

Reproduction in Two Species of Abalone (*Haliotis iris* and *H. australis*) in Southern New Zealand

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Abstract. Gonad development, spawning periodicity, fecundity and recruitment of two species of abalone, *Haliotis iris* and *H. australis*, were examined at two sites. Female *H. iris* spawned in April and September 1986 and March 1987, and decreases in male gonad indices coincided with these events. Oocyte size frequencies showed that the summer–autumn (April 1986, March 1987) spawnings were more pronounced than that in September 1986. Gonad indices of *H. australis* were low in December 1985 and March 1986, but oocyte size frequencies in September 1986 and March 1987 indicated that other spawnings occurred. Gonad development within and between sites was variable, especially for *H. australis*. *H. iris* had a female : male ratio of 1 : 1 at one site and 1.7 : 1 at the other; *H. australis* was 1 : 1 at both sites. In *H. iris*, the smallest females with primary and mature oocytes were 56 mm and 69 mm respectively, and the smallest male with sperm was 80 mm. *H. australis* females had primary and mature oocytes at 61 mm, and the smallest mature male was 65 mm. Fecundity varied between species. At 80–90 mm, *H. iris* had 13 500 eggs and *H. australis* had 2.7 million eggs, but at 140 mm *H. iris* had 7 million eggs. A few recruits of both species were found in May–April 1986, probably the result of the previous September spawnings.

Resumen. Se estudió el desarrollo gónadal, el período de desove, la fecundidad y el reclutamiento de los abulones *Haliotis iris* y *Haliotis australis* en dos áreas. Hembras de *H. iris* desovaron en abril y septiembre de 1986 y marzo de 1987. En estos mismos períodos se observó un decrecimiento del índice gónadal de los machos. Los desoves de verano y otoño (abril 1986, marzo 1987) fueron más intensos que el desove de septiembre de 1986. Los índices gonádicos de *H. australis* fueron bajos en diciembre de 1985 y marzo de 1986. Sin embargo, las frecuencias de tamaño de oocitos en septiembre de 1986 y marzo de 1987 indican que ocurrieron otros desoves. El desarrollo gonadal fue variable, especialmente para *H. australis*. *H. iris* tenía una tasa hembra:macho de 1:1 en un área y 1.7:1 en la otra. *H. australis* tenía una tasa de 1:1 en ambos sitios. En *H. iris* las hembras más pequeñas con oocitos maduros tenían 56 mm en un área, y 69 mm en la otra. Los machos más pequeños con esperma tenían 80 mm en ambas áreas. Hembras de *H. australis* de 61 mm tenían oocitos maduros y primarios, y el macho maduro más pequeño tenía 65 mm. La fecundidad varió entre especies. A 80–90 mm, *H. iris* tenía 13 500 huevos y *H. australis* 2.7 millones de huevos. Se encontraron pocos reclutas en abril y mayo de 1986, probablemente como resultado de los desoves de septiembre del año anterior.

Introduction

Two species of New Zealand paua (abalone), *Haliotis iris* Martyn and *H. australis* Gmelin, are abundant and commercially valuable, but their reproductive biology is not well understood. In particular, information on gametogenesis, its variability between populations, and its relationship to recruitment is incomplete. An understanding of these processes and their variability has become increasingly important because fishery managers focus on population characteristics as criteria for determining catch levels, and because aquaculturalists require reproductive stock for spawnings in shore-based facilities. This paper examines the reproductive cycles of *H. iris* and *H. australis*

in two populations near Dunedin, in the southern part of the South Island of New Zealand.

There is a relatively large literature on the genus *Haliotis* describing the morphology and reproductive system (Crofts 1929; Newman 1967; Young and De Martini 1970), breeding seasons, growth rates, and relationships between age, fecundity and minimum size at first maturity for many species (Ino 1952; Booloatian *et al.* 1962; Cox 1962; Shepherd and Laws 1974). In New Zealand, the annual spawning cycles of *H. iris* and *H. australis* were described and shown to be variable at Banks Peninsula and Kaikoura on the central eastern coast of the South Island. Poore (1973) found that in 1968 both species spawned in late

summer–autumn (March–May) and *H. australis* had a second spawning during spring (September–October). Neither species, however, spawned during the following year. Sainsbury (1982a) also showed that *H. iris* spawned in late summer–autumn in two successive years but subsequently failed to spawn for two years. Poore (1972c) found small recruits in August–December that probably resulted from the preceding late summer–autumn spawnings. North Island populations probably have the potential to spawn during late winter–spring (Schiel, personal observation). Studies elsewhere have shown that spawning cycles of a single species can vary in different populations and that this can affect the timing of recruitment (Webber and Giese 1969; Shepherd *et al.* 1985).

Both *H. iris* and *H. australis* occur along exposed shores throughout mainland New Zealand and the offshore islands but are particularly abundant south of Cook Strait. The cool waters of the Otago district support the largest haliotid fishery in New Zealand, currently 450 t year⁻¹ (Schiel 1992; McShane *et al.* 1994), but little direct information exists on haliotid reproductive habits there. This study was undertaken, therefore, to describe the reproductive cycle, gametogenesis, size at sexual maturity, and sex ratio of *H. iris* and *H. australis* in populations in this region.

Materials and Methods

Study Sites

Two sites, at Seacliff and Warrington within Blueskin Bay (45°42'S, 170°36'E), were selected approximately 1 km apart. The Warrington site is on a large rocky point adjacent to a boulder bay. There is a sloping reef that runs into sand at a depth of 4 m. The Seacliff site is similar to the Warrington site except that the reef slopes more gently and extends further offshore to a depth of 10 m. In Blueskin Bay, south-westerly winds normally prevail during winter and north-easterlies in summer. Southerly swells are common but tend to dissipate in Blueskin Bay, although large swells can occur during north-easterly storms. Inshore water temperatures range seasonally between 7°C and 16°C, being greatest in January–February and lowest in July–August (Jillett 1969).

Study Organisms and Sampling

Haliotis is dioecious, with no discernible sexual dimorphism except for the colour of the gonad. Ripe ovaries of *H. australis* are brown in colour and those of *H. iris* are green. Both of these fade to a cream colour immediately after spawning. Testes in both species are cream in colour throughout the breeding cycle.

Monthly samples of 15–20 individuals of both species were collected for gonad analyses from the full range of adult sizes available at each site at <5 m depth. There is a difference in the maximum sizes of the species that is reflected in the minimum legal fishing size of 125 mm for *H. iris* and 80 mm for *H. australis*. Because of commercial fishing, larger paua were less abundant than were those below the legal size. At Warrington, *H. australis* (70–96 mm shell length) was collected from November 1985 to April 1987 and *H. iris* (107–136 mm) was collected from March 1986 to April 1987. At Seacliff, *H. australis* (66–85 mm) and *H. iris* (105–128 mm) were collected from April 1986 to April 1987. Sea-water temperature was recorded at each sampling date.

All individuals were sexed and measured (mm shell length). Gonads were removed and preserved in 4% formaldehyde. After hardening, a

transverse section was made at one-third of the distance from the tip to the rounded base of the gonad (Poore 1973). The exposed transverse sections showed the gonad surrounding the hepatic gland. The relative sizes of the gonad and hepatic gland were determined by tracing their outlines onto transparent plastic sheets and using an image analyser (Vids General Measurement Program) to calculate their areas. A gonad index was calculated for each individual by using the same formula as Poore (1973): gonad index = [(gonad area)/(total cross sectional area)] × 100.

Histology

Because gonad indices can be inadequate measures of reproductive state, other methods should also be used (Webber and Giese 1969; Gonor 1972). Microscopic examination of gonads was done, therefore, to measure gametogenic activity and to compare this with the seasonal changes in the gonad indices. A subsample of five male and five female gonads from each month's sample was sectioned. Sections were taken routinely from the posterior part of the gonad, after no significant difference in gametogenic activity had been found between two sections from different parts of gonads. Sections were dehydrated in isopropyl alcohol, embedded in paraplast, cut to a thickness of 7 µm, and stained with Lillie–Meyer haemalum and eosin.

The reproductive condition of the ovary was determined monthly by calculating oocyte areas. In sections of five ovaries, areas of the first 50 oocytes encountered with a distinct nucleolus were measured with an image analyser. Oocyte areas for the sets of five individuals were plotted monthly as frequency histograms. Frequency histograms show the initiation of gametogenesis, assuming that the presence of a large number of small oocytes in the smallest size classes is an indication of the start of gametogenesis (Webber and Giese 1969).

For males, five sections of testes from each of five individuals were examined and the thickness of the actual seminal layer consisting of spermatocytes, spermatids and spermatozoa was measured. The relative area (%) of each developmental stage was calculated as an average monthly value.

The size at sexual maturity was determined for both species from a sample collected at Seacliff on 18 January 1987. Gonads from 50 *H. iris* (50–140 mm shell length) and 20 *H. australis* (50–80 mm) specimens were examined histologically. 'Maturity' was determined as the shell length at which gametes first became discernible. Fecundity was determined from the sample by counting the viable eggs from a known mass of gonad by the method of Newman (1967) and Poore (1973). Sex ratio was determined in both species from samples collected throughout the study sites.

Recruitment

To determine the relationship between spawnings and local recruitment, detailed searches for juvenile paua were done at both sites on several occasions in 1986–87. Paua could be reliably found from a size of ~5 mm.

Results

Reproductive Cycles

Haliotis iris. Male and female gonad indices for *H. iris* at Warrington weakly indicate seasonal changes (Fig. 1A). There were three decreases during the year in gonad indices of females. These were not uniform, with small decreases in the index during April and September 1986, suggesting minor spawning events, and a greater average decline to 45% during March 1987. The only clear and discrete decrease in the male gonad index occurred during July–September 1986, with a smaller decrease in April 1986 and a gradual decline from October 1986 to April 1987.

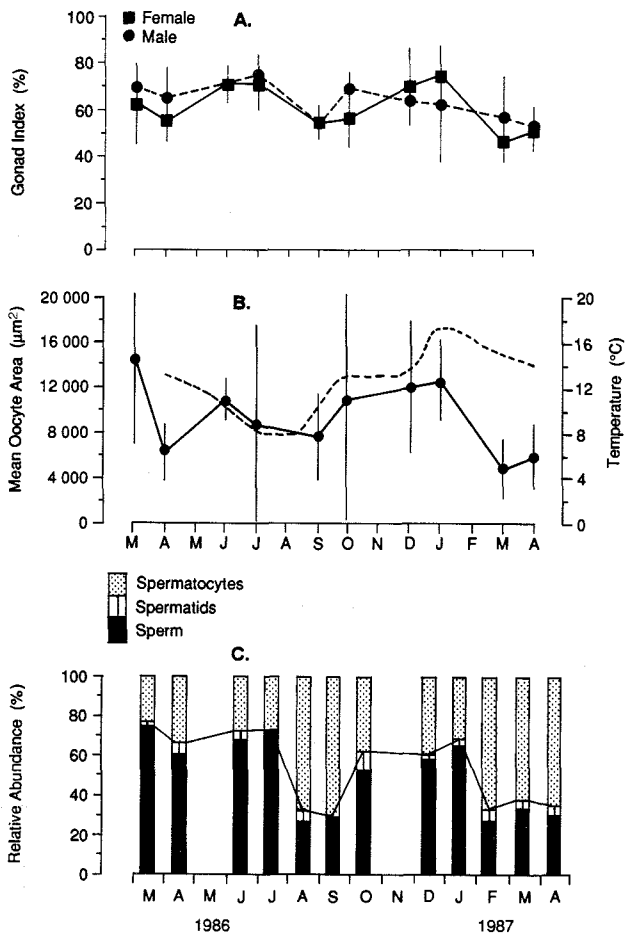


Fig. 1. (A) Gonad indices and (B) oocyte areas (μm^2), \pm 95% confidence interval). (C) Testis indices of *H. iris* from Warrington. Mean sea-water temperature (dashed line) is shown.

The average area of oocytes clearly showed that spawning episodes were coincident with declines in the gonad index (Fig. 1B). A peak in the mean oocyte area of $14\,600\ \mu\text{m}^2$ was recorded when sampling began in March 1986 and was followed by a sharp decrease by April 1986 to a value of $6\,300\ \mu\text{m}^2$, indicating that spawning had occurred. The mean area of oocytes increased to $10\,900\ \mu\text{m}^2$ by June 1986, then fell to $7\,600\ \mu\text{m}^2$ in September, suggesting that another spawning had occurred. An increase in oocyte area occurred after September. A large decrease in March 1987 indicated a major spawning period.

Frequency histograms show that the loss of mature, larger oocytes occurred on three occasions (Fig. 2). Major spawnings occurred during the late summer–autumn periods around April 1986 and March 1987. The spawning around September 1986 was not as pronounced. Gametogenesis, seen as an increase in the number of smaller oocytes, began in April and late June 1986 and March–April 1987.

Male spawnings were more clearly indicated by the proportions of spermatocytes, spermatids and sperm (Fig. 1C) than by the gonad index. Abrupt and large decreases in the proportion of spermatozoa indicated that major spawnings occurred in August–September 1986 and February–April 1987. There was also a minor decline in sperm volume in April 1986.

Gonad indices at Seacliff also indicated three spawnings, although once again the variability was high within each sample (Fig. 3A). Both male and female indices were low during March 1986, a month earlier than at Warrington. The mean female index dropped slightly again in May. The major spawning events as indicated by both indices occurred around September 1986 and the following February, comparable to the timing at Warrington.

Oocyte areas were relatively low at Seacliff for the entire year compared with those at Warrington (Fig. 3B). Two

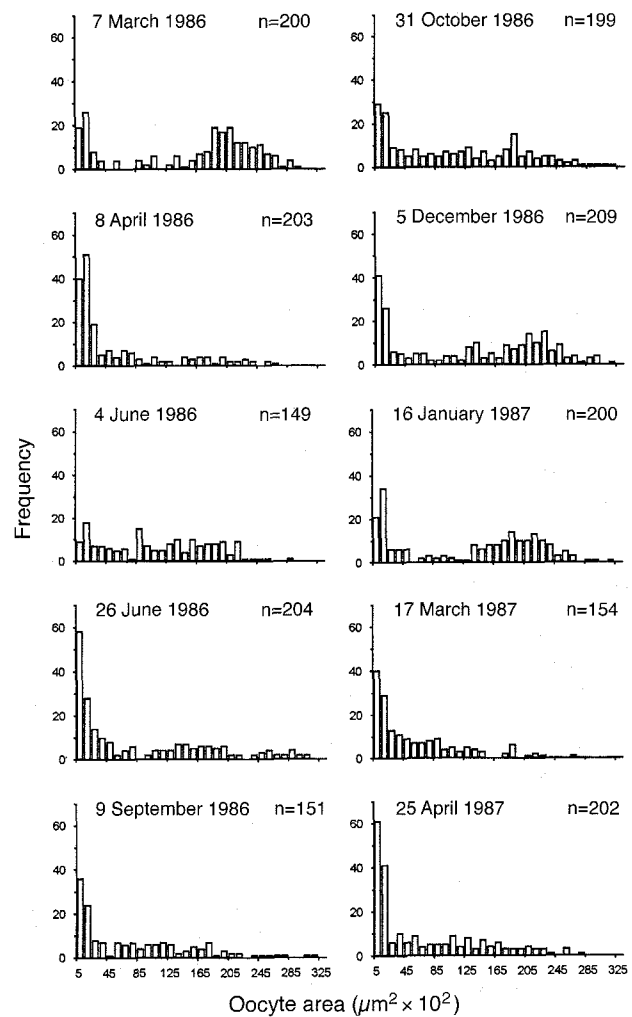


Fig. 2. Oocyte area frequency histograms of *H. iris* from Warrington.

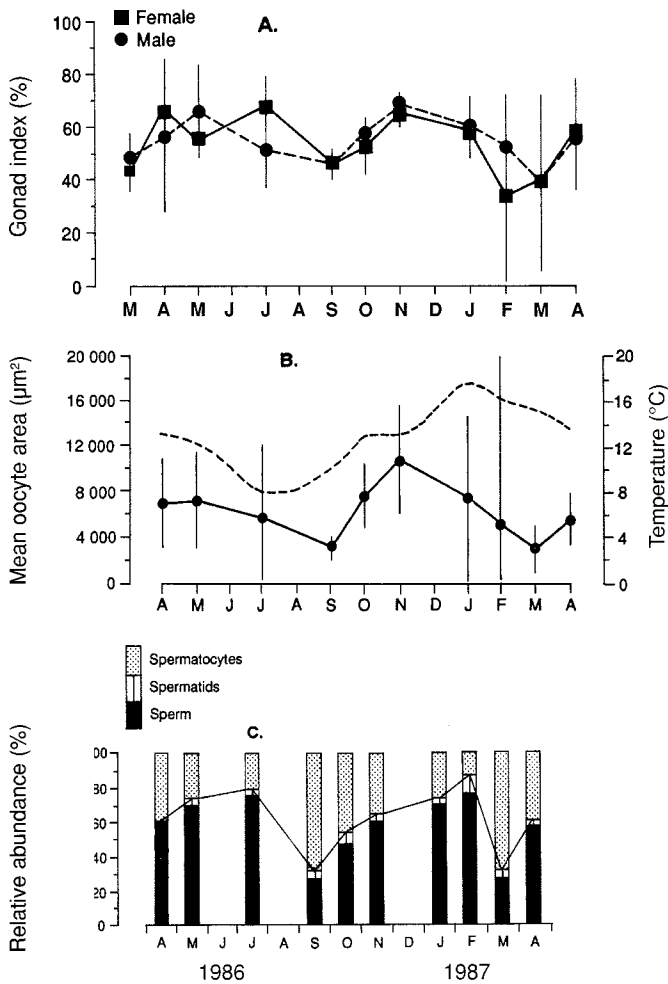


Fig. 3. (A) Gonad indices and (B) oocyte areas (μm^2), \pm 95% confidence interval); (C) testis indices of *H. iris* from Seacliff. Mean sea-water temperature (dashed line) is shown.

distinct declines in the average oocyte area were apparent. One was a gradual fall to $3110 \mu\text{m}^2$ from May to September 1986, suggesting that spawning probably occurred during this time. An increase from September to November 1986 reached a peak of $10717 \mu\text{m}^2$. A second decline from November to March indicated a second spawning.

The frequency histograms of oocyte area from Seacliff (Fig. 4) were generally similar to those for Warrington. Spawning occurred between May and September 1986 and during January–March 1987. The declines in the testis index (Fig. 3C) coincided with those for oocyte area. April 1986 marked the recovery from a spawning event, and the abrupt drops in the volume of spermatozoa during September and the following March indicated that spawning had occurred.

Haliotis australis. The male and female gonad indices at Warrington were very similar (Fig. 5A). A decrease to their lowest value of 39% in December 1985 suggested that spawning had occurred. Gonads then recovered until a

minor drop in March 1986, suggesting a partial spawning. Other minor declines occurred in the following September–December and around March 1987.

The oocyte area index supported the conclusion that females spawned around December 1985, September and December 1986, and March 1987 (Fig. 5B). However, the decline in the gonad index seen in March 1986 was not reflected in the oocyte area index or in the frequency histograms of oocyte area (Fig. 6). Decreases in the number of large, mature oocytes occurred in December 1985, September 1986 and March 1987, but there is little evidence of a spawning event in December 1986. Initiation of gametogenesis, indicated by many smaller-sized oocytes, was evident around the time of spawning.

The spawning cycle of testes showed three declines in the volume of spermatozoa (Fig. 5C). These were around December 1985, to an average sperm volume of 37%, September 1986 (32%) and March–April 1987 (34%).

The gonad indices at Seacliff remained relatively high throughout the year (Fig. 7A). Less synchrony occurred between males and females than occurred at Warrington. The male gonad index showed only a slight drop during January–March 1987, whereas the female gonad index slowly declined after April 1986 to reach its lowest value of

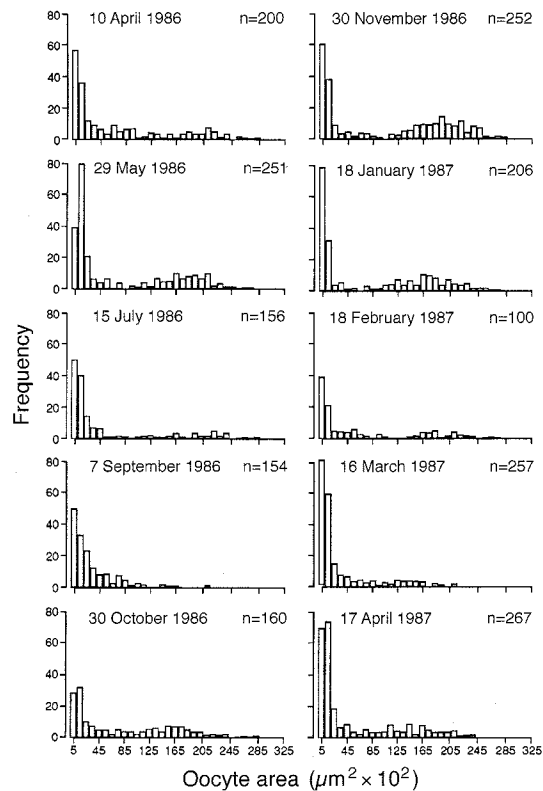


Fig. 4. Oocyte area frequency histograms of *H. iris* from Seacliff.

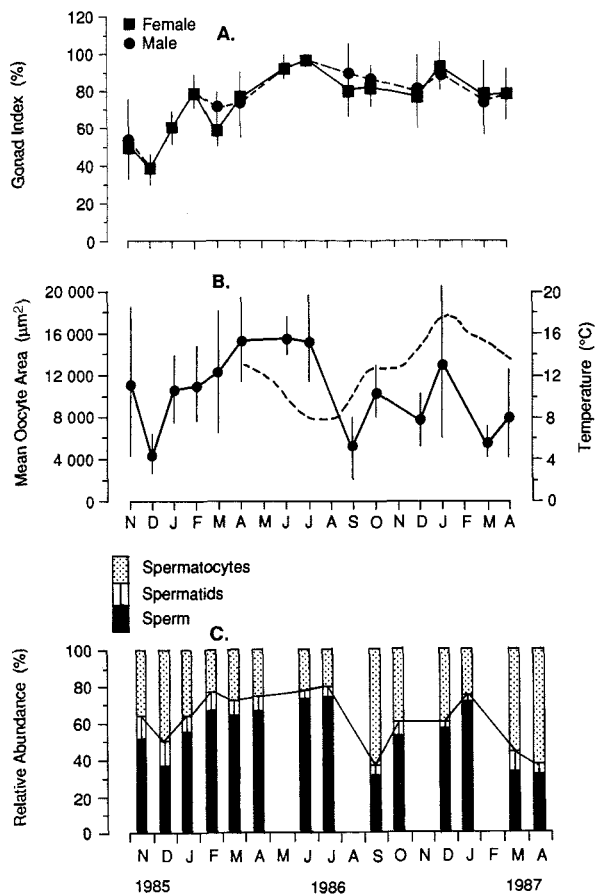


Fig. 5. (A) Gonad indices and (B) oocyte areas (μm^2 , \pm 95% confidence interval); (C) testis indices of *H. australis* from Warrington. Mean sea-water temperature (dashed line) is shown.

56% in September. Partial spawning of the population probably occurred during these months. The average area of oocytes decreased between May and September 1986 (Fig. 7B) and gradually increased from September to November before a second fall in January 1987. It then increased by February 1987 to reach its largest value, followed by a large decline in March 1987.

The oocyte area frequency histograms (not presented) were similar to those from Warrington. Large decreases of mature oocytes occurred between July and September 1986 and during March 1987. The partial spawning suggested for January 1987 by the oocyte area index was not evident in the frequency histograms.

The testis index showed two major declines in sperm volume, during September 1986 and February–March 1987 (Fig. 7C), with no evidence of spawning in January 1987.

For both species at both sites, the temperature profiles were of the same general shape as the mean oocyte graphs

(Figs 1B, 3B, 5B, 7B). However, the drops in temperature relative to spawning events were not sufficiently clear to indicate a correlation ($r_{19} = -0.045$, not significant).

Sex Ratio and Fecundity

The sex ratio of *H. iris* was 1 : 1 at Warrington ($\chi^2 = 0.28$, $P > 0.05$, $n = 91$), but at Seacliff there were 1.7 females to 1 male ($\chi^2 = 9.32$, $P < 0.01$, $n = 139$). *H. australis* had 1 : 1 sex ratios at both sites ($\chi^2 = 0.51$, $P > 0.05$, $n = 97$ and $\chi^2 = 1.95$, $P > 0.05$, $n = 166$).

The minimum size at maturity, as indicated by the lengths of the smallest individuals containing mature eggs on one sampling date, varied slightly between species. The smallest *H. iris* specimen with primary oocytes was 56.4 mm, whereas the smallest individual with mature oocytes was

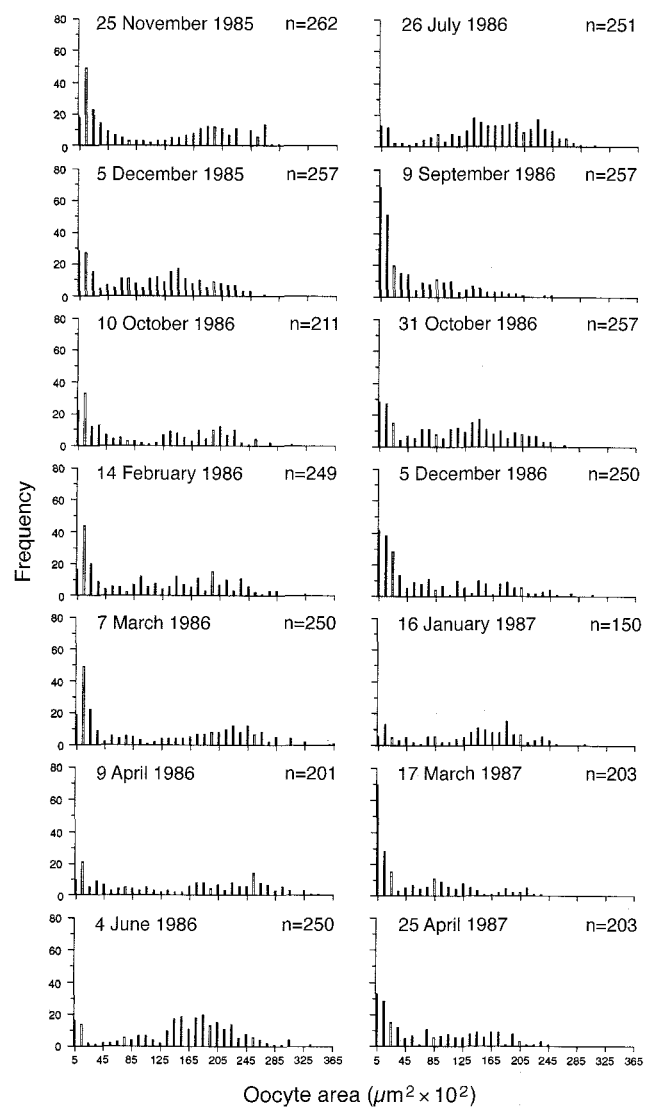


Fig. 6. Oocyte area frequency histograms of *H. australis* from Warrington.

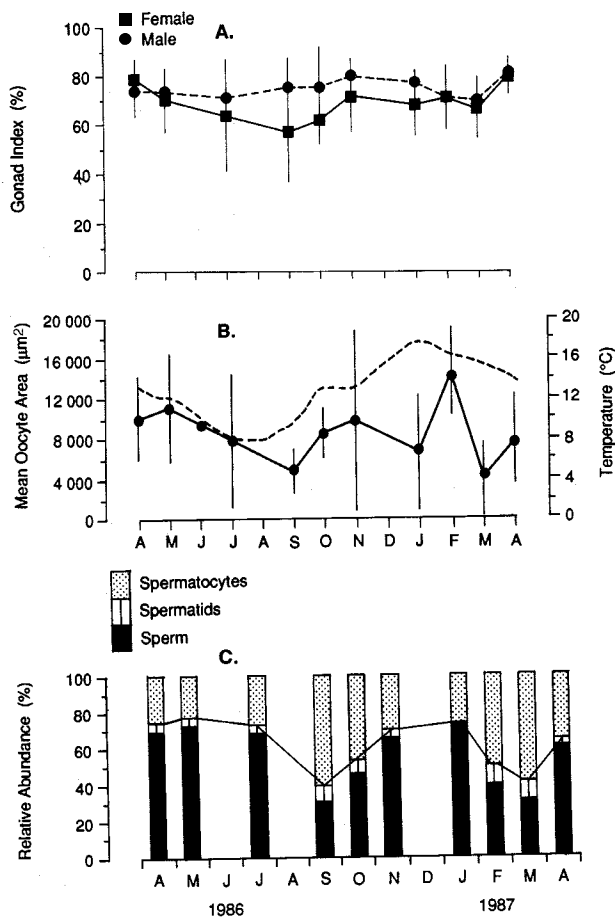


Fig. 7. (A) Gonad indices and (B) oocyte areas (μm^2 , $\pm 95\%$ confidence interval); (C) testis indices of *H. australis* from Seacliff. Mean sea-water temperature (dashed line) is shown.

69.5 mm. The smallest male with a thin testis and small volume of sperm was 79.7 mm. Beyond 80 mm virtually all *H. iris* females contained at least some mature oocytes, whereas all of those >95 mm had gonads packed with mature oocytes. Gonads of males >91 mm were packed with spermatozoa. The smallest reproductive specimen of *H. australis* was 61.4 mm, containing both primary and mature oocytes. All females >63.1 mm contained large numbers of mature oocytes. All males >64.9 mm had abundant spermatozoa.

Although there was a relatively small sample size for determining the fecundity of *H. australis*, this provided an interesting contrast to *H. iris* (Figs 8A and 8B). *H. iris* females at 80–90 mm had 13 500 eggs, whereas *H. australis* females at these sizes had 2.7 million eggs. Large *H. iris* females (140 mm) had 6.8 million eggs, a result similar to that of Poore (1973) except that his counts did not reach 7 million eggs until a size of 150 mm. For both species, the gonad index did not vary significantly with shell length over the size ranges sampled for the earlier gonad analyses (Fig. 8).

Recruitment

Small *H. iris* juveniles (<10 mm) were found at both sites in May 1986. These were probably the result of spawnings during the previous September–October because the paua were too large to have resulted from March–April spawnings (cf. Poore 1972c). Despite extensive sampling at Warrington and Seacliff on four dates between September 1986 and the end of April 1987, no juveniles <10 mm were found that could be ascribed to the major spawning episodes of *H. iris* in September 1986. Two juveniles <10 mm were found at Seacliff in November 1986 that may have resulted from a spawning in March–April 1986. This stands in contrast to the results of Poore (1972c), who found that recruits were present predominantly from August to December at two sites and were the result of March–April spawnings. For *H. australis*, the only juveniles found of about 10 mm size occurred at Warrington in April 1986, probably the result of a December 1985 spawning.

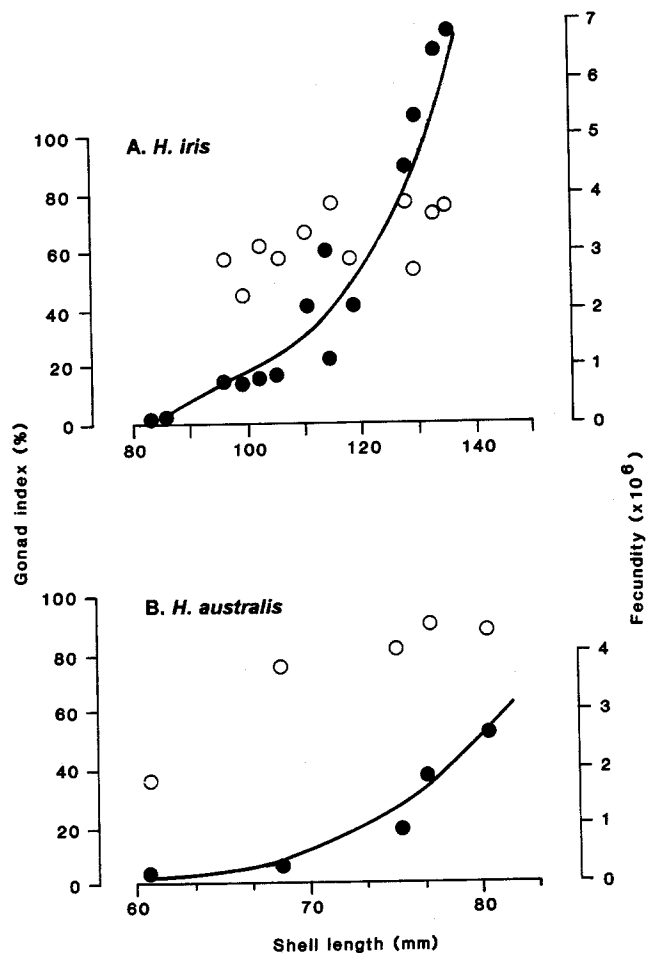


Fig. 8. Relationship between length and (○) gonad index and (●) fecundity for (A) *H. iris* from both sites and (B) *H. australis* from Seacliff.

Discussion

Spawning and Recruitment

Great variability occurs in the spawning periodicity and recruitment of haliotids. Breeding of some species may extend to several months of the year, whereas others are restricted to more discrete periods (Ino 1952; Newman 1967; Webber and Giese 1969; Poore 1973; Shepherd and Laws 1974; Mottet 1978; Tutschulte and Connell 1981). There can also be considerable variation for a single species among years and sites. Two examples illustrate this. *Haliotis rufescens* in California has been shown to spawn during the winter months of January–March (Bonnot 1930; Scofield 1930; Crocker 1931; Carlisle 1962), from November to March (Cox 1962), or throughout the year (Booolootian *et al.* 1962). Recruitment may be much more discrete. Leighton and Booolootian (1963) found small juveniles (6–12 mm) only during April, suggesting that these settled several months earlier and that recruitment may be restricted in time. In South Australia, differences in spawning cycles between sites were seen for *H. scalaris*. Shepherd and Laws (1974) showed that spawning at one site occurred throughout the year but that at another site spawning took place during the late summer–autumn months of February–May (Shepherd *et al.* 1985). Furthermore, by carefully examining rocks from natural habitats, Shepherd *et al.* (1985) found juveniles as small as 1 mm in the months when spawning occurred, indicating successful settlement.

Few studies have tied spawning episodes to recruitment. Poore's (1972a, 1972b, 1972c, 1973) studies are an exception and provide suitable data for comparison with the present study. At two sites, Poore (1973) found that *H. iris* spawned once a year between February and March 1968; *H. australis* spawned during July–October 1967 and again in March–April 1968. No spawning was detected during 1969, a result also recorded by Sainsbury (1982a) during 1974 and 1976. Poore (1972c) found juveniles of 5–12 mm during December 1968 and concluded that these resulted from the spawning period eight months earlier. No recruitment information is available from previous studies on *H. australis* because this species is less abundant and juveniles are scarce. The spawning cycle for *H. iris* in Otago was different from that at Poore's (1973) sites further north, occurring both in late summer–autumn (February–April) and in winter–spring (July–November). The oocyte areas and size frequencies indicated that there can be partial spawnings of populations, probably due to a few active and many resting individuals. Although extensive searches were done, only a few juveniles <10 mm were found during November at one site, and these probably represented settlement from the summer–autumn spawning. Many small juveniles were present on the first sampling date in May 1986 at both sites, pointing to a settlement during

September–November 1985. By the end of April 1987, however, no more juveniles were found that could have settled during the winter–spring spawning period of 1986. During this study, therefore, the spawning and recruitment periods were different from those further north in Kaikoura. Both Poore (1972c) and Sainsbury (1982b) found that the recruitment of *H. iris* was irregular. In *H. australis*, the two annual spawning peaks in Otago were similar to those found by Poore (1973). Some juveniles (10 mm) were found in April 1986 at Warrington that probably settled during the breeding period of the previous November–December.

Reproductive Development

Gametogenesis was usually apparent in the first few months after spawning, but large numbers of small oocytes were often found throughout the year, indicating the ongoing nature of gametogenesis. The total number of primary oocytes shown in the histograms of oocyte area appeared to be great enough to account for the quantity of mature eggs present later in the same cycle. This is contrary to what was found by Tutschulte and Connell (1981) in three Californian abalone species, for which there appeared to be too few primary oocytes. The conclusions from these results are that the maturation of many new primary oocytes takes place within a few months and therefore that oogenesis occurs annually rather than being extended over several annual cycles (Giese and Pearse 1977; Tutschulte and Connell 1981). In *H. australis* and *H. iris*, there was evidence that mature oocytes were being reabsorbed within the reproductive cycle. This implies that not all the decreases in gonad indices were necessarily due to spawning and the release of gametes (cf. Tutschulte and Connell 1981). Resorption was evident in some individuals throughout the reproductive cycle, and in others it was restricted to a few mature oocytes. Resorption was evident in the months associated with spawning, from the lead-up period to the recovery of the ovary after spawning. This could represent the removal of mature oocytes not previously shed.

Regulatory mechanisms for gametogenesis and spawning that have been proposed include sea-water temperature, physical disturbances, food supply, and genetic and hormonal factors (Orton 1920; Webber and Giese 1969; Tutschulte and Connell 1981; Shepherd *et al.* 1985). The only external factor measured at the Otago sites was water temperature. The reproductive cycles of *H. iris* and *H. australis* from Warrington appeared to track generally the change in water temperature, with spawning occurring after a decrease in water temperature. Poore (1973) found that there was a slight correlation between spawning and water temperature during 1967–68 and that an autumn spawn occurred after a drop in water temperature. In 1969, however, the water temperature cycle was similar to that in the previous years but neither species was seen to spawn.

Other studies have concluded there is a good relationship between reproductive cycles and water temperatures (Tomita 1967; Kikuchi and Uki 1974a, 1974b).

The sizes at which *H. iris* and *H. australis* first became sexually mature are comparable between Otago and the northern sites of Poore (1973) and Sainsbury (1982a). These sizes of about 60 mm for *H. australis* and 70 mm for *H. iris* correspond to those at which these species begin to leave their habitats beneath boulders and migrate to deeper portions of reefs (Poore 1972b). This shift may also involve a change in diet from smaller macroalgae to larger drift seaweeds. The few gametes produced when the animals first attain sexual maturity are probably not enough to contribute much to population dynamics. Poore (1973) and Sainsbury (1982a) concluded that only when a female carried more than about 10 500 eggs would it contribute substantially to spawning. Although fecundity estimates varied between studies, the sizes at which females produce sufficient numbers of eggs are 62 mm in *H. australis* and 90 mm in *H. iris*.

The greater proportion of females found at one site is relatively uncommon for haliotids, although several examples have been documented (Shepherd and Laws 1974). Older populations of dioecious molluscs may have more females than males (Fretter and Graham 1964). Both Sinclair (1963) and Shepherd and Laws (1974), however, found populations of *Haliotis* species with a predominance of males.

Conclusion

This study highlights the variability seen within and between populations of paua. As fishing pressure increases, detailed information on reproductive cycles and recruitment episodes becomes crucial (Sainsbury 1982b). Egg-per-recruit and yield-per-recruit analyses used in fisheries management are partially based on this information (Schiel and Breen 1991). Comparisons of populations from different areas of New Zealand will form the biological basis of management schemes (McShane *et al.* 1994).

Acknowledgments

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