INTERSPECIFIC VARIATION IN THE ABUNDANCE, PRODUCTION, AND EMERGENCE OF *DAPHNIA* DIAPAUSING EGGS

Carla E. Cáceres[1]

Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853 USA

Abstract. Despite the ubiquity of dormancy among invertebrates, the demographic ties between the active and dormant stages remain largely unexplored in most systems. Nevertheless, dormant stages could potentially have significant impacts on the ecology and evolution of the active population. In Oneida Lake, New York, populations of the suspension-feeding crustaceans *Daphnia galeata mendotae* and *Daphnia pulicaria* produce large numbers of long-lived diapausing eggs, which accumulate in the sediments to densities of over 2.5×10^4 eggs/m² for *D. galeata mendotae* and 8.0×10^4 eggs/m² for *D. pulicaria.* Sedimentation rates obtained by ²¹⁰Pb dating suggest that these eggs can remain viable for >125 yr and that these two *Daphnia* populations have persisted in this system for >200 yr. Total annual production of new diapausing eggs can range from 0 to over 10^4 new eggs/ m² of sediment. Annual emergence rates back to the water column are also variable but only range between 0 and 25 *Daphnia*/m². Because annual variation in the size of the overwintering water-column population ranges between 0 and 2.5 individuals/L, the contribution of emergence to the development of the spring population is considerable in some years and negligible in others. Despite similar maximum water-column densities, *D. pulicaria* produces and stores more eggs and has a higher rate of emergence than *D. galeata mendotae,* suggesting differences in the benthic–pelagic link of these two species. Diapausing eggs greatly increase the generation time of the populations that produce them and therefore have the potential to substantially alter the outcome of community interactions.

Key words: Daphnia; *diapause; dormancy; egg bank; ephippia; life span; overlapping generations; resting eggs; zooplankton.*

INTRODUCTION

Of the hundreds of studies examining zooplankton population and community dynamics, all but a handful fail to consider the organism's true generation time. Freshwater zooplankton are considered to be short-lived species, with population and community dynamics proceeding on the time scale of a few weeks, months, or years (Allan and Goulden 1980, Lynch 1980, Sommer 1989, Moore et al. 1996). In many species, however, the active stage represents only a small fraction of the total life span, and much of an animal's lifetime is spent in dormancy (Hairston and Cáceres 1996). These dormant stages can be long-lived, and thus can greatly extend the generation time of the species that produce them.

There is increasing, but still primarily anecdotal, evidence to suggest that these diapausing eggs can remain viable for decades or centuries. The diaptomid copepod *Diaptomus sanguineus* produces viable diapausing eggs that have been dated to 400 yr old in Bullhead Pond, Rhode Island, and to 125 yr old in Little Bullhead Pond (Hairston et al. 1995). Two other species of diaptomid copepod produce dormant eggs in Oneida Lake,

New York, that may remain viable for decades (Hairston and Van Brunt 1994). Prolonged dormancy that lasts on the order of a decade or more has also been suggested for freshwater cladocerans (Fryer 1972, el Moghraby 1977, Moritz 1987, 1988, Carvalho and Wolf 1989) and rotifers (Nipkow 1961, Gilbert 1974). In the near-shore marine environment of the Pettaquamscutt estuary, diapausing eggs of copepods, rotifers, and cladocerans were found in sediments that were >40 yr old (Marcus et al. 1994). Most recently, Katajisto (1996) reported copepod diapausing eggs that were at least 10 yr old in the sediment of the Baltic Sea. However, very few detailed studies have examined spatial and temporal variation not only in the dormant eggs but also in the links between the benthic and pelagic phases of the population.

In addition to being extremely long-lived, diapausing eggs can accumulate in densities ranging from 10^3 to 10^6 eggs/m² of sediment in both freshwater and marine systems (reviewed by Hairston 1996). This storage of dormant stages forms an egg bank that is in many ways analogous to the seed banks of various terrestrial plant species (e.g., Leck et al. 1989). One consequence of storing dormant propagules in either a terrestrial or aquatic system is that they create overlapping generations. Therefore, zooplankton population and community dynamics may be better understood by applying theory developed for long-lived iteroparous species

[1] Present address: Center for Aquatic Ecology, Illinois Natural History Survey, Champaign, Illinois 61820 USA.
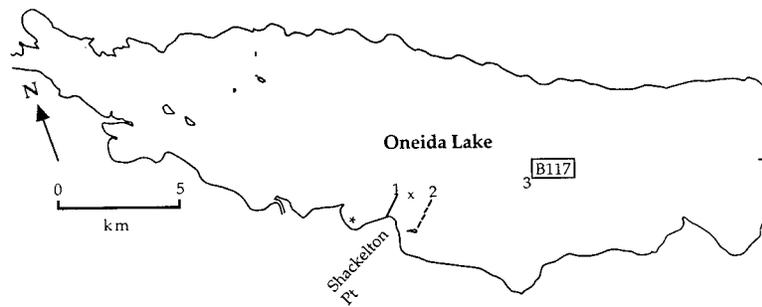
FIG. 1. Oneida Lake, New York. The solid line and asterisk (Billington Bay) indicate the transect of cores taken in 1992. The solid line also represents one of the emergence trap transects, and the dotted line indicates the other emergence trap transect. The "×" represents the main reference station of the Cornell Biological Field Station where *Daphnia* densities were sampled from 1975. Numbers correspond to the sampling stations for the large-diameter cores taken during 1993–1995. The "B117" indicates the placement of Buoy 117 in the New York State Barge Canal.

than by using the traditional seasonal approach. There is an extensive theoretical literature discussing the effects of overlapping generations on the ecology and evolution of populations and communities (e.g., Templeton and Levin 1979, Chesson and Warner 1981, Charlesworth 1994, Cohen 1994, Ellner and Hairston 1994). However, aquatic ecologists have only recently realized these parallels and begun to consider the effects of dormancy in their systems (Hairston and De Stasio 1988, De Stasio 1989, Wolf and Carvalho 1989, Marcus et al. 1994, Hairston et al. 1995).

For example, theory suggests that these long-lived eggs may alter the outcome of ecological interactions such as competition (e.g., Chesson 1983, Warner and Chesson 1985, Cohen 1994). However, a basic understanding of egg bank dynamics is a necessary first step toward quantifying the long-term effects of dormancy on populations and communities. Here I discuss the dynamics of the long-lived egg bank of two competing *Daphnia* species in Oneida Lake, New York. In this lake, both species reproduce by cyclical parthenogenesis. During times of sexual reproduction, females produce two diapausing eggs at a time in a protective case called an ephippium. In assessing the egg bank dynamics of these two *Daphnia* species, I consider not only the abundance and distribution of eggs in the sediment but also the annual timing and rate of diapausing egg production and the rates of emergence back to the active population.

METHODS

Study system

Oneida Lake is a large (206.7 km^2) but relatively shallow lake (maximum depth 16.8 m, mean depth 6.8 m), located on the Ontario Lake Plain in central New York. Annual patterns of phytoplankton, zooplankton, and fish abundance, as well as abiotic factors, have been reported elsewhere (e.g., Mills et al. 1978, 1987, Mills and Forney 1987, Cáceres 1997a, in press). Zooplankton data collected over the past 30 yr demonstrate a striking negative correlation between two suspension-

feeding zooplankton species (Mills and Forney 1987, Braner 1988, Cáceres 1997a, in press). For at least the past three decades, the smaller *Daphnia galeata mendotae* and the larger *Daphnia pulicaria* have alternated as the numerically dominant daphnid species. When one species is abundant in the plankton, the other species remains in very low numbers or is absent from the water column entirely. This negative correlation apparently results from a combination of variable intensities of size-selective predation by fish (Mills and Forney 1987) and interspecific competition (Cáceres 1997a, in press).

Unlike seasonal dynamics in other systems (e.g., DeMott 1983, Hu and Tessier 1995), in Oneida Lake these species do not follow a predictable succession every year. *Daphnia pulicaria* dominates the water column for the entire season in some years, *D. galeata mendotae* dominates in others, and some years involve a spring-to-fall species shift. In addition, in some years the dominant daphnid species maintains an active overwintering population, whereas in others, both species are completely absent from the water column during the winter. The transient dominance of one species over the other has been shown to last for years and in one instance for over a decade (Mills and Forney 1987).

Egg bank size, age, and distribution

On 26 June 1992, I used SCUBA to obtain four sediment cores (7 cm inner diameter) from Oneida Lake. The cores were collected along a transect from near the shore (Billington Bay) to one of the deepest parts of the lake (12 m, Fig. 1). Single sediment cores were obtained in 3, 7, 9, and 12 m of water. In the laboratory, each core was extruded and sliced at 1-cm intervals. To remove the outer edge of sediment that had been dragged along the wall of the core tube, the middle of each slice was extracted with a 5.9-cm circular cookie cutter. Samples were stored in the dark at 7°C until analysis. I began processing samples by filtering them through a 53-μm mesh sieve to remove as much fine sediment as possible. The sediment retained on the

mesh was put into a 15-mL centrifuge tube with a 30% sugar solution and centrifuged at 1085 rpm (~12.8 m/s²) for 1.5 min. This process suspended almost all of the ephippia, which I then poured onto a 75-μm mesh and resuspended in lake water for examination. Ephippia remaining in the pellet at the bottom of the centrifuge tube were removed under a stereo-dissecting microscope. All ephippia were identified to species based on the morphology of the dorsal ridge (C. E. Cáceres, *unpublished data*). To determine the number of eggs in each ephippium (0, 1, or 2), I opened each ephippium with a pair of dissecting needles and scored as viable all eggs that were not clearly degenerated. A subset of these eggs was incubated for up to one year in 24-h light and 8°C conditions to check for hatching. All eggs that appeared to be in good condition were scored as viable whether or not they eventually hatched. Because the hatching cues vary among species and genotypes (Schwartz and Hebert 1987), successful hatching is an unreliable criterion for viability.

To estimate sedimentation rate in Oneida Lake and thus to obtain ages for these eggs, an additional piston core was taken by SCUBA on 24 August 1994 in the same location as the first 12-m core. This core was sliced at 1-cm intervals to 20 cm, at 2-cm intervals from 20 to 40 cm, and at 4-cm intervals from 40 to 87 cm. The outer ring of sediment that had been dragged along the wall of the core tube was also removed from these samples. Sixteen samples in the top 30 cm were analyzed for ²¹⁰Pb by Daniel R. Engstrom (University of Minnesota), and dates and sedimentation rates were calculated by the c.r.s. (constant rate of supply) dating model (Oldfield and Appleby 1984).

To explore the spatial and temporal variability in diapausing egg abundance, 24 large-diameter cores (16 cm internal diameter [id], 0.02 m² surface area) were taken during 1993–1995. In November 1993, May 1994, November 1994, and May 1995, duplicate cores were taken at each of three deep-water (12 m) sites across the east–west axis of the lake (for a total of six cores on each date). Site 1 was part of the original core transect, Site 2 was ~1.5 km east of the first site, and Site 3 was an additional 4 km east, near New York State Barge Canal Buoy 117 (Fig. 1). In the laboratory, I inserted two metal plates vertically into the top of each core to divide it into four pie-shaped wedges (0.005 m² per quarter). I removed the top 2 cm of sediment from each quarter; ephippia were either preserved in sucrose–formalin solution (November 1993) or stored in the dark at 7°C and examined for viable eggs within 2 wk. For each species, changes in diapausing egg density in both space and time were analyzed by ANOVA, with four quarters nested in each of two cores, and each set of cores nested in three sites. Date was treated as a categorical variable.

Diapausing egg production

For the years 1992–1995, I collected replicate zooplankton samples from the main reference station of the Cornell Biological Field Station (12 m). Samples were collected weekly during the ice-free season and less often (every 3–4 wk) during periods of ice cover. In 1992 and 1993, *Daphnia* were collected on each date with a Clarke-Bumpus plankton sampler (manufactured by F. Schueler, Waltham, Massachusetts), with a built-in flow meter and a 75-μm mesh net. Two replicate samples were collected by oblique tow from ~1 m above the bottom to the surface. During 1994 and 1995 and during ice cover in all years, two samples were collected with a 0.5 m diameter conical net (75 or 150 μm) towed vertically from 1 m above the bottom to the surface. The conical net sampled ~2000 L of water whereas the Clarke-Bumpus typically sampled ~1200 L. Samples were preserved in 70% ethanol, and each sample was thoroughly checked for females carrying ephippia. On any given date, the water-column density of females bearing ephippia needed only to exceed 0.0004 individuals/L to be recorded.

Ephippia develop over the course of the female's molt cycle, at the end of which the ephippium is shed with the old carapace. Hence, to convert ephippial densities to daily production rates I divided the number of ephippia per female by the length of the molt cycle (Edmondson 1968, Paloheimo 1974, Braner 1988). To calculate the duration of the molt cycle, on each sampling date I measured the water temperature with a YSI telethermometer (YSI, Yellow Springs, Ohio). Oneida Lake rarely stratifies thermally; therefore, average water-column temperatures were calculated from values recorded at 1-m intervals. Intermolt duration times not only vary with temperature, but can also vary slightly among species. For example, at 15°C, Hall (1964) reports a development time of 4.5 d for *D. galeata mendotae,* whereas Gulbrandsen and Johnsen (1990) report a development time of 3.6 d for *D. pulex.* Consequently, the length of *D. pulicaria*'s molt cycle at each ambient temperature was calculated from the data of Esslová (1959) and Gulbrandsen and Johnsen (1990), whereas Hall's (1964) data were used for *D. galeata mendotae.* By integrating daily production rates over each sampling interval, I calculated weekly production rates. I obtained annual production estimates by summing over all sampling dates. Annual estimates of ephippial production were converted to annual diapausing egg production by multiplying by two eggs per case and correcting for the fact that ~10% of females shed empty cases (C. E. Cáceres, *personal observation*). Lastly, I approximated the variance associated with this annual estimate by summing the variances calculated from each weekly estimate. Between-species differences in the number of eggs produced each year were analyzed with ANOVA.

Emergence

Estimates of hatching from the egg bank were obtained directly by monitoring a series of inverted funnel emergence traps. Twelve emergence traps were in-
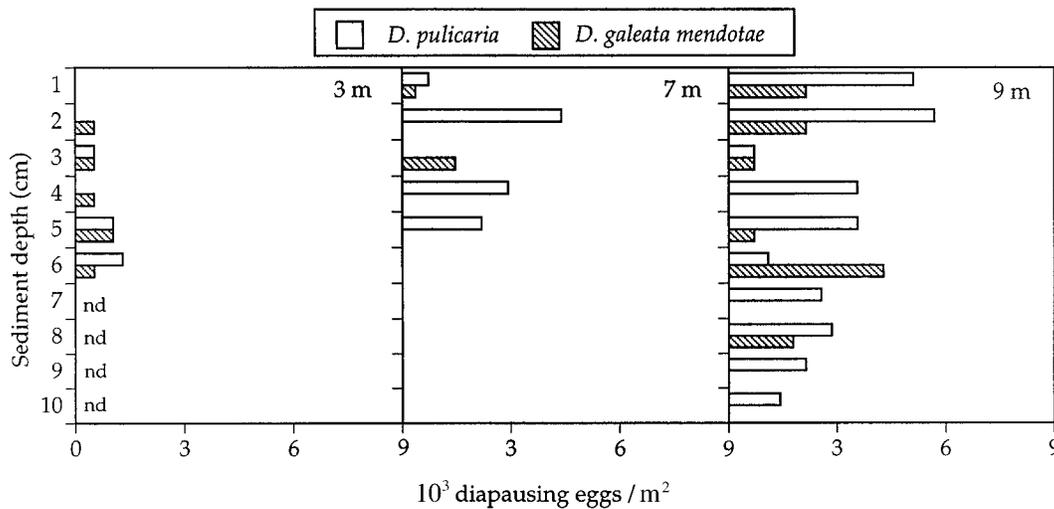
FIG. 2. The abundance of viable diapausing eggs of *D. pulicaria* and *D. galeata mendotae* as a function of sediment depth in cores taken in June 1992 at 3, 7, and 9 m of water. No data were recorded deeper than 6 cm in the 3-m core, while the 7- and 9-m cores were examined down to 11 cm and 25 cm, respectively. No viable eggs or empty ephippia were found below 5 cm in the 7-m core. In the 9-m core, no viable eggs were found below 10 cm, and no empty ephippia were found deeper than 11 cm.

stalled along two transects in 5, 8, and 12 m of water (two traps per site) beginning in June of 1993 and immediately following ice-out in 1994 (19 April) and 1995 (28 March) (Fig. 1). One emergence-trap transect was positioned along the original core transect in an area of the lake frequently sampled by researchers at Cornell Biological Field Station. The other, located ~1.5 km east of the first site, was positioned near enough to the first to allow all six stations to be sampled on the same day. Each trap, constructed from a clear-plastic 5-gallon (~19-L) water bottle with the bottom cut off so as to make a funnel, covered 0.05 m² of sediment. I installed four 75-μm mesh windows in each trap to allow oxygen exchange. To prevent introduction of animals from the surrounding water, the bottom edge of each trap was buried 10 cm into the sediment, and traps were left undisturbed for the duration of the season. The traps were removed from the lake in November of each year.

At the top of each trap I attached a piece of tygon tubing that served as a friction-fitted connection into the neck of a 250-mL tissue culture flask. This exchangeable collection bottle was filled with 225 mL of twice-filtered (75-μm filter) Oneida Lake water. An air bubble was left in each bottle to prevent animal respiration from leading to anoxia (De Stasio 1989). On each sampling date I used SCUBA to remove the sample bottle, which I capped underwater. A new sample bottle was installed immediately, leaving the traps uncovered for only a few seconds each week. *Daphnia* that emerged and were collected in the flasks were isolated in filtered lake water and allowed to mature until a definitive species identification could be made. Samples were collected weekly (1993, March–June 1994–

1995) or every other week (July–November 1994–1995).

In addition, I used the data collected from the 24 large-diameter sediment cores to estimate emergence rates indirectly. I calculated the difference in egg abundance before (November) and after (May) ice cover in 1993 and 1994 as a maximum estimate of emergence. This method most likely overestimates emergence rates because it assumes that all loss from the egg bank results from hatching and ignores other sources such as predation, degradation, and deep burial. Scheffé post hoc tests from the original nested ANOVA were used to analyze the differences in densities between each date. The direct and indirect estimates of emergence rates were then compared to the size of the overwintering population to assess the annual contribution of hatching to the development of the spring water-column population.

All statistical analyses were performed using Data Desk 5.0 for the Macintosh.

RESULTS

The majority of diapausing eggs for both species lay buried in sediments at the deepest part of the lake (Figs. 2 and 3). There were fewer eggs of *D. galeata mendotae* than *D. pulicaria* in all cores except in the sediments closest to shore (*D. galeata mendotae*: 3 m, 3.1×10^3; 7 m, 1.8×10^3; 9 m, 12.1×10^3; 12 m, 26.0×10^3; *D. pulicaria*: 3 m, 2.9×10^3; 7 m, 10.2×10^3; 9 m, 29.3×10^3; 12 m, 83.0×10^3). Total average densities recorded from these four cores indicate that the daphnid egg bank is made up of ~70% *D. pulicaria* eggs.

Results from the ^{210}Pb analysis of the core at 12 m showed an undisturbed sediment column with a fairly
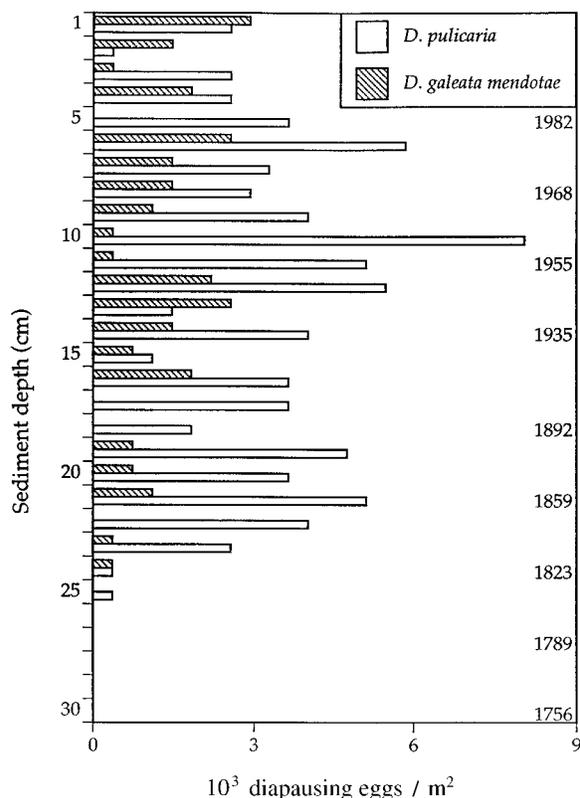
FIG. 3. The abundance of viable diapausing eggs in a sediment core taken in June 1992 at 12 m water depth as a function of both sediment depth and age. No viable eggs of either species were found below 24 cm, but empty ephippia of *D. pulicaria* were found as deep as 30 cm, and those of *D. galeata mendotae* were found as deep as 40 cm (end of core).

VA, $F_{3,68} = 0.97$, $P = 0.410$) whereas that of *D. galeata mendotae* has declined ($F_{3,68} = 22.5$, $P \leq 0.0001$, Fig. 5). For *D. galeata mendotae,* egg density did not differ significantly within cores, between the two cores at each site, or between the three sites. The same was true for *D. pulicaria* when egg density was analyzed with a fully nested model (quarter $F_{18,68} = 1.70$, $P = 0.062$; core $F_{3,18} = 1.49$, $P = 0.250$; site $F_{2,3} = 2.96$, $P = 0.195$). However, when the nonsignificant effects of core quarter and core replication were removed and the ANOVA was calculated with only date and site as the factors, I detected a significant difference in the number of *D. pulicaria* eggs at the three sites ($F_{2,92} = 6.53$, $P = 0.002$). Estimates from Site 1 were often significantly higher than estimates from the other two locations (Fig. 1). As with the cores taken in 1992, results from these cores indicated that the daphnid egg bank is dominated by eggs of *D. pulicaria* (repeated-measures ANOVA of log(egg density), species effect: $F_{1,10} = 52.0$, $P \leq 0.0001$), with $72.4 \pm 4.9\%$ (mean $\pm$ 1 SE) of all eggs belonging to *D. pulicaria.*

Diapausing egg production

There are two distinct periods of sexual reproduction in the Oneida Lake *Daphnia*. Both species produce males and diapausing eggs during late May–early June and during November–December (Fig. 6). This pattern is irregular, however, because each species frequently exhibits prolonged absence from the water column (Mills and Forney 1987). As a result, diapausing egg production in some years is reduced or eliminated en-
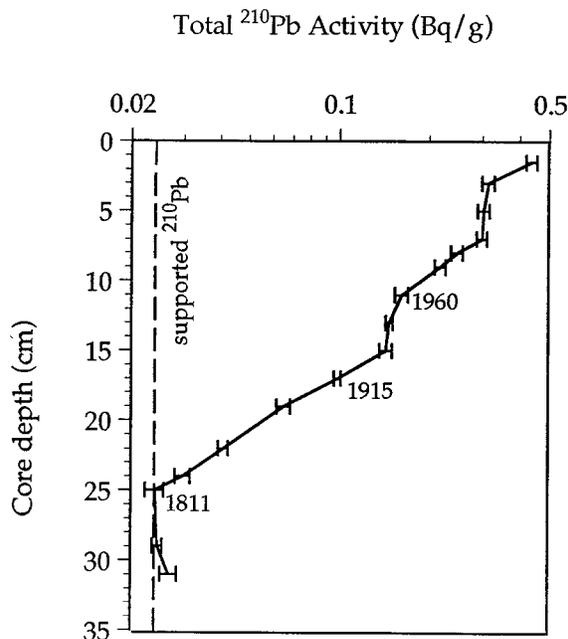
constant sedimentation rate of 0.8 mm/yr before 1935 (15 cm, Fig. 4). After 1935, the ^{210}Pb activity indicates either a sharp increase in sedimentation rate or extensive mixing of the sediment column. From 1960 to 1994, annual sedimentation rate was ~3.9 mm/yr. The average of these rates is 2.35 mm/yr for the top 25 cm, which agrees with the value of 2.3 mm/yr obtained by Moore et al. (1980), who also estimated sediment ages based on ^{210}Pb activity. Ages were assigned to the eggs based on the ages of the sediment in which they were found (Fig. 3). Although the development of these eggs was not followed intensely, up to half of the *D. galeata mendotae* and *D. pulicaria* eggs found as deep as the 18–19 cm slice hatched, indicating that eggs can remain viable in Oneida Lake for >125 yr. Diapausing eggs were not found deeper than 24 cm (169 yr) in the core, but empty ephippial cases of both species were found as deep as 30 cm, suggesting that both species have coexisted in Oneida Lake for >200 yr.

Abundance estimates from the 24 large-diameter cores taken in deep water (12 m) indicate that from 1993 to 1995, the size of *D. pulicaria's* near-surface egg bank (top 2 cm, ~5 yr) remained constant (ANO-

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

FIG. 4. ^{210}Pb activity as a function of sediment depth in a core taken at 12 m water depth on 24 August 1994 (1 becquerel [Bq] = 27.027 pCi [picocuries]). Error bars indicate ±1 SD.
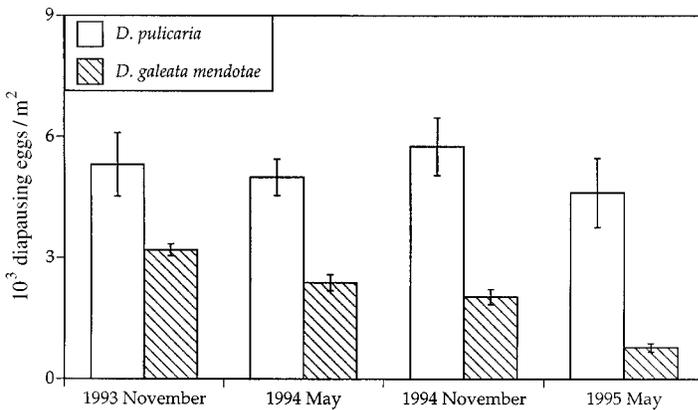
Fig. 5. Abundances of viable diapausing eggs in the top 2 cm (~5 yr) of sediment in Oneida Lake. Histograms represent the mean egg densities (±1 SE) of six large-diameter cores taken at three separate deep-water (12 m) stations (see Fig. 1 for locations).

tirely (Cáceres 1997*b*). In the years 1992–1995, annual production for both species was variable, and the majority of diapausing eggs produced in each of the four years were those of *D. pulicaria* (Table 1). In one year (1995), *D. galeata mendotae* was extremely rare in the water column, and no new diapausing eggs were produced. Over these four years, *D. pulicaria* produced significantly more diapausing eggs than *D. galeata mendotae* (ANOVA, log[number of eggs + 1]: $F_{1,11} = 30.9$, $P < 0.0002$).

Only a small proportion of adults in either population switched to sexual reproduction (Fig. 6). Even during times of peak sexual reproduction, typically <15% of adult female daphnids produced ephippia. At these times of year, the majority (>50%) of the adult females did not carry eggs of either type, and a small fraction of females continued parthenogenetic reproduction.

Emergence

Emergence rates for the daphnid species varied both within and between years, but emergence of either spe-

cies was only detected in the spring (Fig. 7). In 1994, both species emerged from diapausing eggs at all three depths sampled. That year, average emergence over the three depths comprised 3.5 *D. galeata mendotae*/m² and 4.5 *D. pulicaria*/m². Although this represents <1% of the total egg bank, it translates to an annual lake-wide emergence of $>6 \times 10^8$ daphnids of each species. Only *D. pulicaria* emerged in 1995, with an average emergence of 15.6 *D. pulicaria*/m². This increase from 1994 was primarily due to increased emergence at the in-shore stations. In 1995, 28 *D. pulicaria*/m² emerged in shallow water (5 m), whereas only 0.7 *D. pulicaria*/m² emerged from the same stations in 1994. Overall, more juvenile *D. pulicaria* emerged than *D. galeata mendotae* (ANOVA, log(no. *Daphnia* emerged + 1), species effect: $F_{1,10} = 7.76$, $P = 0.019$).

These results suggest that *Daphnia* hatch from diapausing eggs in Oneida Lake only in early spring. It is possible however, that emergence begins during the winter or just prior to ice-out, but no samples were collected during that time of year due to inability to
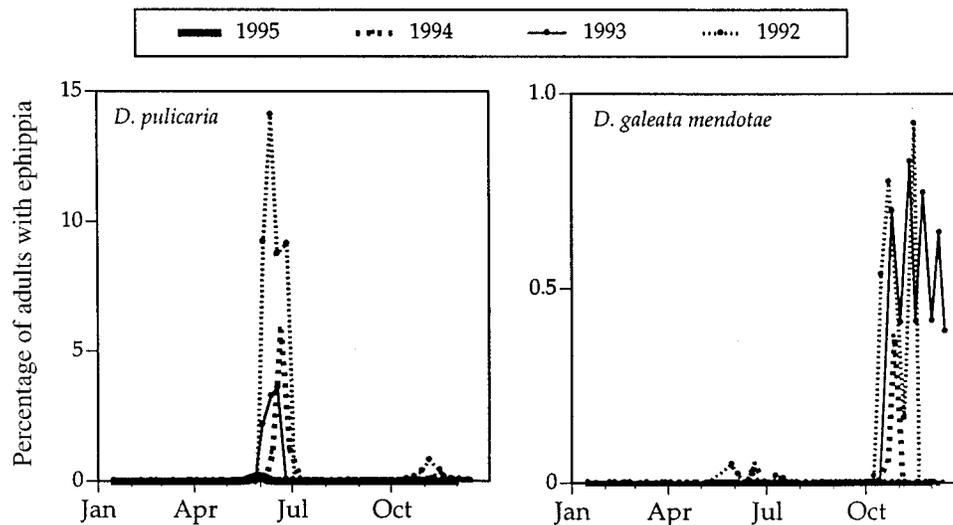

Fig. 6. Annual timing of diapausing egg production by Oneida Lake daphnids based on weekly samples during 1992–1995, expressed as the percentage of females carrying ephippia. Note the difference in scales.

TABLE 1. Number of diapausing eggs (mean ± 1 SD) produced in the water column in each year.

Year	Thousands of diapausing eggs/m²	
	D. pulicaria	*D. galeata mendotae*
1992	3.2 ± 0.3	1.2 ± 0.2
1993	13.7 ± 1.2	0.1 ± 0.02
1994	2.4 ± 0.2	0.1 ± 0.04
1995	2.2 ± 0.1	0.0 ± 0.0

access the traps by SCUBA. Data collected from the traps in 1993 (not shown) further support the conclusion that *Daphnia* does not hatch during the summer or early fall. In that year, emergence traps were sampled from late June through mid-November, but no emergence by either species was observed. The first emergence sample in 1993 was collected 9 wk after the ice had gone out. By 9 wk after ice-out, emergence had ceased in 1994 and 1995, suggesting that I missed the emergence in 1993. Lastly, in a pilot study conducted in 1992, no emergence by either species was recorded in October or early November.

Converting these direct estimates of emergence from number per square meter to number per liter suggests that emergence contributed little to the offshore development of the spring population in 1994 and 1995 (Table 2). In shallower water (5 m), the spring emergence ranged from 0 to 0.006 *Daphnia*/L as a result of higher emergence rates and a shallower water column. The indirect estimates of hatching are higher than the direct estimates and therefore suggest more of a con-

tribution to the water-column population (Table 2). However, estimates of *D. pulicaria* egg densities did not differ significantly across time (ANOVA, $F_{3,68}$ = 0.97, P = 0.410), indicating that there was no significant loss from the egg bank in either spring. In contrast, the size of *D. galeata mendotae*'s egg bank declined significantly over both winters (ANOVA, $F_{3,68}$ = 22.5, $P \leq 0.0001$; Scheffé post hoc tests, P = 0.023 [1993–1994], P = 0.003 [1994–1995]).

DISCUSSION

Egg bank dynamics

Even though diapausing eggs are often thought to have evolved as an adaptation to life in a temporary environment (e.g., Hutchinson 1967, Wiggins et al. 1980), there is a growing body of evidence suggesting that zooplankton egg banks can also significantly affect population dynamics and community structure in permanent systems (Marcus 1984, Herzig 1985, Hairston and De Stasio 1988, Wolf and Carvalho 1989, De Stasio 1989, 1990, Ellner and Hairston 1994, Hairston and Van Brunt 1994, Hairston et al. 1996b). However, the demographic links between the active and dormant phases, as well as the processes affecting the dormant eggs, remain unexplored in most systems. This study provides a detailed investigation of the egg banks of two closely related zooplankton species. Because long-lived dormant eggs can affect the ecology and evolution of the populations that produce them, it is necessary to consider the ties to the dormant stage in order to fully understand the dynamics of the planktonic stage.
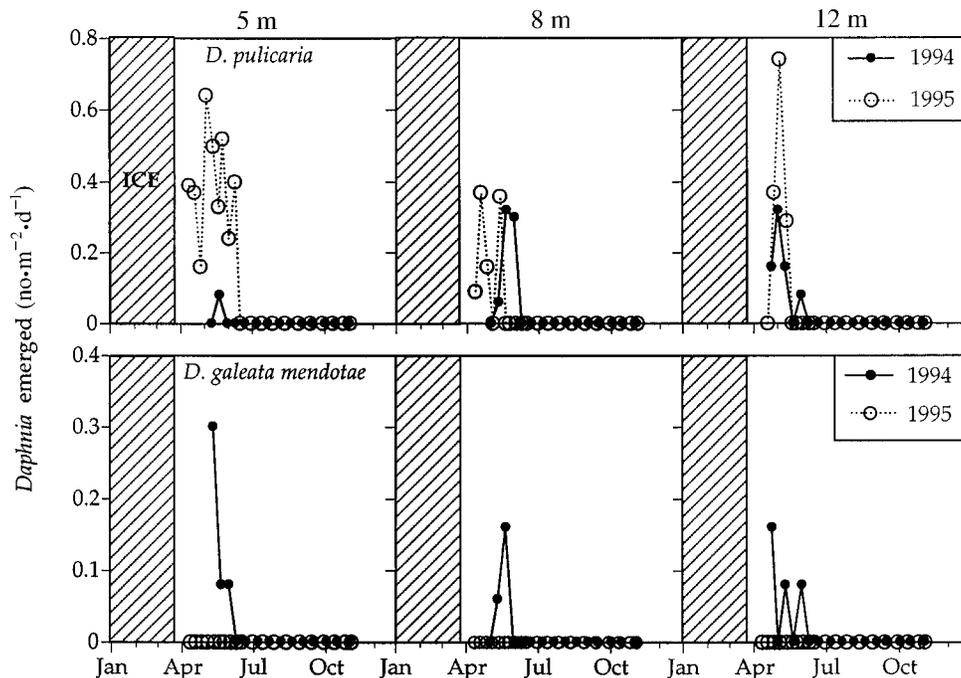

FIG. 7. Emergence rates calculated by sampling in situ emergence traps at 5, 8, and 12 m of water. Each point represents the average of 2–4 traps. Standard errors, omitted for clarity, ranged between 0 and 0.9 *Daphnia*·m⁻²·d⁻¹.

TABLE 2. Estimates of the contribution of emerging *Daphnia* to the development of the spring plankton population. All estimates are for the 12-m sampling station.

	D. pulicaria		*D. galeata mendotae*	
Estimate	1994	1995	1994	1995
Daphnia before ice-out (no./L)	0.001 (21 Mar)	0.038 (24 Feb)	0.006 (21 Mar)	0.000 (24 Feb)
Date of ice-out	16 Apr	23 Mar	16 Apr	23 Mar
Daphnia after ice-out (no./L)	0.004 (19 Apr)	1.156 (29 Mar)	0.090 (19 Apr)	0.000 (29 Mar)
Direct estimate of hatching (no. *Daphnia*/L)	5×10^{-4}	8×10^{-4}	2×10^{-4}	0.0
Indirect estimate of hatching (no. *Daphnia*/L)	0.032	0.096	0.068	0.103

Diapausing eggs and ephippial cases were found in sediments dating to over 100 and 200 yr, respectively, but are these eggs really that old? If sediment mixing (e.g., by invertebrates, fish, or physical processes) rapidly transports young eggs deep within the sediment column, their ages could be overestimated. This does not appear to be the case for the eggs and ephippia below 15 cm (1935) where the ^{210}Pb profile shows no evidence of sediment mixing. In the more recent sediments, however, there are two zones of nearly constant ^{210}Pb activity (Fig. 4), which complicates the interpretation of the sediment profile. This pattern could result from sediment mixing, from a change in sedimentation rate, or from a combination of the two processes. At the deep-water stations, the upper sediments of Oneida Lake are flocculent; this could easily lead to mixing in the top layers. On the other hand, there is also evidence suggesting an increase in sedimentation rate. The opening of the New York State Barge Canal through the lake in 1916 not only changed the hydrology of the lake, but also greatly increased boat traffic. Concurrent increases in development and agriculture within the watershed may also have altered the sedimentation rate. The population along the shores of Oneida Lake increased by an order of magnitude between 1900 and 1960, with the percentage of undeveloped shoreline decreasing from 71% to <50% (Greeson 1971). Even though it is not possible to draw a definitive conclusion about the processes leading to the observed ^{210}Pb profile, it is likely that both an increase in sedimentation rate and sediment mixing were contributing factors. Although the possibility of sediment mixing in the top layers (~30 yr) compromises the age estimates of young eggs, deeply buried eggs nonetheless date to >100 yr old.

Although the potential for sediment mixing complicates analyses of egg ages, it can enhance the contribution of dormant stages back to the active populations. The egg bank for both species extends down 25 cm into the sediment, but it is likely that only the eggs near the surface hatch. Laboratory experiments suggest that exposure to abiotic factors such as light and temperature induce the dormant stages to resume development (e.g., Pancella and Stross 1963, Stross and Hill 1968, Schwartz and Hebert 1987, Chen and Folt 1996).

To receive these types of cues, diapausing eggs need to be near the sediment surface. Therefore, any deeply buried egg is effectively dead unless some localized mixing action brings it back near the surface. The extent of bioturbation by benthic invertebrates in freshwater is typically found to be 2–5 cm (McCall and Tevesz 1982, Cohen et al. 1991, Kearns et al. 1996), but it may be somewhat deeper in Oneida Lake (Fig. 4). The results from the ^{210}Pb profile show a zone of nearly constant activity extending from 2 to 7 cm, which may be the result of sediment mixing. The potential for mixing in the top centimeters of sediment provides a mechanism to keep eggs near the sediment surface longer, thereby increasing their probability of hatching and contributing to the pelagic population.

The near-surface egg bank of *D. galeata mendotae* appears to have declined from 1993 to 1995, while that of *D. pulicaria* has remained fairly constant (Fig. 5). This pattern is not surprising, given the recent inputs to the egg bank by the two species. During 1992–1995, *D. galeata mendotae* produced <1500 dormant eggs/m² in total while *D. pulicaria* produced nearly 20 000 eggs/m². Although this suggests the eventual elimination of *D. galeata mendotae,* long-term production estimates indicate that at times the *D. galeata mendotae* population can produce several thousand eggs per square meter in just one season (Cáceres 1997b). Because many of these eggs remain viable for decades, the *D. galeata mendotae* population needs only to restock its egg bank once over this interval, provided that egg survivorship is high enough to refound the population. Although the density of near-surface eggs may have declined recently due to lack of production, *D. galeata mendotae* still has tens of thousands of older eggs stored in the sediment of Oneida Lake.

In addition, the single core collected at 12 m in 1992 suggests that the near-surface egg bank of *D. galeata mendotae* was larger than that of *D. pulicaria* at that time (Fig. 3). There are at least two possible explanations for this reversal in dominance of the near-surface egg bank. The first is the fact that the densities in 1992 were estimated based on only one small (7 cm id) core as opposed to six large (16 cm id) cores in the other years. Alternatively the date that first core was collected might provide the explanation. In 1990,

1991, and 1992 the water column was dominated by *D. galeata mendotae* and *D. pulicaria* was quite rare (E. L. Mills, *personal communication*). In contrast, for the rest of the study period, *D. pulicaria* tended to dominate the water column.

Annual production estimates during 1992–1995 at times exceeded egg densities found in the sediments and eggs lost to emergence by >100%, thus raising the question: where are the missing eggs? One possibility is that the annual input estimates estimated from water-column densities are too high. The annual production estimates are based on the assumption that all ephippia sink directly to the bottom of the lake. However, the hydrophobic nature of the ephippia increases their probability of sticking in the water's surface tension and being rafted toward the shore. In smaller lakes and ponds, large windrows of ephippia are often seen along the water's edge (Wetzel 1983), but frequent turbulence prevents this in Oneida Lake (*personal observation*). Nevertheless, it is possible that some fraction of the ephippia produced was caught in the surface film instead of sinking to the sediment.

Furthermore, after the ephippia were counted I converted abundance estimates to numbers of diapausing eggs by multiplying by two eggs per ephippium and correcting for empty ephippia. Once a female *Daphnia* is cued to produce sexual eggs and ephippia, she is constrained to that pathway for the duration of that molt cycle. If she does not find a mate, the unfertilized eggs are either reabsorbed (Hutchinson 1967) or quickly degenerate (Zaffagnini 1987), and the ephippium is shed empty. In trying to correct for this I assumed an average of 10% empty cases based on multiple observations from Oneida Lake, but this estimate may be too low.

A different explanation for the apparent loss of dormant eggs involves predation. Mellors (1975) showed that *Daphnia* females with darkly pigmented ephippia suffer from an increased rate of predation by fish. Although many eggs do not survive gut passage, a small fraction of these eggs probably remain viable after being ingested and defecated (Mellors 1975). Thus, vertebrate predation on females carrying ephippia not only can remove eggs from the system, but also can transport the dormant eggs to other parts of the lake. In addition, predation by invertebrates can also result in a loss of dormant eggs from the system. For example, amphipods ingest the ephippia by shredding, thus completely destroying the eggs and their case (Cáceres 1997*a*, Cáceres and Hairston, *in press*).

Diapausing egg production

The cues required to initiate ephippial production are complex, and the work presented here does not explain why daphnids in Oneida Lake switch from parthenogenetic to sexual reproduction. However, of the more typical explanations (e.g., photoperiod, temperature, crowding, food limitation, predation), some seem less probable than others. Crowding is unlikely to induce the switch because the first round of sexual reproduction begins each year during late May to early June whether the daphnid populations contain few individuals (<5 animals/L) or many (>40 animals/L). In addition, there is no evidence for an increase in the per capita frequency of sexual reproduction at higher daphnid densities in Oneida Lake (C. E. Cáceres, *unpublished data*). Because the May switch coincides both with the onset of food limitation (as a result of the clear-water phase) and intense predation by young-of-the-year yellow perch, the field data do not implicate or eliminate either explanation. Furthermore, even though competition or predation may be the ultimate reasons for taking refuge in the sediment, *Daphnia* may be induced to produce diapausing eggs by photoperiod or temperature, as has been suggested for other plankton taxa (e.g., Hairston and Olds 1984, Maier 1989, Hairston and Kearns 1995, Santer and Lampert 1995, Chen and Folt 1996).

The spring round of sexual reproduction is potentially quite a valuable strategy, given the frequent mid-summer elimination of *Daphnia* from the water column (Mills and Forney 1987), which would pre-empt end-of-the-year egg bank deposits. Moreover, the fact that *D. galeata mendotae* typically produces the majority of its dormant eggs in the fall while *D. pulicaria* produces the majority in the spring (Fig. 6) may partially explain the differences in annual input to the egg bank. Not only do fewer *D. galeata mendotae* than *D. pulicaria* females switch to sexual reproduction (Fig. 6), but fall population densities are typically much lower than those observed in the spring.

The late fall switch to sexual reproduction comes at a time when food is increasing, population abundances are generally low, and temperature and photoperiod are declining. The fact that the temperature and photoperiod combination of late spring is much different from that of fall might seem to weaken the argument that a precise temperature and photoperiod interaction induces the daphnids to initiate sexual reproduction. However, it is possible that different genotypes within the populations respond to these different cues, as found by Ferrari and Hebert (1982) and Carvalho and Hughes (1983); it is also possible that a single genotype can respond to more than one combination of cues.

Contributions to community structure

Dormant eggs have the potential to influence both the genetic composition of a population and the species structure of a community (e.g., Herzig 1985, De Stasio 1990, Ellner and Hairston 1994, Hairston et al. 1996*a*), but to do so they obviously must be induced to resume development. Unfortunately, the lack of information regarding the cues required to terminate dormancy in the field make addressing the within- and between-year variance in *Daphnia* emergence rates pure speculation. If a precise set of environmental factors is needed to induce these eggs to develop, then it is not surprising

that emergence occurs only over a narrow window in the spring. A prior study of Oneida Lake *D. pulicaria* also suggested that these eggs return to the water column only in the spring. In examining multi-locus genotypes in the Oneida Lake *D. pulicaria* population over four seasons (1983, 1984, 1990, and 1991), M. G. Boileau (*unpublished manuscript*) found that the populations conformed to Hardy Weinberg expectations on the first spring sampling date each year, but not again thereafter. He attributed this result to the hatching of sexually produced dormant eggs early in the season, followed by clonal replacement.

In contrast, the emergence results in this study suggest that *D. galeata mendotae* do not return to the water column every season. However, given that only 88 daphnids were caught in the emergence traps over the two years, the hatching of *D. galeata mendotae* in 1995 might have been below detection limits. Nevertheless, the failure to record *D. galeata mendotae* from the plankton in 10 of the last 32 years (Mills and Forney 1987) indicates that in many years either this species does not emerge, or too few individuals hatch to found a planktonic population. The number of individuals that need to hatch to found this planktonic population obviously depends on conditions in the water column such as predation, resources, and the size of the overwintering daphnid population.

The contribution of the egg bank to the development of the spring population depends on two parameters: the size of the overwintering population in the water column and the number of emerging daphnids. At one extreme, emergence can have a negligible effect on water-column population dynamics due either to a low emergence or to large overwintering populations. At the other extreme, when the overwintering population is undetectable, any detectable emergence will contribute significantly to the development of the spring population. In the years 1964–1995, *D. pulicaria* failed to overwinter in 6 yr and *D. galeata mendotae* in 12 yr (Mills and Forney 1987; E. L. Mills and J. L. Forney, *unpublished data*), indicating a large contribution of emergence in these years. In contrast, the largest overwintering population was 2.5 *Daphnia*/L. In 12 m of water, 12 000 *Daphnia*/m^2 would need to emerge to found a population of just 1 daphnid/L. Because there are <6000 eggs in the top 2 cm of sediment, a contribution of this magnitude is unlikely.

Over the period studied here (1992–1995), the indirect estimates of emergence suggest a minimal contribution to the spring population (Table 2). In fact, given the average number of eggs found in the top 2 cm of sediment, a complete emergence of all eggs would only give rise to ~0.5 *Daphnia*/L for *D. pulicaria* and 0.25 *Daphnia*/L for *D. galeata mendotae*. Since the May core samples show that the near-surface egg bank is not depleted each year, overwintering populations must be on the order of 1 daphnid/100 L or less for the egg bank to make a substantial contribution

to the offshore plankton assemblage. However, because more daphnids tend to emerge from nearshore sediments (Fig. 7) and there are fewer total daphnids in the overlying water-column (because it is not as deep), the contribution of emergence to the plankton will be higher in these areas.

The links between the benthic and pelagic phases of these two populations seem to differ somewhat in Oneida Lake. Although maximum water-column densities of the two species are comparable (Mills and Forney 1987), *D. pulicaria* produces and stores more dormant eggs than *D. galeata mendotae* in addition to having a higher emergence rate. Furthermore, over the four years of this study, *D. pulicaria* produced new diapausing eggs in every year, whereas no new diapausing eggs were detected for *D. galeata mendotae* in 1995. That *D. galeata mendotae* was absent from the water column for six consecutive years in the 1970s (see Fig. 2.4 of Mills and Forney 1987) further suggests that there are years in which this species has no new recruitment to the egg bank. These results suggest that without multiple-year dormancy, *D. galeata mendotae* could not persist in Oneida Lake. In contrast, *D. pulicaria* rarely experiences years of failed recruitment, as judged by its presence in the water column for at least some fraction of each of the years 1964–1995. Thus, in Oneida Lake, this species may rely upon diapause to persist from season to season rather than across multiple seasons, as *D. galeata mendotae* does in this lake. Apparently, both species have an adequate tie between the benthic and pelagic phase because both species have persisted in Oneida Lake for at least the past 200 yr.

Clearly these *Daphnia* are not uniformly short-lived animals. Long-lived diapausing eggs greatly increase the generation time of the species that produce them, which can lead to long-term population persistence in a variable environment. Theory suggests that the overlapping generations established by an egg bank, in combination with environmental variation, may promote the maintenance of both genetic and species diversity within a community (Chesson and Warner 1981, Ellner and Hairston 1994, Hairston et al. 1996*a*). The egg bank dynamics presented here indicate that dormancy plays a key role for the Oneida Lake daphnid populations where one or the other species repeatedly disappears from the water column. Although processes such as variable predation and competition undoubtedly influence their water-column dynamics, the long-term persistence of these species would not be possible without the reliable colonization source provided by the egg bank (Cáceres 1997*b*).

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