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REPRODUCTIVE BEHAVIOR OF THE GREEN-LIPPED MUSSEL, *PERNA CANALICULUS*, IN NORTHERN NEW ZEALAND

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ABSTRACT

Wild populations of mussels, *Perna canaliculus,* in northern New Zealand supply the majority of seed mussels to the >70,000 tonnes per annum green-lipped mussel aquaculture industry. However, surprisingly little is known about the reproductive cycle in this mussel species or in these northern populations at Ninety Mile Beach. An extensive histological study of *P. canaliculus* found that their reproductive biology was similar to that recorded for other mussels. The mussels were dioecious with a 1:1 sex ratio throughout all sizes; only one hermaphrodite individual was found. Mussels began to mature from 27 mm shell length, and by 40–50 mm, most individuals were sexually mature. Both female and male mussels appeared to have a consistent gonad cycle of gamete development, discharge, and redevelopment. Both sexes were well-synchronized reproductively, with a prolonged spawning season from June to December (Austral winter-spring) when water temperatures were at their lowest and rising. However, a small proportion of mussels was found spawning ripe gametes throughout the year, which could account for the continuing appearance of mussel seed outside the main spawning season. The spawning-spat catching season is more extensive at Ninety Mile Beach than has been recorded in more southerly parts of New Zealand, and these differences may be related to the generally warmer water conditions recorded in northern areas.

Knowledge of reproductive patterns of natural mussel populations is important for mussel aquaculture, which in New Zealand depends entirely on wild-caught seed. For example, the frequency and duration of spawning events may be used to predict spat settlement and spatfall events within a particular population. However, there are great geographical and seasonal variations in reproductive cycles within mussel populations (Newell et al., 1982; Snodden and Roberts, 1997), and reproductive patterns cannot be generalized from one population to another. There is limited published data on the reproductive cycle of the New Zealand green-lipped mussel, *Perna canaliculus*, except for indirect observations on spat settlement (Greenway, 1975; Meredyth-Young and Jenkins 1978; Buchanan, 1994; Buchanan and Babcock, 1997), body condition index (Flaws, 1975; Hickmanand Illingworth, 1980; Buchanan, 1998), and initial histological work by Flaws (1975), Tortell (1976), and Buchanan (1998). The full gametogenic cycle of the genus *Perna* has been well studied in tropical regions (Virabhadra Rao et al., 1975; Walter, 1982). Several investigations report on the reproductive cycles of various temperate species of *Perna*, and most have used indirect methods such as larval appearance in the plankton (Booth, 1977), and settlement of spat (Greenway, 1968; 1969; 1975; Zaouali, 1973; Berry, 1978; Abda-Boudjema and Mouèza, 1981). These methods do not provide the precise assessment of mussel gonad development that can be attained with histological sections of gonad tissues (e.g., as for Moroccan *Perna* species in Shafee, 1989). In conjunction with environmental measurements such as water temperature and nutrient availability, histological gonad sections can provide information about the influence of exogenous and endogenous factors affecting the initiation and duration of various stages in the gametogenic cycle (Vélez and Epifanio, 1981; Newell et al., 1982; Nichols, 1996). For dioecious species with external fertilization such as mytilids, examination of histological sections may elucidate sex ratios, hermaphroditism, and level of gamete synchrony in the population (Brousseau, 1982; Jasim and Brand, 1989; Villalba, 1995).

Ninety Mile Beach, North Island, New Zealand, is the main source of wild mussel spat for commercial farms in Marlborough Sounds, South Island. About 100,000 tonnes yr^{-1} of mussel spat, attached to seaweed, are collected from Ninety Mile Beach and transported about 1,000 km to farms in Marlborough Sounds, where they provide about 80% of mussel farm spat requirements (Jeffs et al., 2000). However, the detailed reproductive cycle of wild populations of mussels at Ninety Mile Beach is largely unknown. Buchanan (1998) investigated the reproductive condition in *P. canaliculus* at French Pass, Marlborough Sounds, with the aim to compare histological and visual techniques that could be used to measure mussel condition in farms. However, no other studies have focused on the reproductive patterns and potentials of the wild mussel populations that provide the bulk of seed mussels to the farms. The present study investigates the reproductive cycle of *P. canaliculus*, the major commercial shellfish product of New Zealand, through histological sections of gonad tissues, which were prepared and analyzed from natural intertidal and subtidal green-lipped mussels from the main spat-source region of Ninety Mile Beach, northern New Zealand. Results are provided on the reproductive behavior of mussels from 6 sites along the 90 km length of Ninety Mile Beach. More specific comparisons of reproductive variability among sites are presented elsewhere (Alfaro et al., in prep.).

METHODS AND MATERIALS

Mussel specimens were gathered for histological analysis from a total of six sites at Ninety Mile Beach, in northern New Zealand (Fig. 1). Collections from four rocky intertidal sites at Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point represented the sum total of all major intertidal mussel populations that occur along Ninety Mile Beach. Two subtidal sites at Wizard Rock and Blue House were chosen for additional sampling because these were the only subtidal populations known at the outset of the study (Fig. 1). Temperature records were obtained from a data logger placed 0.5 m below low water level at the south end of the study area at 35°10.8′S and 173°5.3′E.

Approximately 70 adult mussels (62–114 mm in length) were collected monthly from each of the six sites, for a total of about 420 mussels sectioned per month. Sampling took place from July 1998 to April 2000, with 21 mo sampled. Exceptions to this regular sampling scheme took place only when weather conditions prevented access to the sites. In addition, 96 juvenile mussels (3–60 mm in length) were collected on 8 July 1998 and 24 April 2000 to determine the minimum size at sexual maturity. Intertidal mussels were collected haphazardly during low tide and subtidal mussels were dredged when weather conditions permitted. Immediately after collection, the mussels were sectioned dorsoventrally through the mid-body and fixed in Bouin's solution. Mussel tissues were embedded in paraffin, sectioned with a microtome at 5–7 μm, and stained with Haematoxylin-Eosin. The histological sections were viewed under a compound microscope to identify sex and stage of gametogenic development. Gonad developmental stages were identified for each sex according to a modified classification scheme based on Shafee (1989). Gonad tissues mostly were uniform in their stage of development, and mussels were assigned a developmental stage according to the state of the majority of the follicles in the gonad tissues. The presence of hermaphroditism and parasitism was recorded throughout the sampling period.

A 1:1 sex ratio in the mussels was tested with a Chi-square, goodness-of-fit test. Gonad indices were calculated according to King et al. (1989) and Galinou-Mitsoudi and Sinis (1994) with the following formula:

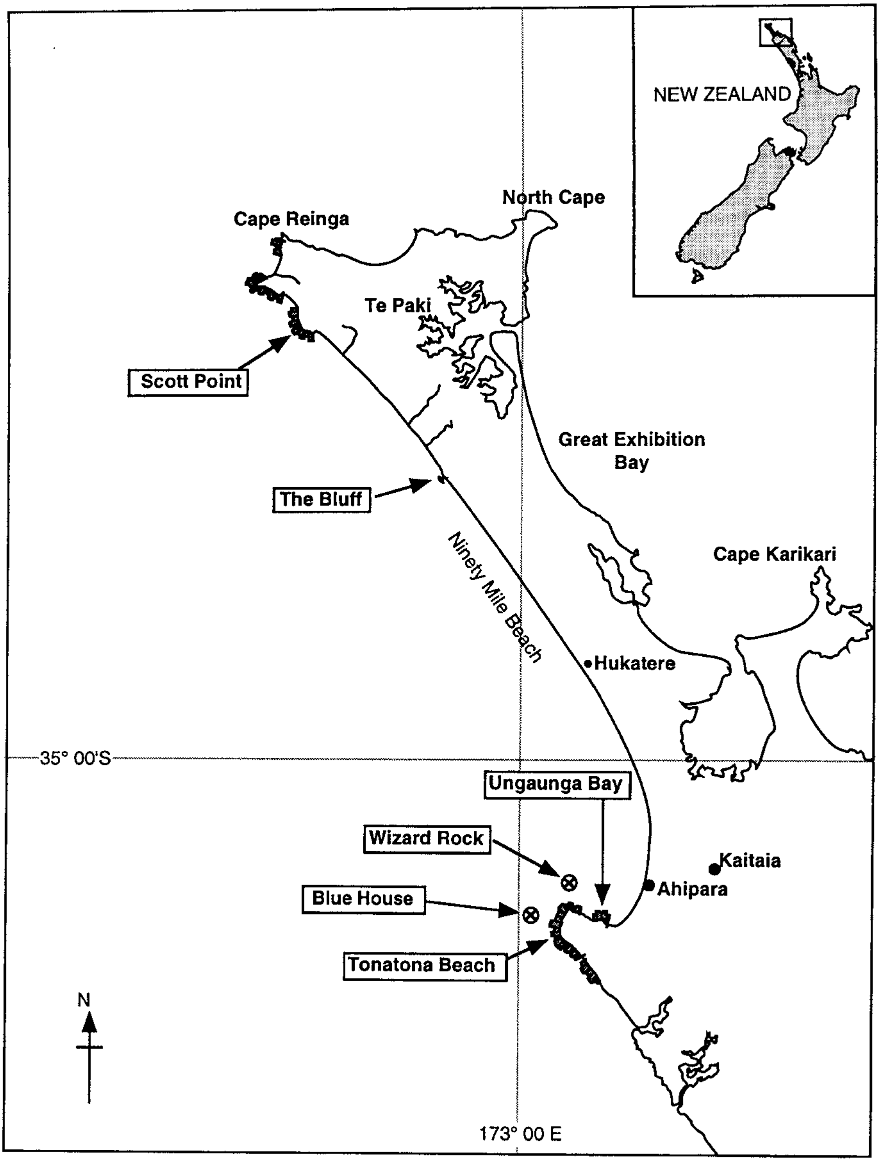

Figure 1. Map of study area at Ninety Mile Beach, northern New Zealand. Four intertidal collection sites are Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point. Two subtidal collection sites are Blue House and Wizard Rock.

$$\text{G.I.} = \frac{\text{(number in each stage) (rank of stage)}}{\text{total sample size}} \times 100$$

where the rank system was:

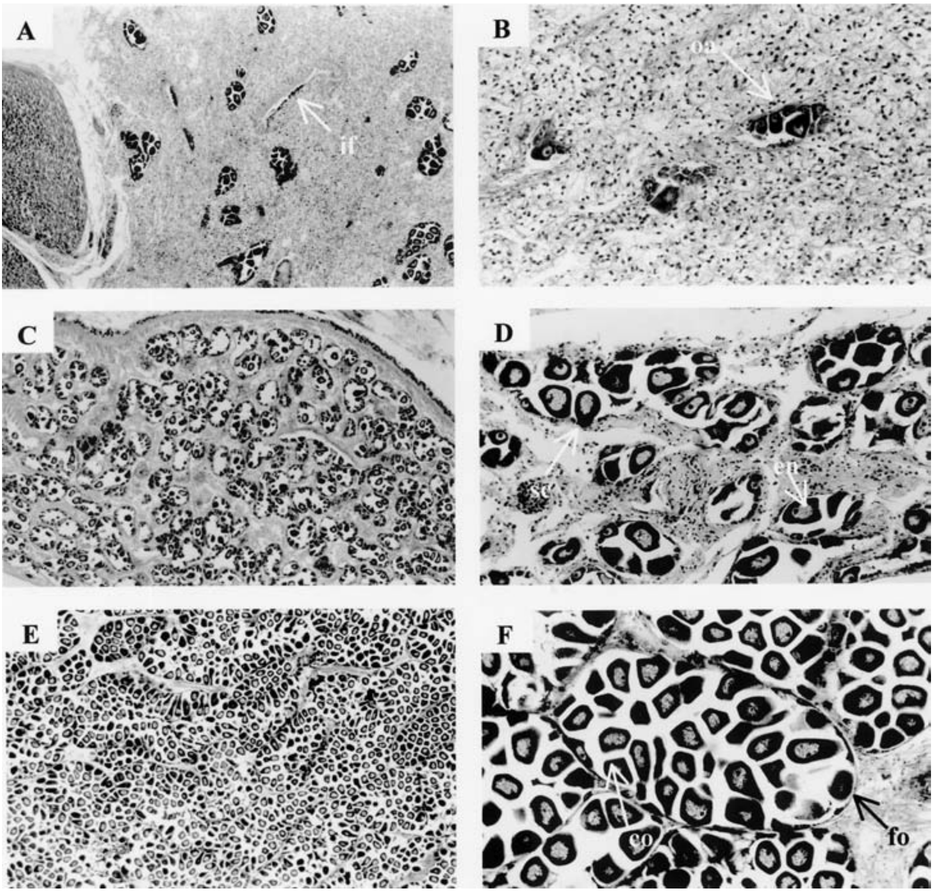

Figure 2. Histological sections showing 3 gonad developmental stages for female mussels. A) Early stage showing irregular follicles (if) with small oocytes; 4×, and B) oocytes attached to follicle wall (oa); 16×. C) Late stage of development showing larger follicles; 4×. D) stalk of cytoplasm (sc) between oocyte and follicle wall, and enlarged nuclei (en); 16x. E) Ripe stage with oocytes covering mantle area; 4×, and F) compressed free oocytes (co) inside follicles (fo); 16×.

Resting stage	0
Early development stage	1
Late development stage	2
Ripe stage	3
Spawning stage	2
Redevelopment stage	2
Spent stage	1

Frequency distribution graphs, including all developmental stages, were constructed to identify seasonal patterns of gametogenic and breeding activities.

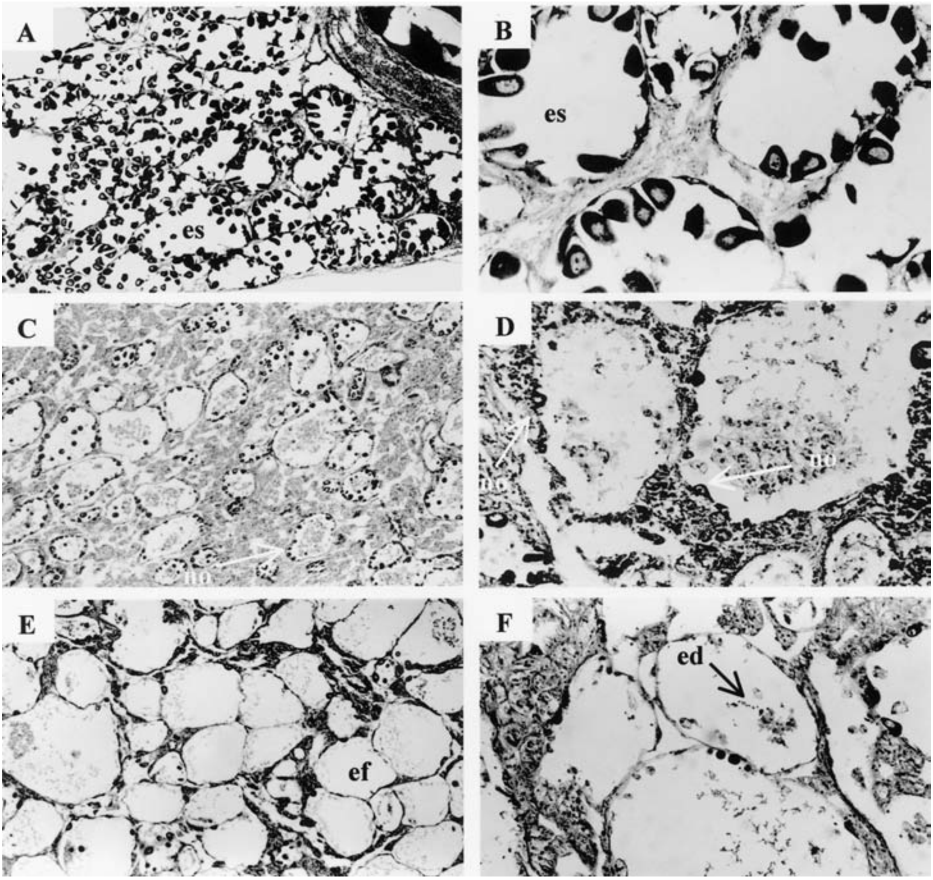

Figure 3. Histological sections showing 3 gonad developmental stages for female mussels. A) Spawning stage showing empty spaces (es) inside follicles left by spawned oocytes; 4×. B) Spawning stage with empty spaces (es) inside follicles; 16×. C) Redeveloping stage with new oocytes (no) present in large follicles; 4×. D) new oocytes (no) inside follicles; 16×. E) Spent stage of development showing empty and degenerate follicles (ef); 4×, and F) remaining cellular debris (ed); 16×.

RESULTS

Examination of gonad tissues of female and male mussels allowed delineation of six distinct development stages for each sex (Figs. 2–5). An indeterminate stage was recorded for mussels which showed no signs of follicle development in the tissues sectioned.

FEMALE GONAD.—Early developing stage (Fig. 2A,B): Small groups of germinal cells are scattered in the mantle. The follicles are irregular in size. Oogonia line the follicle wall. Mostly small, irregular-shaped oocytes bulge from the follicle wall. A few large oocytes are attached to the follicle wall by a cytoplasmic stalk. Oocyte nuclei are large and clear.

Late developing stage (Fig. 2C,D): The follicles are larger and more numerous than in previous stage. Oocytes have begun to accumulate yolk and have grown considerably.

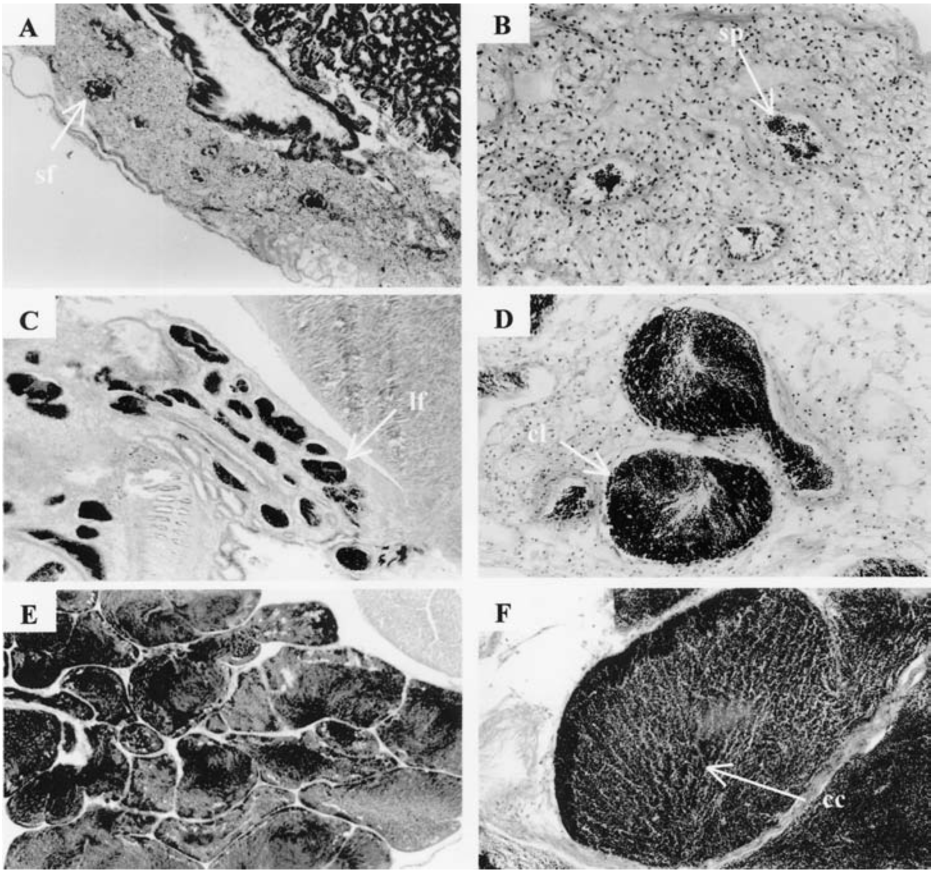

Figure 4. Histological sections showing 3 gonad developmental stages for male mussels. A) Early stage of development with small follicles (sf); 4×, and B) spermatogonia inside follicles (sp); 16×. C) Late stage showing larger follicles (lf); 4×, and D) concentric layer (cl) of spermatogonia; 16×. E) Ripe stage showing mantle filled with follicles; 4×, and F) spermatozoa converging at the center of the lumen; 16×.

Early oocytes are still attached to the follicle wall by a slender stalk of cytoplasm. Some mature oocytes are free in the lumen. Oocyte nuclei are enlarged.

Ripe stage (Fig. 2E,F): The mantle is nearly filled with follicles. Most oocytes have reached maximum size, have become free from the follicle wall, and are now packed in the lumen. Oocytes have become compressed inside the follicle.

Spawning stage (Fig. 3A,B): A great number of ripe oocytes are still present in the expanded follicles. However, there is a reduction in the density of gametes which have left numerous empty spaces in the lumen. Some follicles have ruptured and a few oocytes may be left.

Redeveloping stage (Fig. 3C,D): Follicles do not occupy all the available mantle area. Remaining oocytes are arranged loosely in the follicle. New oocytes are visible along the follicle wall. More connective tissue is evident in this stage than before initial spawning.

Spent stage (Fig. 3E,F): Follicles collapse and degenerate. Amoebocytes attack unspawned gametes, often resulting in the lumen of the follicle becoming filled with a mass of cellular debris.

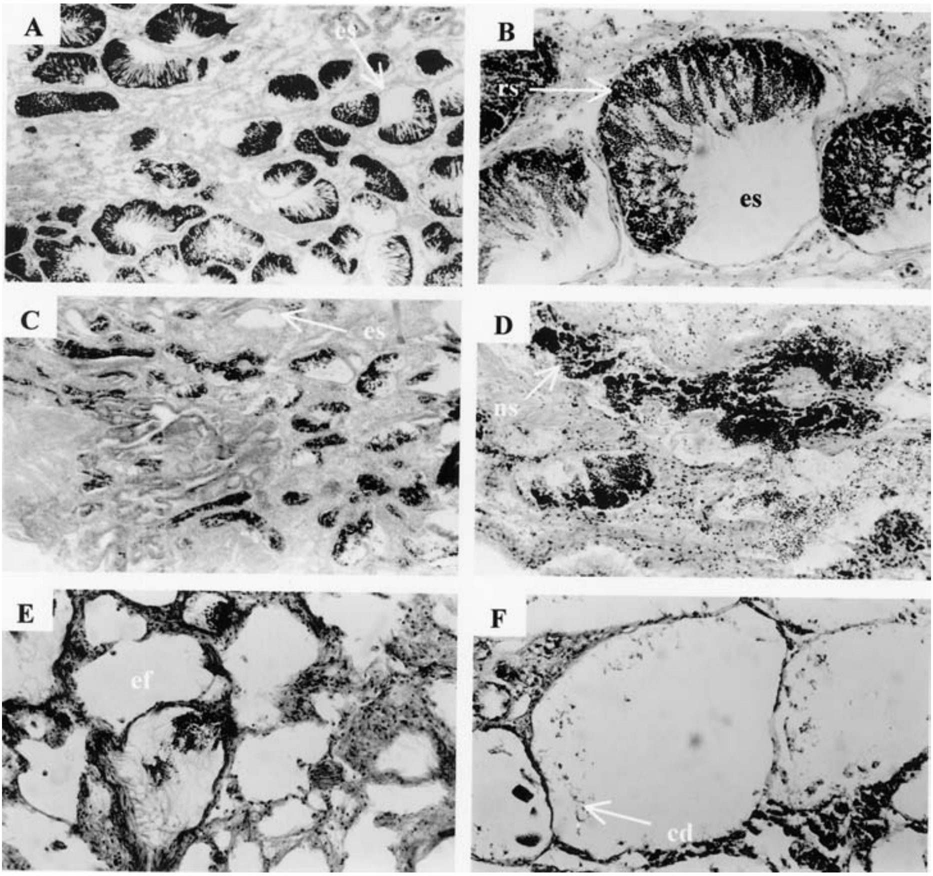

Figure 5. Histological sections showing 3 gonad developmental stages for male mussels. A) Spawning stage of development showing empty spaces (es) inside follicles after ejection of spermatocytes; 4×, and B) some ripe spermatozoa (rs) are still present; 16×. C) Redevelopment stage showing empty spaces (es) inside follicles; 4×, and D) new spermatids (ns) forming. E) Spent stage with empty follicles (ef); 4×, and F) cellular debris (cd) left inside follicles after spawning; 16×.

MALE GONAD.—Early developing stage (Fig. 4A,B): Small groups of germinal cells are scattered in the mantle. The follicles are often small and elongate. Spermatogonia line the follicle wall. The follicles start to fill with spermatocytes and spermatids. A few spermatozoa can be seen in the middle of the lumen.

Late developing stage (Fig. 4C,D): The follicles occupy a large portion of the mantle. Wide concentric layers of spermatogonia, spermatocytes, and spermatids are evident. Spermatozoa are apparent in the lumen, but they are not well organized.

Ripe stage (Fig. 4E,F): The mantle is nearly filled with follicles. A thin layer of spermatogonia line the follicle wall, although in some follicles this layer is not visible. Spermatocytes and spermatids are less apparent. Spermatozoa are clear and neatly arranged in layers, converging at the center of the lumen.

Spawning stage (Fig. 5A,B): A dense band of ripe spermatozoa is still present. The spermatozoa are less organized in a partially empty lumen. Very few or no spermatocytes and spermatids remain.

Table 1. Numbers and percentages of mussels (*Perna calaniculus*) (3–69 mm in length) within seven size classes.

Size range (mm)	Total number	Number with gonads (%)	% of total
3–9	11	0	0
10–19	16	0	0
20–29	16	5 (31)	10
30–39	17	12 (71)	24
40–59	15	14 (93)	28
50–59	12	11 (92)	22
60–69	9	8 (89)	16
Total	96	50 (52)	100

Redeveloping stage (Fig. 5C,D): Densely staining bands of spermatids give rise to new lamellae of spermatozoa, although gaps within the follicles are still present. Large follicles do not occupy all the available mantle area. More connective tissue is evident in this stage than before initial spawning.

Spent stage (Fig. 5E,F): Follicles collapse and degenerate. Amoebocytes attack unspawned gametes, often resulting in the lumen of the follicle becoming filled with a mass of cellular debris.

Reproductive Cycle.—Maximum shell length measurements of adult mussels showed no differences in mean shell lengths between female and male individuals. The range of shell length for both female and male mussels was the same at 70–145 mm, and the mean (± SE) for each sex was 91 ± 12 mm. Furthermore, similar numbers of females to males were found within the samples of adult mussels ($\chi^2 = 0.34$, $P > 0.05$).

Histological examination of small mussels (3–69 mm in length), from both intertidal and subtidal populations, indicated that about 50% of mussels from about 27 mm in length contained identifiable gonad tissues (Table 1). A Chi-square test for all female and male mussels between 3–69 mm in length indicated no statistical difference from a 1:1 sex ratio ($\chi^2 = 2.00$, $P > 0.05$). Both sexes were equally represented within the mussel size range, which suggests that female and male mussels mature at about the same size.

The gonad index analyses suggest that female and male mussel reproductive cycles were well synchronized across all sites (Fig. 6). A two-way ANOVA comparing gonad indices between all female and male mussels for the interval from July 1998 to April 2000 (sex and month as factors) showed no statistical difference in reproductive state between sexes (ANOVA; $F(1,134) = 0.003$, $P > 0.05$) and the interaction (ANOVA; $F(19,134) = 0.007$, $P > 0.05$), but highly significant monthly differences among sampling periods (ANOVA; $F(19,134) = 6.119$, $P < 0.05$) (Fig. 6).

The frequency distribution of all reproductive stages indicated a similar seasonal trend for female and male mussels (Figs. 7,8). Generally, gonad development started in December, with the early stage becoming increasingly dominant until around February. The late stage of development predominated in March. By April, mussels in the ripe stage became more numerous, and these were most abundant in May. The number of ripe mussels continued to be high through August–September. Spawning appears to have begun in June–July, with spawning continuing through December. Redevelopment of gonad tissue was present throughout the year, but was most significant from August to December (Austral winter-spring). No major inter-annual variations were observed between the 1998, 1999, and 2000 reproductive cycles. The number of mussel gonads in the resting stage of

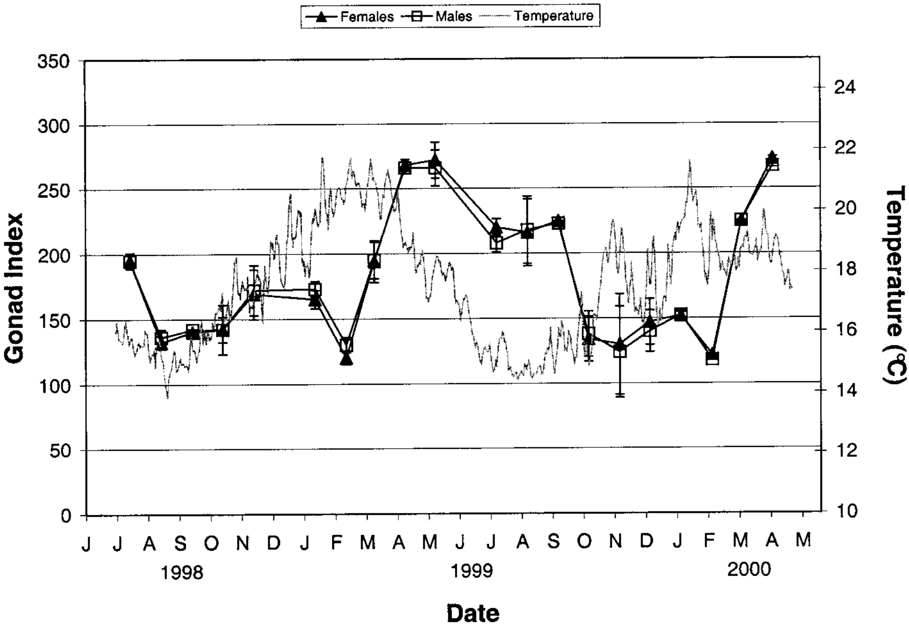

Figure 6. Mean (± SE) gonad indices for female and male mussels (combined data from 6 sites) and water temperature records for Ninety Mile Beach, northern New Zealand between July 1998 and April 2000.

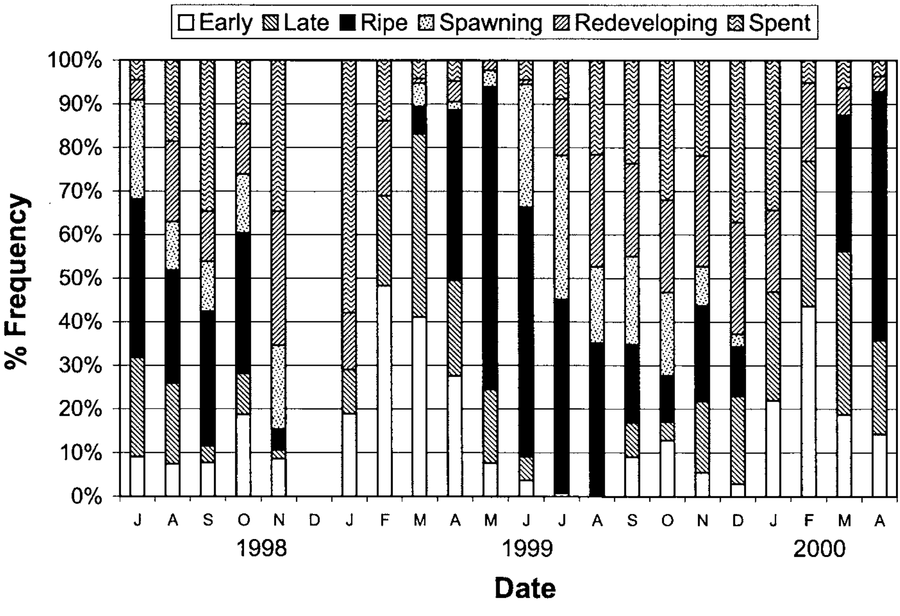

Figure 7. Percent frequency of the six female gonad developmental stages in the monthly samples from July 1998 to April 2000.

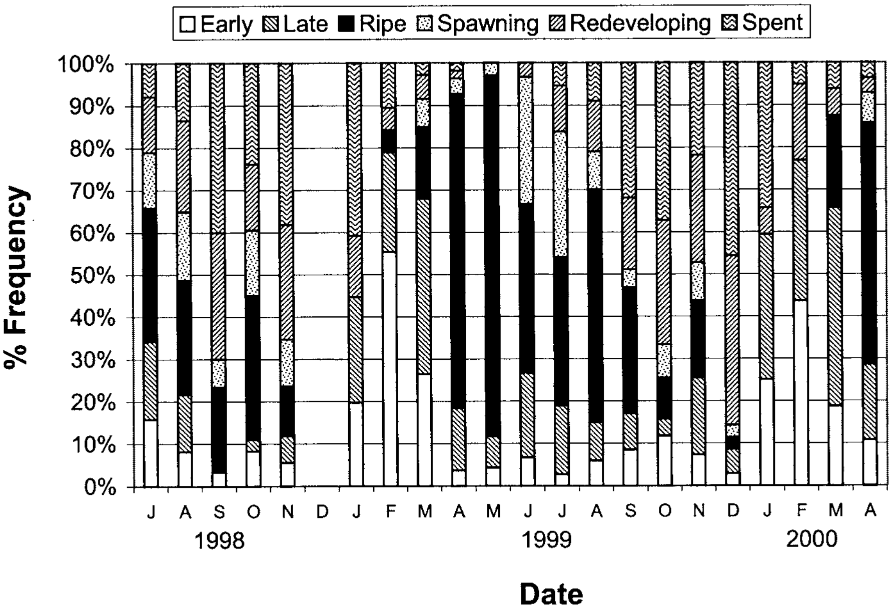

Figure 8. Percent frequency of the six male gonad developmental stages in the monthly samples from July 1998 to April 2000.

development was similar for female and male mussels. These resting gonads were more abundant (7 ± 4%) from January to March, which is when high numbers of gonads were in the early stage of development. During the rest of the year, the percentage of resting gonads fluctuated between 0 to 4%.

Only one hermaphrodite mussel was found among 6720 mussels examined. The mean (± SE) number of parasitized mussels per site per month was 3.6 ± 5.3 mussels, but with > 30% of parasitized mussels within a single monthly sample. Parasitized mussels were most common in samples taken in October 1999, July 1998 and April 2000. Two different parasites were found in the samples; *Bucephalus* sp. and *Nematopsis* sp., were equally abundant in the number of mussels they infested (66 and 57 respectively, of the 6720 mussels). No differences were observed in the level of parasitism between female and male mussels ($\chi^2 = 1.72$, $P > 0.05$), although in most cases the sex was not identifiable.

Water temperature records at Ninety Mile Beach ranged from 14°C in winter to 22°C in summer and had a mean (± SE) of 17 ± 2°C throughout the sampling period (Fig. 6).

DISCUSSION

Understanding the reproductive patterns of the wild mussel populations at Ninety Mile Beach is particularly important because their spat production is of considerable commercial importance to the extensive New Zealand mussel farming industry. Reproductive cycles of local mussel populations, together with oceanographic data (i.e., ocean currents, tidal range, and upwelling dynamics) and weather information (i.e., wind and temperature), may allow for temporal and spatial predictions of both spatfall events and the health of adult source populations.

The 1:1 sex ratio and synchronized reproductive development between sexes throughout the year in intertidal and subtidal populations at Ninety Mile Beach have been observed in other *P. canaliculus* populations in New Zealand (Flaws, 1975; Tortell, 1976; Buchanan, 1998), and is found among other mussel species (Heffernan and Walker, 1989; Villalba, 1995; Nichols, 1996; Darrigran et al., 1999). Furthermore, no differences in maximum shell length, nor size at maturation, were found between females and males. These results suggest that female and male *P. canaliculus* respond to similar spawning cues to ensure maximum chances of fertilization and larval production.

The shell length at onset of sexual maturity for wild mussel populations at Ninety Mile Beach appears to be around 27 mm, which indicates early development of gonad tissue. Hermaphroditism was rare, as in other wild mussel populations (Sunila, 1981;Villalba, 1995). By contrast, up to 5% hermaphroditism has been found in farmed mussels in Coromandel that were sourced from the same Ninety Mile Beach spat (Alfaro et al., unpublished). The overall level of parasitism of the mussel gonads was 3%, but differences were observed among the six sites (Alfaro et al., in prep.).

Gonad indices that are based on gonad developmental stages have been used extensively as a quantitative way to identify the larval/spat production of shellfish populations, and to compare results from different studies (Gabbott and Bayne, 1973; Kautsky, 1982; Brown, 1988; Borcherding, 1991). Results from Ninety Mile Beach gonad indices indicate that the potential production of larvae is low from about October to February, and productivity is highest in April–May.

The reproductive cycle of *P. canaliculus* at Ninety Mile Beach reveals a spawning season starting in June and continuing through December. Together, the extended spawning season, and the large percentage of ripe and redeveloping mussels through most of the year, suggest that gonad production in mussel populations at Ninety Mile Beach is occurring in optimal environmental conditions. Prolonged reproductive periods have been observed in other mussel populations in tropical and subtropical waters (Lubet, 1981; Lee, 1986), but marked differences in the timing and frequency of spawning events have been reported in other mussel populations, even within the same species (Flaws, 1975; King et al., 1989; Villalba, 1995; Nichols, 1996). The prolonged spawning season of *P. canaliculus* at Ninety Mile Beach greatly differs from the two spawning periods (early summer and autumn–spring) observed six degrees latitude to the south in Marlborough Sounds, New Zealand (Flaws, 1975; Tortell, 1976; Buchanan, 1998).

Water temperature has been suggested to be one of the most important factors responsible for spawning in marine bivalves (Kautsky, 1982; Newell et al., 1982; Brown, 1988; Dame, 1996). Rapid temperature changes (up or down) have been observed to trigger spawning events in many bivalves, including mussels (Newell et al., 1982; Hawkins et al., 1985; Grant, 1994; Hooker and Creese, 1995; Nichols, 1996). Furthermore, marked differences in spawning behavior have been attributed to regional climatic differences from one population to another (Shafee, 1989). In general, warm water mussels spawn throughout the year according to sudden climatic fluctuations such as favorable temperature changes (opportunistic behavior), whereas in temperate regions, gonad development and spawning are continuous through a season or conservative in behavior (Shafee, 1989). In the present study, spawning activity started in June-July, which corresponds to water temperatures of about 15°C, a value close to the lowest temperatures of the year (Figs. 6–

8). Spawning continued through the warmer months in spring, until December, when water temperatures reached their highest values of 18–20°C.–A factor that contributes to the extended spawning season of *P. canaliculus* at Ninety Mile Beach is that water temperature rarely drops below 14°C, which is well above the temperature range (10–12°C) at which larval production ceases for other mussel species (Fraleigh et al., 1993; Nichols, 1996). Mean water temperatures in Marlborough Sounds of 10–11°C in winter and 20–21°C in summer (Tortell, 1976; Jenkins, 1985) may account for the observed differences in spawning patterns of mussels between these warmer northern and cooler southern regions of New Zealand. Thus, the shorter spawning intervals of Marlborough Sounds populations appear to be constrained by the relatively cooler climatic conditions they experience. Conversely, the less marked seasonality in reproductive cycle of the northern populations may be a result of the warmer subtropical climate of the area. Results from this study confirm that reproductive variability is great from one region to another in New Zealand, and that generalizations about the seasonal reproductive behavior may not be appropriate for this mussel species.

The presence of a clear redeveloping stage in Ninety Mile Beach mussels suggests that multiple spawning events take place throughout the year, and implies high reproductive output in these mussel populations. This potential high productivity, together with the prolonged spawning season from winter to spring, is consistent with the observation that Ninety Mile Beach has the highest wild spat abundances in the country (Jeffs et al., 2000). Finally, the extended spawning period of *P. canaliculus* at Ninety Mile Beach has significant ecological implications for the maintenance of mussel populations in northern New Zealand. A better understanding of the factors that control spawning allows elucidation of geographic differences among regions, and may help overcome current difficulties in conditioning and spawning mussels in commercial hatcheries.

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