AGE AND SURVIVORSHIP OF DIAPAUSING EGGS IN A SEDIMENT EGG BANK[1]

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Abstract. We determined the densities of diapausing eggs of the copepod *Diaptomus sanguineus* in sediments from two small freshwater lakes in Rhode Island. Sediment cores, sliced at 1-cm intervals, showed that egg densities ranged between 4×10^4 and 8×10^4 eggs/m^2 near the sediment surface and declined to very low values at depths of 10–15 cm in both lakes, although eggs were found as deep as 30 cm in the sediment of one lake. Between 10 and 50% of these eggs hatched in short-term laboratory experiments, and actual egg viability is probably higher. ^{210}Pb-dating revealed relatively constant sedimentation rates in both lakes, and we use this information to estimate egg ages. In one lake, the mean diapausing-egg age is 70.4 yr (median age = 45.9 yr) and the maximum age of eggs we hatched was 332 yr. In the other lake, the mean egg age is 48.9 yr (median age = 35.9 yr) and the maximum age of eggs we hatched was 112 yr. We calculated egg mortality rates by regressing ln(egg density) on the age of the sediment from which the eggs were taken to obtain estimates of 1.1 and 1.5% mortality/yr for the two lakes. Diapausing eggs of zooplankton represent a long-lived life history stage of an otherwise short-lived organism. They provide generation overlap that can have substantial significance for both ecological and evolutionary dynamics.

Key words: diapausing eggs; Diaptomus sanguineus; *egg bank; egg mortality; generation overlap; ^{210}Pb-dating; life-span; zooplankton.*

INTRODUCTION

Most freshwater zooplankton are typically thought of as short-lived animals with high potential population growth rates (Fenchel 1974, Allan and Goulden 1980, Banse and Mosher 1980), an ability to respond rapidly to changing environments (Peters 1983), and a high sensitivity to anthropogenic disturbance (Moore and Folt 1993, Locke and Sprules 1994). One feature of many species of zooplankton that is often overlooked in this characterization is their ability to make diapausing eggs. The natural life-span of these dormant stages has been little investigated, but existing data suggest that the duration may be at least on the order of decades. Aside from anecdotal descriptions of zooplankton diapausing eggs surviving for extended periods on laboratory shelves and other unnatural locations (e.g., Gilbert 1974, el Moghraby 1977), there are four studies reporting viable eggs taken directly from lake sediments of known age. Nipkow (1961) hatched diapausing eggs of seven species of rotifers from the varved sediments of Zürichsee, Switzerland, obtaining maximum egg ages of between 15 and 35 yr, and Moritz (1987) found viable eggs of *Ceriodaphnia pulchella* as old as 14 yr in ^{137}Cs-dated sediments of Pilburger See, Austria. More recently, Marcus et al. (1994) obtained viable diapausing eggs of a variety of zooplankton taxa,

including copepods, a cladoceran, and a rotifer with maximum ages between 5 and 40 yr in ^{210}Pb-dated sediments of a meromictic lake at the upper end of the Pettaquamscutt estuary, Rhode Island, USA, while Hairston and Van Brunt (1994) found viable eggs of diaptomid copepods in ^{210}Pb-dated sediments of Oneida Lake, New York, USA in large numbers at sediment depths aged at 22 yr and still present in sediments nearly 90 yr old. In addition to being long lived, the densities of these eggs in lake sediments can be extremely high, typically ranging between 10^3 and 10^6 eggs/m^2 (Lampert and Krause 1976, Hairston and De Stasio 1988, Carvalho and Wolf 1989, De Stasio 1989, Ban 1992, Hairston and Van Brunt 1994). Similar densities are found in near-shore marine sediments (Kasahara et al. 1975, Kankaala 1983, Lindley 1990, Marcus et al. 1994).

The diapausing eggs in lake sediments thus represent an "egg bank" analogous to the seed banks of many terrestrial plants (Hairston and De Stasio 1988, De Stasio 1989, Marcus et al. 1994). Depending on the probability that sediment eggs receive the cue to hatch (typically some combination of light, temperature, and oxygen [Gilbert 1974, Stross 1987]), prolonged diapause has the potential to extend substantially zooplankton generation times. This, in turn, can slow the rate of elimination of a species from a system when conditions for individuals in the active stages become uninhabitable, and can increase the rate of return of a species

to the water column once suitable conditions are restored.

Here we report the presence of centuries-old viable copepod diapausing eggs of *Diaptomus sanguineus* in the sediments of two small north-temperate lakes in Rhode Island: Bullhead Pond and Little Bullhead Pond. The presence of egg banks in these two populations has been demonstrated in the past, first by showing that eggs are present in the surface sediments of both lakes in densities exceeding 2×10^5 eggs/m^2, and second by documenting the emergence of nauplii over a 3-yr period from sediments into which no new input of eggs was possible (Hairston and De Stasio 1988, De Stasio 1989). Now, by using ^{210}Pb-dating we are able to obtain a more long-term picture of egg age. In addition, from knowledge of both the densities and the ages of eggs, we calculate the mortality rates of the eggs in the sediments. This is a critical component of any effort to understand the dynamics of an egg bank and its potential impact on ecological and evolutionary processes.

METHODS

Diaptomus sanguineus, a small (≈ 1 mm) calanoid copepod, has a distribution spanning much of North America (Wilson and Yeatman 1957). In Rhode Island it lives in temporary ponds, and semi-permanent and permanent lakes. In temporary ponds, it makes diapausing eggs in spring, apparently as a mechanism to avoid summer dry periods (Hairston et al. 1985), whereas in permanent water bodies it makes the eggs to avoid summer predation by fish (Hairston and Walton 1986, Hairston 1987). The eggs, which are ≈ 100 μm in diameter, possess a thick chitinous chorion that permits them to survive both desiccation and passage through the guts of predators (Hairston and Olds 1984). Of the two lakes investigated here, Bullhead Pond (surface area 2.4 ha, maximum depth 4.0 m) is permanent (i.e., never dries), and Little Bullhead Pond (0.15 ha, 1.5 m) is semi-permanent, having dried completely in 1981 and probably several times earlier (Hairston 1988).

Bullhead Pond

A core (35 cm long, 7 cm diameter) was taken by SCUBA diver on 23 August 1990 at the deepest part of the lake (4.0 m). The core was returned to the laboratory wrapped in aluminum foil and stored in the dark at 4°C until 14 January 1991 when funds were available to process the sediments and analyze them for copepod diapausing egg densities. The core was extruded and sliced in 1-cm intervals down to 19 cm; below this depth, only the 24–25 cm and the 30–31 cm slices were analyzed. For each slice, the outer layer of sediment that had dragged along the wall of the core tube was trimmed using a cookie cutter (5.9 cm diameter) and discarded. For analysis of egg densities, all eggs in each slice were counted. Eggs were separated from sediments by suspending each subsample in water and sonicating using a Branson probe sonifier set at low intensity. After re-

moving the water, the sediment and eggs were resuspended in a 30% sucrose solution, centrifuged at 650 rpm (≈ 7.7 m/s^2) for 1.5 min, and the supernatant was filtered (75-μm mesh) and resuspended in filtered lake water. Processed samples were searched for eggs under a stereo-dissecting microscope. Eggs were identified as viable if they were the dark brown or red color typical of diapausing eggs just after they are laid, or if they contained distinctly visible "eyed" embryos. It is our observation that dead eggs decompose very quickly. Eggs scored as viable were isolated in glass-fiber-filtered lake water and placed in a controlled environment chamber at 3°C under continuous illumination by daylight fluorescent lamps and monitored at least twice monthly for hatching for 9 mo.

A second, piston core (74 cm long, 7 cm diameter) was taken in Bullhead Pond on 13 November 1993 in the lake center for establishing sedimentation rates and hence, indirectly, egg ages by ^{210}Pb dating. The core was extruded the day following collection and sliced at 1-cm intervals in the top 20 cm, 2-cm intervals between 20 and 40 cm, and at 4-cm intervals below 40 cm. Core slices were vigorously stirred and subsampled. ^{210}Pb was measured on 12 selected slices by ^{210}Po distillation and alpha spectrometry methods (Eakins and Morrison 1978). Dates and sedimentation rates were calculated according to the c.r.s. (constant rate of supply) and cf:cs (constant flux : constant sedimentation) models (Appleby and Oldfield 1983); both models yielded virtually the same results.

Little Bullhead Pond

Hairston and De Stasio (1988) report egg densities in a core (20 cm long, 7 cm diameter) taken by diver during summer 1987 at the deepest part of Little Bullhead Pond (1.5 m). The methods and data are summarized here for comparison with the data from Bullhead Pond, and because new results on egg hatching and sediment age are presented. The core was extruded in the laboratory and sliced 1 cm at a time in 1-cm intervals down to 12 cm with additional slices taken at 13–14 cm and 19–20 cm. The methods for analyses of egg densities and egg hatching were the same as for the Bullhead Pond core, except that core slices were subsampled in triplicate, and eggs were monitored monthly for hatching for 7 mo.

In 1989, samples of sediment from the slices of the 1987 core were sent to the Wadsworth Center for Laboratories and Research (Albany, New York) for ^{210}Pb dating. Water content was not determined on this material, and so we assume here that it is constant in order to calculate sediment age. ^{210}Pb activity was measured for eight of the core slices.

RESULTS

In both Bullhead and Little Bullhead Ponds, there are tens of thousands of eggs per square metre for each centimetre of sediment depth near the sediment surface.
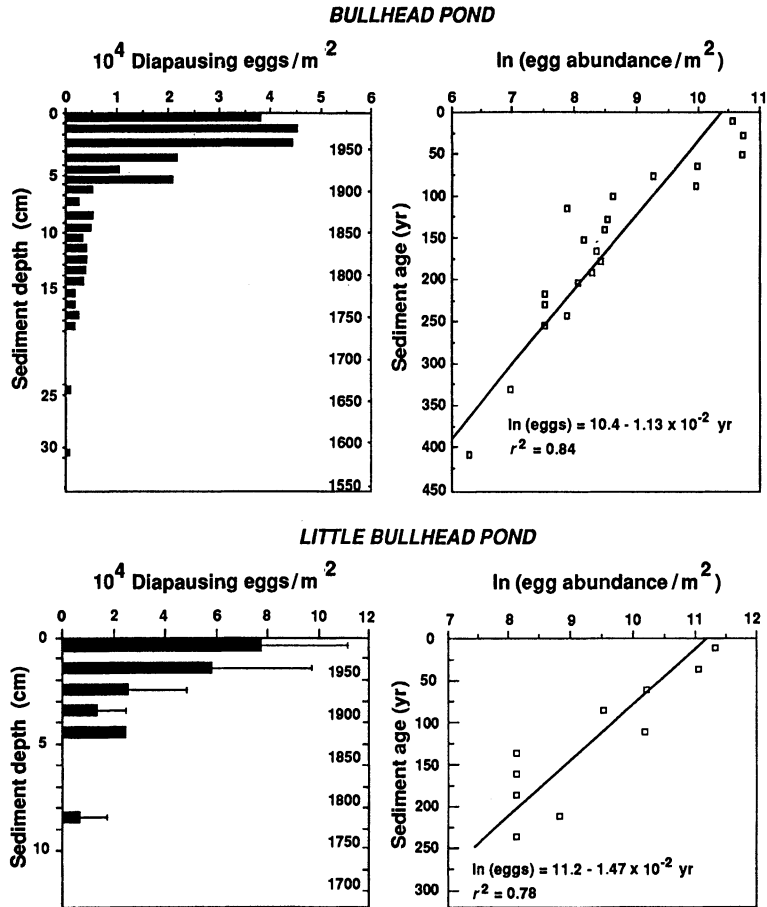
FIG. 1. (Left graphs) The abundance of *Diaptomus sanguineus* diapausing eggs as a function of sediment depth (left axis) and sediment age (right axis) of Bullhead Pond and Little Bullhead Pond. For Bullhead Pond, the depth axis is adjusted slightly in order to account for variation in sedimentation rate with depth, and to make the age axis linear. (Right graphs) The mortality rate of diapausing eggs is calculated as the slope of the regression of ln(egg density) on time.

Below this, egg densities decline, but in Bullhead Pond, eggs remain present down to 31 cm and in Little Bullhead Pond they are present down to 9 cm (Fig. 1). In Bullhead Pond, two transects (shallow to deep water) of seven previous short cores from the lake (top 5 cm only) gave similar egg numbers in the surface sediments at the center of the lake but lower densities near shore (De Stasio 1989). A calculation of the total number of viable diapausing eggs of *D. sanguineus* in the sediments of Bullhead Pond (drawing on both past [De Stasio 1989] and present data) yields 6.52×10^9 living animals waiting to hatch. A similar calculation, based only on the single core in Little Bullhead Pond, gives a highly tentative estimate of 0.77×10^9 viable diapausing eggs in that population. By comparison, the mean maximum population size of adult *D. sanguineus* is 0.35×10^9 in Bullhead Pond and 3.3×10^6 in Little Bullhead Pond.

In Bullhead Pond, we found a near constant sedimentation rate of 6.8 mg·cm^{-2}·yr^{-1} for the entire dated core, which translates (correcting for sediment density)

to a linear accumulation rate of 0.51 mm/yr for the upper 3 cm of the core and 0.78 mm/yr below 3 cm (Fig. 2). Because ^{210}Pb cannot be used to date sediments older than ≈ 150 yr (11 cm sediment in Bullhead Pond), sediment ages below 11 cm were obtained by extrapolating the 0.78 mm/yr value below the last dated interval. We conclude that the diapausing eggs of *D. sanguineus* can live in the sediments of Bullhead Pond for as long as 400 yr (30–31 cm core slice). The median egg age is 45.9 yr and the mean is 70.4 yr. In Little Bullhead Pond, a regression of unsupported ^{210}Pb activity on sediment depth (without correction for sediment density, see above), gives a sedimentation rate of 0.40 mm/yr (Fig. 2). Assuming a constant sedimentation rate below 6 cm (= 150 yr), we find that the oldest viable eggs in Little Bullhead Pond are on the order of 210 yr old, with a median age of 35.9 yr and a mean of 48.9 yr.

DISCUSSION

Are these eggs really that old? Because *D. sanguineus* diapausing eggs are small and roughly the same
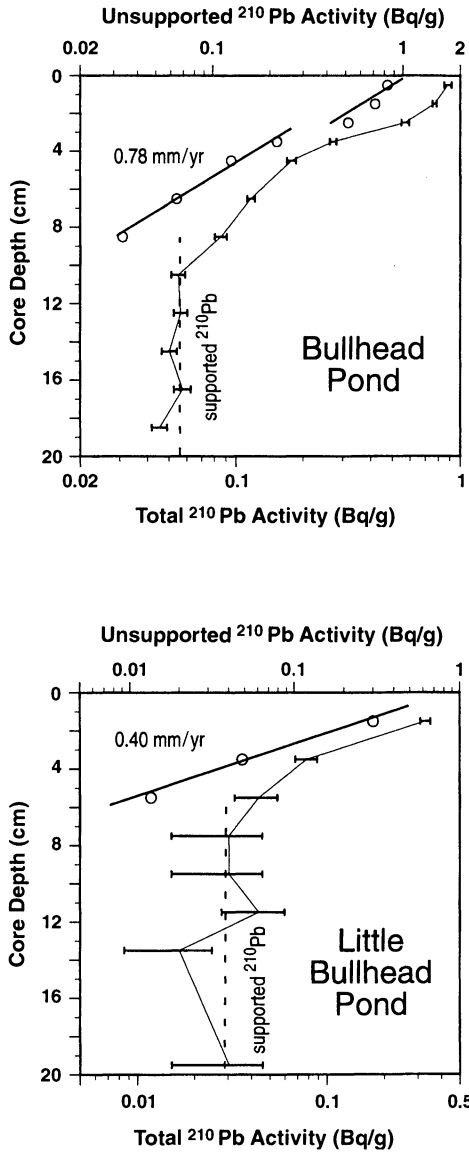
Unsupported ^{210}Pb Activity (Bq/g)

Total ^{210}Pb Activity (Bq/g)

Unsupported ^{210}Pb Activity (Bq/g)

Total ^{210}Pb Activity (Bq/g)

FIG. 2. Profiles for total (bars) and unsupported (circles) ^{210}Pb activity as a function of depth in Bullhead (top) and Little Bullhead (bottom) Ponds. Mean accumulation rates based on the cf:cs model are shown for both curves. (1 becquerel [Bq] = 27.027 pCi [picocuries].)

density (specific gravity 1.03) as the sediments surrounding them, we have no reason to expect that they are selectively transported within the sediments. In addition, direct measurements of sediment mixing indicate little vertical movement, as follows. In July 1992, 8.5×10^8 polystyrene beads of the same size and specific gravity as the copepod diapausing eggs were introduced to the water column of Bullhead Pond, yielding a bead density (mean $\pm$ 1 SD) on the surface sediments at the deepest portion of the lake of 2.54×10^4 $\pm$ 1.34×10^2 beads/m². Duplicate cores taken 1.3 yr later (November 1993) show mean bead densities of

$2.70 \times 10^4 \pm 1.73 \times 10^4$ beads/m² at 0–1 cm, $1.77 \times 10^3 \pm 2.50 \times 10^3$ beads/m² at 1–2 cm, and 6.00×10^2 $\pm 8.50 \times 10^2$ beads/m² at 2–3 cm. Below this no beads have been found. Thus downward mixing is present but slow. These observations are strongly supported by the ^{210}Pb results which show no evidence of bioturbation or sediment mixing in either Bullhead or Little Bullhead Ponds (Fig. 2) that would otherwise produce a zone of constant ^{210}Pb near the top of the core.

Are these eggs really viable? Only those containing a visible eyed embryo, or of the reddish brown color typical of eggs in an earlier stage of development were counted. In laboratory studies, these eggs can frequently be induced to hatch, whereas nonviable eggs decompose very rapidly. Many of the diapausing eggs that were extracted from the cores and incubated at 3°C hatched within the 7–9 mo period of study. There appears to be a decline in fraction hatching with sediment depth (regression for Bullhead Pond, $P < 0.01$; Fig. 3), though low sample size leads to uncertainty at greater sediment depths. The oldest eggs observed to hatch were aged 330 yr (24–25 cm core slice) in Bullhead Pond, and 112 yr (4–5 cm core slice) in Little Bullhead Pond. Eggs that did not hatch within the period of study were not necessarily dead. Many continued to look healthy and simply may not have been stimulated to hatch. In addition, no hatching was observed in either lake for eggs that looked viable and were taken from sediment deeper than 19 cm (Bullhead Pond) or 5 cm (Little Bullhead Pond). Our confidence in this result is low, however, because only 4 eggs total were isolated from these depths.
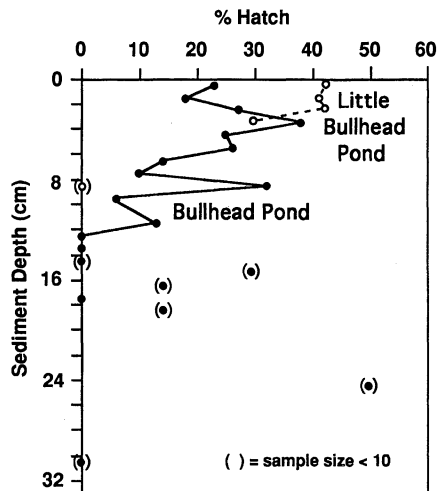
% Hatch

FIG. 3. The percentage of eggs in the cores from Bullhead and Little Bullhead Ponds shown to hatch within 7–9 mo after isolation (see *Discussion*). Note that these are minimum hatching percentages because many eggs remained unchanged and apparently viable at the end of the study. Hatch percentages in parentheses are unreliable due to low sample size, but are illustrated here to show that some eggs hatched even from deep in the Bullhead Pond core.

The mortality rate of the diapausing eggs in the sediments can be calculated by regressing ln (egg density) on the sediment age at which the eggs were collected (Fig. 1). This approach assumes a constant (or at least not a systematically varying) rate of egg input over time. Indeed, for Bullhead Pond, we can calculate the numbers of diapausing eggs produced annually by *D. sanguineus* from the results of weekly zooplankton samples obtained between 1979 and 1986. For this rather brief period, egg production showed no directional change and a modest coefficient of variation (71%, 1.60 × 10^5 ± 1.14 × 10^5 eggs·m^{-2}·yr; mean ± 1 SD). Per capita egg mortality (the regression slope) is thus estimated for the Bullhead Pond population to be 0.011 yr^{-1}, or 98.9% survival of eggs between years. For the Little Bullhead Pond population, the rate is comparable: 0.015 yr^{-1}, or 98.5% annual egg survival.

Diapausing eggs of zooplankton with the ability to survive over multiple years are usually thought of as adaptations to life in temporary ponds where they provide a means of surviving a series of years of completely failed recruitment. The discovery that they exist in large permanent bodies of water, both freshwater and marine (e.g., Grice and Marcus 1981, Hairston and Van Brunt 1994, Marcus et al. 1994), raises the question of whether this trait is an adaptation to unpredictable recruitment in these less extreme environments, or simply an artifact of egg burial (i.e., they must be close to the sediment surface to hatch). By analogy with seed bank theory, we expect that when survivorship of the diapausing eggs is high, even fairly modest recruitment fluctuations between years will lead to the evolution of prolonged diapause (Ellner 1985). Knowing the extent of recruitment fluctuations will thus be essential for evaluating whether the egg bank is an adaptation or an artifact. Ultimately it will be necessary to learn the cues involved in inducing hatching of diapausing eggs and then to see if egg hatching is delayed after repeated exposure to these cues. The extent to which diapausing eggs may contribute to future recruitment depends on the rate of sediment burial and the probability that eggs at depth get returned to the sediment surface by disturbance of the lake bottom. In lakes with very slow sedimentation rates such as Bullhead and Little Bullhead Ponds, diapausing eggs remain within 5 mm of the sediment–water interface for a decade or longer. The flocculent sediment surface is easily entrained into the water column by physical and biological forces, so that recruitment from eggs representing multiple generations must be common. Disturbances of deeper sediment layers that bring very old eggs to the sediment surface are undoubtedly less frequent, but nevertheless occur through localized events such as burrowing by bullhead catfish, tree falls, and setting of boat anchors by fishermen and limnologists.

The fact that many eggs in lake sediments are of great age suggests that the average generation time of zooplankton taxa may be much longer than previously suspected. Increased generation time is likely to be accompanied by an increase in the amount of generation overlap, calculated as: $\gamma = Hs_r + (1 - H)s_d$, where H is the fraction of eggs that hatch each year, and s_r and s_d are the survival of hatched and diapausing portions of the population, respectively (Ellner and Hairston 1994). Generation overlap is, in turn, a central component in the coexistence of species within a community (Chesson and Warner 1981) and genotypes within a population (Ellner and Hairston 1994) because it permits types that suffer relatively poor recruitment in one year to be well represented in other years for which recruitment may be better. Finally, because large s_d clearly has the effect of increasing generation overlap, prolonged diapause (whether or not it is an adaptation), may turn out to be a key component in the maintenance of biotic diversity (Hairston et al. 1995).

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