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Lynda D. Corkum · Jan J.H. Ciborowski
Ray G. Poulin

Effects of emergence date and maternal size on egg development and sizes of eggs and first-instar nymphs of a semelparous aquatic insect

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Abstract We examined whether or not sizes of eggs and offspring were related to emergence date or maternal size in a semelparous aquatic insect (the burrowing mayfly, *Hexagenia*) in which parental care is lacking and oviposited eggs are passively dispersed. We quantified the size of males and female imagos over the emergence span at a site on the Detroit River, Canada, and investigated relationships between emergence date and female size and (1) egg size and (2) size of first-instar nymphs. Although size of female imagos (*H. limbata* and *H. rigida* combined) declined significantly ($P < 0.025$) over the emergence season, there was no significant relationship between body length and emergence date for males of either species. Males were significantly ($P < 0.001$) smaller than females. *H. limbata* eggs, subsampled from three individuals from each of three size classes of female imagos collected on seven sampling dates, were measured using video image analysis. Eggs ($n = 100$) oviposited by each of 63 *H. limbata* imagos were inspected daily for hatching. Newly hatched nymphs were removed, counted and measured. Egg size ($P < 0.001$) and size of first-instar nymphs ($P < 0.001$) varied significantly with emergence date, but not maternal size. The largest eggs and newly hatched nymphs occurred at peak emergence of adults. The synchronous release of larger (faster-sinking) eggs may result in reduced predation. Plasticity in egg development time and egg and nymph size may account for the ability of this taxon to recover from episodes of massive population reduction.

Key words Reproductive strategy · Maternal effects · Propagule size · Offspring size · Ephemeroptera

Introduction

Body size has important ecological and evolutionary implications for adult insects (Peters 1983). Genetic constraints determining insect body size are often less important than environmental conditions (Sebens 1987), and adult insects can show considerable variation in body size. One assumption of life history theory is that limiting resources lead to trade-offs between different structures and activities (Avelar 1993). In a phenotypic trade-off, there is a differential allocation of resources between traits, such that an individual that devotes more resources for one trait will have fewer resources to invest in another (Avelar 1993). Smith and Fretwell (1974) suggested that maternal size may influence offspring growth since females of different sizes have different amounts of resources to allocate to offspring. Larger females could have either more eggs, larger eggs, or both more and larger eggs than small females (Berrigan 1991).

Although parental fitness is often maximized by producing an intermediate number of offspring, fitness of individual progeny is increased when clutch size is small (Pianka 1983). Assuming larger eggs result in greater offspring fitness, there may be a trade-off between the number and size of eggs produced by a female (Smith and Fretwell 1974; Parker and Begon 1986).

Researchers have assumed that egg size in insects is constant and independent of clutch size (Parker and Begon 1986); yet, egg size does vary systematically in some insects (Capinera 1979; Roff 1992). Moreover, larger eggs are characteristic of females developing at lower temperatures in many ectothermic organisms including insects (*Drosophila*, Avelar 1993), amphipods (*Gammarus*, Kolding and Fenchel 1981), and fish (*Oncorhynchus kisutch*, Fleming and Gross 1990). Although egg size is often correlated with body size in fish (Fleming and Gross 1990), and large eggs produce large juveniles (Fowler 1972; Beacham et al. 1985), a similar association using aquatic insects has not been tested.

L.D. Corkum (✉) · J.J.H. Ciborowski · R.G. Poulin
Department of Biological Sciences,
University of Windsor, Windsor, Ontario, Canada N9B 3P4
Fax: (519) 971–3609; e-mail: corkum@server.uwindsor.ca

Ephemeroptera (mayflies) spend most of their lives as aquatic nymphs, then emerge as adult winged forms (subimago and sexually mature imago) to reproduce (Edmunds et al. 1976). Most temperate species are univoltine, but some spend two or more years as nymphs. All growth occurs during the nymphal stage (Brittain 1982), and the number of nymphal instars ranges from 12 to 45 depending on the species (Fink 1980). Adults cannot feed (the alimentary tract inflates with air) and seldom live more than 2 days, during which time they may disperse, mate, and the females oviposit (Corkum 1987). Mayflies are semelparous, they breed once and then die.

Significant size variation in adult mayflies has been observed over the entire emergence period and on individual sampling dates (Benech 1972; Clifford and Boerger 1974; Brittain 1982). Sweeney et al. (1995) suggested that size variation in adults reflects random processes that affect egg development and growth of early instars. Earlier, Rowe and Ludwig (1991) hypothesized that fitness of univoltine mayflies depended on mass at maturity and time of maturity.

In mayfly species having an extended emergence period, early emerging females are typically larger and more fecund than those emerging later in the season (Sweeney 1978; Brittain 1982). There is a positive correlation between maternal size and number of eggs for several mayfly species (Clifford and Boerger 1974; Brittain 1982; Giberson and Rosenberg 1994). Most mayfly species have fecundities in the range of 500 to 3,000 (Brittain 1990).

Hexagenia limbata (Serville), a burrowing mayfly, is abundant throughout North America in lakes and large rivers where the substrate is composed of soft mud and clay (Edmunds et al. 1976). Although the number of instars of *H. limbata* is not known, estimates of about 30 for other large burrowing mayflies likely apply (Ide 1935; Hunt 1953). Life history interpretation of *H. limbata* is difficult because populations have a protracted emergence (Corkum and Ciborowski 1995), and often show multiple cohorts (Heise et al. 1987), delayed hatching of eggs, differential growth of males and females (Wright et al. 1982), and a wide variability in growth rates of individuals from the same egg mass (Hunt 1953). *H. limbata* frequently co-occurs with *H. rigida* or with *H. bilineata*, contributing further to the complexity of life history analysis, since identification of early instars is difficult or impossible. *H. limbata* imagos collected at similar latitudes to the present study have 2,300–7,700 (mean: 4,000) eggs per female (Hunt 1953). Parental care is not exhibited, except perhaps in the broadest sense in that females may select oviposition sites. Parental care is typically defined as an association between parent and offspring after fertilization that enhances offspring survivorship (Sargent and Gross 1993).

There is tremendous size variation in nymphs of *Hexagenia* from any egg mass reared in the laboratory (Corkum and Hanes 1992; Hanes and Ciborowski 1992) and from samples collected from the field (Schloesser and Hiltunen 1984; Heise et al. 1987; Giberson and Rosenberg 1994). Several factors have been suggested to explain size variation in nymphs, including temperature, photoperiod, degree days, food, and density (Sweeney 1984; Corkum and Hanes 1992; Hanes and Ciborowski 1992; Giberson and Rosenberg 1994). With the exception of temperature, many of these exogenous factors seem to alter growth of *Hexagenia* later in development (i.e., after 90 days growth) (Hanes 1992). In contrast, an endogenous factor such as maternal size may influence nymphal growth early in development (Hanes 1992).

Although Giberson and Rosenberg (1994) observed a positive correlation between female (subimago) body length of *Hexagenia* (*H. limbata* and *H. rigida* combined) and the number of eggs, the associations between egg and offspring size and maternal size have not been examined. In other organisms where egg size is related to adult body size, there is evidence of parental care (Wooton 1994) or of habitat selection by propagules (McGinley et al. 1987). The argument may or may not apply to *Hexagenia*, an organism with high fecundity and no parental care or habitat selection (oviposited eggs are passively dispersed by water currents).

Researchers have often assumed that juvenile size is a function of egg size. Large eggs may give rise to immatures that are superior in some way (e.g., in the ability of newly hatched individuals to survive until food resources are found) to those individuals hatching from smaller eggs (Ito 1980). Large eggs produce large juveniles in some fishes (Fowler 1972; Beacham et al. 1985). However, because we were unaware of any studies focusing on the association between egg size and size of first instars in insects, we examined the relationship between these variables in *Hexagenia*.

In this paper, we explore previously unstudied aspects of mayfly reproductive biology. We quantify the size of male and female imagos of *H. limbata* over the emergence span. We also examine possible effects of emergence date and female size on egg size and size of first-instar nymphs as well as the relationship between sizes of eggs and newly hatched nymphs.

Materials and methods

We collected male and female imagos of *Hexagenia* weekly for 7 weeks throughout the emergence span (17 June–28 July 1993) from the Lakeview Park Marina lighthouse, where Lake St. Clair enters the Detroit River, in Windsor, Ontario, Canada (42°20′27″N, 82°56′56″ W). Sampling began the first week of June and continued until late August to ensure that specimens from the entire emergence span were included in the study. No imagos were observed before 17 June. On 4 August, there was one female imago and ten male imagos (*H. rigida*). No other imagos were observed at the sampling site throughout the remainder of August. Eggs were retrieved from females at the time of collection. Each female was grasped by the wings and placed into a 180-ml Whirlpac bag containing aerated, dechlorinated water. Female imagos immediately released eggs into the water. Fifty females and their oviposited eggs were collected into individual bags on each date. Females and their oviposited eggs were also mass collected by placing 25–30 individuals in heavy plastic 6-l bags containing about 2 l of aerated, dechlorinated water. Females were subsequently removed from the collection bags and preserved in 70% ethanol. Body length (excluding cerci) measurements of male and female imagos were made using digital calipers to the nearest 0.01 mm. We used body length as a measure of size because bodies were consistently intact, easy to measure, and historically used in our laboratory for comparative studies.

In the laboratory, eggs stored in collection bags were cooled in 4°C steps to 8°C for incubation (Friesen 1981). Cold storage induced dormancy. Friesen et al. (1979) indicated that *H. rigida* eggs could be stored at 8°C for 1 year with little or no change in development. We randomly removed eggs after 9 months of cold storage and placed them in water-filled petri dishes at room temperature (about 22°C) for measurement and hatching. Photoperiods during hatching mimicked natural lighting; Brittain (1982) showed that photoperiod does not influence development time in mayfly eggs.

Three different size classes [small (12.2–18.7 mm), medium (17.8–22.9 mm), large (21.5–27.3 mm)] of female imagos of *H. limbata* (identified by chorionic sculpture of eggs, Koss 1968) were selected from all individuals collected on any one sampling date. Three individuals (the maximum number of specimens consistently available) were selected from each size class on each of the seven sampling dates. The surface areas of 30 eggs subsampled from each individual were measured (at × 50 magnification) beneath a Wild dissecting microscope upon which was mounted a Panasonic WV 1854 high-resolution video camera. Video signals were digitized with a Targa 64 grabber card. Surface areas and images of eggs were quantified using a Java image analysis system.

In addition, a subsample of 100 eggs from each of 63 individual females of *H. limbata* (three size classes × three individuals/size class × seven sampling periods) were placed in covered petri dishes (diameter 55 mm) containing aerated, dechlorinated water. Eggs were inspected daily (0930 hours EDT) for hatching using a dissecting microscope. Newly hatched nymphs were removed, counted, and measured. Up to 30 first-instar (1-day-old) nymphs per dish that hatched on any given day were measured. Total body length (excluding cerci) of each nymph was determined (× 50) using the image analysis system.

Results

Relationships between body size of imagos and emergence date

Individuals of both *H. limbata* and *H. rigida* were found at our sampling site. There was a linear regression ($Y = \mathrm{A} + \mathrm{B}X$) relationship between body size (Y) and emergence date (X; days after 17 June) for these insects. Body lengths of *Hexagenia* females (both species combined) obtained from individual and mass collections ($n = 1,176$) declined significantly ($Y = 23.51 - 0.73X$; $R^2 = 0.78$, $P < 0.025$, $n = 7$) throughout the emergence period, 17 June–28 July 1993 (Fig. 1). There were no significant relationships between body length and emergence date for males of *H. rigida* ($Y = 19.8 - 0.26X$; $n = 133$) or *H. limbata* ($Y = 20.96 - 0.40X$; $n = 74$). The ratio of *H. rigida* to *H. limbata* males was 1.8:1. When regression lines were compared, there were significant differences among intercepts (ANCOVA; $P < 0.025$; females were larger than males), but not among slopes (ANCOVA; $P > 0.05$).

Variation in egg size

Results from a two-way ANOVA indicated a significant effect of emergence date on mean egg size ($df = 6, 59$, $F = 5.23$, $P < 0.001$). Neither maternal size ($df = 2, 59$, $F = 0.57$, $P > 0.05$) nor its interaction with date ($df = 12, 59$, $F = 1.11, P > 0.05$) influenced egg size. Egg size increased during the first three sample weeks for all three size classes of females (Fig. 2). For 5 years, including

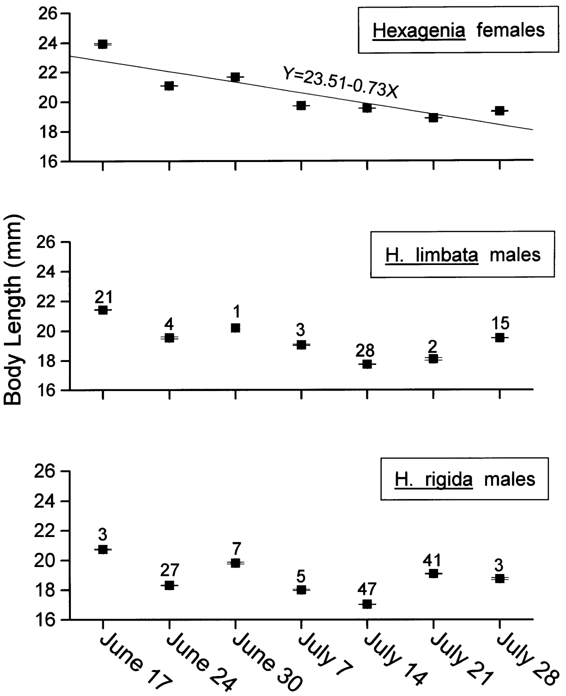

Fig. 1 Relationships between imago body length (excluding cerci) and sampling date for female *Hexagenia* (*limbata* and *rigida* combined) ($R^2 = 0.78$, $P = 0.023$), males of *H. limbata* ($R^2 = 0.48$, $P = 0.09$), and *H. rigida* males ($R^2 = 0.21$, $P = 0.30$)

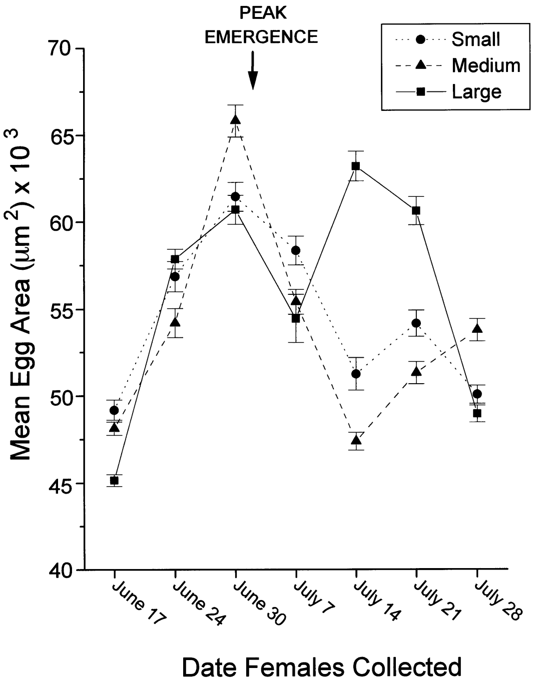

Fig. 2 Mean (± SE) egg size (surface area) obtained from small, medium, and large female imagos (adults) of *H. limbata* collected on seven sampling dates. Peak emergence occurred during the first week of July

1993, peak emergence (the date at which maximum numbers of *Hexagenia* adults were observed at the study site) has occurred during the first week of July (L.D. Corkum, personal observation). After peak emergence, the size of eggs obtained from small and mid-sized females declined until mid-July and then levelled off (Fig. 2). In contrast, large eggs were obtained from large females collected during the middle 2 weeks of July.

Egg development

Development of eggs from all size classes of *H. limbata* adults showed variation in mean hatch duration (4–16 days from warming to hatching), hatch success (22–94%) and day of first hatch (day 1–day 9) (Table 1). Without cold storage, eggs from oviposited females hatch in about 22 days at room temperature (L.D. Corkum, personal observation). Following cold storage, eggs from females of all size classes collected in the first 3 weeks of emergence hatched immediately; eggs from females collected during the last 4 weeks of emergence were delayed in their hatching by 1 week (Table 1). With one exception (hatch of eggs from large females collected on June 24: 16 ± 3.8 days mean ± SE), mean hatch duration was 2 weeks or less (Table 1).

Variation in size of first-instar nymphs

Results of a two-way ANOVA indicated that emergence date was significantly related to the size of first-instar nymphs ($df = 6, 59$, $F = 4.5$, $P < 0.001$). Neither female size ($df = 2, 59$, $F = 1.1$, $P > 0.05$) nor its interaction with date ($df = 12, 59$, $F = 1.3$, $P > 0.05$) significantly influenced the size of first-instar nymphs. The largest nymphs were observed from females collected just prior to peak emergence (June 30) (Fig. 3). Nymph size declined after peak emergence.

The relationship between mean egg size and mean body length of newly hatched nymphs was established for small, medium, and large females on each of seven sampling dates, with the exception of July 7, when no nymphs hatched from eggs obtained from large female imagos. There was a weak, positive association ($r = 0.45$, $P < 0.05$, $n = 20$) between mean egg size and mean body length of newly hatched (1-day-old) nymphs, although neither variable alone was related to maternal size (Fig. 4).

Discussion

Relationships between body size of imagos and emergence date

Mean female size (*H. limbata* and *H. rigida* combined) decreased significantly over the emergence span from mid-June until the end of July. A decline in adult mayfly size during the emergence period is common (Sweeney and Vannote 1981; Brittain 1982). Females present early in the emergence period are larger and more fecund than

Table 1 Egg development in *Hexagenia limbata* from small, medium, and large female imagos, collected throughout the emergence span (June 17–July 28), for day of first hatch, hatch duration, and percentage hatch. Values presented are mean ± SE (in parenthesis). Total number of eggs = 63,000; number of replicates = 3

Date (1993)	Female imago size	Day of first hatch	Percent hatch	Hatch duration (days)
June 17	Small	1.3 (0.33)	32.3 (11.79)	10 (1.53)
	Medium	1.3 (0.33)	73.7 (10.49)	8 (3.21)
	Large	1 (0)	45 (13.05)	7.7 (0.30)
June 24	Small	2 (0)	21.7 (9.24)	3 (0)
	Medium	1.3 (0.33)	38.7 (8.57)	11.7 (2.60)
	Large	1.7 (0.33)	41.3 (7.31)	16 (3.79)
June 30	Small	1 (0)	50 (13.89)	14 (1)
	Medium	1 (0)	50 (18.18)	8.3 (0.88)
	Large	2.3 (0.33)	52.3 (7.62)	9 (2.08)
July 7	Small	8.3 (0.33)	58.3 (12.13)	10 (2.31)
	Medium	8.3 (0.33)	56.3 (9.87)	4.7 (0.33)
	Large	8.5 (0.50)	66.5 (15.50)	7 (1.63)
July 14	Small	6 (0.58)	91.7 (2.73)	7.6 (0.88)
	Medium	6.3 (0.33)	93.7 (2.60)	5.3 (0.88)
	Large	6.3 (0.67)	94.3 (0.33)	7.7 (1.20)
July 21	Small	8.3 (0.33)	76.3 (12.12)	4.3 (0.33)
	Medium	9 (1.0)	33 (7.09)	5.3 (0.33)
	Large	9 (0.58)	54.7 (19.20)	9.3 (2.90)
July 28	Small	8 (1.0)	69.7 (11.20)	4 (0.58)
	Medium	7 (0)	59.3 (14.34)	7.3 (1.76)
	Large	8.7 (0.33)	62.7 (3.38)	8 (1.15)

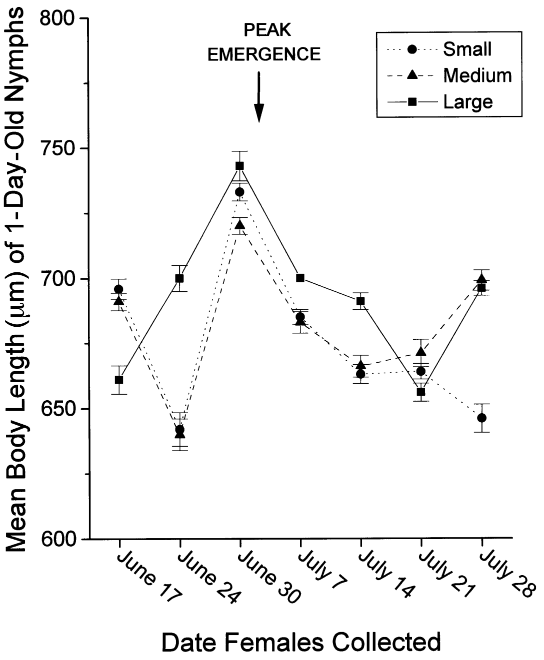

Fig. 3 Mean (± SE) body length of 1-day-old nymphs hatched from eggs obtained from small, medium, and large female imagos (adults) of *H. limbata* on seven sampling dates. Peak emergence occurred during the first week of July. No nymphs hatched from eggs obtained from large-sized adults, July 7

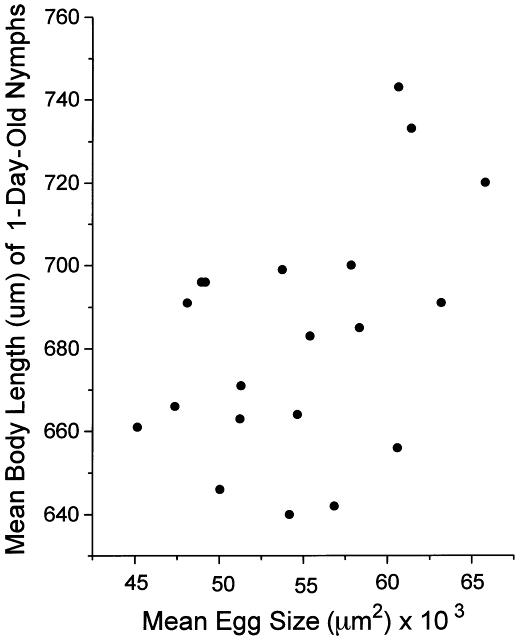

Fig. 4 Relationship between mean body length of 1-day-old nymphs and mean egg size ($n = 20$, $r = 0.45$, $P < 0.05$)

those that emerge later (Clifford and Boerger 1974; Sweeney 1978; Giberson and Rosenberg 1994). Clifford (1969) suggested that when nymphs of the mayfly *Leptophlebia cupida* reached a "mature" stage, they could moult to a subimago regardless of size. Rowe and Ludwig (1991) suggested that decrease in size at maturity was an adaptive response to "the conflict between size and age at maturity (emergence)". An advantage of a small imago emerging 1 year earlier (albeit at the end of the emergence span) may offset the cost of producing a smaller clutch, by avoiding mortality of overwintering nymphs. Also, under density-independent conditions, accelerating generation time is far more effective in raising the intrinsic rate of natural increase than increasing fecundity (Stearns 1976).

In contrast to that of females, male *Hexagenia* body length was unrelated to emergence date. Males of *H. limbata* and *H. rigida* were also smaller than females in both species (Fig. 1). Sexual dimorphism is prevalent in insects, especially in aquatic insect species that do not feed as adults; in these cases, female mass may be double that of males (Butler 1984 and references therein). Although eggs in the abdomen of females contribute much to their excess mass compared to males, it is curious that males are not larger since nymphs of both sexes experience the same environmental conditions (Butler 1984). Butler (1982) suggested that male larval chironomids (Diptera) may cease feeding before females, but continue with development. Since the main function of mayfly male imagos appears to be sperm production and mating, the smaller male size may be related to the lower energy cost of sperm than of egg production. Small size in male insects may be selected for greater maneuverability in mating swarms (McLachlan 1985; Corkum 1987). Males, in other insect orders that feed as adults and contribute to parental care through feeding of young or in territorial defense, have body sizes that approach or exceed female size (Ricklefs 1973).

Variation in size of eggs and first-instar nymphs

McGinley et al. (1987), using a simulation model, showed that habitat choice is necessary for the evolution of variable propagule size in a spatially heterogeneous environment; a single egg size was favored under conditions of random dispersal. A soft mud/clay substrate is essential for the survival of burrowing mayfly offspring (Edmunds et al. 1976), but habitat selection resulting from the passive dispersal of eggs is unlikely. Moreover, an association between egg and offspring size and maternal size seems unlikely since adult mayflies do not provide parental care. Despite the lack of both parental care and habitat selection by propagules, we found that significant differences existed in both egg size and the size of first-instar nymphs of *H. limbata* throughout the emergence period. Although emergence date was significantly related to offspring size, other unknown seasonal factors related to date may account for the size differences observed. The occurrence of largest egg and nymphal size at the time of peak emergence suggests not only greater mating success, but potential for greater overall propagule fitness at this time. Peak, synchronous emergence of adults may result in the swamping of aerial predators (Sweeney and Vannote 1982). The synchronous release of eggs at night possibly reduces exposure to planktivorous predators and may also swamp nocturnal predators. For small particles of comparable density, the rate of sinking is proportional to size (Stokes' law). Therefore, large eggs will sink faster than small ones, perhaps resulting in a further reduction in predation intensity.

Although numerous taxon-specific hypotheses have been presented to account for seasonal variation in propagule size, "differences among taxa in seasonal pattern of propagule size argue against any general explanation" (Roff 1992, p. 391). Nevertheless, the observed relationship between offspring size (size of eggs and first-instar nymphs) and emergence date may help to explain the broad size variation and occurrence of overlapping cohorts observed in nymphs of *H. limbata* found in lakes (Flannagan 1979; Heise et al. 1987), reservoirs (Hudson and Swanson 1972; Horst and Marzolf 1975), and rivers (Schloesser and Hiltunen 1984).

There was no significant relationship between female size of *H. limbata* and egg size or between female size and size of first-instar nymphs. Interestingly, positive correlations exist between egg size and female size in teleost fishes exhibiting parental care (Sargent et al. 1987; Sargent and Gross 1993). Such associations are not found in either pelagic fish spawners (Wooton 1994) or, as we have shown, in *Hexagenia* that oviposit on surface waters and whose eggs are dispersed by water currents.

Egg development

Duration of egg development in nondiapausing aquatic insects is often inversely related to temperature and is typically described by a power function (Humpesch and Elliott 1980; Sweeney 1984). However, hatching success may be highest at some intermediate temperature and low at the higher and lower temperature extremes (Elliott and Humpesch 1980; Brittain 1990). Hunt (1953) reported that hatching success of *H. limbata* from Michigan lakes was > 90% at about 20°C. Giberson and Rosenberg (1992) reported that the optimum temperature for hatching for the same species was 20°C or greater. In this study, we examined egg development at about 22°C, the optimum temperature for development in *Hexagenia* eggs.

There may be a bet-hedging strategy in adult *Hexagenia* to prevent completely synchronous egg hatching. In this study, mean hatch duration ranged from 3 to 16 days. Extended hatching periods in mayflies have been recorded in Europe and Australia (Brittain and Campbell 1991), the U.S.A. (Hunt 1953) and Costa Rica (Jackson and Sweeney 1995). Hunt (1953) reported that egg hatch in *H. limbata* from Michigan lakes was 10–21 days depending on temperature and oxygen conditions. This range of hatching duration partially accounts for the developmental variability and overlapping cohorts of nymphs that others have reported (Hudson and Swanson 1972; Flannagan 1979; Heise et al. 1987; Giberson and Rosenberg 1992).

Summary

The body size of female *Hexagenia* declined significantly over the emergence span (mid-June to the end of July). Male body size, which was significantly smaller than that of females, did not change with time. In this semelparous insect, where eggs disperse passively and in which parental care is lacking, egg size and size of day-old nymphs were unrelated to maternal size. However, emergence date (or some unknown seasonal factor related to date) accounted for significant size differences in eggs and first-instar nymphs. The largest eggs and newly hatched nymphs occurred at peak emergence of imagos (the first week of July). The synchronous release of larger (faster-sinking) eggs may result in reduced predator intensity. The plasticity in egg development time along with size variation in egg and offspring may account for the great variability in life cycle pattern seen in this taxon and in its ability to recover from episodes of massive population reduction.

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