

Winter storms: Sequential sediment traps record *Daphnia* ephippial production, resuspension, and sediment interactions

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Abstract

For species that do not over-winter, an essential part of the life cycle is the production of diapausing eggs. We use sequential sediment traps in southern Lake Michigan (1997–2000) to capture settling *Daphnia* ephippia and sediments, characterizing ephippial production and sediment interactions during hazardous conditions. Each year, there was an enormous pulse of *D. mendotae* ephippia (ca. 7.2×10^{13} ephippia, 1.2×10^{14} diapausing eggs) that coincided with autumn population decline. Most ephippia settled through the water column, although a few were captured at the water surface and blown shoreward. The duration and amplitude of the autumn ephippial fluxes were similar among years. Ephippial production was positively correlated with water column depth, a consequence of *Daphnia* spatial abundance. In contrast, resuspension of ephippia was inversely related to water column depth and spatially complex, influenced by waves, coastal currents, and offshore gyre circulation. Large winter storms created nearshore sediment plumes, could resuspend vast numbers of ephippia (e.g., 10 March 1998 storm; 1.9×10^{12} ephippia and 3.1×10^{12} diapausing eggs), and were important in the formation of “egg banks.” Almost all newly produced and resuspended diapausing eggs came from *D. mendotae*, with very few from two other species (*D. retrocurva*, *D. dentifera*) that dominated waters 12 yr ago. These observations suggest a relatively short relaxation time for species cycling out of egg banks in Lake Michigan (<10 yr), due in part to (1) differential resuspension of unconsolidated versus consolidated sediments and (2) the spatially restricted nature of “high-sedimentation” zones. Our study is the first use of sequential sediment traps to document diapause egg production.

Studies of planktonic communities traditionally emphasize seasonal population growth, describing how the balance of births and deaths in the water column alters pelagic species abundance and maintains community composition (Kerfoot 1980; Lampert and Sommer 1997). An equally important life history stage is seasonal dormancy and the longer term formation of “egg banks” (Marcus 1984; DeStasio 1989; Marcus et al. 1994; Hairston 1996). For species that do not over-winter, a typical north temperate cycle features fall production of diapausing eggs followed by spring hatching.

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During this process, some eggs become buried in lake sediments, surviving for decades or even centuries (Herzig 1985; Hairston et al. 1995; Weider et al. 1997; Kerfoot et al. 1999). This long-term storage phenomenon has potential implications for maintaining both genetic diversity within species and species diversity within communities (Chesson 1983; Elner and Hairston 1994; Hairston et al. 1996; Cáceres 1997). However, documenting critical components of yearly or longer processes (diapausing egg production, dispersal, resuspension, formation, and purging of egg banks) has proved difficult.

Seasonal recruitment into the pelagic population and formation of a long-term buried egg reservoir is intimately tied to yearly production of diapausing eggs, water column stratification, particle dispersal, processes of sedimentation and resuspension, and bioturbation of benthic sediments. Yet our basic knowledge of component processes is limited, even for well-known pelagic species (Marcus 1979; Herzig 1985; Hairston 1996). For example, pelagic population dynamics of the widespread freshwater cladoceran *Daphnia* are documented extensively in many small and some large lakes.

However, the fate of their diapausing eggs, cast off in a “saddle-like” ephippium, is poorly known (Cáceres 1998). Basic questions cover yearly production, dispersal, and burial. When and where are diapausing eggs produced? Do ephippia remain near the site of production or do they float soon after release, drifting along windrows or rafting onto shorelines (Jankowski and Straile 2003)? A second set of questions relates to resuspension. In north temperate regions, how many ephippia are resuspended and dispersed during dimictic periods of water column mixing (e.g., December–January prior to ice formation; spring April–May ice-off)? How do physical processes, such as resuspension, scale with lake size? In large lakes that do not freeze over during winter, to what degree is resuspension and dispersal of diapausing eggs dependent upon late-season or spring storms?

Over a longer time span, there are additional questions. How frequent are severe storms that purge egg banks? Do these events maintain diverse communities by resurrecting buried species, or does occasional reintroduction of species come from other sources (e.g., river or coastal lake discharges; bird or ship dispersal)?

There are relatively few studies that have attempted to directly document diapausing egg production (e.g., DeStasio 1989). Most investigations use the incidence of diapause egg-carrying females in late-season plankton tows to calculate temperature-dependent release rates (Carvalho and Wolf 1989; Cáceres 1998; Jarnagin et al. 2004). Sampling is usually incomplete, and calculations involve numerous assumptions simply because ephippia are produced, dispersed, and resuspended when conditions for routine water column collections are very hazardous, due to winter storms and surface ice formation. In addition, application of egg ratio techniques to autumn diapausing egg production might be flawed, if declining populations under severe physiological stress depart from laboratory-derived molting schedules.

Computer-sequenced sediment traps (Fig. 1A,B) allow direct monitoring of diapausing egg production, dispersal, and resuspension. The traps permit measurement of settlement fluxes for extended periods and can be preprogrammed for taking samples during dangerous winter storm conditions (Fig. 1C). Moreover, the traps provide information on sediment interactions, since they capture both resuspended ephippia and sediment. Here we document production, dispersal, and resuspension patterns for *Daphnia* ephippia in southern Lake Michigan, setting the stage for longer term (sediment core) investigations. Our studies suggest that typical cycling of diapausing eggs in this system is relatively short (<10 yr), although winter storms play important roles in dispersing eggs and in creating sedimentary conditions for egg bank formation.

Materials and methods

Lake Michigan has a surface area of 57,800 km² and a volume of 4920 km³, making it the third largest North American Great Lake and the sixth largest lake in the world. We concentrated on the southern basin of the lake. The locations of zooplankton sampling transects, sequential sediment trap,

ponar, and coring sites are shown in Fig. 2. Starting with 10 traps at 7 sites, eventually 12–17 sequential sediment traps were deployed at 9–11 sites in Lake Michigan during three seasons, 1997–2000, as part of the 5-yr National Oceanic and Atmospheric Association/National Science Foundation episodic events Great Lake experiments, coastal oceans project effort (NOAA/NSF EEGLE CoOP). Yearly totals were 1997–1998 (10 traps at 7 locations), 1998–1999 (17 traps at 11 locations), and 1999–2000 (13 traps at 9 locations). Deep-water locations (T12, T27, T28) remained the same for three seasons, but shallow-water traps were repositioned, concentrating on the eastern high deposition regions during the later two seasons. In addition, although numbers of traps might appear high, many of the coastal traps were devoted to sediment resuspension studies and were not deployed until December, after the ephippial production period.

Zooplankton collection and enumeration—Plankton were sampled by replicate vertical tows ($n = 2$ samples) with a metered 0.5-m diameter 153- μm Nitex plankton net. On many dates, an additional two replicates were taken with a 64- μm Nitex plankton net. The latter samples aided efforts to determine ephippial incidence. Zooplankton were washed into a cod end and preserved in 4% formalin/sucrose for later laboratory enumeration. Analysis of samples emphasized tows from the St. Joseph, Muskegon, and central basin stations, although transect surveys covered additional coastal waters, river mouths, and harbors. Extensive winter sampling of zooplankton was done to examine copepod interactions with winter sediment plumes. The winter cruises (17 cruises over 3 yr) verified *Daphnia* absence during winter (Bundy et al. in press).

Historical changes in zooplankton composition (Fig. 3) provide an excellent setting for investigating “system memory.” The *Daphnia* species composition of Lake Michigan is well documented from numerous studies and has changed over the past half-century. Two of the resident species (*Daphnia mendotae*, *D. retrocurva*) were recorded from plankton tows since the 1880s, whereas a third species, *D. longiremis*, was reported as present, but scarce, between 1966–1973 (Balcer et al. 1987). Originally *D. mendotae* and *D. retrocurva* dominated offshore waters (Wells 1970). In the 1970s, *D. retrocurva* was more abundant than *D. mendotae* (Evans and Jude 1986). In 1981, following an alewife decline, *D. pulicaria* appeared and was abundant for 6 yr (1981–1986), after which the assemblage returned briefly to a mixture of *D. mendotae* and *D. retrocurva*. In 1986, an exotic predaceous cladoceran, *Bythotrephes cederstroemi*, colonized the lake, mediating a shift toward *D. mendotae* (Lehman and Cáceres 1993). Since 1987, *D. mendotae* has dominated cladoceran biomass, with *D. retrocurva* and *D. pulicaria* only occurring sporadically in open-water samples, although populations exist in river mouth and harbor collections (Agy 2001; Vanderploeg et al. 2002).

Sequential sediment traps, ephippial and sediment processing—Details of the Great Lakes Environmental Research Laboratory (GLERL) sequential sediment trap design and calibration are discussed in Muzzi and Eadie (2002). The trap was field tested prior to 1997 (Eadie 1997; Muzzi and Eadie

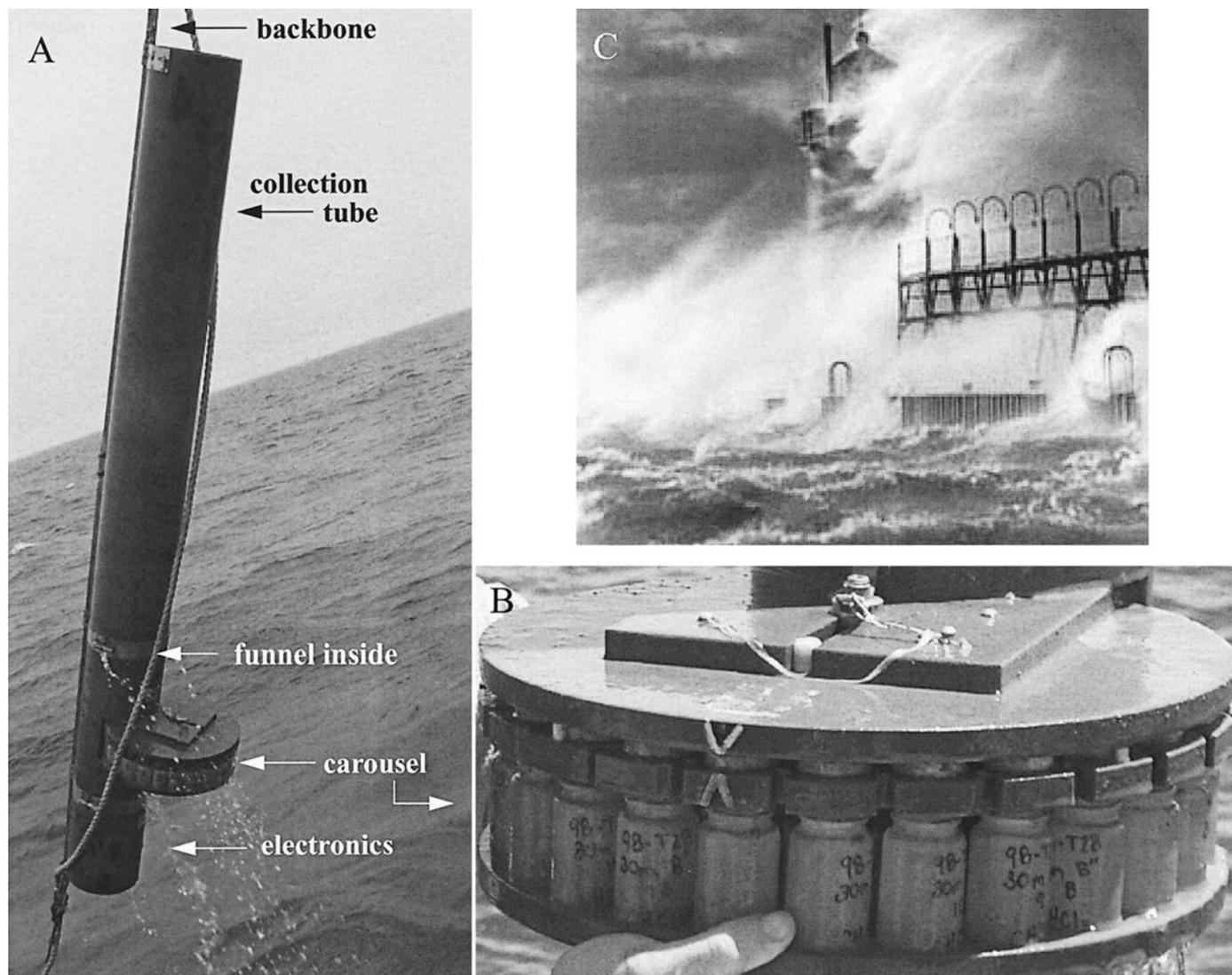


Fig. 1. Sequential sediment traps and the environment: (A) trap retrieval from Lake Michigan, noting essential components; (B) close-up of carousel, showing labeled 60-ml Nalgene collection bottles; (C) winter storm impacting harbor entry, South Haven, Michigan (courtesy Muskegon Chronicle).

2002). The trap design (Fig. 1A,B) was cylindrical with an aspect ratio (height: width) of 8: 1. It was constructed from a 160-cm length of standard 8-in. diameter PVC pipe with an inner diameter of ca. 20 cm (exact collection area = 318 cm²). A 20-cm diameter funnel (Nalgene), with 45° sloped sides and a relatively large diameter stem, was located at the bottom of the pipe. The top lip of the funnel was beveled to produce a continuous, sloping surface.

A computer-controlled carousel contained twenty-three 60-ml (Nalgene) polyethylene sample bottles that rotated under the funnel at preprogrammed intervals. An upper, circular PVC plate shielded bottles until time for exposure to the funnel. Each bottle used a nylon insert with an o-ring to seal against sediment seepage. The collection bottles were poisoned with 6 ml of chloroform (Lee 1992) and filled with distilled water immediately prior to deployment. Sampling frequency was set at 8–14 d during critical fall and winter

seasons and 30 d for stratified spring and summer seasons. Although a battery pack potentially allowed up to 2 yr of operation, in the EEGLE project we retrieved traps after 4–6 months of operation. Data were subsequently binned into 2-week intervals for the autumn ephippial production season and monthly for the spring–summer stratified season. Construction of a single trap cost ca. US \$14,000–\$17,000.

Traps were deployed at various sites (Fig. 2) as anchored arrays using subsurface buoyed 0.95-cm steel cable. In deeper waters, bottom traps were anchored 5 m above sediments, whereas top traps were tethered 30 m below the water surface. Arrays were deployed with groundlines of 180–360 m between two anchors. Retrieval was accomplished by snagging the groundlines with brass grapples, then hauling up the arrays. An acoustic release often served as a backup, if grappling was unsuccessful. During the project, retrieval of traps was nearly 100%, although data were lost from several traps

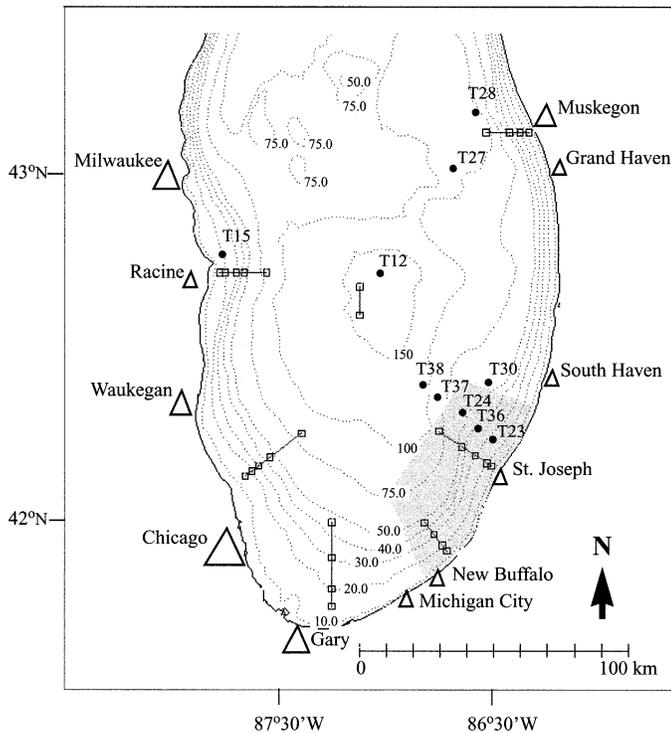


Fig. 2. Location of sequential sediment traps (black dots) and coastal and central transect stations (connected hollow squares). Transect sites are positions of zooplankton samples, ponar, and preliminary sediment core samples. Coastal transects are named for the closest large city (e.g., St. Joseph, Muskegon). Later in the study, emphasis focused on the high-sedimentation region, off St. Joseph (shaded portion). Sites of sequential sediment traps are numbered.

during 1998–1999 due to battery failure and from several coastal sites due to sediment plugging of funnel openings.

After arrival at the lab, trap samples were allowed to settle in a 4°C controlled temperature incubator for a day. The overlying water was siphoned off and the sample sieved through 350- μm Nitex netting to remove *Daphnia* ephippia. Ephippia were filtered onto small (45 mm) Whatman filter pads, placed in small (60 \times 15 mm) Petri dishes, and kept at low temperature (4–6°C) and dark conditions (no illumination) prior to laboratory enumeration and identification.

The remaining sediment was further sieved into size fractions, freeze-dried, and weighed on an analytical balance calibrated to within <1 mg. During winter, collected samples usually contained >100 mg sediment, with masses measured to a precision <1% (coefficient of variation [CV]). To check for replication, pairs of 20-cm traps were tethered at 30 m on a 100-m deep station for 10 months in 1992, using sampling intervals of 14 d. The mean mass flux ranged between 0.1 and 7.7 $\text{g m}^{-2} \text{d}^{-1}$ for the 22 sampling intervals. The 20-cm traps (8:1 aspect ratio) replicated with a mean difference between pairs of 10.5%. A second deployment in 2000 recorded sediment fluxes that varied between 4.4 and 18.5 $\text{g m}^{-2} \text{d}^{-1}$, with a mean difference between pairs of 9.5% (Muzzi and Eadie 2002). These values (9.5–10.5%) were similar to those of nonsequencing traps of comparable dimension that replicated with a mean difference between pairs

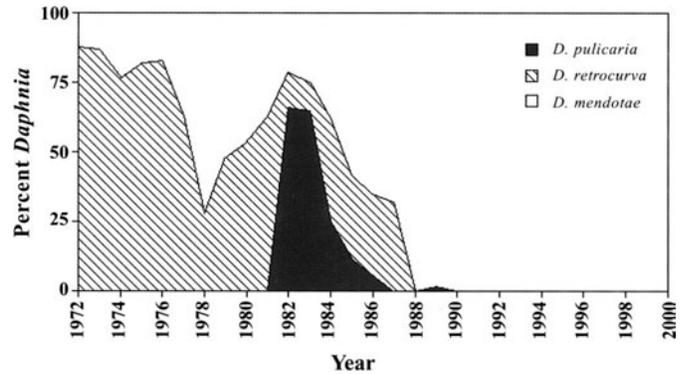


Fig. 3. Shift in *Daphnia* species abundance in southern Lake Michigan. In the 1970s and mid-1980s, *D. retrocurva* and *D. pulicaria* were abundant. Since 1987, *D. mendotae* has dominated collections. Sequence between 1972 and 1990 compiled from published studies of Evans and Jude (1986) and Lehman and Cáceres (1993). Records from 1990 to 2000 come from unpublished (1990–1996, Vanderploeg pers. comm.) and EEGLE (1997–2000) samples.

for sediment of 14% (Eadie 1997). Counts of ephippia in replicate traps at the same depth (four cases, $n = 2\text{--}3$ traps, 22 sampling intervals) gave coefficients of variation (CV) that ranged between 5.8 and 38.6, with a mean difference of 19.4%.

Gyre circulation and winter sediment plumes—Water circulation in Lake Michigan is highly episodic because it is almost entirely wind driven. Wind direction during winter is predominantly from the north to northwest, propagating two counter-rotating gyres: a counterclockwise-rotating (cyclonic, south basin) gyre to the right of the wind and a clockwise-rotating (anticyclonic, north basin) gyre to the left of the wind (Bennett 1974; Schwab et al. 2000; Beletsky and Schwab 2001). The gyres are separated by a convergence zone along the downwind shore (Grand Haven to Muskegon) with resulting offshore flow and a divergence zone along the upwind shore with onshore flow. In the late 1980s, coastal zone color scanner (CZCS) imagery revealed a 10-km wide plume of resuspended sediment that extended over 100 km along the southern shore, following the cyclonic gyre (Mortimer 1988). Since becoming routinely available in 1992, advanced very high resolution radiometer (AVHRR, NOAA TIROS-N series, NOAA-10 and NOAA-11) imagery has confirmed coastal sediment plumes every year in March–April, although the spatial extent and duration varies greatly from year to year (Chen et al. 2002; Eadie et al. 2002; Ji et al. 2002).

As a part of the EEGLE project, we processed all available AVHRR (1992–2001) and sea-viewing wide field-of-view sensor (SeaWiFS, 1997–2000) imagery on winter plume development. The latter sensor has a scan coverage of 2800 km local area (LAC), a nadir resolution of 1.1 km^2 , and is sensitive to wavelengths at 412, 443, 490, 510, 555, 670, 765, and 865 nm (Hooker et al. 1995). The first six visible channels provide R_{RS} , and the two near infrared channels (765 and 865 nm) are used to remove atmospheric contamination. The R_{RS} at 555 is used here to estimate total suspended material (TSM, McClain et al. 1998) and is applied

to help visualize the development of yearly sediment plumes after storm events. Ship-based TSM samples were collected from January to November 1998–2000 along five transects off Racine, Chicago, Gary, St. Joseph, and Muskegon, with additional data from the four offshore stations (Fig. 2). Between 1 and 3 liters of lake water were filtered (preweighed Whatmann GFF 47-mm filters). Filters were dried at 70°C for at least 24 h, then reweighed on a five-place Mettler analytical balance. This ground-truth effort provided an empirical nonlinear relationship between R_{RS} (555) and total suspended matter ($R_{RS} = 5.975 \log(\text{TSM}) + 2.005$, $r^2 = 0.891$, S.E. = 0.387, Param/S.E. = 15.4, $n = 31$) over the observed range of 1–12 mg L⁻¹. The logarithmic fit covered saturating values in the high-concentration coastal plume, while revealing patterns for low concentration levels in offshore waters.

Time series SeaWiFS imagery was processed using SeaWiFSMAP image processing software (Stumpf 2001; Warrington 2001) and a modified IDL/SeaDAS code, which includes the 1998 sensor calibration (McClain et al. 1998) and the coastal atmospheric correction scheme (Stumpf et al. 2000). We use only selected SeaWiFS images in this paper to illustrate the complex spatial development of coastal plumes and offshore incursions. Additional satellite maps from the processed AVHRR and SeaWiFS imagery are available from the authors.

For the 10 March 1998 storm event, the total mass of resuspended sediment in the southern basin was estimated through sediment mass flux into sequential and standard (8:1 aspect ratio, 20-cm aperture) sediment traps. Plume extent was determined from SeaWiFS images, then mass flux was multiplied by the areal extent of the plume (Schwab et al. 2000; Eadie et al. 2002). From the sequential sediment trap data, we determined the number of ehippia per gram of sediment, then multiplied by the estimated kilograms of resuspended sediment to estimate the number of resuspended ehippia during the plume event.

Preliminary coring established that buried egg banks were restricted to the “high-sedimentation” zones along the eastern coast. Ponar and core samples were taken at scattered locations throughout the southern basin, yet subsequent sampling focused on the high-sedimentation region between St. Joseph and New Buffalo, where coastal sequential sediment traps (T23, T24, T30, T33, T36, T37, T38) were later clustered. Since the *Daphnia* assemblages had changed over the past two decades in Lake Michigan, we took ponar samples along the St. Joseph transect to check the species composition of diapausing eggs. The eggs might be resuspended if local egg bank sediments were purged by large winter storms, such as the 10 March 1998 event. Sediments were sieved through 350- μm Nitex netting to retrieve ehippia with viable-appearing diapausing eggs. Additional sieving through 75- μm Nitex netting ensured that all ehippia were retained. The condition, color, and dimensions of ehippia were noted. Ehippia were sorted to species morphological categories, and a certain number hatched under long daylight conditions (14:10 light:dark [L:D]) to confirm species identity. Diapausing eggs from various *Daphnia* species in egg bank samples were compared with the incidence of *Daphnia* assemblages in traps (resuspended ehippia).

All statistical calculations were run on SYSTAT, version 9 (Wilkinson 1989). Differential initiation and spatial movement of traps made full scale ANOVA on count and sedimentation parameters very difficult, although we were able to examine subsets with regression, correlation, and contingency tests.

Results

Daphnia abundance—Open-water plankton samples were dominated by a single species of *Daphnia*, *D. mendotae*, that was highly seasonal in southern Lake Michigan. Individuals appeared in the water column during May–June and became abundant by July. Population abundance (individuals m⁻²) in the entire water column was highest in the deep central waters, 1–2 orders of magnitude greater than in shallow coastal waters (Table 1). Over the three seasons of sampling, deep-water abundance (entire water column) peaked at 1.0–2.4 $\times 10^5$ individuals m⁻². The population maximum usually occurred in July–September, followed by a rapid population decline from late October to December. During the decline, water temperature dropped rapidly, decreasing from 15°C to 4°C in middepth strata (Beletsky and Schwab 2001; Chen et al. 2002). Numerous dead or dying cladocerans were characteristic of zooplankton samples taken between late October and mid-November. The entire water column became isothermal by late December to early January (Chen et al. 2002). Only a few stragglers were present by early December and none by the end of December.

Daphnia mendotae exhibited a simple pattern of ehippial production. Females showed almost no sexual activity until late September to early October (Table 2), although males were recorded sporadically throughout July, August, and early September (0–7% of adults). The major pulse of ehippial production in October and November occurred during the population crash and enhanced period of sexual activity. Over the 3-yr interval in the offshore region, abundance of individuals in the water column declined from a mean of $98.5 \pm 46.5 \times 10^3$ *Daphnia* m⁻² (mean \pm 95% confidence level [CL]; $n = 9$) in September to $33.8 \pm 15.5 \times 10^3$ ($n = 18$) in October, $2.9 \pm 2.2 \times 10^3$ ($n = 7$) in November and $2.2 \pm 2.0 \times 10^2$ ($n = 5$) in December. Ehippial incidence (percentage adults) increased from 0.2% (SD = 0.5%; $n = 10$) in September to 10.3% (SD = 12.8%; $n = 15$) in October and 24.7% (SD = 27.3%; $n = 6$) in November, then declined to 14.0% (SD = 4.3%; $n = 3$) by December. Multiplying abundance times ehippial incidence in the entire population (including juveniles) produced a peak ehippial concentration in the water column during October (3,046 ehippia m⁻²) and November (674 ehippia m⁻²) with much lower values in September (140 ehippia m⁻²) and December (31 ehippia m⁻²). Using the Edmondson–Paloheimo technique for estimating production of ehippia in offshore waters gave an expected flux of 17.2×10^3 ehippia m⁻² yr⁻¹. The incidence of males increased to 11–36% of the adult population by late October. Sexual females and males dominated during the decline from late October to mid-November. By November to December, males often made up 57–94% of the remaining adult population.

Table 1. *Daphnia mendotae* abundance (10^3 individuals m^{-2}) along the St. Joseph (15, 45, 80 m water column depth) and Muskegon (15, 45, 110 m water column depth) transects in southern Lake Michigan. Mean and standard error (parentheses) given for replicate samples ($n = 2-4$) at the various stations. Dates for the St. Joseph transect are along the left-hand margin, whereas dates for the Muskegon transect are along the right-hand margin.

Date	J15	J45	J80	M15	M45	M110	Date
3 Feb 98	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 Feb 98
16 Mar 98	0 (0)	0 (0)	0 (0)	0 (0)		0 (0)	19 Mar 98
22 May 98	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	22 May 98
7 Jul 98	ns	ns	ns	ns	89.2 (5.1)	52.2 (6.4)	7 Jul 98
19 Aug 98	ns	ns	ns	6.7	38.2 (0.8)	21.3 (23.3)	19 Aug 98
23 Sep 98	2.0 (0.5)	45.9 (4.2)	124.8 (12.7)	ns	63.3 (16.1)	216.6 (2.6)	14 Sep 98
28 Oct 98	0 (0)	2.5 (0.4)	60.2 (11.1)	ns	31.6 (9.1)	31.8 (4.0)	19 Oct 98
21 Nov 98	0.3 (0.2)	0 (0)	ns	ns	0 (0)	3.0 (2.5)	17 Nov 98
1 Dec 98	ns	ns	ns	ns	0 (0)	0 (0)	8 Dec 98
18 Feb 99	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	18 Feb 99
8 Apr 99	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	8 Apr 99
27 Apr 99	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	27 Apr 99
5 Jun 99	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 Jun 99
29 Jul 99	0	207.6 (27.8)	243.3	1.4 (1.9)	8.0 (0.3)	50.3 (20.7)	30 Jul 99
11 Sep 99	0.3 (0.07)	20.9 (5.2)	89.3 (16.0)	1.5 (0.5)	76.7 (10.4)	126.1 (21.7)	12 Sep 99
20 Oct 99	0 (0)	1.8 (0.9)	48.4 (17.8)	0 (0)	3.4 (2.5)	ns	20 Oct 99
14 Dec 99	0 (0)	0 (0)	ns	0 (0)	0.6 (0.7)	0 (0)	13 Dec 99
21 Feb 00	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	23 Feb 00
11 Mar 00	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	15 Mar 00
11 Apr 00	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5 Apr 00
16 May 00	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	15 May 00
7 Jun 00	0 (0)	0 (0)	1.3 (0.6)	0 (0)	0 (0)	2.7 (0.1)	7 Jun 00
10 Jul 00	0 (0)	3.8	12.7 (2.5)	5.4 (0.7)	201.3 (43.3)	101.0 (18.7)	20 Jul 00
10 Aug 00	0 (0)	4.3 (0.2)	1.9 (0.6)	0 (0)	7.5 (0.6)	16.1	9 Aug 00
21 Aug 00	ns	ns	ns	1.4 (0.3)	15.8 (5.2)	75.2 (19.1)	21 Aug 00
8 Sep 00	0.40 (0.02)	16.6 (1.3)	25.2 (0.3)	1.1	15.3 (6.4)	25.5	9 Sep 00
21 Sep 00	ns	ns	ns	0.5 (0.1)	28.7 (7.0)	68.1 (13.5)	21 Sep 00
5 Oct 00	ns	ns	ns	0 (0)	15.9 (7.0)	57.8 (10.2)	5 Oct 00
23 Oct 00	ns	ns	ns	0 (0)	22.9 (3.8)	89.8 (1.9)	23 Oct 00
5 Nov 00	0 (0)	0 (0)	8.6 (3.4)	0 (0)	0.8 (0.9)	39.2 (13.9)	6 Nov 00

The previous dominants (*D. retrocurva* and *D. pulicaria*) occurred only sporadically in water samples. To place their relative abundance into perspective, during the first processing of pelagic zooplankton samples, 6517 *D. mendotae* were counted, but only 22 *D. retrocurva* and 15 *D. pulicaria*. Records of *D. retrocurva* came mainly from the Saint Joseph and Muskegon transects (five individuals, 23 September 1998 J10 0–8 m; 4, 23 September 1998 J80 0–83 m; 2, 10 August 2000 J45 0–40 m; 2, 8 July 1998 G90 0–100 m; 1, 30 July 1999 M15 0–13 m; 1, 7 June 2000 M15 0–13 m; 1, 9 September 2000 M15 0–13 m; 1, 20 July 2000 M15 0–15 m; 1, 20 July 2000 M15 0–15 m; 2, 21 August 2000 M15 0–15 m; 3, 21 August 2000 M15 0–15 m). The same was true for *D. pulicaria* (one individual, 23 September 1998 J10 0–8 m; 1, 23 September 1998 J80 0–83 m; 1, 5 June 1999 J45 0–43 m; 1, 5 June 1999 J80 0–77 m; 3, 17 May 2000 J80 0–77 m; 1, 7 June 2000 J45 0–43 m; 1, 10 August 2000 J45 0–40 m; 2, 22 May 1998 M15 0–15 m; 1, 25 June 1998 M45 0–35 m; 2, 17 July 1998 M45 0–40 m; 1, 4 June 1999 M15 0–14 m). The occasional Muskegon transect records were not surprising, since both species (*D. retrocurva* and *D. pulicaria*) occur in Lake Muskegon, which discharges into coastal waters off Muskegon. More discussion of harbor and river incidence is found in Agy (2001).

Ephippial production—During 4 yr of continuous monitoring, incidental capture of ephippia was very low during summer stratified periods (June–August), when young were produced almost exclusively by parthenogenesis. All recorded summer and fall *Daphnia* ephippia were from *D. mendotae*, with none from any other *Daphnia* species. Total ephippia captured in sequential sediment traps during 3 yr of stratified spring–summer conditions were June (4), July (20), August (23), and September (39). These represent very low total numbers compared to the October–November period of ephippial production.

At deep-water sequential sediment trap sites (T12, T27, T28), yearly production of *D. mendotae* ephippia came as a distinct, late-season pulse, coinciding with population decline (Fig. 4). The abundance of *Daphnia* (central south basin site, T12) was inserted above ephippial histograms on Fig. 4 as a spindle diagram to illustrate the timing of population decline relative to ephippial deposition. In the spindle diagram, width is proportional to pelagic *Daphnia* abundance, with the abundance graphed on a log scale (0–100,000 individuals m^{-2}). Based on trap records, the timing and duration of peak ephippial production was similar throughout the three seasons of trap deployment. Ephippial production began in late September to early October, reached

Table 2. Frequency of males and ephippial females in samples of *Daphnia mendotae*, taken from deep-water stations, southern Lake Michigan (M, Muskegon transect; J, St. Joseph; G, Grand Haven; D, central, deep water). Samples arranged by date of the year, with total individuals (n) counted, and frequency of mature males and ephippial females. Smaller mesh net samples (64 μm) marked by an asterisk.

Station	Date	n	Percent males	Percent ephippial females
M110	14 Sep 98	286	3.1	0.0
J80	23 Sep 98	268	1.1	0.0
M110	22 Oct 98	139	27.3	0.7
J80	28 Oct 98	251	33.5	4.0
J80	28 Oct 98	286	36.4	2.1
J80	28 Oct 98*	230	23.5	2.6
J80	28 Oct 98*	234	32.9	3.4
M110	29 Oct 98	550	11.1	7.5
G90	30 Oct 98	390	7.2	1.5
G90	30 Oct 98	481	6.9	6.2
M110	17 Nov 98	287	17.1	62.0
M110	17 Nov 98	123	26.0	55.3
M110	18 Nov 98	14	71.4	21.4
M110	8 Dec 98	28	85.7	10.7
M110	8 Dec 98	48	70.8	12.5
M110	14 Dec 98	4	100.0	0.0
J80	29 Jul 99	245	0.8	0.0
J80	11 Sep 99	213	0.0	0.0
J80	11 Sep 99	261	0.0	0.0
J80	11 Sep 99	226	1.3	0.0
J80	19 Oct 99	148	16.2	10.8
J80	19 Oct 99	147	26.5	14.3
J80	19 Oct 99*	41	14.6	12.2
J80	19 Oct 99*	25	16.0	8.0
M110	13 Dec 99	7	57.1	14.3
M110	13 Dec 99	5	60.0	40.0
M110	7 Jun 00	9	0.0	0.0
M110	9 Jul 00	101	0.0	0.0
M110	9 Jul 00	151	0.0	0.0
M110	20 Jul 00	170	0.6	0.0
M110	9 Aug 00*	52	0.0	0.0
M110	21 Aug 00	101	1.0	0.0
M110	21 Aug 00	191	0.5	0.0
D150	8 Sep 00	222	7.2	0.0
M110	9 Sep 00*	43	0.0	0.0
M110	9 Sep 00	125	1.6	0.0
M110	21 Sep 00	141	3.5	0.0
M110	21 Sep 00	118	2.5	1.7
M110	5 Oct 00	162	1.9	1.9
M110	23 Oct 00	222	25.7	45.9
M110	23 Oct 00	248	30.2	33.1
J80	5 Nov 00	51	84.3	2.0
J80	5 Nov 00	50	94.0	2.0
J80	5 Nov 00*	8	94.4	5.6

a peak between late October and early November, then tailed off through November to December. Mean numbers for deep-water traps were always large, although totals for individual trap sites could vary (e.g., the T12, 30 m trap catch in 1999–2000 was very high). The mean number of diapausing eggs/ephippium from deep-water and coastal loca-

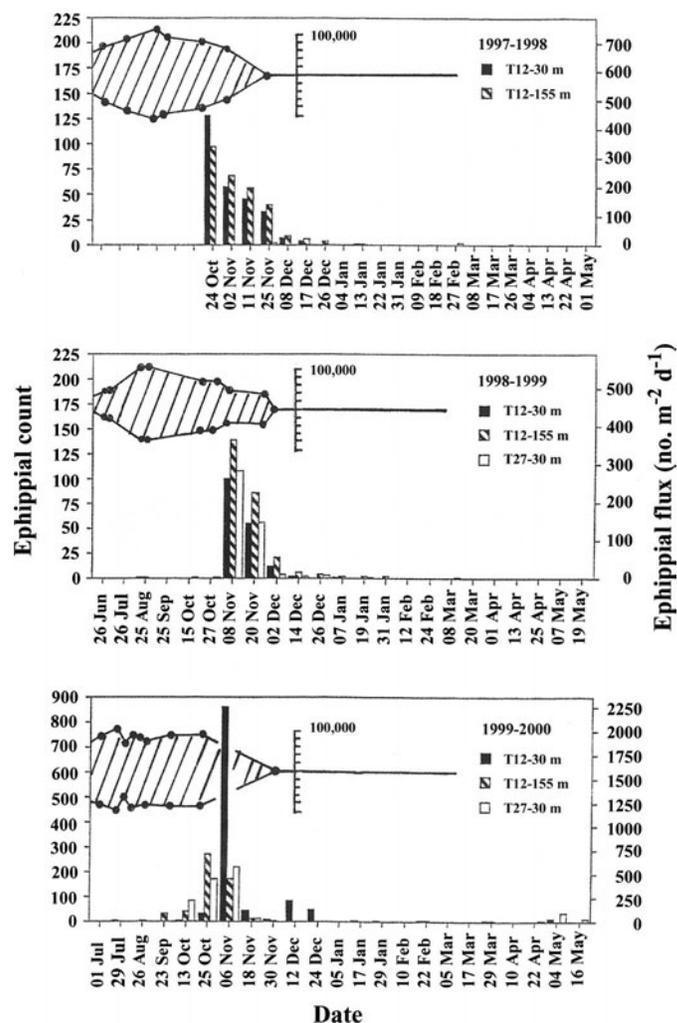


Fig. 4. Production of ephippia relative to autumn population collapse. Ephippial count and flux presented for various deep-water sediment traps as histograms. *Daphnia* abundance in the water column (central south basin site) given as spindle diagrams, where width of spindle is proportional to abundance (number m^{-2}) on a log scale (symmetrical about axis, 0 at axis to 10^5 outer value).

tions was similar (ca. 1.6) over the three seasons of collection (Table 3).

During the deep-water production period, mean accumulation of ephippia in shallow-tethered traps was very similar to totals from deeper tethered traps (mean \pm 95% CL = 30 m, 624 ± 419 ephippia; 100–200 m, 599 ± 417 ephippia). This observation suggests considerable dispersal throughout the water column via turbulence at peak release times (late October–November).

Out-of-season ephippial capture during winter was low at deep-water stations. In a supplemental follow-up deployment during 2000–2001, some sites contained traps tethered at three depth levels, providing more detailed depth comparisons. Moreover, arrays were suspended at a northern basin site (T29) for comparison with sites in the southern basin. Table 4 records the time sequence for ephippial captures at various depths in the north basin arrays (T29) compared with central south basin (T12) and Grand Haven (T27) arrays.

Table 3. Incidence of diapausing eggs in selected ephippial samples. All *Daphnia* ephippia in production and resuspension assemblages came from *D. mendotae*. Mean and standard deviation (parentheses) given for production and resuspension averages.

Trap date	Depth (m)	Ephippia	Eggs	Eggs per ephippia
Production				
97 T12	30	282	508	1.80
98 T12	30	123	183	1.49
98 T12	155	338	512	1.51
98 T27	30	602	848	1.41
98 T28	30	147	223	1.51
99 T12	30	1053	1894	1.80
99 T27	30	644	1090	1.69
99 T28	30	713	1173	1.65
00 T12	30	2036	3674	1.80
00 T12	100	1102	1984	1.80
00 T27	30	237	358	1.51
00 T27	95	598	1027	1.72
Mean				1.65 (0.15)
Resuspension				
99 T24	30	53	80	1.51
99 T27	30	52	90	1.73
99 T33	30	17	26	1.53
99 T37	71	29	52	1.79
99 T38	95	35	60	1.71
Mean				1.65 (0.13)

Ephippial tallies for the northern basin (T29) corresponded closely in timing and numbers with southern sites (T12, T27), although in this comparison deep-tethered traps seemed to have higher tallies during the trapping interval. At deep-water sites over the regular three-season period, with only one exception (T12, 30 m vs. T12, 155 m 1999–

2000, $r^2 = 0.002$), time-sequence tallies for traps on the same tether line were highly correlated (r^2 range 0.307–0.943, mean = 0.764, $n = 23$ time intervals), and only slightly higher than the correlation between traps at different locations (r^2 range 0.192–0.971, mean = 0.641, again $n = 23$ time intervals). That is, the correspondence of tallies through time was quite good for offshore traps tethered at different depths. However, total accumulation at offshore (>100 m water column) sites was much higher ($3.8\text{--}63.9 \times 10^3 \text{ m}^{-2} \text{ yr}^{-1}$; mean \pm 95% CL = $18.5 \pm 7.8 \times 10^3 \text{ m}^{-2} \text{ yr}^{-1}$) than at coastal sites (<76 m depth; range $0.3\text{--}4.1 \times 10^3 \text{ m}^{-2} \text{ yr}^{-1}$; mean = $1.3 \pm 0.7 \times 10^3 \text{ m}^{-2} \text{ yr}^{-1}$). The observed flux in offshore traps ($18.5 \pm 7.8 \times 10^3$ ephippia $\text{m}^{-2} \text{ yr}^{-1}$) corresponded well with the expected flux from the Edmondson–Paloheimo technique (17.1×10^3 ephippia $\text{m}^{-2} \text{ yr}^{-1}$).

Over the entire southern basin, there was a positive, non-linear relationship between water column depth and total ephippial production, which is, the deeper the water column the more ephippial production. Logarithmic transformation equalized variance (Fig. 5, Table 5) and produced a highly significant linear regression ($\log \text{ prod} = 0.014 \text{ depth} + 0.2.164$, $r^2 = 0.593$, $p < 0.01$). The general pattern with water column depth reflected the greater total abundance of *Daphnia* in deeper waters at the time of ephippial production. Using the ephippial production versus depth relationship, we integrated production over depth contours for the Lake Michigan region south of Muskegon. The mean number of ephippia produced per year in the southern basin was about 7.2×10^{13} ($\times 1.65 = 1.2 \times 10^{14}$ diapausing eggs), an enormous number.

During the project, we uncovered another feature that contributes to dispersal of ephippia. Ephippial dimensions for *D. mendotae* were 1.07 (length) \times 0.77 (height) \times 0.47

Table 4. Comparison of north and south basin deepwater traps. Tallies record ephippia deposited in sequential sediment traps (all *D. mendotae*). Trap 29–100 did not function after 2 Dec 01. The dates (date in) record when the collection bottle rotated into position.

Date in	South basin T12			South basin T27			North basin T29		
	100 m	155 m	30 m	100 m	155 m	30 m	100 m	200 m	
1 Jul 00	2	0	1	2	0	2	0	0	
15 Jul 00	0	0	0	0	0	1	0	0	
29 Jul 00	0	0	0	0	0	0	1	0	
12 Aug 00	1	0	1	0	0	2	2	1	
26 Aug 00	0	1	0	0	0	3	1	3	
9 Sep 00	1	1	0	0	2	1	2	3	
23 Sep 00	0	0	1	0	2	2	1	0	
7 Oct 00	19	4	53	88	58	3	41	30	
21 Oct 00	312	247	117	508	244	14	233	203	
4 Nov 00	827	273	28	156	210	37	275	89	
18 Nov 00	79	69	51	80	51	20	14	10	
2 Dec 00	6	2	8	4	7	3	—	3	
16 Dec 00	1	2	1	12	15	4	—	0	
30 Dec 00	0	1	1	0	2	4	—	0	
13 Jan 01	1	0	0	12	3	7	—	1	
27 Jan 01	1	0	0	0	2	1	—	0	
10 Feb 01	0	0	0	0	2	2	—	0	
24 Feb 01	0	3	0	4	7	0	—	0	

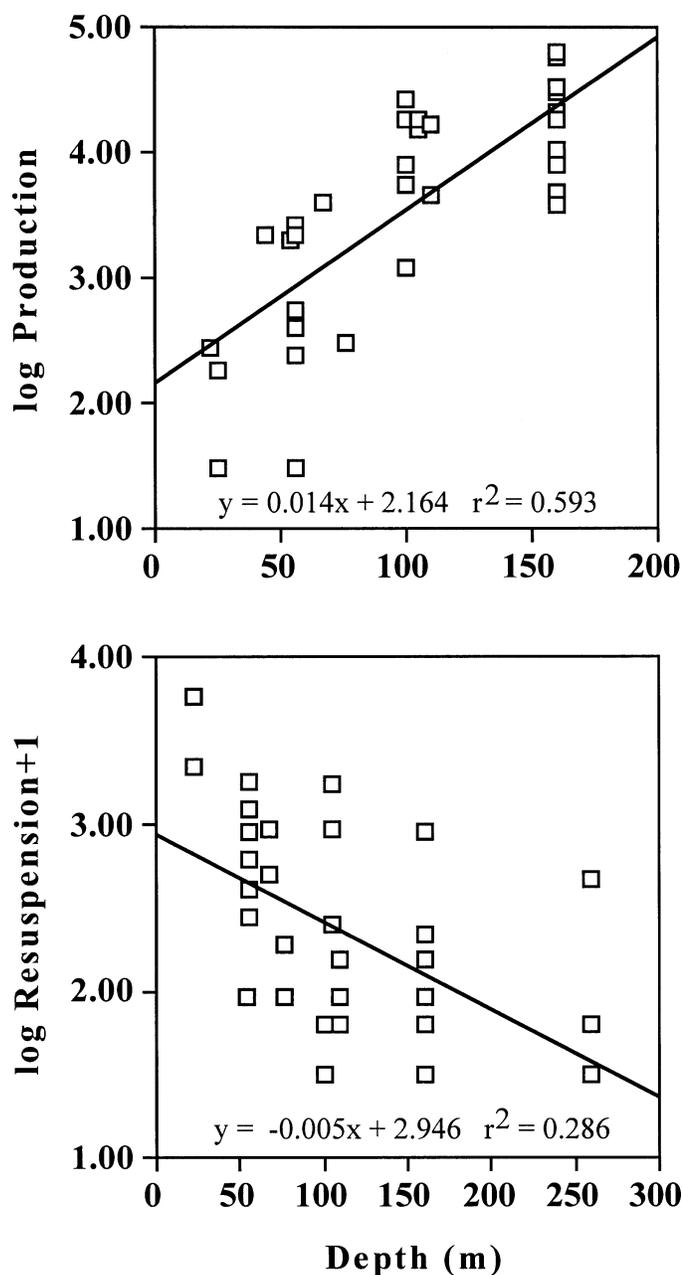


Fig. 5. Depth relationships of ephippial production and resuspension. Depth is water column depth in meters at the trap site. Regressions are fit to log transformed ephippial production (in season) and resuspension (out of season) totals. Log transformation helps to equalize residual variance and fit with a linear regression. Parameters of log regressions are given in Table 5. Note the y-axis scale difference in both plots, as production totals greatly exceed resuspension totals. The production regression is used to estimate total ephippial production for the entire southern basin of Lake Michigan. Each symbol represents the seasonal total of ephippia in a single trap. Points come from all 4 yr and various tethered depths.

(width) mm. Under quiet laboratory conditions, ephippia settled with a mean speed of 3.0 ± 0.2 mm s⁻¹ (mean \pm 95% CL; $n = 72$), slightly faster than the smaller ephippia of *D. retrocurva* (2.6 ± 0.2 mm s⁻¹, $n = 30$). These are relatively

large values for suspended particles, since under quiet-water conditions both types of ephippia would reach the bottom of southern Lake Michigan in 1 d ($259\text{--}225$ m d⁻¹). However, offshore environments are rarely quiet waters in late October to November. During production, a few ephippia circulated into the bubble zone near the water surface and were captured by surface film and drifting scum. Field samples of Langmuir foam lines revealed modest numbers of ephippia (5–100 per 20 m tow), although we were unable to estimate total surface transport because the incidence of Langmuir spirals through time was irregular and the patterns too small to be picked up by our remote sensing techniques. Foam samples were taken (1) by plankton net tows from ship casts and (2) along the shoreline, off jetties and beaches. When 243 ephippia from foam samples were cleared of externally attached bubbles and immersed in water, most ($n = 231$, 95.1%) sank, i.e., were negatively buoyant particles. This simple observation demonstrated that the vast majority of surface-transported ephippia would sink if not suspended by surface film or foam bubbles. Yet a few ephippia ($n = 12$, 4.9%) with small internal gas or lipid vacuoles would float as positively buoyant particles. The potential importance of foam transport is that surface dispersal provides a vector more sensitive to wind direction and with interesting ecological ramifications. Foam could adhere to bird's feathers, or transport ephippia onto beaches, along strand lines. The total number of ephippia transferred into the littoral zone by surface rafting was probably not large relative to settlement in deep waters, since coastal traps did not record large tallies (Fig. 5). Contrasting with some genera of cladocerans that drop transparent ephippia (*Bosmina*, *Eubosmina*) or individual eggs (*Holopedium*), surface transport of *D. mendotae* ephippia is a potential option, since a patch of melanin is placed over the eggs, affording protection against UV exposure.

Resuspension of sediment in offshore regions—Did resuspension of sediment contribute to the ephippia found in autumn traps? One way to check for an influence of resuspension is to compare the amount of sediment coming into shallow-tethered traps with the observed patterns of ephippial flux. Figure 6 compares the mass flux of sediment and ephippia into 30-m tethered open-water traps (T12, T27). The peak in ephippial production came well before isothermal conditions and before resuspended sediments began to accumulate in traps. Fine sediments (resuspended) settled into traps in early January, after the onset of isothermal conditions (see thermal modeling and records in Beletsky and Schwab 2001; Chen et al. 2002).

Thus ephippial production came as a pulse during population decline in late October to early November, coincident with thermocline descent but preceding isothermal conditions. In offshore waters during winter, sediment mass flux ranged between 1 and 20 g m⁻² d⁻¹, peaking during isothermal intervals in January and March–April (Fig. 6). Sediment flux was highly correlated among offshore shallow-tethered traps (e.g., T12, 30 m vs. T27, 30 m; $r = 0.74$; $p < 0.001$; $n = 68$). In these traps, there was also a weak, inverse correlation between ephippial flux and sediment flux (e.g., T12, 30 m 1997–1998, -0.305 ; 1998–1999, -0.220 ;

Table 5. Regressions for ephippial production and resuspension versus water column depth. Values are in season and out-of-season ephippial accumulations for individual traps, log transformed for production and log ($n + 1$) transformed for resuspension.

Effect	Coefficient	SE	t	p (two tail)	Source	Sum of squares	df	Mean square	F ratio	p
Production ($n = 34, r^2 = 0.593$)										
Constant	2.164	0.224	9.64	0.000	Regression	14.9	1	14.9	46.6	0.000
Depth	0.014	0.002	6.82	0.000	Residual	10.2	32	0.3		
Resuspension ($n = 34, r^2 = 0.286$)										
Constant	2.946	0.188	15.685	0.000	Regression	3.7	1	3.7	12.8	0.001
Depth	-0.005	0.001	-3.578	0.001	Residual	9.2	32	0.3		

1999–2000, 0.110; T27, 30 m 1998–1999, -0.127; 1999–2000, -0.200; $n = 22-23$; $p > 0.05$ for individual traps, but $p < 0.05$ for the combined set, $n = 114$). Although this relationship seems intriguing, cause and effect is probably spurious. The amount of suspended sediment in the water column during late September, October, and early November is low because whiting (CaCO_3) precipitation in July and August removes suspended particles from epilimnetic waters (Robbins and Eadie 1991).

Sediment flux into offshore traps during winter (January–April) was less in shallow-tethered traps compared with deep-tethered traps. For example, the mean \pm 95% CL for the 1997 T12, 30 m trap was $1.5 \pm 0.8 \text{ g m}^{-2} \text{ d}^{-1}$, whereas that for the 1997 T12, 155 m trap was $9.3 \pm 3.8 \text{ g m}^{-2} \text{ d}^{-1}$. Likewise, mean sediment flux for the 1999 T38, 30 m trap was $2.0 \pm 0.9 \text{ g m}^{-2} \text{ d}^{-1}$, whereas that for the 1999 T38, 95 m trap was $15.8 \pm 8.2 \text{ g m}^{-2} \text{ d}^{-1}$. The correlation of mass flux was lower between top and bottom traps (e.g., T12, 30 m vs. T12, 155 m; $r = 0.57$; $p < 0.001$; $n = 83$) than among top traps. Greater sedimentation of TSM into deep traps and greater heterogeneity of deep traps between sites is a well-known consequence of the deep nepheloid layer (Eadie et

al. 1984; Robbins and Eadie 1991; Eadie 1997). However, we must stress that resuspension of ephippia was quite low in offshore traps. Apparently ephippia are behaving as large particles that are difficult to resuspend in a deep water column. Out-of-season incidence of total ephippia was greatest in January and April: during three seasons, 36 ephippia settled in January (24.5%), 19 in February (12.9%), 34 in March (23.1%), and 58 in April (39.5% of winter total).

Resuspension of ephippia along coastal margins—In general, ephippial resuspension exhibited a distinctly different spatial and temporal pattern than ephippial production. Resuspension was noted when ephippia settled into traps between January and May, after the November–December population crash. Most resuspended ephippia were clean and with eggs, suggesting that they were from the previous fall’s ephippial production, i.e., freshly deposited ephippia lying in the benthic nepheloid layer or sitting on the sediment–water interface at shallow depths prior to resuspension. Deeply buried ephippia resuspended from consolidated sediments could be distinguished because their ephippial surfaces appeared discolored (coated with surface bacteria and sediment), and co-occurred with benthic microfossils (planarian, oligochaete egg cases; benthic diatoms) characteristic of bottom sediments. From a practical standpoint, purging of the egg bank took place with accompanying telltale clues.

In deep waters, resuspension of sediments during winter generally came during isothermal periods, between January and April, although peaks were year-specific and subject to storm conditions. Long-term (1961–1998) records from St. Joseph and Chicago water treatment plant coastal intakes documented two peaks of maximum seasonal turbidity in southern Lake Michigan, one in mid-December to mid-January and another in March to April (Eadie et al. 2002).

Out-of-season accumulation (resuspension) of ephippia in the southern basin was inversely related to water column depth and highly variable from year to year (Fig. 5). The variability had both temporal and especially spatial components. Contrasting with deep-water trap patterns, which normally had low out-of-season ephippial accumulation (Fig. 4), winter resuspension was pronounced along coastal margins (trap locations T15, T20, T23, T24, T30, T33, T36, Fig. 2) that coincided with development of coastline sediment plumes. Sediment flux into coastal traps was related to storm events and could reach values as high as $800 \text{ g m}^{-2} \text{ d}^{-1}$, 20–40 times maximum offshore sediment flux values.

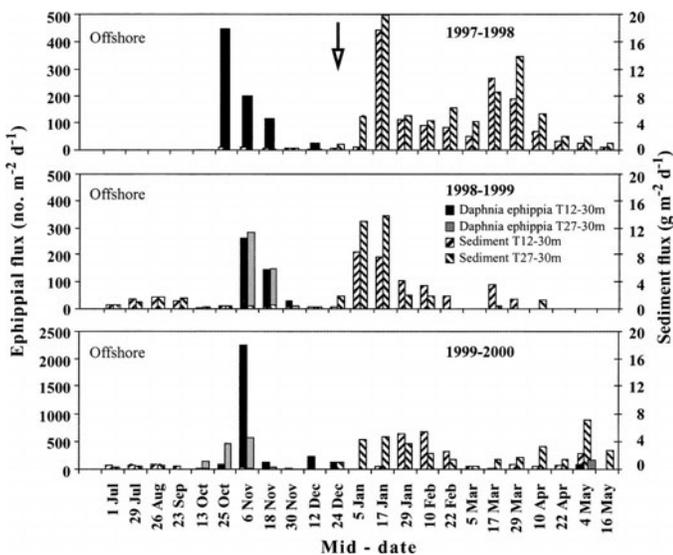


Fig. 6. Seasonal ephippial and sediment flux into offshore sediment traps. Shaded histograms record ephippial flux, whereas crosshatched histograms record sediment flux. Superimposed arrow marks the onset of isothermal conditions in the water column.

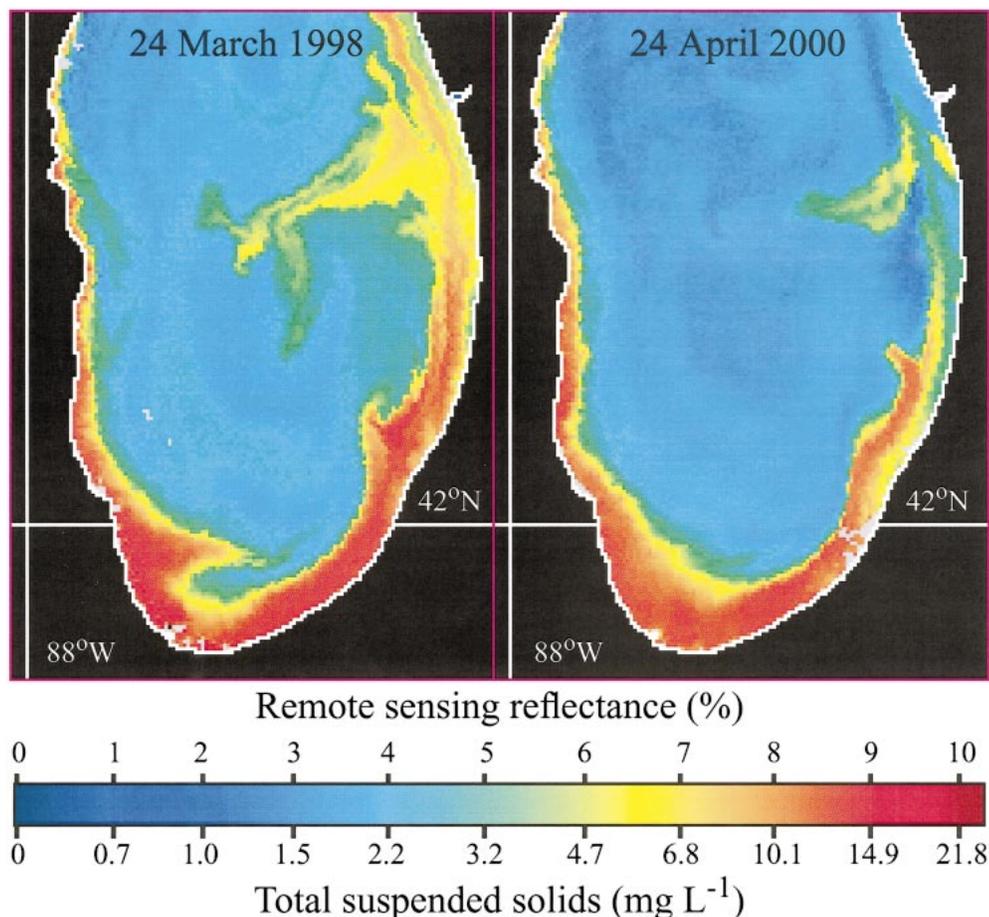


Fig. 7. Heterogeneous spatial distribution of resuspended sediment during the plume season (March–April). Prevailing gyre rotation after winter storms (north–northwest wind) is counterclockwise in southern Lake Michigan. The southern coastal plume contains $>10 \text{ mg L}^{-1}$ TSM and expands up the eastern coastline, depositing sediment into high-sedimentation zones off St. Joseph, Grand Haven, and Muskegon. During severe storms, plume sediments are captured in the two-gyre convergence zone near Grand Haven–Muskegon and moved offshore.

The importance of winter storms is acknowledged in the literature. Some consider that large storms, despite their infrequent occurrence, are responsible for much, probably most, of the sediment transport in large lakes (Hermanson and Christensen 1991; Lick et al. 1994). Resuspension is related to the forcing of currents and wave action by wind speed and to the frequency of large storms, since resuspension of bottom sediments is a very nonlinear function of wind speed. Shear stress at the sediment–water interface due to currents and wave action is approximately proportional to the square of the magnitude of the currents and wave action, whereas the mass of sediment resuspended per unit surface area is approximately proportional to the cube of the shear stress. Hence the amount of sediment resuspended for a particular wind speed is approximately proportional to the sixth power of the wind speed ($\varepsilon \propto U^6$; Lick et al. 1994). The nonlinear scaling can be appreciated when we consider that if the wind is doubled, the amount of sediment resuspended is increased by a factor of 64, whereas if the wind is increased fourfold, the amount of sediment resuspended increases 4096-fold. In practice, the exact amount of resus-

pended sediment will be subject to geomorphic complexities of individual basins, the details of gyre circulation patterns, bottom surface roughness characteristics, and the cohesive nature of sediments (MacIntyre et al. 1990). In the EEGLE project, there was direct monitoring of wind and current speed, wave action, resuspended sediments, and shear stress at several locations during winter storm events.

The observed pattern of sediment resuspension was spatially heterogeneous. Prevailing winter winds (northerly to westerly) set up a dual-gyre circulation pattern, a counterclockwise gyre in the southern basin and a clockwise gyre in the northern basin. Fine sediments tended to be moved off the western and southern portions of the basin and deposited along the eastern shoreline. Each year, storm energy was sufficient to create a lengthy coastal sediment plume from Racine, Wisconsin, to St. Joseph, Michigan, that generally appeared in March and disappeared by late April (Figs. 2, 7). In Fig. 7, note that the logarithmic scale emphasizes the extremely high TSM concentrations for the southern coastal plume, while revealing very slight differences in TSM during dilute offshore incursions.

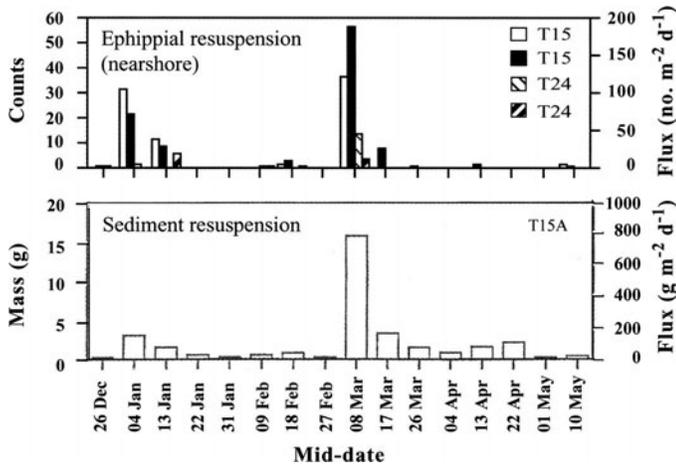


Fig. 8. Resuspension of ephippia and sediment during the winter of 1997–1998, illustrating the impact of the 10 March 1998 storm. Nearshore traps T15 and T24 were at water depths of 22 and 56 m, respectively, within the coastal sediment plume. Dates mark the middle date of deployment intervals.

During the three-season field study, the 8–10 March 1998 storm event was one of the largest on record, a one in 12-yr meteorological event (Schwab et al. 2000). Several days of intense storms produced 17 m s^{-1} southward winds and generated waves over 5 m high. Alongshore current speeds, which typically averaged $2\text{--}3 \text{ cm s}^{-1}$, surged above $20\text{--}30 \text{ cm s}^{-1}$, as wind/current action created $10\text{--}30 \text{ mg L}^{-1}$ TSM (Rao et al. 2002). The initial plume appeared on 9 March 1998. Resuspension increased again on 18 March during a sustained southward wind of 10 m s^{-1} and persisted for almost 2 months, disappearing in late April. The well-developed coastal plume extended over 300 km from Milwaukee, Wisconsin, to Muskegon, Michigan (Figs. 2, 7). Examples of ephippial and sediment deposition patterns from 1997–1998 coastal traps (T15, T24) at plume locations are illustrated in Fig. 8. In contrast to open-water traps, the pattern for out-of-season deposition of ephippia in coastal traps was strongly correlated with episodes of sediment resuspension and deposition (e.g., T15, 1997–1998 season, $n = 23$, $r = 0.958$, $p \ll 0.01$, ephippia vs. g sediment). During the March event, the estimated total resuspended sediment mass was $7.53 \times 10^9 \text{ kg}$ (sediment trap data; Schwab et al. 2000; Eadie et al. 2002). With the ratio of ephippia to grams of sediment captured in traps at that time ($Y = 0.252X + 0.349$, $r^2 = 0.918$, $p \ll 0.01$), this event resuspended an estimated 1.9×10^{12} ephippia, i.e., 1.9 trillion ephippia. Given the frequency of diapausing eggs in winter ephippial collections, the event resuspended 3.1 trillion diapausing eggs. However, over the long run (1997–2000), yearly ephippial resuspension averaged only $4.4 \pm 2.2 \times 10^2$ (mean \pm 95% CL) ephippia $\text{m}^{-2} \text{ yr}^{-1}$, much lower (2–4%) than yearly production.

Under prevailing north to northwest winds, sediments resuspended from wave action would rotate counterclockwise around the southern basin with the plume moving offshore near St. Joseph, largely a consequence of shoreline irregularities (Fig. 7). As the resuspended sediment and ephippial

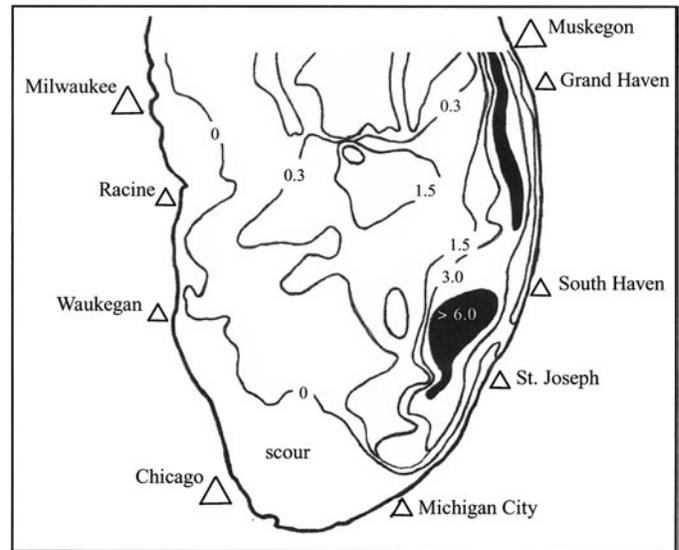


Fig. 9. Deposition of postglacial sediments in southern Lake Michigan (after Foster and Colman 1992). Contours represent thickness of postglacial sediments in meters. Western portions of the basin are scour surfaces, whereas the eastern high-sedimentation regions are shown in solid black.

mixture from the high-energy coastal zone settled, it helped to bury ephippia into the sediment. This same process was repeated at other locations along the eastern coast. Thus winter storms had an important routine consequence of ensuring egg bank formation in the high-sedimentation zones, a narrow band of troughs that lies along the eastern coastline (Fig. 9; after Foster and Colman 1992). The high-sedimentation region corresponded to less than 10% of the bottom surface area of southern Lake Michigan.

When winter storms were very intense, a second episodic process could be distinguished (Fig. 7). The two rotating gyres set up a convergence zone along the downwind shore that drew material offshore. The large 10 March 1998 storm created greater wave action and stronger counterclockwise alongshore currents. The combination of wave action and currents encouraged plume development well past St. Joseph up to Muskegon, where the coastal plume was captured in the convergence zone of the two-gyre system and drawn far offshore. Plume advection into the southern gyre created a spectacular swirling eddy on 12–20 March 2000, whereas a smaller storm in April of 2000 (24 April 2000 image) produced a less pronounced incursion (Fig. 7). Deployed arrays (acoustic Doppler current profilers [ADCP], smart acoustic current meters [SACM], vector-averaging current meters [VACM], Argonne National Laboratory [ANL] tripod) along the eastern coastline documented that during incursions alongshore currents increased from a mean of $2\text{--}3 \text{ cm s}^{-1}$ to over 20 cm s^{-1} , whereas cross-shore currents increased to 4 cm s^{-1} (Murthy et al. 2002). At South Haven, when current speed was over 30 cm s^{-1} and TSM over 10 mg L^{-1} , wave-current shear stress was over 6 dynes cm^{-2} . Above 20 cm s^{-1} , TSM would start to resuspend (Lesht and Hawley 2001).

However, relatively few ephippia were deposited in open-water traps T27 and T12 following these events, as the trans-

Table 6. *Daphnia* diapausing egg assemblages in sediment egg bank compared with out-of-season captures in sequential sediment traps. Egg bank incidence is based on ponar samples from high sedimentation site (J45, St. Joseph transect, eastern trough). Resuspension totals are significantly different from egg bank values (4×3 contingency test, $df = 6$, $\chi^2 = 96.7$, $p \ll 0.01$).

Total	<i>D. mendotae</i>	<i>D. retrocurva</i>	<i>D. pulicaria</i>
Egg bank			
1102	1013 (91.9%)	84 (7.6%)	5 (0.5%)
1725	1634 (94.7%)	83 (4.8%)	8 (0.5%)
561	532 (94.8%)	20 (3.6%)	9 (1.6%)
Resuspension			
1023	1022 (100%)	1 (0%)	0 (0%)

ported sediment consisted mainly of very fine material (Figs. 4, 6). An influx of 38 ephippia into T27, 30 m did occur as the April 2000 offshore incursion intercepted one set of traps (4–28 April interval). SeaWiFS images captured the incursion, again emphasizing the spatially heterogeneous nature of TSM transport.

Resurrection from egg bank regions?—Only in the high-sedimentation regions did we find viable diapausing eggs with depth in bottom sediments. Sieved core and ponar samples from the high-sedimentation region along the St. Joseph transect confirmed the presence of an egg bank. Diapausing eggs from several species (three *Daphnia* species, *Bosmina*, *Bythotrephes*, *Alona*) extended down into sediments several centimeters. For example, at 110 m water depth the 0–10-cm deep portion of a core (SJ110A) contained 417 total *Daphnia* ephippia with 13 diapausing eggs. A comparable core taken at 45 m water depth (SJ45A) contained 322 total *Daphnia* ephippia in the 0–10-cm zone, with 53 diapausing eggs. From these totals, it is clear that the majority of initially deposited eggs hatched previously or aborted (SJ100A, expected = 417×1.65 eggs per ephippium = 688 eggs initially deposited, observed = 13, so 13/688 or only 2% of total remains; SJ45A, expected = $321.5 \times 1.65 = 530$, so observed = 53/530 or only 10% of initially deposited).

The diapausing egg pool in the egg bank region contained species not found in autumn ephippial production records for 3 yr, although individuals were sporadically captured in plankton net tows. Table 6 presents egg tallies sieved from the high-sedimentation site along the St. Joseph transect (J45, 45 m water depth). At this site, the replicate samples contained diapausing eggs from three different species: *D. mendotae*, *D. retrocurva*, and *D. pulicaria*. Thus the assemblages verified historical contributions from previous plankton communities in southern Lake Michigan (Fig. 3). However, *D. mendotae* dominated the pool, making up 92–95% of the diapausing eggs, whereas *D. retrocurva* and *D. pulicaria* contributed only 4–8% and 0.5–2%, respectively. Two additional types of *Daphnia* ephippia were distinguished, but these were scarce and contained no viable diapausing eggs, hence we could not confirm the identity of these species with hatching experiments.

We inspected all out-of-season ephippia to determine species affinity. Despite the clustering of sediment traps in the

high-sedimentation region, out of hundreds to thousands of ephippia with eggs, all except a single ephippium with one egg (*D. retrocurva*, 13 May 1999, T20) were from *D. mendotae*. Moreover, the ratio of diapausing eggs/ephippia was very similar to the value observed during autumn production (Table 3), again suggesting that almost all resuspended eggs came from the previous autumn's production. Two additional ephippia from *D. retrocurva* (April 2000, T24) and one from *D. pulicaria* (March 1998, T15) were found in midwinter samples, but these did not contain diapausing eggs.

Discussion

Thus the pattern of ephippial production of *Daphnia* in southern Lake Michigan was a prominent late fall pulse by *D. mendotae* that coincided with pelagic population decline. Production was highest in late October to early November, then tailed off into December. The tail coincided with the disappearance of the last few *Daphnia* in the water column. In offshore waters, observed ephippial flux into traps matched values expected from Edmondson–Paloheimo egg ratio calculations. On an areal extent, the rain of ephippia was most pronounced in deeper waters, a simple consequence of greater abundance of individuals in that region. Ephippia were produced during a period of increased water column turbulence and thermocline descent, prior to the development of isothermal conditions. In offshore regions there was high correlation between ephippial fluxes in shallow-tethered and deep-tethered traps, similar mean numbers captured, and high temporal correlation between sites. That is, the production pulse was well defined and broadly distributed throughout the basin. Most of the ephippia settled onto the benthic bottom surface, although a few rafted across the surface onto shorelines. This yearly production pulse provided a pool of ephippia that was subject to resuspension and cycling during winter and early spring. Our observations suggest that resuspension cycling of the new pulse lying on the bottom layer and within the benthic nepheloid layer should be distinguished from ephippia contained within cohesive sediments (egg bank ephippia).

The observation of a large, pulsed ephippial event has both life history and practical implications. The enormous production may be necessary to ensure spring recruitment in a species that does not over-winter, especially if propagules are subject to predation during winter. A variety of freshwater benthic organisms, especially amphipods (Cáceres and Hairston 1998), are known to consume diapausing eggs. Production of trillions (10^{12}) of diapausing eggs within a relatively short period of time, flooding the environment, may be important, as in plants, to ensure adequate spring hatch (Harper 1977). Such a pattern could satiate potential consumers, guaranteeing that a sufficient number survive to hatching (Janzen 1967), yet predation experiments in Lake Michigan with the dominant amphipod *Diporeia* are necessary to confirm this conjecture. The production of large numbers of diapausing eggs might also guarantee “priority effects,” i.e., a large flush of hatching in the spring to ensure dominance in the water column. To our knowledge, this type of density-dependent priority effect has not been experimen-

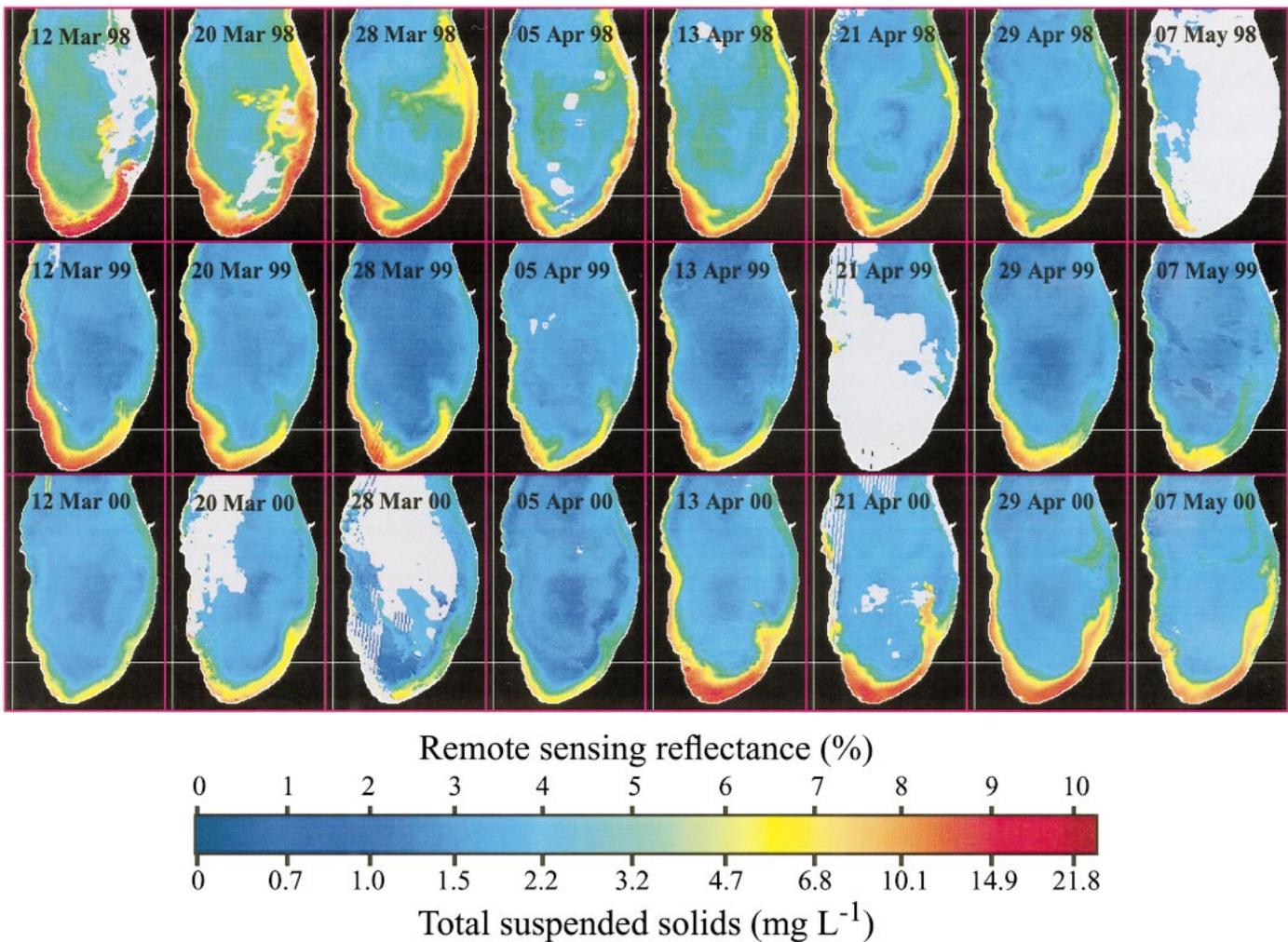


Fig. 10. Consolidated SeaWiFS images of winter sediment plumes, stretching over the three seasons of fieldwork. Winter storms in March–April set up a sediment plume around the southern coast from Racine, Wisconsin, to St. Joseph, Michigan. Each year, the sediment plume moved offshore at St. Joseph, following a topographic irregularity. The sediment buried ephyppia in the high-sedimentation zone, creating an egg bank in consolidated sediments. The winter of 1999 was relatively moderate compared to 1998 and 2000, when storms moved coastal plumes into the convergence zone of the two rotating gyres. The convergence zone drew sediments offshore where they were captured by the southern counterclockwise (cyclonic) gyre. The 9–10 March 1998 storm was very strong, judged as a one in 12-yr event. Gray areas are cloud-masked regions.

tally evaluated, although competition is established as an important summer interaction in modest-sized lakes (DeMott and Kerfoot 1982; DeMott 1983; Hu and Tessier 1995).

In terms of anthropogenic dispersal, a flush of ephyppia suspended in the water column has implications for ballast-water transport, since ocean-going vessels routinely take on ballast water in southern Lake Michigan (Chicago Port) before proceeding up to Thunder Bay and Duluth ports in Lake Superior (MacIsaac et al. 2002). *Daphnia* (*D. mendotae* and *D. retrocurva*) colonization of the coastal zone in Lake Superior about 150 yr ago might be due to original up-bound ship traffic through the Sault St. Marie Locks (Kerfoot et al. in press; Kerfoot and Weider 2004). Understanding when diapausing eggs are produced and dispersed has implications for ballast-water regulations, since there is growing recognition that diapausing eggs in ballast tank sediments are

probably responsible for much of the microcrustacean transfer (MacIsaac et al. 2002; Bailey et al. 2003).

If a one in 12-yr storm (10 March 1998) resuspends trillions of eggs, what is the frequency and impact of even larger storms? Over the interval of study, only three major storms occurred, primarily in 1998 and 2000, whereas 1999 was relatively quiet (Fig. 10). Evidence for major storms may be found in the sedimentary record as a uniform ^{210}Pb anomaly (Lake Erie, Robbins et al. 1978; Lick et al. 1994; Lake Michigan, Hermanson and Christensen 1991; Lake Superior, Evans et al. 1981). The homogenous vertical values in a uniform ^{210}Pb anomaly suggest purging of preexisting sediments at the sediment–water interface and subsequent simultaneous deposition. The anomalies described from Lake Erie correspond in time to five periods of major storms (1913–1918, 1940, 1951, 1953, 1966–1971; Lick et al.

1994), whereas those in Lake Michigan correspond to three episodes of major recorded storms (1888–1905, 1940–1945, and 1975; Hermanson and Christensen 1991). Evidence from meteorology suggests strong storms in the Great Lakes in 1905, 1913, 1916, 1918, 1919, 1940, 1952, 1958, and 1975 (Donn 1959; Murty and Polavarapu 1975; Evans et al. 1981; Lewis 1987). Thus large winter storms occur on a frequency of 1–17 yr, whereas ^{210}Pb anomalies appear at 2–30-yr intervals. Further research is needed to reconcile the two estimates, although the severe nonlinear relationship between wind stress and shear stress at the sediment–water interface may account for the differences.

As isothermal conditions developed from January to April, fine sediments were dispersed throughout the lake. However, as opposed to small lakes, the patterns of sediment resuspension and transport were spatially complex. Resuspended sediments and “out-of-season” ehippial fluxes were poorly correlated in offshore waters, largely because so few ehippia were resuspended in deep waters. Major erosion of sediment may occur in a different location of the lake than burial, since particles of different sizes are transported different distances following advection into the water column. Resuspension of sediments and ehippia was highly correlated in nearshore waters, largely as a consequence of storm severity. High-energy near-shore sediment plumes created mixtures of sediments and ehippia that directly contributed to egg bank formation in the high-sedimentation zones. Off-shore incursions of fine sediments from coastal regions, entrained along convergent zones of gyres, delivered relatively few ehippia to offshore traps. That is, convective forces were not sufficient to resuspend and transport larger particles such as ehippia across broad expanses during incursions, whereas finer particles were dispersed tens of kilometers into and around interior portions of gyres.

An intriguing observation deals with “memory” of the system. Since *D. retrocurva* and *D. pulicaria* were numerically dominant in the 1970s and 1980s, persisting through 1987 (Fig. 3), we initially anticipated that in a large lake subject to winter storms, ehippia from several species might be circulating during resuspension episodes. In contrast, what we observed was the virtual absence of *D. retrocurva* and *D. pulicaria* ehippia circulating during major resuspension events. The ratio of species in the plankton corresponded to the ratio of diapause eggs in traps (1,000:1), rather than to the ratio in the egg bank (100:1). This disparity probably resulted from the energy necessary to resuspend unconsolidated versus consolidated sediments. One concern of ours is that only thousands of the circulating trillions of ehippia were sampled. Use of 1-m diameter traps (e.g., Parflux Mark 78H-21 sequential sediment traps), which collect 25× the number of ehippia, might remedy the problem of detecting rare species. However, the 10 March 1998 storm did not produce a spring penetration of *D. retrocurva* or *D. pulicaria* into the zooplankton community or alter dominance of *D. mendotae* during the summer of 1998. Instead, our observations suggest that most circulating ehippia were produced rather recently and that resuspension was a small fraction of production (2–4%). Several factors could explain low circulation in open waters: (1) the great water depth of large lakes, requiring very large storms to resuspend even

moderate-sized particles; (2) the difficulty of resuspending consolidated (egg bank) versus unconsolidated sediments; (3) the restricted spatial extent of high-sedimentation zones (<10% of the lake’s bottom surface area), where egg banks are found; and (4) the relatively low incidence of diapausing eggs from both previously dominant species (*D. retrocurva*, 4–8%, and *D. pulicaria*, 0.5–2%) in consolidated surface sediments within the high-sedimentation regions. By contrast, in small- or medium-sized lakes during spring and fall overturn, resuspension circulates more old microfossils than new production (e.g., pollen, Frains Lake, 2–4×; Sayles Lake 10×; Davis 1968, 1973).

Do the hydrodynamic and sedimentary processes that control deposition in large lakes actually shorten, rather than extend, temporal community continuity? Almost all of the ehippia circulated by winter storms seem to be the previous autumn’s production. If much of the lake bottom is erosional, with over-wintering propagules exposed to benthic predation, are only a few diapausing eggs ending up in the egg bank? Is the system zooplankton memory (decaying time constant for recycled recruitment) actually less than 10 yr? The relatively short memory of egg banks contrasts with previous work on radiotracers in Lake Michigan. Studies of radiotracer cycling by Lerman (1979), Eadie et al. (1984), and Robbins and Eadie (1991) have also shown that radiotracer concentration is primarily the result of an annual cycle of sediment resuspension and redeposition releasing constituents from sediments back into the water. The long-term decline of ^{239}Pu and (decay corrected) ^{137}Cs in Lake Michigan has about a 20-yr time constant (Wahlgren et al. 1980; Edgington and Robbins 1990), which is interpreted as characterizing the net rate of incorporation of the tracers into permanent sediments (Robbins 1982).

Although expensive to construct and more difficult to maintain, sequential sediment traps offer numerous advantages over conventional sediment traps and alternative techniques. Sequential sediment traps can be deployed for extended periods (e.g., 6-month intervals), while taking collections at discrete, programmed short time intervals. Using these devices, we could document the details of temporal patterns of diapausing egg production. This technique complements less precise, although valuable, studies of egg or ehippial density changes in surface sediments (e.g., Lampert and Krause 1976; Uye 1983; Onbé 1985; Ban 1992). Moreover, the use of rotating bottles to capture samples ensures that periods of increased turbulence in large lakes do not purge previously sampled material, as might happen in conventional sediment traps left over long intervals. If applied widely, the devices will allow direct comparisons across lakes of different size. For example, our results can be compared with those of DeStasio (1989), who used conventional sediment traps to study egg bank dynamics in a small (2.3 ha) Rhode Island pond, Bullhead Pond. DeStasio’s detailed work on the copepod (*Diaptomus sanguineus*) was facilitated by life history events. The copepod over-wintered as adults and produced diapausing eggs in spring (May). This species’ life cycle thus reduced difficulties with severe weather and ice. In the small pond, there were indications of sediment focusing, i.e., resuspension of eggs from shallow to deep waters in spring, although most captured eggs

seemed to be new production. In the small pond studies (Little Bullhead Pond, Bullhead Pond), there was much more active exchange between living populations and the egg bank (ca. 20% per year), enough to slow evolution (Hairston and DeStasio 1988). Are circumstances different in larger, deeper lakes? Does the low exchange between living populations and the egg bank in Lake Michigan release populations for more rapid evolution?

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