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LOCALIZED SYNCHRONOUS SPAWNING OF *MYTILUS CALIFORNIANUS* CONRAD IN BARKLEY SOUND, BRITISH COLUMBIA, CANADA

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ABSTRACT Although *Mytilus californianus* is a dominant intertidal species along most exposed rocky shores of the northwest coast of North America and has been studied extensively, no direct observations of spawning by this species in the field have been reported. This paper presents the first report of synchronous spawning in the field by the mussel *M. californianus.* Two synchronous spawning events were observed in Barkley Sound on the west coast of Vancouver Island, British Columbia, Canada. On both occasions several thousand mussels spawned profusely at low tide, leaving masses of gametes on their shells or concentrated in tidepools and surge channels. In the 2002 spawning event 35% of the mussels spawned, for an estimated 54,000 spawning mussels, and fertilization rate in a surge channel was ~80%. Both spawning events, however, were highly localized, occurring within 24–41 m lengths of shoreline; no mussels spawned along adjacent areas of the shore. The timing of these 2 spawning events showed no consistent relationship with tidal and lunar phases, seawater temperature or cloud cover, and mussels in adjacent parts of the shoreline did not release gametes when exposed to spawned material. Localized synchronous spawning might be common in *M. californianus,* involving a patchwork of spawning events occurring intermittently over periods of a few months or throughout the year. This could provide the benefits of synchronous spawning as well as the advantages of the continuous production of recruits.

KEYWORDS: life cycle, reproduction, fertilization rate, gametes, broadcast spawning, *Mytilus*

INTRODUCTION

Among aquatic organisms, the synchronous release of gametes or larvae by many individuals of a population can provide increased fitness (see review by Olive 1992) by enhancing fertilization rates in broadcast spawners (Pennington 1985, Babcock 1995), taking advantage of hydrodynamic conditions that optimize fertilization or dispersal (Pennington 1985, Olive 1992), reducing larval mortality by predator satiation (Harrison et al. 1984, Slattery et al. 1999), and synchronizing the timing of planktotrophic larval development with that of algal blooms which the larvae use as food (Starr et al. 1990). Knowledge of whether a species spawns synchronously is therefore important in elucidating its population dynamics. In addition, an understanding of how environmental factors influence the timing of spawning can help predict future spawning events or determine how changes in environmental conditions can affect reproductive success (Minchin 1992, Olive 1992, Watson et al. 2000).

Synchronous spawning has most commonly been reported in anthozoans (Harrison et al. 1984, Babcock et al. 1986, 1992, Brazeau & Lasker 1989) and various echinoderms (Pearse et al. 1988, Babcock et al. 1992, Lamare & Stewart 1998) but also occurs in other marine invertebrates such as bivalves (Babcock et al. 1992, Minchin 1992, Grant & Creese 1995), gastropods (Counihan et al. 2001) and polychaetes (Caspers 1984, Hardege 1999, Watson et al. 2000). Sightings of natural spawning, however, are most often chance observations and, as a result, many species that do spawn synchronously may simply not yet be known to do so. This paper reports the first observations of synchronous spawning by the mussel *Mytilus californianus.*

Mytilus californianus is a dominant intertidal species on exposed rocky shores along the northwest coast of North America, forming extensive mussel beds from British Columbia to California (Suchanek 1981). Studies based on gonad condition or laboratory spawning indicate that this species is capable of spawning throughout the year (Young 1945, Kelly et al. 1982, Dittman & Robles 1991) and that the peak spawning period in British Columbia occurs in the summer (Kelly et al. 1982). A study of male gonad development in *M. californianus* in British Columbia concluded that many individuals are trickle-spawners (Kelly et al. 1982). However, no direct observations of spawning by this species in the field have been reported. This paper (1) reports 2 synchronous spawnings by *Mytilus californianus,* one in 1992 and the other in 2002, (2) quantifies the spawning rate and fertilization rate for the 2002 event, and (3) examines the relation of these 2 events with tidal, lunar, seawater temperature and cloud cover conditions.

METHODS AND RESULTS

The 2 spawning events described herein occurred in Barkley Sound on the west coast of Vancouver Island, British Columbia, Canada, and were discovered while visiting the sites at low tide. Tide levels for periods when the spawning events occurred were obtained from the Canadian Hydrographic Service (1991, 2001) tide tables. Surface seawater temperature data for Cape Beale (48°47′20″N, 125°12′95″W) and Amphitrite Point (48°55′25″N, 125°32′50″W), for 1992 and 2002, were obtained from the Fisheries and Oceans Canada online database for BC lighthouses (http://www-sci.pac.dfo-mpo.gc.ca/osap/data/SearchTools/Searchl ighthouse_e.htm). Amphitrite Point data was used for 2002 because seawater temperature measurements at Cape Beale ended in 1998.

1992 Spawning Event

The first spawning event was observed at Kirby Point (48°50′85″N, 125°21′40″W) on 22 June 1992. A large number of mussels had spawned profusely and several tidepools were clouded with sperm and lined with a coating of orange oocytes. Mussels outside of tidepools had masses of gametes on their shells near the siphons. Spawning was limited to a 24 m section of shoreline in which the mussel bed ranged in width from 3.0 m to 14.5 m; the surface area within which spawning occurred was ~214 m^2. No spawning mussels were found within 100 m on either side of the spawning area. In addition, to determine if spawning was stimulated by exposure to spawned material from other mussels, 3–4 l of water from a tidepool with an abundance of spawned material was transferred to each of 3 other small tidepools several metres away, in which no spawned material was apparent. Each tidepool contained 10–30 mussels. No spawning was observed over the following 2 h in the 3 tidepools receiving spawned material. This spawning event occurred at a time when the tidal amplitude was modest (Fig. 1A), with the moon in its last quarter. The weather that morning was sunny, and surface seawater temperature had been increasing for over 2 weeks (Fig. 1B).

2002 Spawning Event

The second spawning event was observed during a collecting trip to the intertidal zone at Cape Beale on the morning of 8 August 2002. Large numbers of emersed mussels were found with masses of gametes at the margin of their shell near the siphons. The water in several small tidepools as well as in a surge channel running parallel to the shoreline was yellowish-brown from the high densities of gametes. This spawning event occurred during very high amplitude tides (Fig. 2A) at new moon. The weather that morning was overcast, and surface seawater temperature had been relatively stable over the 5d preceding the spawning event, with a slight increase on the day of spawning (Fig. 2B). To further characterise the event 4 sets of observations and measurements were taken.

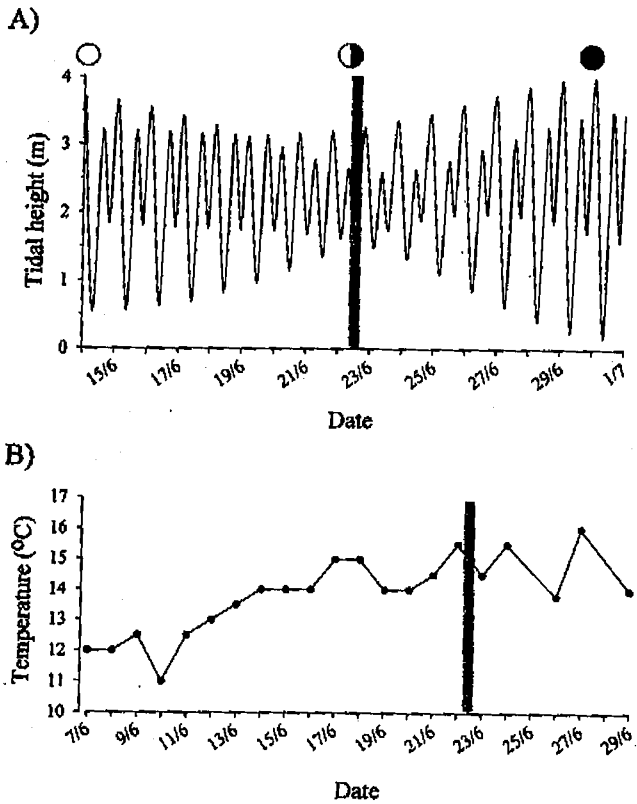

Figure 1. Environmental conditions prior to and after the synchronous spawning event of *Mytilus californianus* in 1992. The dashed areas in each graph represent the time of the spawning event. (A) Tidal heights and lunar phases; (B) surface seawater temperatures measured at the Cape Beale lighthouse.

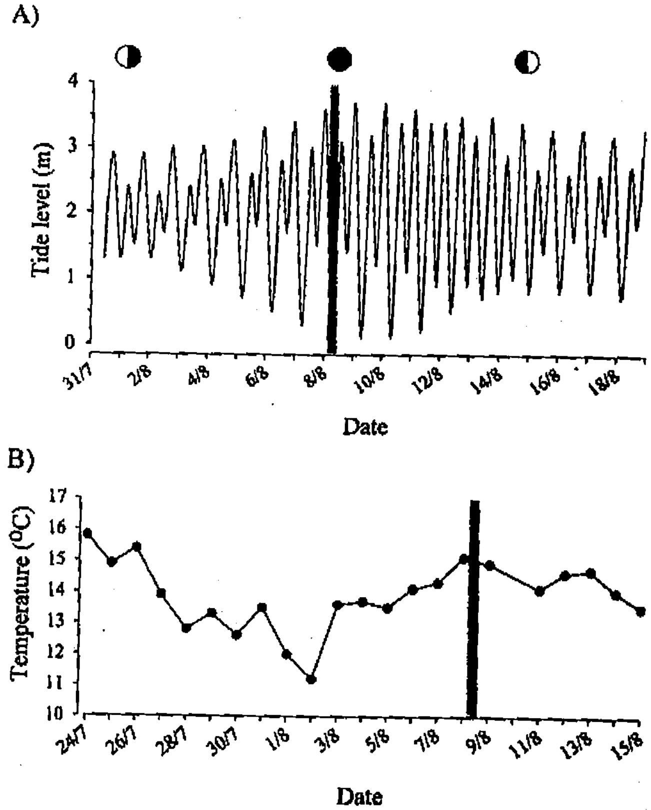

Figure 2. Environmental conditions prior to and after the synchronous spawning event of *Mytilus californianus* in 2002. The dashed areas in each graph represent the time of the spawning event. (A) Tidal heights and lunar phases; (B) surface seawater temperatures measured at the Amphitrite Point lighthouse.

Mussel Densities and Proportion of Mussels that Spawned

To quantify mussel densities and the proportion of mussels that spawned, observations were made along 2 separate transects running parallel to the shoreline within the mussel bed. Each transect consisted of five 25 × 25 cm quadrats set at 1 m intervals. In each quadrat I counted the total number of visible mussels and the number of mussels having spawned to determine the proportion of mussels that had spawned. Spawned gametes, when present, were located at the margin of the shell near the siphons or, when located elsewhere on the shell, a shiny slime coating could be observed running from the shell margin to the spawned material. Mussels were not dislodged for these observations; if small juvenile mussels were present deeper within the mussel bed they would not have been detected. *Mytilus californianus* densities in individual quadrats within the mussel bed ranged from 392 to 984 mussels m^{-2} and averaged 678 mussels m^{-2} (Table 1). Although densities varied among the 2 transects, the proportion of *M. californianus* that had spawned was consistent, averaging ~35% in each transect. No spawned material was present on low intertidal mussels that were exposed to wave wash, but the abundant gametes in the nearby water indicated that many of these had also spawned.

TABLE 1.

***Mytilus californianus*. Densities and percent of mussels found to have spawned at Cape Beale on 8 August 2002.**

	Mussel Density m^{-2} (±SD)	% Spawned (±SD)
Transect 1	520.0 ± 119.6	33.0 ± 15.4
Transect 2	836.8 ± 122.45	36.1 ± 4.8
Overall	678.4 ± 202.2	34.51 ± 10.9

Smallest Spawning Mussel

The mussel bed was closely examined for 15 minutes to search for and measure the smallest mussels with spawned material. The smallest spawning mussel measured 28 mm shell length, which is within the reported size range (25–30 mm) at which *Mytilus californianus* reaches maturity (Suchanek 1981). Several 30–50 mm mussels had also spawned. Mussel sizes at that site ranged from 10.2 mm to 150.0 mm, with most mussels measuring 60 mm to 120 mm. Few were smaller than 30 mm. The spawning event thus appears to have included all mussel sizes present in the bed.

Number of Mussels Spawning

Mussels with spawned gametes were found only along a 41 m section of shoreline. The width of the mussel bed along that section of shoreline ranged from 1.8 m to 14.2 m, for a surface area of the bed where spawning occurred of ~231 m^2. No spawning mussels were found over ~100 m on either side of the spawning area. Using an average mussel density of 678.4 m^{-2} and an average of 34.51% of mussels spawning (Table 1), the total number of mussels spawning in this event is estimated at 54,080 individuals.

Oocyte and Egg Density and Percent Fertilization in a Surge Channel

The combined density of oocytes and eggs as well as percent fertilization was determined by collecting a 60 ml sample of seawater from a surge channel formed by a rocky outcrop running parallel to the shoreline. The swell entering the channel caused continuous and substantial turbulence, thoroughly mixing the water throughout the channel. Oocytes and eggs were counted in the laboratory within five 0.1 ml subsamples. In addition, I estimated the proportion of oocytes that had been fertilized from the proportion that had undergone cleavage at 1:15 PM the same day, approximately 5–10 h after they had been spawned. Combined oocyte and egg density in the channel running parallel to the mussel bed was 885 ± 80.1 ml^{-1} (average ± SD). Based on measurements of length, width and depth of the channel, the volume of water in the channel at the time the sample was taken was estimated to be ~60,800 l. Using 885 eggs ml^{-1} as an estimate of density throughout the channel, the water in that channel would have contained ~5.4 H 10^{10} oocytes and eggs. In the sample returned to the laboratory, 80.7 ± 12.3 % (average ± SD) of these developed at least to the 2-cell stage. Using 80.7% as an estimate of fertilization rate, the channel would have contained ~4.3×10^{10} fertilized eggs. This constitutes the output of only the lower part of the mussel bed, as approximately two-thirds of the mussel bed was above the splash zone at the time of sampling and the gametes produced by those mussels were not suspended until later by the rising tide.

DISCUSSION

Localized Synchronous Spawning in *Mytilus californianus*

Mytilus californianus have the capacity to spawn at any time of the year (Young 1945, Kelly et al. 1982, Smith & Strehlow 1983, Dittman & Robles 1991). It has also been suggested, based on observations of juvenile recruitment throughout the year, that *M. californianus* spawns continually releasing small amounts of gametes throughout the year (Suchanek 1981) and a study of gonad condition in male mussels revealed that about half of the males are probably 'trickle' spawners (Kelly et al. 1982). None of these conclusions, however, are based on observations of spawning in the field. Despite its widespread occurrence and ecological importance along the rocky shores of the northwest coast of North America, there are no reports of *M. californianus* spawning in the field. In the present study, more than 50,000 mussels spawned in the 2002 event. Mussel densities were not quantified in 1992; however, assuming an average density similar to that observed at Cape Beale in 2002 of 678.4 mussels m^{-2}, the total number of mussels in that section of mussel bed would have been ~145,000 individuals. The number of mussels spawning in the 1992 event was thus likely in the order of several thousand. These findings reveal that events in which large numbers of individuals spawn synchronously do occur in this species. This is the first report of synchronous spawning in *M. californianus* and the first such report for a species in the genus *Mytilus*.

The 80.7% fertilization rate observed during the 2002 spawning event is consistent with the expectation that synchronous spawning in a population favours high fertilization rates (Pennington 1985, Olive 1992, Babcock 1995). This particularly high fertilization rate, however, was possibly due to the retention and continuous mixing within the limited volume of the surge channel, as fertilization rate should decrease with dilution of the gametes (Pennington 1985, Levitan et al. 1992). Particularly intriguing, however, is the fact that both spawning events were very localized. While a high proportion of mussels in a given area of shoreline spawned, mussels in adjoining areas of the shoreline did not. The boundary between spawning and non-spawning areas of the mussel bed occurred over 1–2 m, and there was no apparent physical difference in the shoreline or in the size or health of the mussels between areas with and without spawning mussels.

In addition, it is not clear why the mussels spawned at low tide; why not release the gametes at high tide when fully submerged? One might expect the viability of gametes released at low tide to be decreased due to exposure to air and ultraviolet radiation. Given the rarity of observations of spawning by *Mytilus californianus* in the field, it may be that spawning usually takes place at high tide and that low tide spawning events are rare occurrences.

Factors Influencing Spawning Synchrony

Several factors have been reported to induce or synchronize spawning in marine invertebrates, including tidal and lunar phases (Caspers 1984, Babcock et al. 1986, Slattery et al. 1999, Watson et al. 2000), changes in seawater temperature (Minchin 1992), mechanical stimulation by water flow (Desrosiers & Dubé 1993) or by wave action (Young 1945), clement weather (Watson et al. 1986), and water-borne chemicals released by other spawning individuals (Young 1945, Atkinson & Atkinson 1992, Hardege

1999) or by phytoplankton (Breese & Robinson 1981, Smith & Strehlow 1983, Starr et al. 1990, Parsons et al. 1992). The present study therefore documented tidal and lunar phases, seawater temperature (measured 1–3 km from the spawning sites) and weather (cloud cover) to determine if the 2 spawning events occurred under similar conditions. None of these factors, however, were the same on both spawning events. Finally, water transferred from tidepools with spawned gametes to tidepools in which mussels had not spawned did not induce spawning, although it is possible that those mussels had spawned on previous days and thus were unable to spawn that morning.

Ecological Significance of Synchronous Spawning by *Mytilus californianus*

Observations of the two spawning events described herein were serendipitous. I have frequently visited various rocky intertidal sites colonized by *Mytilus californianus* in Barkley Sound over the last 14 years but only observed mussels spawning on these 2 occasions. These observations nevertheless reveal that synchronous spawning of several thousand *M. californianus*, and by as much as 35% of the individuals of a mussel bed, does occur. It may be that such events are not rare, but happen mostly at night or when the mussels are submerged, and therefore spawning goes unnoticed. If localized synchronous spawning is common in *M. californianus*, reproduction in this species could involve a patchwork of spawning events occuring intermittently over periods of a few months or throughout the year, which would be consistent with Suchanek's (1981) observations of recruitment throughout the year on the northern coast of Washington State. This strategy would allow the species to benefit from the advantages of synchronous spawning as well as from the continued production of recruits allowing the opportunistic colonization of habitats as they become available, free space being a limiting resource on these exposed rocky shores, made periodically available by disturbance events such as storms and impacts by floating logs (Dayton 1971, Paine 1974).

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