

Sex change in a giant endemic limpet, *Patella kermadecensis*, from the Kermadec Islands

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Abstract

Sex-ratios of the limpet *Patella kermadecensis* Pilsbry, collected at three times of the year during 1984 and 1985 at Raoul Island in the Kermadecs group, varied with the size of the limpets. Small limpets were predominantly male, while amongst larger ones about half were female. The presence of hermaphroditism in *P. kermadecensis* was confirmed by microscopic examination of gonad material from over 50 limpets, which revealed a high percentage of individuals with both male and female gametes in their gonads. It is postulated that protandric sex change occurs in this large limpet, and that this phenomenon is related to a change in habitat from the backs of large shells (limpets less than approximately 50 mm) to bedrock (larger limpets). The pattern of sex change in *P. kermadecensis* is compared with that in other species of limpet, and it is suggested that a reproductive system consisting of gonochoristic males and sequential hermaphrodites may be particularly advantageous for a large, slow-growing species that has a very restricted geographical range.

Introduction

Limpets often dominate mid- and low-intertidal regions of rocky shores around the world, and can have significant effects on the overall biological structure of these areas (see reviews by Underwood 1979, Branch 1981, Hawkins and Hartnoll 1983; and references therein). These effects are likely to be most pronounced for large species of limpet which also occur in large densities. Such situations may lead to intense inter- and/or intra-specific interactions, which, in

turn, are thought to have resulted in the evolution of territoriality and specialised feeding behaviours. Two particularly well-documented examples involve a suite of large South African patellids (Branch 1975, 1976) and the large Californian acmaeid *Lottia gigantea* (Stimson 1970, 1973). The occurrence of protandric sex change is often associated with these large species (Branch 1974, Wright and Lindberg 1982, Lindberg and Wright 1985), although it is also known to occur amongst smaller patellids (Branch 1981).

A pilot ecological survey of intertidal and shallow subtidal reefs at Raoul Island in the remote Kermadec Island Group was made during 1984 (Schiel et al. 1986) to quantify the patterns of distribution and abundance of the major organisms present. *Patella kermadecensis* Pilsbry was identified as the most abundant limpet. This species is known to be endemic to the Kermadec group (Powell 1973), but is thought to be a relict of a species that was widespread throughout New Zealand during the Tertiary (Fleming 1973). Its presence at Raoul Island had been noted in previous studies (Oliver 1915, Knox 1963). No information was available on its ecology or reproductive biology, however, largely because of the geographic isolation of the Kermadecs and the generally inaccessible nature of the rocky shores that occur there. In Schiel et al.'s (1986) survey, *P. kermadecensis* was found to reach peak abundances subtidally (0 to 2 m depth), attain sizes in excess of 130 mm shell-length, and occupy obvious home scars. Characteristically, the smaller limpets occurred on the shells of larger limpets (see also Fig. 2 of present paper).

Preliminary examination of samples collected during the expedition in March 1984 suggested that some form of sequential hermaphroditism might occur in *Patella kermadecensis* (Schiel et al. 1986). Because of its large size, very restricted geographical range and complete dominance of low intertidal and shallow subtidal reefs, a more detailed examination of the sexual characteristics of this species would provide additional information on sex change phenomena in limpets. Because *P. kermadecensis* is one of the world's largest limpets, it also provides an opportunity to

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examine these phenomena in the light of general models relating the adaptive significance of sex change to the size of an organism (Ghiselin 1974, Warner 1988).

Materials and methods

The Kermadec Islands are a small group of subtropical islands lying 750 km to the northeast of New Zealand (Fig. 1). *Patella kermadecensis* Pilsbry, collected during the initial visit to Raoul Island in March 1984, was supplemented by two further samples obtained in October 1984 and August 1985.

In March 1984, three samples were obtained from closely adjacent sites in Boat Cove (Fig. 1). Each sample comprised all individuals collected from an area of rock, and contained 30 to 50 large limpets and many more smaller ones. The samples were immediately preserved in 10% formalin in seawater.

The material collected in October 1984 consisted of 12 very large *Patella kermadecensis*, obtained from various locations within the Kermadec group. These limpets were not immediately placed in preservative, but were simply frozen during their return trip to Auckland. They were placed into preservative (10% formalin in seawater) immediately on arrival at the laboratory. The material obtained in August 1985 was a single sample of 29 large limpets collected from an area of approximately 3 m² in the vicinity of Boat Landing, Raoul Island (Fig. 1). This material was treated in the same way as that from October 1984. For the material obtained on these latter two occasions, each large limpet was kept in a separate container so that the juvenile limpets associated with each large shell were retained with that particular individual.

In the laboratory, the shell length of each individual limpet was measured with vernier calipers to the nearest 1 mm. The limpet was then removed from its shell, weighed to the nearest 0.1 g and dissected. The gonad, if present, was removed, weighed to the nearest 0.01 g, and sexed macroscopically according to its colour and outward appearance.

Gonads which could not be reliably sexed by these criteria were checked under a dissecting microscope; if female, oocytes could be clearly seen at a magnification of $\times 10$. Some gonads were then placed in Bouin's fixative for later histological examination. Sections were cut at 4 to 10 μm from paraffin blocks and examined microscopically at $\times 40$ and $\times 100$. Although the sections cut from limpets frozen during transportation were of poor quality, they were adequate to verify the sex of selected individuals and to identify hermaphrodites. Where possible, notes were also made of the state of development of the gametes. For each limpet with a sexable gonad, a gonad index was calculated as (gonad weight:somatic weight) $\times 100$.

In the samples from October 1984 and August 1985, records were also kept of the shell length, body weight, gonad weight and sex of all juvenile limpets found on the shell of each large *Patella kermadecensis*. This was also done for the March 1984 samples where possible, but some small limpets were loose in the collection container and it was not possible to determine from which adult they had come. To resolve this problem, additional measurements were made of the size of juvenile home scars on the large shells (see examples in Fig. 2), which allowed some evaluation of a limpet's size in relation to its microhabitat.

Results

In *Patella kermadecensis*, male gonads are creamy white in colour and female gonads pinkish brown. Very small gonads were often a dark brown colour, but could always be unequivocally assigned to one sex or the other after examination under low power. The gonads from the sample collected in March 1984 had a sex ratio strongly biased in favour of males (Table 1). Over all samples, males outnumbered females by approximately 3 to 1 (Table 1). The ratio of males to females, however, varied with size. Only the sample from March 1984 had enough limpets over the entire size range to quantify this variability. The use of equally spaced size-categories, however, resulted in large numbers in the small

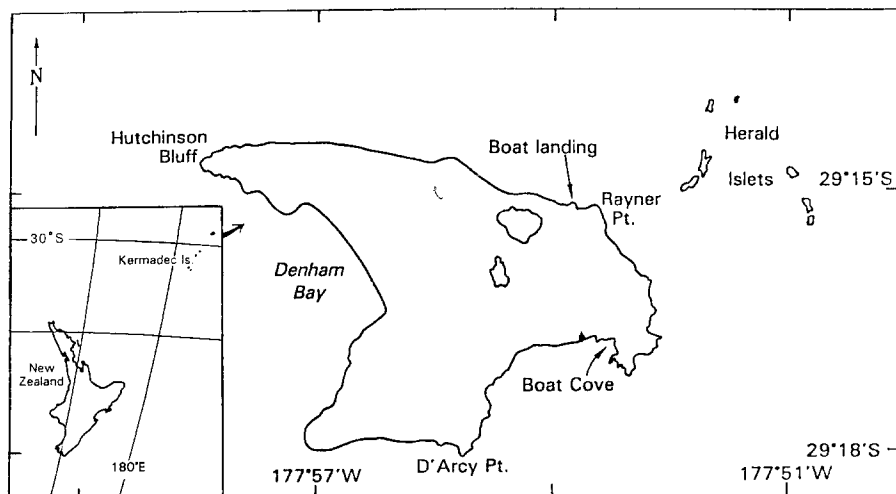


Fig. 1. Location of Kermadec Islands (inset), and main sampling sites on Raoul, the most northerly island in the group

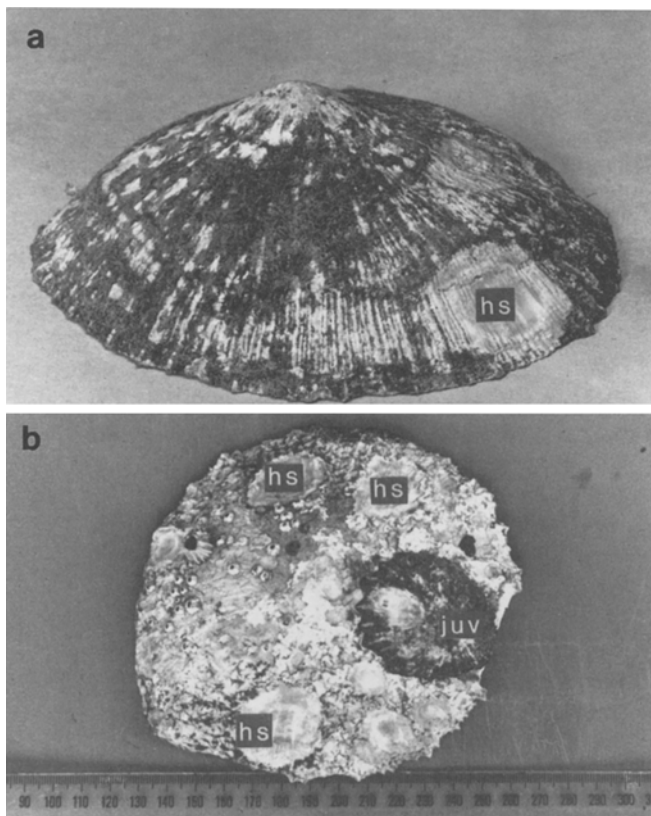


Fig. 2. *Patella kermadecensis*. Shells of large adults (a) Limpet (110 mm) covered with turfing algae and one home scar (hs; 24 mm). (b) Limpet (136 mm) with one juvenile (juv; 50 mm) *in situ* and several home scars, three of which are marked (hs); note that the juvenile also has a scar (21 mm) on its back

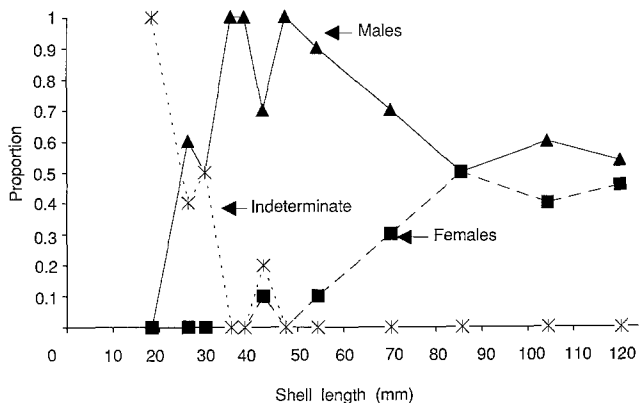


Fig. 3. *Patella kermadecensis*. Proportion of each size group ($n=10$ limpets in each group; see “Results” for details of grouping procedure) in three sex categories, based on macroscopic examination of gonads collected in March 1984

size-classes and low numbers in the large classes (see Fig. 4a). A more accurate method of illustrating changing sex-ratios with size involved ranking all 123 limpets according to the lengths of their shells, from the smallest to the largest. They were then divided into groups of ten, and the mean size and sex-ratio for each group were calculated. The final group, which ranged in size from 116 to 129 mm, had

Table 1. *Patella kermadecensis*. Sex ratios determined from macroscopic examination of gonads (Ind.: indeterminate). Asterisks indicate juvenile individuals attached to the shells of adult limpets

Sample	Ind.	Male	Female
March 1984			
Sample 1 ($n=41$)	4	33	4
Sample 2 ($n=50$)	11	29	10
Sample 3 ($n=32$)	6	20	6
October 1984			
Sample 1 ($n=12$)	0	4	8
Sample 1* ($n=9$)	8	1	0
August 1985			
Sample 1 ($n=29$)	8	13	8
Sample 1* ($n=539$)	538	1	0
Overall	575	101	36

13 limpets rather than 10. By plotting the proportion of individuals of each sex against the mean size for the group, the changing pattern of sex distribution with size became apparent (Fig. 3). All limpets smaller than 23 mm did not have a recognisable gonad (10 individuals), and even some individuals in the 40 to 45 mm size range were of indeterminate sex. The smallest female had a shell length of 42 mm; the next largest was 60 mm. Males clearly predominated in the smaller size classes, with 58 individuals <65 mm compared with only 3 females. The proportion of females in the population increased above this size and was close to 50% in the larger size classes (Fig. 3).

The sample collected in October 1984 contained 12 large specimens (65 to 160 mm). Most of these were females (Table 1), including 3 of the 4 limpets which were >110 mm. All but one of the small limpets on the backs of the larger shells (hereafter called “hitchhikers”) were of indeterminate sex. In August 1985, the sex-ratio of sexable specimens favoured males (Table 1), but again there were more females amongst limpets >110 mm (7 females, 5 males). There were many small hitchhikers in this sample, but all but one was of indeterminate sex. As with the October 1984 sample, the only juvenile with a recognisable gonad was a male (Table 1).

The indeterminate sex of small limpets was confirmed histologically. The eight indeterminate hitchhikers from October 1984 and a subsample of ten from August 1985 were sectioned right through the visceral mass. None showed any distinguishable gonadal tissue.

In August 1985, there was a clear delineation in size between those limpets occurring on the rock (67 to 155 mm shell length) and hitchhikers (5 to 55 mm) (Fig. 4b). This distinction could not be made for limpets collected in March 1984, because we could not determine whether a small limpet had been collected from the rock or had fallen from the shell of a larger limpet after collection. Because *Patella kermadecensis* has very prominent home scars, however, it was possible to measure the length of scars on the larger shells (Fig. 2). Although most of these scars were obviously unoccupied at the time of collection, the data show that the

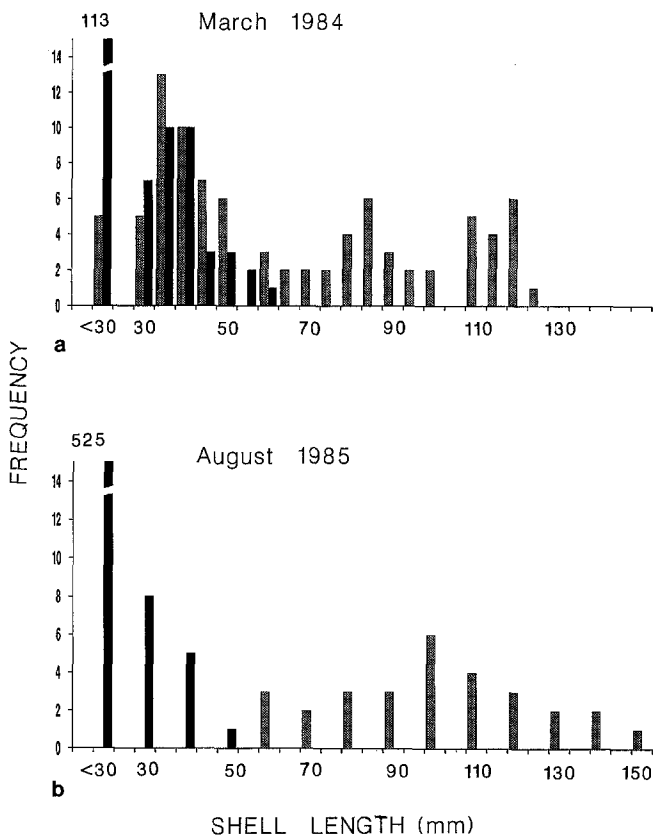


Fig. 4. *Patella kermadecensis*. Length-frequency histograms for two samples. For March 1984, data are for actual limpets (stippled bars) and for home scars on shells of larger individuals (filled bars). For August 1985, data are for limpets occurring on the rock (stippled bars) and for “hitchhikers” (filled bars)

Table 2. *Patella kermadecensis*. Sexual characteristics determined from histological sections (n = no. of gonads sectioned). Numbers of gonads are given for three main categories, with three further divisions within the last category. Asterisk indicates mosaic hermaphrodite (Fig. 6 c); other hermaphrodites are transitional (Fig. 6 d, e). Shell lengths (mm) of limpets with hermaphroditic gonads are given in parentheses

Gonad category	Mar. 1984 ($n=18$)	Oct. 1984 ($n=12$)	Aug. 1985 ($n=21$)
All male	8	2	10
All female	4	5	8
Hermaphrodites	6	5	3
Male with some oocytes	5 (31,37,45,49,50)	1 (143)	3 (73,105,128)
Female with some sperm	0	3 (84,99,110)	0
Approx equal male/female	1* (87)	1 (64)	0

largest hitchhiker in this sample was about 60 mm (Fig. 4 a). The largest hitchhiker encountered was 74 mm, and was found on the shell of a 143 mm limpet in October 1984.

The gonad indices (Fig. 5) showed no consistent patterns. In October 1984 and August 1985, limpets smaller

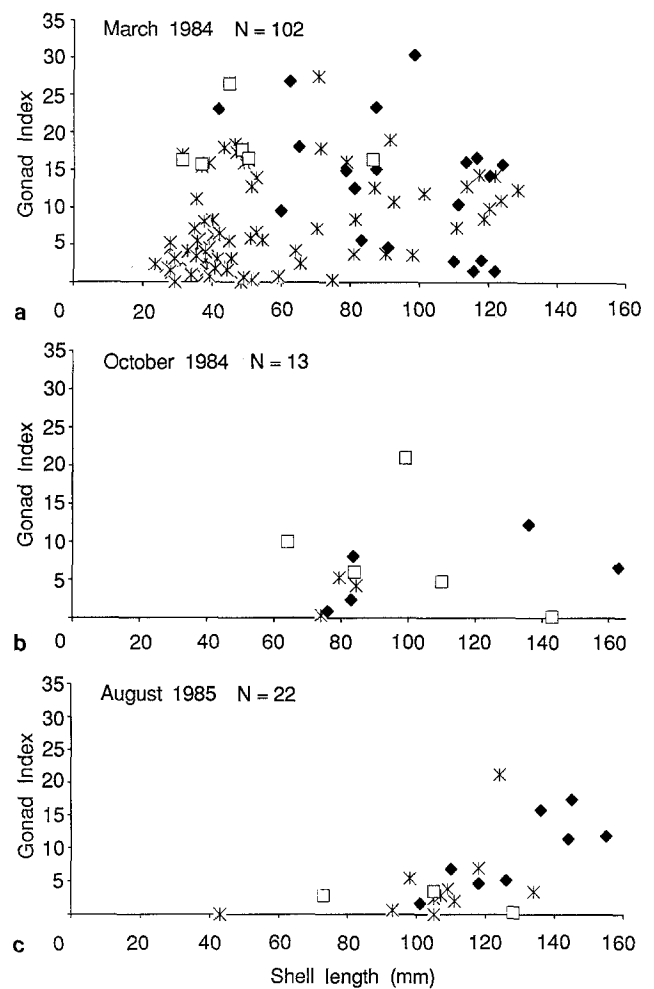


Fig. 5. *Patella kermadecensis*. Gonad indices for populations sampled on three different occasions. Only limpets with determinate gonads included. *: males; ♦: females; □: hermaphrodites

than 70 mm rarely had sexable gonads, and the gonad index increased with increasing shell length above a size of 80 to 90 mm. Females in these two samples contained a large proportion of immature oocytes, and none showed signs of a recent spawning. In March 1984 many limpets as small as 25 mm had recognisable and large gonads, but there was no significant relationship between gonad index and shell length over the whole range of sizes. Some females had very ripe gonads full of mature oocytes, whereas others contained a relatively small proportion of mature eggs, suggesting that these individuals may have recently spawned. This variability may also indicate non-synchronous oogenesis among females.

In both sexes of *Patella kermadecensis*, the gonad is a compact layer encased in a thin membrane on the ventral surface of the visceral mass. The structure of the gonads is identical to that described for other patellids (e.g. Branch 1974), and examples of mature male and female gonads are shown in Fig. 6 a, b.

During macroscopic examination of the March 1984 sample, however, one limpet (87 mm) was found that had a gonad composed of both male and female components. A

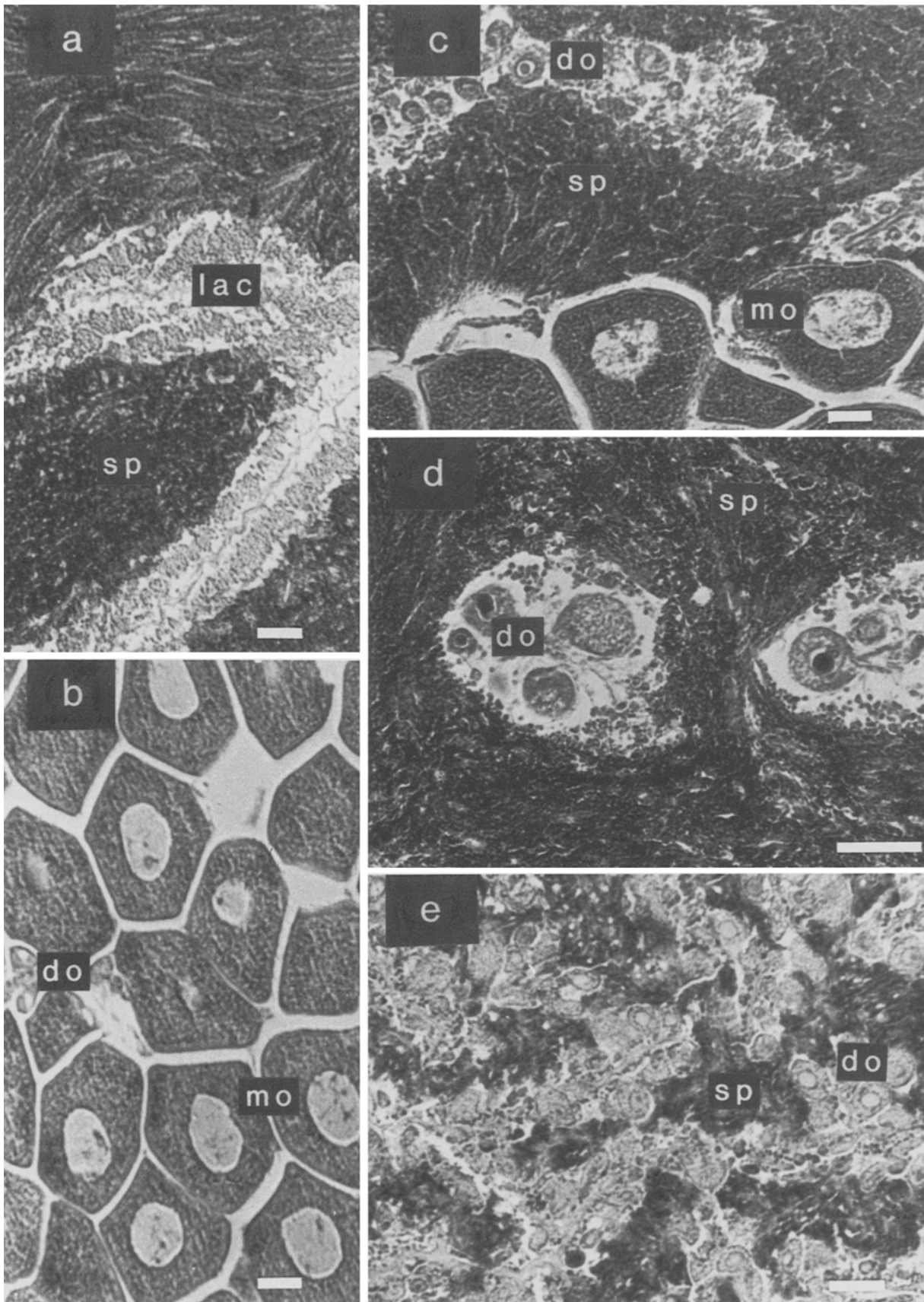


Fig. 6. *Patella kermadecensis*. Histological sections of gonads. (a) Mature testis; (b) mature ovary; (c) mosaic hermaphrodite; (d) transitional hermaphrodite (early stage); (e) transitional hermaphrodite

(late stage). do: developing oocytes; lac: lacuna of testis; mo: mature oocyte; sp: sperm. All scale bars = 50 μ m

layer of oocytes occurred on the dorsal surface of an otherwise male gonad. Subsequent microscopic examination confirmed that this limpet had mature spermatocytes and oocytes (Fig. 6c), and also revealed that immature oocytes were common in the lacunae of the testicular part of the gonad. Further examination of sectioned material revealed more hermaphroditic gonads (Table 2). Predominantly male gonads containing immature oocytes (Fig. 6d) were found in five small limpets in March 1984, one very large limpet in October 1984, and three large limpets in August 1985. In addition, the October 1984 sample contained three large limpets which were predominantly female but also contained small pockets of sperm, and one small limpet which had a gonad comprised of almost equal portions of male and female tissue (Fig. 6e).

Discussion

The existence of protandric sex change amongst molluscs has long been recognised (Coe 1953, Hoaglund 1978), and several species of limpet are thought to exhibit this form of sexual development (Branch 1981). This suggestion is often based solely on a changing sex ratio with increasing size; males predominate in the smaller size classes and females in the larger ones. Such patterns have been demonstrated for the European patellids *Patella vulgata* (Orton et al. 1956), *P. aspera* (Thompson 1979) and *P. coerulea* (Bacci 1947), for the South African species *P. argenvillei*, *P. longicosta* and *P. oculus* (Branch 1974), and for the Californian acmaeid *Lottia gigantea*. Differential rates of growth and/or mortality may also give rise to these patterns (Branch 1981), however, and additional evidence is required to verify the existence of sex change.

The relationship between sex-ratio and size in *Patella kermadecensis* suggests that protandric sex change is likely. In March 1984, there were 54 limpets between 30 and 60 mm, 51 of which had discernible gonads, but only one (42 mm) was a female (see Fig. 5a). As there is virtually no overlap in size between neuter individuals and females, female *P. kermadecensis* are not likely to arise from neuter individuals but from individuals that were previously male (Fig. 3). Unfortunately, in the other two samples, only one limpet smaller than 60 mm had a gonad, and that limpet was a male hitchhiker, so this pattern could not be confirmed for another time of year. Of the limpets previously described as changing sex, only two had a range of sizes where the whole population had sexable gonads, but females were either absent or extremely rare. For *P. vulgata* this occurred between 20 and 30 mm shell length, and in *P. oculus* between 2.5 and 5 g wet flesh weight (Branch 1981).

The hypothesis of sex change in *Patella kermadecensis* is further strengthened by histological evidence of transitional hermaphrodites in the population. Branch (1974) recognised two forms of hermaphrodites in *P. oculus*: transitional and mosaic. The first type had morphologically uniform gonads which were predominantly male, but which had small oocytes scattered throughout and arising from the germinal

epithelium. Eventually, all sperm were either shed or resorbed, and the limpet became entirely female. This situation has been reported for *P. oculus* (Branch 1974) and *P. coerulea* (Bacci 1947). There was a high incidence of this form of hermaphroditic gonad (as illustrated in Fig. 6d, e) in *P. kermadecensis* (Table 2), and this can best be interpreted as an intermediate stage in the transformation of a male gonad into a female one (sequential hermaphroditism). Mosaic hermaphrodites, however, contained some patches of gonad that were functionally female and some that were functionally male (i.e., simultaneous hermaphrodites). This form of hermaphroditism has a small, sporadic incidence in many *Patella* spp. from South Africa (Branch 1974), England (Dodd 1956) and elsewhere, but this is not necessarily related to sex change (Branch 1981). One mosaic hermaphrodite was encountered in the samples of *P. kermadecensis* (Fig. 6c), and this was almost certainly associated with sex change in this case: a transitional gonad in which resorption of sperm had not occurred for some reason and a hermaphroditic condition had been retained.

Unfortunately, samples of *Patella kermadecensis* were not available over a sufficient portion of the year to allow the incidence of hermaphroditism to be related to the spawning cycle. Branch (1974) was able to do this for *P. oculus*, and hence provide additional evidence for protandric sex change. Because transitional hermaphrodites of *P. kermadecensis* were found at three different times of the year, however, and in the absence of a clearly defined spawning event, it is unlikely that sex change is closely linked with spawning. If this is the case, it represents a different pattern of sex-change from three other well-documented patellid limpets (Branch 1981): in *P. vulgata* the transition takes place in the resting phase between spawnings so that transitional hermaphroditic gonads are never encountered, and in *P. oculus* and *P. coerulea* transitional gonads are only encountered after spawning.

A direct test of the presence of protandric sex change in limpets has been provided only for *Lottia gigantea*. Wright and Lindberg (1982), using a syringe to sample gonad tissue from live limpets (Wright and Lindberg 1979), observed some limpets that were initially male but were female when sampled a year or two later. The inaccessibility of the Kermadec Islands, especially during the summer months when reproductive activity of small limpets appears to be most pronounced (Fig. 5a), has so far precluded such *in vivo* sampling of gonad tissue in *Patella kermadecensis*. Despite the absence of a direct test, it is interesting to note several similarities between *P. kermadecensis* and *L. gigantea*. This latter species also reaches sizes >100 mm, with the largest individuals maintaining regularly spaced territories on the rock (Stimson 1970). Sex change in *L. gigantea* is related to its territorial behaviour, and the incidence of sex change increases with decreasing densities (Lindberg and Wright 1985, Wright 1989). These authors argued that environmental factors (including the social interactions among conspecifics) could exert some control over sex change. Such mechanisms are well known in species of *Crepidula*, in which protandric sex change has been well studied (Coe 1953,

Hoaglund 1978), but they are not usually considered for sex-changing archaeogastropod limpets (Lindberg and Wright 1985). Like *L. gigantea*, *P. kermadecensis* is regularly spaced on the rock (see Fig. 7d in Schiel et al. 1986), and probably also maintains feeding territories (Creese and Cole in preparation). In addition, young limpets were found only on the backs of adults (as illustrated in Fig. 2b) in collected material (Fig. 4b) and field samples (Schiel et al. 1986), and must presumably move from this microhabitat to the open rock at a size of 35 to 75 mm. Because the sex of so few hitchhikers is known at present, it is not possible to relate the time of sex change to a change in habitat. Nevertheless, it seems likely that most, if not all, hitchhikers develop as males, and that sex change occurs after the young males move on to the rock and establish territories of their own. Further sampling is needed to substantiate this, but we suggest that, like *L. gigantea* (Lindberg and Wright 1985, Wright 1989), protandric sex change in *P. kermadecensis* may be at least partly controlled by environmental factors. It is unlikely to be merely a function of growth, as the sizes of the hermaphroditic limpets varied considerably; between 31 and 143 mm (Table 2).

In reviewing the size-advantage hypothesis (Ghiselin 1974) as an explanation of the adaptive significance of sequential hermaphroditism, Warner (1988) argued that protandry would be favoured if males functioned better when small and/or females functioned better when large. In limpets, there is an exponential relationship between gonad weight and length, and fecundity increases with size irrespective of sex (Creese 1980, Branch 1981). It has been hypothesised, therefore, that there will only be a distinct advantage for limpets to concentrate production of eggs in the larger individuals if males are sufficiently plentiful not to limit fertilisation (Hughes 1986). This is certainly true in *Patella kermadecensis* and, because it can grow to such a large size, this relative reproductive advantage for large females is likely to be particularly pronounced. For example, the four females in the August 1985 sample that were over 13 cm long had gonads ranging from 9 to 17 g, which represents a potential reproductive output of 2.5 to 5×10^6 eggs (W. J. Ballantine personal communication). On the other hand, it may be disadvantageous to be a small female because it is energetically more expensive to produce eggs than sperm (Branch 1981, Hughes 1986). In a situation where young *P. kermadecensis* at the time of sexual maturity (25 to 40 mm) may have a limited supply of energy for reproduction by virtue of the limited grazing surface available on adult shells, production of sperm would be favoured. By rapidly and inexpensively developing a male gonad, young individual *P. kermadecensis* could participate in a non-trivial way in at least some spawning activity before making the probably hazardous transition from adult shell to rock surface.

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