

Depensatory Mortality, Density-Dependent Growth, and Delayed Compensation: Disentangling the Interplay of Mortality, Growth, and Density during Early Life Stages of Yellow Perch

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Abstract.—We present long-term (>40-year) patterns in the density of age-0 yellow perch *Perca flavescens* in Oneida Lake at four early life stages (at egg deposition, at the attainment of a total length of 18 mm, on 1 August, and on 15 October), from which we calculated mortality and growth rates during the three intervals between these early life stages. At each of these stages, age-0 yellow perch densities have been lower in recent years than in the 1960s and 1970s. Mortality rates showed no time trend from egg to 18 mm (interval 1 [the larval stage]), increased from 18 mm to 1 August (interval 2 [the limnetic stage]), and decreased from 1 August to 15 October (interval 3 [the demersal stage]). We also tested previous hypotheses for density-dependent effects on mortality and growth using the entire long-term data set. Contrary to expectations from the 1960s, the mortality rates of age-0 yellow perch in Oneida Lake are no longer depensatory. Overall, the growth rate of age-0 yellow perch has increased over time and become density dependent. Also contrary to common expectations of size-selective mortality, greater average total length is not associated with decreased instantaneous daily mortality for two early life stage intervals. The combined effect has been a decline in age-0 yellow perch density and an increase in average total length by the end of their first year. Although increased growth has not sufficiently compensated for increased mortality during the first year of life, obtaining a larger end-of-year size should reduce subsequent mortality during the winter period, providing for a process of delayed compensation that helps stabilize density at age 1.

Fish recruitment has long been the subject of inquiry, with some studies focusing on the processes affecting survival during early life stages and potential spawner–recruit relationships (Chambers and Trippel 1997; Fuiman and Werner 2002). Because the condition and size of the mature fish stock should at least partially determine the production of young, the relation between spawning stocks and numbers of recruits has been examined for numerous species and system types, but the results have not revealed consistent patterns (Myers and Barrowman 1996). The variability in these relationships implies that recruitment is also influenced by factors other than the reproductive potential of the parental stock. Additional factors that have been identified as important for at least some freshwater fish include

hatch date (Garvey and Stein 1998), temperature and climate (Clapp et al. 1997; Casselman 2002), changes in habitat and hydrology (Sammons et al. 2002), food supply and competition (DeVries and Stein 1992; Hoxmeier et al. 2004), and predation (Brandt et al. 1987; Guy and Willis 1991; Kim and DeVries 2001). These factors can act independently or in association to affect recruitment (Paukert et al. 2002) and can regulate the number of age-0 fish that successfully transition through early life stages. Resulting mortality events may either dramatically reduce year-class strength in a short episode or act subtly to remove individuals over longer periods of time (Houde 1989).

Recruitment analyses often consider growth rates because achieving an increased size through rapid growth is usually believed to reduce the mortality of young fish. Achieving an increased size through rapid growth reduces the time spent in vulnerable early life stages (Houde 1994; Sogard 1997), decreases the sensitivity of young fish to fluctuations in the physical environment (Roseman et al. 1999), allows for consumption of larger and potentially more energetically profitable prey (Schael et al. 1991), and reduces vulnerability to smaller and potentially more abundant predators (Miller et al. 1988). In general, a “bigger is better” hypothesis is often assumed for young fish (Sogard 1997). However, increased foraging activities

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that produce more rapid growth can also lead to greater exposure to predators and therefore higher risk of mortality (Walters 2000). As a result, individual fish probably experience a tradeoff between increasing resource acquisition and reducing mortality risks, particularly during early life stages (Sogard 1997; Walters 2000).

For young fish, the interplay of mechanisms that affect mortality and growth can determine whether the transition through the first year of life is successful. These mechanisms can be density dependent and either increase survival at low densities (compensatory) or decrease survival at low densities (depensatory). Depensatory mechanisms will increase the difference between weak and strong year-classes, whereas compensatory mechanisms will decrease this difference (Forney 1971; Houde 1994). As an example, predation-driven depensatory mortality can disproportionately reduce the density of a small cohort (Forney 1971). Conversely, compensation can alleviate the effects of early life stage mortality through increased growth if the individuals remaining experience decreased subsequent mortality (Sogard 1997). In this regard, some factors that increase mortality during one life stage may reciprocally act to increase survival during a later life stage (Pepin 1991; Sogard 1997). As such, early mortality events may not solely determine cohort success, and the stage at which year-class strength is set can vary among species and across systems (Houde 1994). Given the complexities associated with identifying the determinants of year-class success, recruitment variability may be better understood by evaluating patterns in both mortality and growth rates (Houde 1987) because these rates are critical for successful transitions across early life stages.

In this study, we consider both mortality and growth rates within sequential early life stage intervals for young yellow perch *Perca flavescens* in Oneida Lake, New York. Such consideration is possible given the long-term studies supported by the Cornell Biological Field Station (CBFS) since the 1950s. Consequently, these studies have become textbook examples for percid interactions (Mills and Forney 1988; Craig 2000; Diana 2004). Specifically, we consider long-term data (>40 years) for age-0 yellow perch at sequential early life stages and during the intervals between these stages. Following earlier analyses of portions of this data set, we estimated the density of age-0 yellow perch at the egg stage, at a larval stage corresponding to the attainment of an 18-mm total length, and at two later times during the first year of life: 1 August and 15 October (e.g., Forney 1980; Mills and Forney 1988; Rose et al. 1999). For completeness, we also include the densities of the same cohorts at age 1, as observed

during the following spring (Fitzgerald et al. 2006). First, we present densities of age-0 yellow perch at multiple early life stages and of age-1 yellow perch at the following spring. We then consider long-term trends in mortality and growth rates over time for multiple early life stage intervals (larval, limnetic, and demersal). Using these trends, we test a priori hypotheses that both mortality and growth rates are negatively related to density of age-0 yellow perch (Forney 1980; Mayer et al. 2000). Next, we examine the relationship between average individual total length and mortality rate within two early life stage intervals to explore the temporal presence of compensation. Finally, we use these analyses to discuss implications for future abundance of yellow perch and the relevance of potentially important ecological changes to this population.

Study Site

Oneida Lake is relatively shallow (mean depth = 6.8 m), yet has the largest surface area (207 km²) of any lake entirely inside the borders of New York State. It supports important recreational fisheries for several species, including yellow perch, walleye *Sander vitreus*, and black basses *Micropterus* spp. The lake has a rich history of ecological study across multiple trophic levels (Mills et al. 1978; Forney 1980) and has experienced notable ecological changes and perturbations to its food web during the past half-century. The signing of the Great Lakes Water Quality agreement in 1972 helped to reduce nutrient loadings, allowing Oneida Lake to shift over time from eutrophic to mesotrophic status (Mayer et al. 2002). During the 1980s, invasive white perch *Morone americana* and gizzard shad *Dorosoma cepedianum* displayed periodic high production of young (Fitzgerald et al. 2006). By 1992, zebra mussels were found in high abundance, which has led to increased water clarity and macrophyte coverage across the lake (Mayer et al. 2002; Zhu et al. 2006). During the zebra mussel period, double-crested cormorants *Phalacrocorax auritus* also increased in abundance; current management aims to reduce double-crested cormorant numbers to lessen their piscivory (Rudstam et al. 2004). Throughout this most recent period, the density of adult yellow perch has remained low, as has the density of adult walleyes (Rudstam et al. 2004).

Methods

Surveys of age-0 yellow perch.—Spawning by yellow perch occurs in shallow areas of Oneida Lake, and their eggs typically hatch during May (Mills and Forney 1988). Annual egg deposition estimates for the Oneida Lake population were based on an equation

relating fecundity to weight, estimates of weight and abundance at age, and the proportion of mature females per age-class (for additional details see Clady 1976). For most of the data series mature yellow perch were age 3 and older, but in the 1990s–2000s some age-2 yellow perch were also included in the calculations of egg deposition, given the increased growth rates observed during these more recent years.

Each spring, a survey of larval yellow perch was conducted when pilot sampling indicated that the larval yellow perch cohort had reached a mean total length of approximately 18 mm (usually in mid-June). Sampling at a total length of 18 mm was selected in the 1960s, to catch relatively large larval fish at a size before their avoidance ability became too great for the Miller sampling gear. Larval yellow perch were collected at multiple depth strata and locations by means of four high-speed Miller samplers (see Noble 1970 and Rudstam et al. 2002 for additional details). Because the date of larval surveys varied somewhat from the time larval yellow perch achieved a mean total length of 18 mm, we standardized these collections to a uniform size to compare densities over time (e.g., Jackson and Noble 2000). To standardize annual larval density estimates to the attainment of 18 mm, we calculated daily larval growth and mortality rates from a subset of years when additional Miller sampling was performed earlier in the spring. These additional surveys targeted larval yellow perch at a total length of approximately 8 mm, when the near absence of yolk sac larvae indicated cohorts were fully recruited to the pelagic population ($N = 11$ years; 1968–1977, 1998, 2001). For these years, we estimated rates of daily growth ($N = 11$; mean \pm SE = 0.48 ± 0.02 mm/d) and instantaneous mortality ($N = 9$; 0.042 ± 0.005) from the time of the 8-mm survey to that of the 18-mm survey and used these increments to adjust the density estimates to the time a cohort attained a total length of 18 mm for each year (henceforth called the standardized 18-mm survey). Because a direct measure of yellow perch hatch dates was not available for most years, we used the estimated daily growth rate from 8 to 18 mm to estimate the duration of the period between hatching (assumed to occur at 4 mm because larval yellow perch <5 mm have been captured in Oneida Lake; e.g., Clady 1976) and the attainment of 18 mm as about 29 d. Use of this time period allowed us to calculate larval mortality as an instantaneous daily rate (on a comparable scale as estimates for both limnetic and demersal intervals; see below). The resulting estimated hatch dates indicated that hatching of yellow perch occurs during May, which is consistent with earlier observations for Oneida Lake (e.g., Mills and Forney 1988).

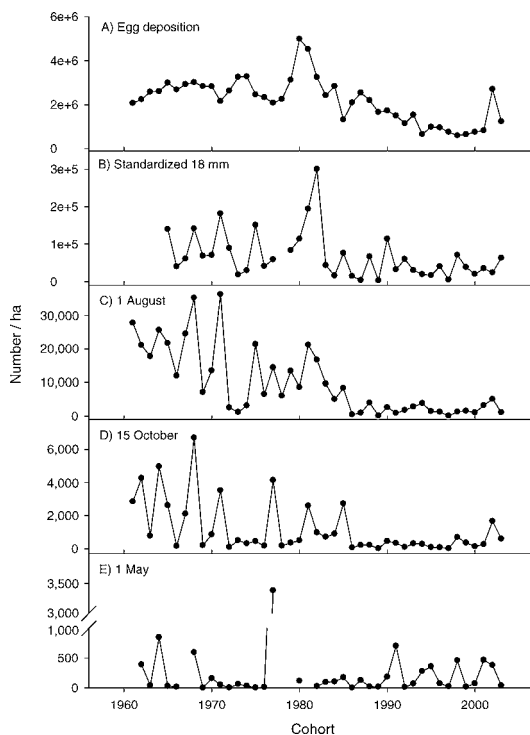


FIGURE 1.—Estimated annual density of age-0 yellow perch in Oneida Lake during four early life stages—(A) at egg deposition, (B) at the attainment of an average total length of 18 mm, (C) on 1 August, and (D) on 15 October—along with (E) that of age-1 yellow perch during the following spring (1 May). Note the differences in the scale of the y-axes.

The density and mean total length of age-0 yellow perch on both 1 August and 15 October were calculated from weekly bottom trawl collections at 10 standardized sites (see Forney 1971; Nielsen 1983; and Fitzgerald et al. 2006 for additional details). Year-specific catch curves for yellow perch, developed from trawl catches throughout the growing season by assuming a constant instantaneous mortality rate for that year, were used to estimate density on 1 August and 15 October of each year. Occasionally, dates with low catches (associated with low oxygen levels in deepwater sites) were excluded. A subsample of yellow perch collected in bottom trawls were measured for total length (to the nearest millimeter). Each year, the average total length of age-0 yellow perch was plotted across the collection dates as annual growth curves to estimate mean size of age-0 yellow perch on both 1 August and 15 October.

We then used the long-term data series of age-0 yellow perch at four early life stages (at egg deposition, at the attainment of a total length of 18 mm, on 1

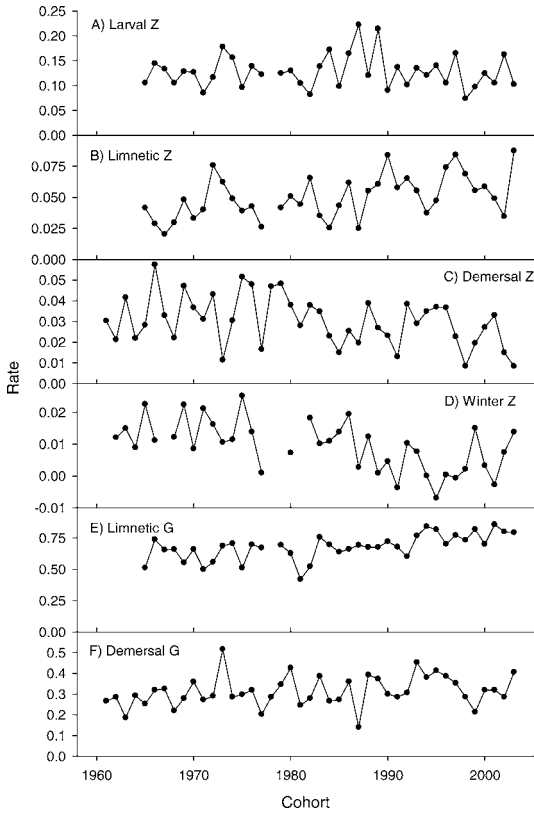


FIGURE 2.—(A–C) Instantaneous daily mortality rates (Z) for three early life stage intervals of age-0 yellow perch, (D) the instantaneous winter mortality rate, and daily growth rates (G) for the (E) limnetic and (F) demersal intervals. Note the differences in the scale of the y-axes.

August, and on 15 October; Figure 1A–D) to calculate mortality and growth rates for specific early life stage intervals (interval 1 [egg to 18 mm; the larval stage]; interval 2 [18 mm to 1 August; the limnetic stage], and interval 3 [1 August to 15 October; the demersal stage]; Figure 2). An instantaneous daily mortality rate for each interval was calculated as

$$Z_i = \log_e \left(\frac{D_i}{D_{i+1}} \right) / t_i$$

where D is the density of age-0 yellow perch during early life stage i and t is the number of days elapsed during that interval. Likewise, interval-specific growth rates were calculated as

$$G_i = \frac{L_{i+1} - L_i}{t_i}$$

where L is the average total length of age-0 yellow perch.

Because growth measures were not directly available for the larval stage, we calculated larval growth rates from the 8-mm survey to the 18-mm survey for 11 years whenever these data were available. For both the limnetic and demersal stages, a measure of fish size was calculated as the average of age-0 yellow perch total length at the start and end of the interval.

For completeness, we also report estimates of a winter mortality index and of the yellow perch cohorts once they reached age 1 (sampling during early May; see Fitzgerald et al. 2006 for the initial presentation of these data and a more complete discussion of the winter period). The winter period extends from the end of the demersal stage to the following spring, and spring trawling followed the same procedures (e.g., bottom trawling at standardized sampling sites) as described for the autumn age-0 yellow perch collections.

We also present springtime water temperature data in relation to the day of the year on which larval yellow perch attained an average total length of 18 mm. Water temperature was recorded at a station near the CBFS at a depth of 2 m. In a few cases, when daily temperature values were not available throughout the interval of interest (whether from equipment malfunction or late deployment), we interpolated between weekly estimates to obtain daily values before we calculated the averages. We evaluated temperature specifically because of the particularly important role it can play during early life stages of fish (e.g., by potentially reducing the time spent in vulnerable periods when thermal conditions are optimal).

Statistical analyses.—We used simple linear regression to determine whether mortality and growth rates exhibited temporal trends during multiple early life stage intervals. The use of regression to evaluate temporal trends is perhaps simplistic, but it helps identify early life stage intervals when long-term changes in important demographic rates may have occurred over time. We also used simple linear regression to test for density-dependent mortality and growth. In this case, we hypothesized that mortality and growth rates would be negatively related to density. Estimates of larval yellow perch density were not available before 1965 or for 1978; therefore, mortality and growth rates were calculated for fewer years during the larval and limnetic intervals than during the demersal interval (which also includes data from 1961–1964 and 1978). Linear regression was also used to evaluate the day of the year yellow perch attained an average total length of 18 mm and to relate that timing to springtime water temperature. All regression procedures were performed using the REG procedure in SAS version 9.1.

Results

The density of age-0 yellow perch has typically remained low during recent years at all of the early life stages included in this study (Figure 1A–D). However, springtime collections of age-1 yellow perch have not shown this sustained period of relative low density (Fitzgerald et al. 2006; Figure 1E). No temporal trend was evident for mortality during the larval interval ($N = 38$, $R^2 < 0.001$, $P = 0.945$; Figure 2A). However, the recent low density of larval yellow perch coincides with a general increase over time in instantaneous daily mortality during the limnetic interval ($N = 38$, $R^2 = 0.234$, $P = 0.002$; Figure 2B). Instantaneous daily mortality rates have decreased over time for a later early life stage (demersal: $N = 43$, $R^2 = 0.123$, $P = 0.021$; Figure 2C). Likewise, the winter mortality index has decreased over time ($N = 38$, $R^2 = 0.301$, $P < 0.001$; Figure 2D). The daily growth rates of age-0 yellow perch have increased significantly during the limnetic interval ($N = 38$, $R^2 = 0.378$, $P < 0.001$; Figure 2E) and marginally during the demersal interval ($N = 43$, $R^2 = 0.069$, $P = 0.089$; Figure 2F). The limited data for growth rates between the 8- and 18-mm larval surveys failed to indicate a temporal trend ($N = 11$, $R^2 = 0.044$, $P = 0.538$). In combination, the increased age-0 growth rates during both the limnetic and demersal intervals have led to larger age-0 yellow perch on both 1 August and 15 October during recent years.

Contrary to a priori hypotheses, daily mortality rates were not related to density during any early life stage interval when all available years of data were included (larval interval: $N = 38$, $R^2 = 0.024$, $P = 0.353$; limnetic interval: $N = 38$, $R^2 < 0.001$, $P = 0.927$; demersal interval: $N = 43$, $R^2 = 0.022$, $P = 0.348$; Figure 3A–C). We had expected mortality during early life stages of yellow perch to be depensatory, the mechanism identified for cohorts from the 1960s (Forney 1971, 1980; filled triangles in Figure 3C). However, the anticipated negative relationship between age-0 yellow perch density and mortality was not evident when all available data were considered. The disruption of the depensatory-mortality relationship, particularly for demersal age-0 yellow perch, was the result of several years with low mortality and low density (Figure 3C).

Growth from the 8-mm to the 18-mm survey also was not related to the density of larval yellow perch at 8 mm ($N = 11$, $R^2 = 0.129$, $P = 0.278$; Figure 3D). For this larval interval, the most recent (2001) estimate of growth rate was the lowest observed during the 11 years for which data were available (Figure 3D). However, the growth rates of age-0 yellow perch during the subsequent early life stages were highly density dependent, especially during the period from

18 mm to 1 August (limnetic interval: $N = 38$, $R^2 = 0.507$, $P < 0.001$; demersal interval: $N = 43$; $R^2 = 0.136$; $P = 0.015$; Figure 3E–F). During these later early life stage intervals, recent growth rates were typically high or at least moderate (Figure 3E–F).

In recent years, age-0 yellow perch have typically achieved a greater total length during each of the early life stage intervals considered here (Figure 4A–C). Even so, decreased mortality rates for years with larger mean body lengths were not evident for limnetic age-0 yellow perch ($N = 38$, $R^2 = 0.016$, $P = 0.444$; Figure 4A). During the demersal stage, instantaneous mortality rates were slightly lower during years with larger fish, but unexplained variability was high ($N = 43$; $R^2 = 0.101$; $P = 0.038$; Figure 4B). To a greater extent, winter mortality was inversely related to larger end-of-year total length ($N = 38$; $R^2 = 0.382$; $P < 0.001$; Figure 4C).

Over the several decades considered here, larval yellow perch are generally attaining a total length of 18 mm on an earlier date during the spring ($N = 38$, $R^2 = 0.121$, $P = 0.032$; Figure 5A). Earlier dates of attaining 18 mm are associated with warmer May water temperatures ($N = 35$, $R^2 = 0.605$, $P < 0.001$; Figure 5B).

Discussion

Our measures of age-0 yellow perch at multiple early life stages revealed a recent sustained period of low densities in Oneida Lake. Egg deposition has declined over time with the decline in the adult population (Rudstam et al. 2004), but larval mortality was variable across years, showing no distinct temporal trend. Use of egg deposition estimates is the same as assuming a constant rate of hatching success across years. Annual density estimates of eggs at the time of hatch were not available for this study, but such a measure would perhaps be a better starting point for the larval period. Through frequent sampling of individual cohorts across several decades, we observed increased mortality of limnetic age-0 yellow perch during the transition from the larval stage to August 1, followed by a moderate decline in demersal mortality rates. The shift from increasing limnetic mortality to decreasing demersal mortality may indicate a change in the localized environments experienced by these early life stages in Oneida Lake. Theoretically, such a change could reduce the vulnerability of demersal age-0 yellow perch to predation through direct separation of their habitat from that of potential predators later in the year, when alternative prey species (e.g., age-0 white perch and gizzard shad) are more pelagic than age-0 yellow perch. Reduced vulnerability could also occur indirectly through reduced activity levels, the result of

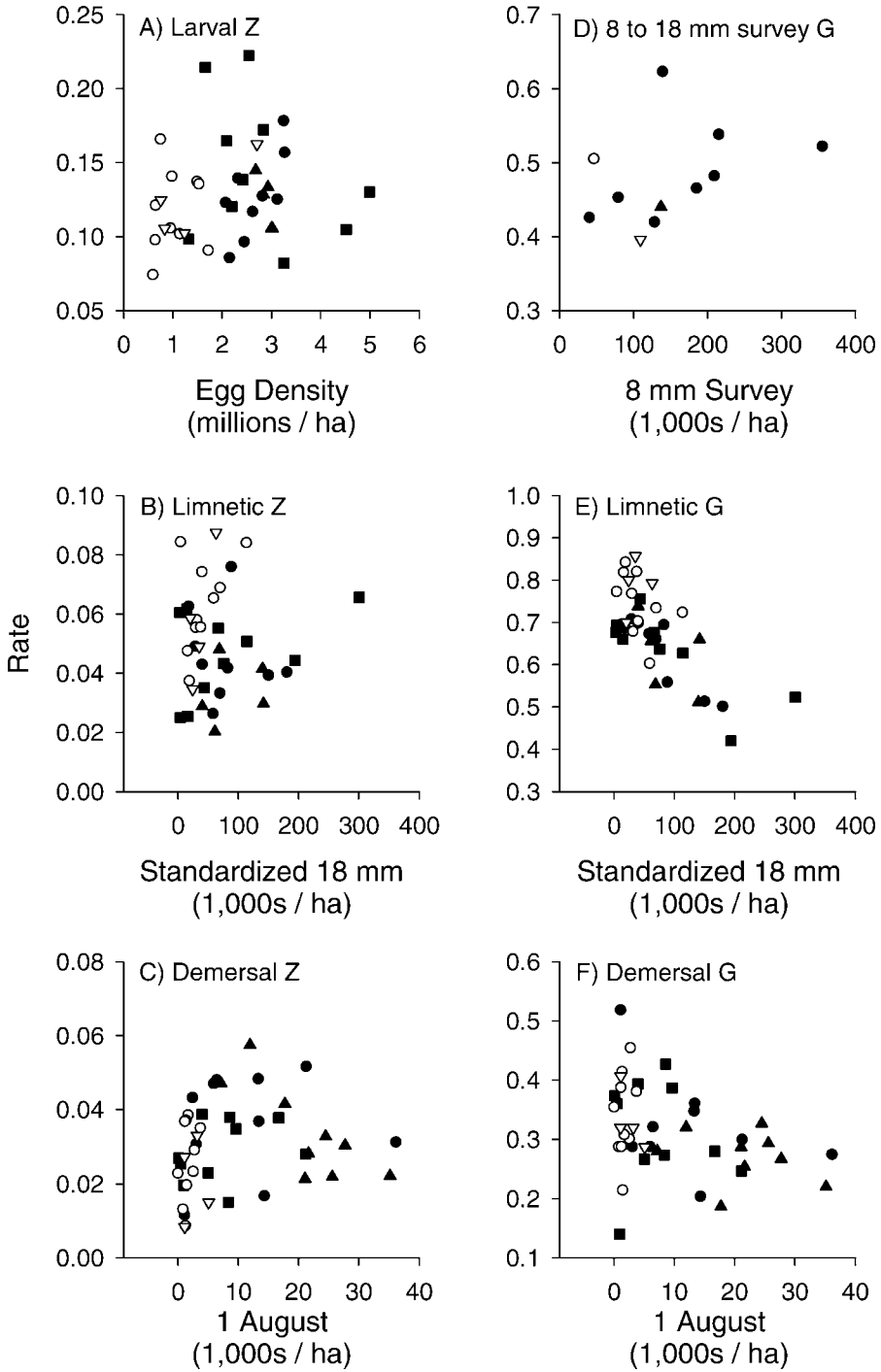


FIGURE 3.—(A–C) Instantaneous daily mortality (Z) and (D–F) growth (G) rates relative to the density of age-0 yellow perch at several early life stages. Note the differences in the scale of the y-axes. The different symbols represent different decades: filled triangles = the 1960s; filled circles = the 1970s; squares = the 1980s; open circles = the 1990s; and open and inverted triangles = the 2000s).

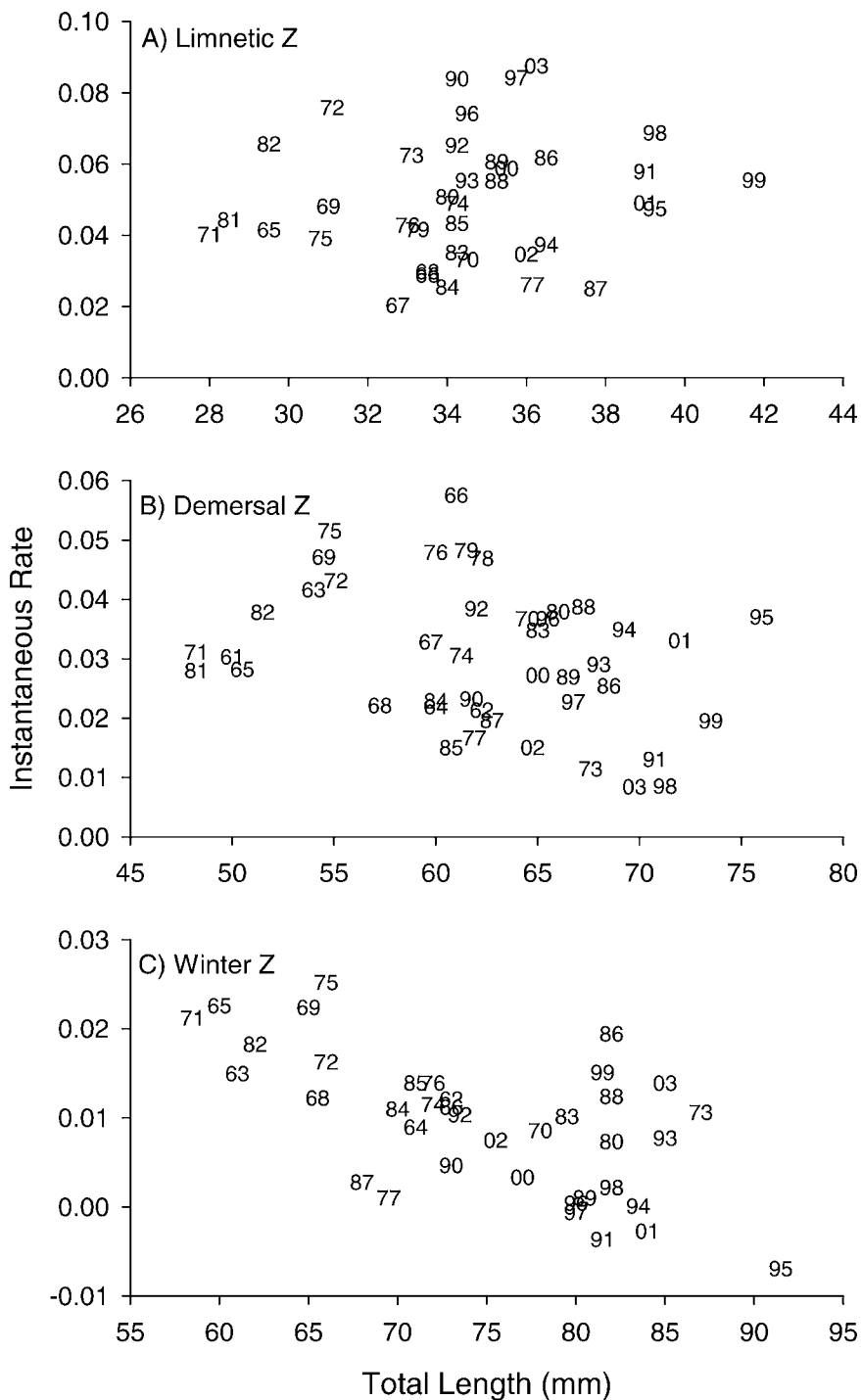


FIGURE 4.—Instantaneous daily mortality rates (Z) of age-0 yellow perch during the (A) limnetic and (B) demersal early life stage intervals relative to their average size within the interval and (C) the instantaneous winter mortality rate during the first overwinter period relative to total length on 15 October. Note the differences in the scale of the y-axes. Year cohorts are denoted by the two-digit numerals.

we saw the opposite trend in Oneida Lake: depensatory mortality was strongly evident when predation by walleyes was the primary regulator of the age-0 yellow perch population (Forney 1971, 1980; filled triangles in Figure 3C). In those years, mortality decreased at high yellow perch densities because the feeding rate of individual walleyes reaches a limit and increasing the number of walleyes involves a time lag of several years. In Oneida Lake, we have not typically measured high mortality for dense cohorts of age-0 yellow perch during any early life stage interval; therefore, we think it unlikely that previous high densities of age-0 yellow perch affected activity levels to the point of increasing mortality, as suggested by Walters (2000).

The disruption of depensatory mortality may reflect fluctuations in other prey species. In Oneida Lake, alternative prey (e.g., white perch and gizzard shad) may buffer walleye predation on young yellow perch for some early life stages (Rose et al. 1999; Fitzgerald et al. 2006), and direct competition during larval stages is unlikely because white perch and gizzard shad hatch later than yellow perch (Prout et al. 1990; Roseman et al. 1996). Walleye predation on yellow perch may be buffered from the time when alternative prey hatch to around 1 August, because both white perch and gizzard shad are capable of rapid growth and achieve a large end-of-year size. Increased buffering of predation provides immediate short-term benefits for some age-0 yellow perch but also could lead to time-delayed indirect negative effects (e.g., apparent competition; Holt 1977). For example, alternative prey species probably buffer cannibalism by walleyes in addition to buffering predation on yellow perch. Therefore, the walleye population may increase over time relative to that of the yellow perch population (Forney 1980; Rose et al. 1999). In such an instance, walleyes may eventually exert greater predation pressure on yellow perch than was the case before increases in alternative prey, particularly when buffering species have inconsistent recruitment; walleyes still consume mainly age-0 yellow perch during early summer (Lantry et al. 2008). This mechanism would be consistent with the observation of increased mortality during early life stages for years after the increase in gizzard shad in 1983 (Hall and Rudstam 1999).

Growth rates were density dependent for both limnetic and demersal age-0 yellow perch, but density-dependent growth was not evident in the more limited data available from the 8-mm to 18-mm larval surveys. That larval growth was not density dependent during the first interval is not surprising, given that newly hatched larvae are initially endogenous feeders and their low total biomass makes them unlikely to regulate their prey (Post et al. 1992). For example,

larval yellow perch frequently first consume adult and naupliar copepods but transition to a broader diet as they grow (e.g., Whiteside et al. 1985). The density-dependent growth observed during the limnetic and demersal stage suggests that there was competition for food resources. In Oneida Lake, growth of age-0 yellow perch has been shown to be positively correlated with biomass of the larger *Daphnia* species (Mills and Forney 1988). However, growth of age-0 yellow perch at high densities may also have been suppressed because of the more localized food limitations associated with formation of dense schools. If the energetic costs of schooling are particularly high relative to the amount of food available to dense aggregations of yellow perch, then growth rates should improve at reduced yellow perch densities (e.g., Eggers 1976; Boisclair and Leggett 1989).

Changing ecological conditions in Oneida Lake have altered the environment experienced by age-0 yellow perch. One of the major changes is a decrease in chlorophyll-*a* and an increase in water clarity associated with the invasion of zebra mussels in 1992 (Idrisi et al. 2001). In Oneida Lake, increased water clarity has also contributed to increased diversity and extent of submerged aquatic vegetation in the littoral zone (Zhu et al. 2006), which could affect both mortality and growth of young yellow perch when they occupy these inshore areas (during limnetic and demersal stages). The increased complexity and distribution of macrophytes may alter the availability of littoral prey items for young yellow perch while promoting a new suite of potential predators (e.g., black basses). These relationships may be especially important if young fish select structurally complex habitats in clear waters (Snickars et al. 2004). Furthermore, clearer water may drive size-specific differences in foraging behavior and vulnerability. Utne-Palm (2002) summarized potential size-dependent effects of turbidity on predator-prey interactions and suggested that small predators, which forage upon prey in close proximity, benefit from both the increased contrast between a nearby potential prey and its background as well as from the protective cover of turbid water (see also Johnson and Hines 1999). On the other hand, larger predators, with a greater reactive volume, experience a limited visual field under the same conditions (Utne-Palm 2002). In Oneida Lake, the foraging success of both limnetic age-0 yellow perch and their larger predators appears to have increased with higher water clarity; we observed both higher growth rates and higher mortality rates with increased water clarity. The exact role of water clarity in relation to mortality and growth of age-0 yellow perch remains unclear.

Temperature also is an important influence on fish

and can even contribute to regional patterns in year-class strength (Koonce et al. 1977; Casselman 2002). The average water temperature in Oneida Lake during the growing season of age-0 yellow perch has increased over time. Over the past several decades, the duration of winter ice cover on Oneida Lake has decreased, and complete ice cover did not occur during the winter of 2001–2002—an extremely rare event according to records dating from the mid 1800s (Magnuson et al. 2000; Fitzgerald et al. 2006). Changing springtime warming patterns would probably affect the timing of yellow perch spawning, hatching period, and duration of the larval period. In Oneida Lake, larval yellow perch are generally reaching 18 mm earlier in the spring (Figure 5A), and this shift in timing is related to warmer May water temperatures (Figure 5B). Because we do not have annual estimates of hatch date, we have not determined whether the earlier attainment of 18 mm is due to an earlier hatch date, an increased growth rate after hatching, or both. Clady (1976) found increased survival of prolarval yellow perch during years with higher mean temperatures and noted that survival was more strongly correlated to mean temperature than to the observed daily warming rates. Warmer temperatures probably allow for a more rapid transition through the interval with the highest daily mortality rates. In the end, ecological changes may modify spatial and temporal overlap between predators and prey (e.g., Winder and Schindler 2004) and may either increase or decrease early mortality. When multiple observed ecological changes trigger both increases and decreases in mortality, distinguishing the effects of each on recruitment will be difficult.

Growth and mortality of age-0 yellow perch in Oneida Lake interact through a process of delayed compensation; although early increased mortality further reduces density, increased growth results in a larger end-of-year size, which benefits overwinter survival (Fitzgerald et al. 2006). As a result, measures of age-1 yellow perch during the spring and summer have remained surprisingly stable (Rudstam et al. 2004; Fitzgerald et al. 2006), given the dramatic decline in age-0 densities documented here. The winter mortality of recent cohorts has decreased despite the lower density of young-of-year yellow perch, the lowest observed winter mortality rate being that for the 1995 cohort, which is also the cohort that had achieved the largest observed mean total length by autumn. Previously, compensation in the Oneida Lake yellow perch population was attributed to the buffering of walleye predation on age-1 yellow perch during spring and summer by abundant age-0 cohorts (Nielsen 1980). However, this mechanism may no longer be operating, because we have not observed high densities of age-0

yellow perch in recent years. Consideration of stage-specific mortality and growth rates for age-0 yellow perch indicates that they are now probably less tightly coupled to traditional primary prey resources and predators (e.g., *Daphnia* spp. and walleyes) than previously reported (e.g., Mills and Forney 1988). The likely causes include establishment of nonindigenous species (and associated ecological changes) and climate warming. It appears that delayed compensation, resulting in reduced mortality through the first winter and second spring, is now more important than depensation for the Oneida Lake yellow perch population. These analyses also indicate that density-dependent growth during the first year of life is resulting in the attainment of larger end-of-year size by age-0 fish before their first winter (see also Fitzgerald et al. 2006).

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