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Mass spawning by the sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea) in a New Zealand fiord

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Abstract A mass synchronous spawning of the sea urchin *Evechinus chloroticus* (Valenciennes) was observed in situ in Doubtful Sound, a large New Zealand fiord. Spawning occurred between 17:30 hrs and 18:30 hrs on 27 January 1994 and coincided with a full moon, spring tides and a period of decreasing sea temperatures. During spawning, the sea urchins formed a dense spawning aggregation of both sexes, with >90% of the urchins observed spawning at the time. Spawned gametes clouded the water column, and some were eaten by small labrid fish species. The spawning, which may have been as widespread as 40 km, marked a 42 to 50% decrease in gonad indices and resulted in a widespread, dense cohort of *E. chloroticus* larvae within the fiord.

Introduction

Gametogenic cycles in echinoderms are generally well understood and relatively easy to determine from gonad indices and histological examination (Giese et al. 1987). Much less is known about the processes of gamete release and in situ fertilization rates in this group of animals. Successful fertilization of gametes may be a limiting event in the life histories of marine invertebrates that have external fertilization (Pennington 1985; Levitan 1991). While these animals can have very high fecundity, the rapid dilution of gametes in the water column can greatly reduce fertilization success and subsequent larval production (Denny and Shibata 1989). Spawning behavior is one factor that can influence fertilization rates.

The cues that trigger gamete discharge, how synchronous spawning is, and the duration of spawning are processes that are ill understood. Information on these processes requires both experimental manipulation and in situ observation of gamete release. As spawning cues are poorly understood in echinoderms, very few in situ observations exist and these are typically serendipitous. For example, after questioning over 100 individuals, including investigators at various marine stations, Pennington (1985) could record only seven reports of direct observations of spawning. Examples of in situ spawning observations have been reported for holothuroid (McEuen 1988; Babcock et al. 1992), crinoid (Fishelson 1968; Hendler and Meyer 1982; Babcock et al. 1992), echinoid (Randall et al. 1964; Pennington 1985; Levitan 1988; Minchin 1992) and asteroid (Minchin 1987; Babcock et al. 1992, 1994; Minchin 1992) species. Two exceptional observations of spawning were made by Hendler and Meyer (1982), who observed spawning in three tropical echinoderms; and by Pearse et al. (1988), who documented simultaneous spawning in six species of echinoderms in Barkley Sound, British Columbia. By their nature such chance observations cannot incorporate rigorous experimental design; however, they yield information essential to the examination of fertilization dynamics.

This paper describes chance observations of a mass, synchronous spawning of the regular sea urchin *Evechinus chloroticus* (Valenciennes). This species is dioecious, with an equal sex ratio (Dix 1970; Lamare 1997). It has an annual gametogenic cycle, releases gametes during mid-to-late-summer (Dix 1970; Walker 1982), and has a planktotrophic larval stage lasting for 30 to 60 d (Dix 1969; Walker 1984). Details on the nature of spawning, pre- and post-spawning changes in gonad indices, and the resultant larval densities are reported here. The cues for spawning, and possible optimal spawning strategies in this species are discussed.

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Materials and methods

Study site

Doubtful Sound–Thompson Sound complex (166° 58′ 45″E; 45° 18′ 00″S) is one of a series of fiords indenting the southwestern coast of South Island, New Zealand (Fig. 1). The fiord is ≃ 110 km long in total, and 2 km wide, with a 40 km main channel and five secondary arms. The hydrography of Doubtful Sound is complex. The fiord has a large input of freshwater, with an average rainfall of 465 mm mo^{-1}, an average riverine input of 135 m^3 s^{-1}, and an average anthropogenic input of 350 m^3 s^{-1} (Bowman and Dietrich 1995). The freshwater input results in a thin, low-salinity surface layer throughout the fiord, which has typical salinities of 5 to 10‰. The tidal cycle at Espinosa Point is semi-diurnal and has a maximum vertical range of 1.4 m. Sea temperatures in Doubtful Sound at 10 m depth typically range from 9 to 17°C annually.

Spawning observations

Adult *Evechinus chloroticus* (Valenciennes) populations in Doubtful Sound were frequently monitored by SCUBA divers during a 4 wk period from mid-January to mid-February 1994. Observations of spawning were made during a 60 min SCUBA dive at 3 to 5 m on the north wall of Doubtful Sound at a site north of Fergusson Island (Fig. 1) on 27 January 1994, between 17:30 and 18:30 hrs.

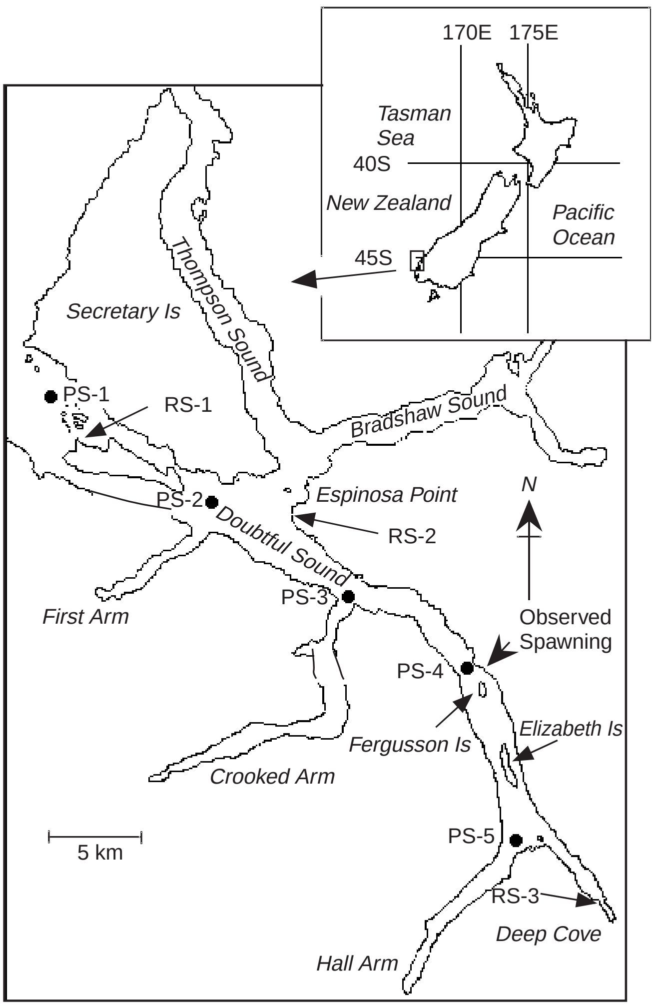

Fig. 1 Doubtful Sound, showing location of observed 27 January 1994 spawning [*RS-1*, *RS-2*, *RS-3* = *Evechinus chloroticus* populations sampled to determine gonad indices (Causet Cove, Espinosa Point, Deep Cove, respectively); *PS-1 to PS-5* = five sites where plankton samples were taken]

Environmental parameters

Sea temperatures at 10 m depth were recorded at Tricky Cove (Espinosa point; Fig. 1) every 280 min between 10 January and 14 February 1994 using a Hobotemp® data logger. Tidal cycle and the phase of the moon over the same period were calculated from the New Zealand Nautical Almanac (1994).

Gonad indices

Gonad Indices (GI) were recorded for *Evechinus chloroticus* in three populations (RS-1 to RS-3) in Doubtful Sound (Fig. 1) on 3 December 1993 (55 d pre-spawning), on 1 February (5 d post-spawning), and on 28 March 1994 (60 d post-spawning). For each sea urchin, the drained wet weight (drained of perivisceral fluid; g) and total gonad wet weight (g) were measured. The gonad index (%) was calculated as:

$$\text{Gonad index (\%)} = \frac{\text{total gonad wet weight (g)}}{\text{total drained wt weight (g)}} \times 100.$$

Sample size on each date was 10 for two of the populations (RS-1 and RS-3), while 20 sea urchins were sampled in the third population (RS-2).

Plankton sampling

Plankton samples were collected on 14 February 1994 (18 d post-spawning). Two replicate 100 m vertical larval tows were taken at five sites in Doubtful Sound (Fig. 1) using a 100 µm mesh UNESCO WP2 plankton net (UNESCO 1968) with a 50 cm-diam opening; the net was hauled at a rate of 30 cm s^{-1}. All samples were immediately preserved in 4% buffered formalin, and returned to the laboratory where the number and development stage of *Evechinus chloroticus* larvae in each sample were recorded using a dissecting microscope.

Results

Spawning observations

During spawning on 27 January, large numbers of *Evechinus chloroticus* (≃ 70 to 90 mm test diameter) were observed aggregating in a band ≃ 1 m wide immediately below the interface of the low-salinity layer and the more dense seawater. The low-salinity layer/seawater interface was at a depth of 3 m. Previous surveys at Fergusson Island (Lamare 1997) indicated that *E. chloroticus* typically occur randomly between depths of 3 and 15 m, at mean densities (± SE) of 1.55 ± 0.14 m^{-2}. Individuals aggregated in patches in shallow depths attaining densities of 20 to 30 individuals m^{-2} during spawning. At the beginning of the dive at 17:30 hrs, ≃ 10% of both male and female sea urchins were observed to be discharging gametes. It was not known which sex initiated spawning. Over the ensuing 30 min, ≃ 90% of the sea urchins present were releasing gametes. The spawning event was observed along the entire length of shoreline travelled during the SCUBA dive (100 m).

Both male and female gametes were neutrally buoyant and clouded the water from the low-salinity/seawater interface to ≃ 0.5 m below the spawning aggregation. Large numbers of small fish, notably spotties *(Notolabrus celidotus)*, were observed feeding on the gametes, either directly as the gametes were discharged from the sea urchins, or by swimming repeatedly through the cloud of gametes.

Environmental parameters

Prior to spawning, sea temperatures peaked on 16 January 1994 at a temperature of 15.6 °C (Fig. 2). From this time until the 27 January spawning, sea temperatures decreased to 14.8 °C. *Evechinus chloroticus* spawning coincided with the start of a period of rapid cooling temperatures, which decreased by 2.3 C° over a 10 d period.

Spawning occurred during a transition between a neap tide on 21 January 1993 (0.43 m tidal range) and a spring tide on 29 January 1993 (1.07 m tidal range) (Fig. 2). Maximum tidal ranges occurred two days after the observed 27 January spawning. Spawning had commenced by 17:30 hrs, which was ≃ 20 min prior to low tide. A new moon phase started on 12 January 1994, with a full moon occurring on 28 January.

Gonad indices

Gonad indices of *Evechinus chloroticus* increased to prespawning maxima on 3 December 1993 (Table 1). Indices of 20.0, 18.3 and 19.1% were recorded in the Causet Cove (RS-1), Espinosa Point (RS-2) and Deep Cove (RS-3) populations, respectively. Immediate post-spawning indices of 8.8, 9.6 and 11.2% were recorded on 1 February in the three populations respectively. Minimum gonad indices of 6.8, 6.5 and 11.1% for each population, respectively, were recorded on 28 March 1994.

Plankton sampling

Evechinus chloroticus larvae were present at all five sites sampled on 14 February (Table 2). Mean densities ranged from 613.5 to 2743.0 larvae tow^{-1}, with the maximum number of larvae in a tow being 3312 (taken in the central site in the fiord: PS-3). A single cohort of larvae

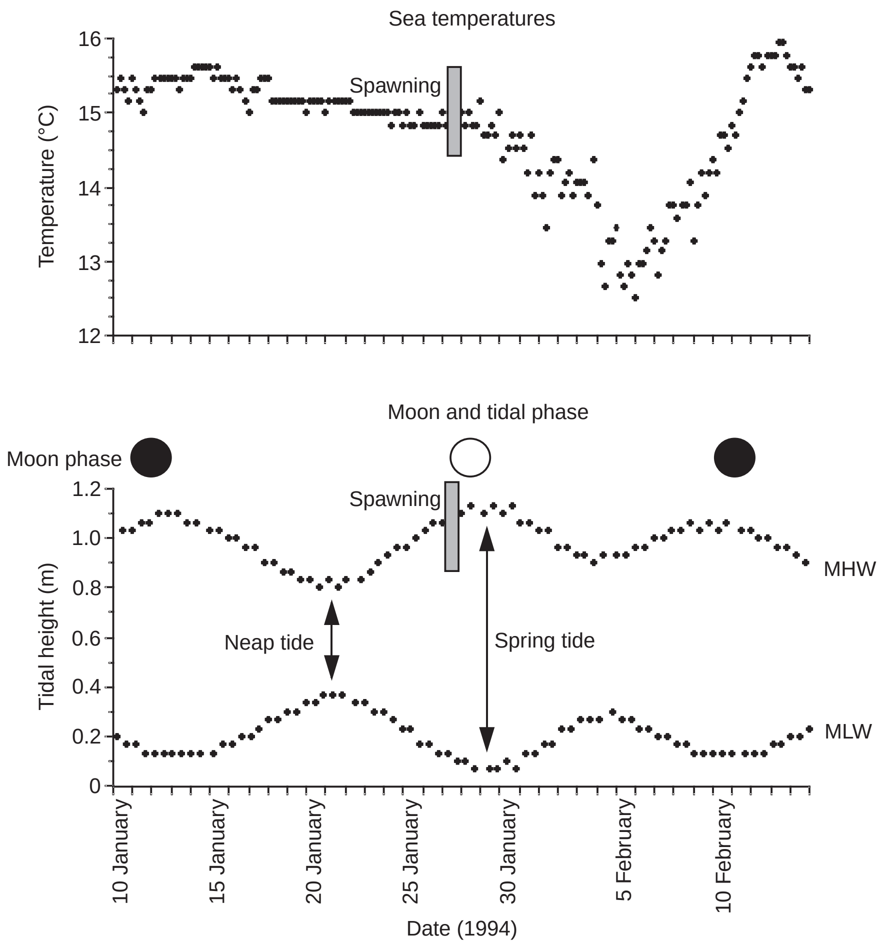

Fig. 2 Changes in sea temperature, moon phase and tidal height during 36 d period prior to and following 27 January spawning of *Evechinus chloroticus* (● new moon; ○ full moon)

Table 1 *Evechinus chloroticus*. Mean (± SE) pre-spawning (3 December 1993) and post-spawning (1 February, 28 March 1994) gonad indices in three populations in Doubtful Sound (*n* no. of individuals sampled)

Site	3 December 1993	1 February 1994	28 March 1994
RS-1: Causet Cove ($n = 10$)	20.0 (2.1)	8.8 (1.3)	6.8 (0.9)
RS-2: Espinosa Point ($n = 20$)	18.3 (0.7)	9.6 (0.9)	6.5 (0.5)
RS-3: Deep Cove ($n = 10$)	19.1 (1.5)	11.2 (0.9)	11.1 (0.6)

made up of equally-aged larvae was present throughout the fiord (99% of the larvae sampled were at the four-armed pluteus stage).

Discussion

Synchronous spawning of *Evechinus chloroticus* coincided with a full moon and spring tides and occurred during an extended period of decreasing sea temperatures. Spawning was accompanied by a 42 to 56% drop in gonad indices of *E. chloroticus* throughout Doubtful Sound. Gonad indices were taken at two-monthly intervals and, therefore, cannot provide information on the exact timing or degree of synchrony of spawning. The observed decreases in gonad indices throughout the fiord during the period of the observed spawning is, however, consistent with a widespread synchronous spawning throughout the fiord. This suggestion is supported by the presence of a widely-dispersed equally-aged cohort of *E. chloroticus* larvae throughout Doubtful Sound 18 d post-spawning. These larvae were almost entirely in the late four-armed pluteus stage (99%), a similar stage to 15 d old larvae reared in the laboratory (Dix 1969; Lamare 1997). It is possible, therefore, that spawning was synchronous over a distance of at least 40 km.

Spawning behaviour will influence fertilization success in echinoderm species that have external fertilization. Populations can increase fertilization success by forming spawning aggregations, spawning synchronously, and spawning under favourable environmental conditions (i.e. minimal water movement to reduce the dilution of gametes) (Giese and Pearse 1974; Levitan et al. 1992). Observations made in Doubtful Sound suggest that *Evechinus chloroticus* had adopted at least two of these strategies during gamete release in 1994. *E. chloroticus* aggregated in patches in shallow water, and were observed releasing gametes in a mass synchronous spawning event that occurred over a relatively short space of time. The aggregation of individuals at the low-salinity boundary may have further enhanced gamete concentration (and hence fertilization rate), as the gametes' upper depth distribution was apparently bounded by the low-salinity layer.

Table 2 *Evechinus chloroticus*. Mean density of larvae at five sites in Doubtful Sound on 14 February 1994. Percentage of larvae in four-armed pluteus stage on this date is indicated for each site

Site	Mean no. larvae tow^{-1}	(% of larvae in 4-armed pluteus stage)
PS-1	613.5	(99.6)
PS-2	1732.0	(98.5)
PS-3	2743.0	(99.6)
PS-4	1732.0	(98.6)
PS-5	366.0	(98.6)

The question as to whether *Evechinus chloroticus* adopted the third strategy (the use of more favourable conditions) requires an understanding of the proximate cues that trigger spawning in this species. Possible cues that initiate gamete release in echinoids are water temperature (Fenaux 1968; Byrne 1990; Kobayashi 1992; Minchin 1992), lunar cycles (Fox 1923; Pearse 1975; Emlet 1986; Kobayashi 1992), phytoplankton abundance (Himmelmann 1975, 1978), intensity of illumination (Pearse et al. 1988), and the presence of gametes or pheromones (Pearse et al. 1988). Cues for spawning in *E. chloroticus* are not well understood, but have been discussed by several researchers. Dix (1970) examined spawning times in relation to lunar cycles, sea roughness and sea temperature, and concluded that peaks in gonad indices occurred just prior to full moon. While this may indicate some lunar periodicity, Dix observed that little or no spawning actually occurred on full moons, with spawning coinciding with the end of calm seas, and after a period of increasing sea temperatures. Walker (1982) noted that because spawning times varied spatially over small areas (< 5 km), the factor(s) that induce spawning must operate within a population or over small distances. Mead (1996) reviewed the anecdotal evidence of spawning in *E. chloroticus*, and questioned commercial sea urchin fishermen about their observations of spawning in this species. The results of this survey showed that mass spawnings in this species have often been observed, and are frequently associated with rough sea conditions and changes in sea temperature. In addition, large spawning events are often triggered by the spawning of an initially small number of conspecifics within a population.

The present study examined sea temperature, tidal cycle and moon phase as physical factors providing cues for spawning. As these environmental variables do not change independently, they are difficult to separate as individual cues. Significantly, the 27 January spawning occurred during full moon, at the onset of spring tides as the tide turned, and coincided with an extended period of decreasing sea temperatures. In addition, the percentage of individuals spawning in the population increased from 10 to 90% over the observation period, which suggests some conspecific-induced spawning.

Given these and previous observations, a possible sequence of spawning events in *Evechinus chloroticus* is: (1) Lunar cycles provide proximate cues for spawning, with gonads maturing and reaching maximum size at full moon; (2) spawning is finally triggered by changes in sea temperatures and/or sea state; (3) cues from the spawning of conspecifics may enhance spawning synchrony.

In situ spawning in the echinoid *Paracentrotus lividus* occurs after increases in sea temperature (Minchin 1992). In Minchin's study, gametes were shed once a threshold temperature of 14 °C had been reached. In the current study, sea temperature decreased from 15.6 to 14.8 °C during the 11 d prior to spawning, with spawning coinciding with the start of rapidly cooling temperatures. Therefore, it is possible that a lower threshold temperature for spawning exists for *Evechinus chloroticus*. *E. chloroticus* gonad indices generally decrease in late summer (Dix; 1970; Lamare 1997), supporting the suggestion that gametes are shed during decreasing sea temperatures.

Evidence that temperature is a proximate cue for spawning in *Evechinus chloroticus* requires experimentation. Changes in sea temperature and/or sea state can vary over relatively short distances; therefore, as final cues for spawning, they are consistent with observations of differences in spawning times over small areas (<5 km). Furthermore, spawning cues which are graded in intensity (e.g. temperature changes) are more likely when temporal differences in the duration of spawning are considered. In this respect, large synchronous spawning would represent a strong or rapid change in the cues, while fractional spawning, (which is also observed in *E. chloroticus*) could represent weaker, or slowly changing, cues.

Full moon, spring tides, rapid changes in sea temperature and rough sea conditions all represent periods of increased water movement. While this may be advantageous for *Evechinus chloroticus* by increasing the dispersal of fertilized gametes, several workers suggest that successful spawning requires periods of low water movement to minimize the rapid dilution of gametes (Pennington 1985; Petersen 1991; Levitan 1991). Interestingly, *E. chloroticus* commenced spawning $\simeq 20$ min prior to low tide when water movement (and hence gamete dispersal) would be minimal in Doubtful Sound. *E. chloroticus* may have utilized the favourable conditions of little water movement at the turn of the tide with high fertilization rates, and then taken advantage of the spring tides to disperse the fertilized gametes.

The nature of the *Evechinus chloroticus* spawning observed in this study probably resulted in a high rate of fertilization. Mead (1996) examined in situ fertilization in *E. chloroticus* and concluded that a fertilization rate of $>94\%$ would be achieved in a synchronous spawning aggregation. A comparable rate may have occurred in Doubtful Sound, with the presence of a widespread cohort of *E. chloroticus* larvae (up to 2743 tow^{-1}) 2 wk after spawning confirming that successful fertilization occurred. This study may provide an example of optimal spawning strategies resulting in high fertilization rates and successful larval production.

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