Journal of Fish Biology (2006) **68,** 681–694
doi:10.1111/j.1095-8649.2006.00946.x, available online at http://www.blackwell-synergy.com

Natural disturbance and life history: consequences of winterkill on fathead minnow in boreal lakes

A. J. Danylchuk* and W. M. Tonn

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada

(Received 4 November 2004, Accepted 12 August 2005)

Age, growth and reproductive characteristics of fathead minnow *Pimephales promelas* populations inhabiting four lakes that varied in the extent and frequency of winterkill were studied in the boreal region of western Canada. The lifespan of fathead minnows inhabiting lakes prone to winterkill was 1–2 years shorter than those in less disturbed lakes. In populations prone to winterkill, fish displayed faster growth rates and grew to a larger size-at-age, particularly during the first year of life. Although lower population densities in winterkill lakes probably contributed to this increased growth, adults in these populations tended to spawn earlier in the season than the smaller adults in more stable populations. Fathead minnows in lakes prone to winterkill also matured at an earlier age and allocated a greater proportion of their body mass to gonads than conspecifics in the more benign, stable lakes. These trends are consistent with predictions for organisms in variable, unpredictable environments and, because fathead minnows are tolerant to a wide range of environmental conditions, suggest that variation in life-history traits among populations is probably a product of both selection and phenotypic plasticity.

Key words: boreal lakes; fathead minnow; life-history; winterkill.

INTRODUCTION

Winter conditions in northern regions can decrease oxygen concentrations in lakes. Extended periods of ice and snow cover and the decomposition of organic matter contribute to the development of winter hypoxia, especially in shallow, productive lakes (Greenbank, 1945; Barica *et al*., 1983). In turn, winter hypoxia is a natural disturbance that can have dramatic impacts on fish populations and assemblages, including the death, or winterkill, of large numbers of fishes when their oxygen requirements are not met (Casselman & Harvey, 1975; Tonn & Paszkowski, 1986; Fox & Keast, 1990).

Absolute oxygen requirements in fishes are size-dependent, and larger fishes are typically more susceptible to winter hypoxia (Moyle & Cech, 1996). As such, winterkill often affects the size structure of populations by reducing the number of large individuals (Casselman & Harvey, 1975; Fox & Keast, 1990). Moreover,

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*Author to whom correspondence should be addressed at present address: Cape Eleuthera Institute – RSD c/o Twin Air, 498 SW 34th Street, Ft. Lauderdale, Florida 33315, U.S.A. Tel.: +1 242 359 7625; fax: +1 954 252 2440; email: andydanylchuk@islandschool.org because of lower absolute oxygen demands and physiological and behavioural adaptations (Gee *et al.*, 1978; Klinger *et al.*, 1982; Magnuson *et al.*, 1985), small-bodied fishes tend to cope with winter hypoxia more effectively than large-bodied species. This, in turn, can affect the species composition of fish assemblages, with only small-bodied fishes persisting in lakes prone to winter hypoxia (Tonn & Magnuson, 1982; Robinson & Tonn, 1989).

Although more tolerant, even small-bodied fishes can be affected if winter oxygen depletion is severe (Klinger *et al.*, 1982). Population densities and size structures of small-bodied fishes are more variable from year-to-year in lakes prone to severe and frequent oxygen depletion than in lakes that develop hypoxia only occasionally, or not at all (Danylchuk & Tonn, 2003). Given the higher density-independent mortality and consequently shorter expected life spans of fishes in lakes prone to winterkill, life-history theory predicts that selection should favor earlier maturity and a higher reproductive investment (MacArthur & Wilson, 1967; Stearns, 1992). In pumpkinseed *Lepomis gibbosus* (L.) for example, populations inhabiting beaver ponds prone to winter hypoxia differed in life-history traits from a population in a larger, more stable, lake in the direction predicted by theory (Fox & Keast, 1990, 1991). Large environmental differences between beaver ponds and lakes, however, combined with a limited ability to deal with low oxygen levels, probably contributed to the development of different life histories among pumpkinseed populations. It is unknown whether similar differences in life-history characteristics hold true among populations of small-bodied fishes, such as minnows (Cyprinidae), that often dominate small north-temperate lakes. Environmental similarities, however, are considerably greater among small lakes along a winterkill gradient than the pond-lake contrast of Fox & Keast (1990, 1991). These similarities therefore facilitate a more direct examination of the role that winterkill plays in creating and maintaining life-history differences.

The purpose of this study was to examine the effects of winter hypoxia on life-history characteristics of fathead minnow *Pimephales promelas* Rafinesque populations inhabiting a series of small boreal lakes that varied in frequency and intensity of winterkill, thus resulting in populations that displayed a gradient of densities and variations in density (Danylchuk & Tonn, 2003). Based on life-history theory (Stearns, 1992), it was predicted that fathead minnows in lakes prone to winterkill (lower densities and greater variation) would have a shorter average lifespan than populations in lakes where winter oxygen depletion is less severe or frequent. In response to higher adult mortality, it was also predicted that fathead minnows in more disturbed populations would grow faster, mature at younger ages and allocate more resources to reproduction than those in more stable populations. As well, greater growth and reproductive allocation may permit earlier spawning in winterkill populations, which could feed back positively into greater growth of young-of-the-year (YOY), increasing their overwinter survival and ultimately parental fitness (Post & Evans, 1989; Shuter & Post, 1990). Conversely, because hypoxia can disrupt endocrine functions in fishes and potentially reduce overall reproductive success (Wu *et al.*, 2003), fathead minnows in lakes prone to winterkill might show different reproductive traits when compared to those in more stable lakes. Thus, seasonal patterns in spawning activity were also examined to determine if differences among populations were linked to the disturbance regime (frequency and intensity of population declines) and to differences in other life-history traits.

MATERIALS AND METHODS

STUDY LAKES AND POPULATIONS

Four populations of fathead minnow were studied over a 5 year period (1995–1999). These populations inhabited lakes, accessible only by an all-terrain vehicle, located in the Boreal Plains Ecozone of western Canada, *c.* 200 km north of Edmonton, Alberta. The lakes, designated SCL20, SCL100, SCL200 and SCL800, are located within 30 km of each other, and are all relatively small (<110 ha), shallow (mean depth 0·6–4·6 m) and naturally eutrophic (Table I; Devito *et al.*, 2000; Prepas *et al.*, 2001). Small-bodied species dominate the fish assemblages. SCL20 contains an allopatric population of fathead minnow, while the other three lakes are inhabited by fathead minnow, brook stickleback *Culaea inconstans* (Kirtland) and finescale dace *Phoxinus neogaeus* Cope. In some years, SCL200 also contains a small, transient population of white sucker *Catostomus commersoni* (Lacépède).

Population estimates derived from mark-recapture surveys showed that densities varied greatly across populations, as did the year-to-year variability in density (Table I). Variability among lakes and years was largely driven by the extent of winter oxygen depletion, as large declines in fathead minnow density (47–94%) were documented in lakes following winters of notably low dissolved oxygen levels (Danylchuk & Tonn, 2003). Of the four study lakes, SCL800 and SCL200 experienced the most dramatic (>80%) and frequent overwinter declines in fathead minnow density. The population in SCL20 experienced one significant decline (47%), while the population in SCL100 was relatively stable from year to year. Thus, the four populations represent a gradient of populations at risk of winterkill, from high (SCL800) to low (SCL100); this gradient was well reflected in the coefficients of variation (CV) in population density over the 5 years (Table I).

TABLE I. Physical and chemical characteristics of the four study lakes (data are from the TROLS project core sampling programme; Prepas *et al.*, 2001) and densities, year-to-year variations in density and number of major winterkills of fathead minnows inhabiting the four study lakes from 1995 to 1999 (data summarized from Danylchuk & Tonn, 2003)

Lake	Latitude (°N)	Longitude (°W)	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Total phosphorus (μg l^{-1})	Chlorophyll *a* (μg l^{-1})
SCL100	55·13	111·66	18	3·5	7·6	24	11
SCL20	55·19	113·66	52	4·8	12·0	46	19
SCL200	55·10	113·73	109	0·6	2·1	58	12
SCL800	55·38	113·63	75	2·1	3·0	55	8·8

Lake	Mean density (number m^{-3})	Range in density (number m^{-3})	CV (%)	Number of large (>47%) declines over a 5 year period
SCL100	1·92	1·35–2·44	22·8	0
SCL20	3·75	2·22–5·37	33·6	1
SCL200	0·72	0·17–1·10	56·9	1
SCL800	0·14	0·02–0·37	93·5	2

LIFE-HISTORY CHARACTERISTICS

From 1995 to 1998, unbaited Gee minnow traps (2 cm trap openings, 5 mm mesh) were used to collect fathead minnows from each lake early in the spring, shortly after ice-off and before the onset of reproductive activity. Fish >38 mm (total length, L_T) were susceptible to the traps. Traps were set in the late afternoon at randomly selected sites within the 0–2 m depth stratum (where fathead minnows concentrate; unpubl. data), and retrieved the following day. A sub-sample of *c.* 60 fish per lake and year were euthanized with tricaine methanesulphonate (MS 222), stored on ice, and subsequently frozen until time of processing.

After thawing with cold tap water, fish were measured (L_T to the nearest mm), and mass determined (to nearest 0·001 g). To determine gender and stage of maturity, all specimens were dissected and the physical condition of the gonads assessed by macroscopic observation. Fish were considered mature if testes were white and enlarged or ovaries contained yolked eggs. Gonads were removed and weighed (nearest 0·001 g). Both lapilli otoliths were also removed, cleaned, and stored dry until they were processed for ageing.

To prepare otoliths, each lapillus was mounted whole on a glass microscope slide. The slide was warmed on a hot plate (45–55° C) and a thin layer of thermoplastic cement (Buehler No. 40–8100) was applied to one end of the slide. As the cement thickened, an otolith was placed in it with the convex lateral surface facing up. After cooling, otoliths were ground using a sequence of progressively finer wet sandpaper (600, 1200 and 1500 grit) until the primordium was clearly visible. Lapilli were then polished with diamond paste (8000 mesh equivalent) and a felt polishing cloth. Lastly, the slide was reheated and a thin layer of molten thermoplastic cement spread over the otoliths as a clearing agent.

Otoliths were examined in transmitted light at ×20 magnification and measurements were made with an ocular micrometer. The otolith radius (O_R) and distance to each annuli were measured using a longitudinal axis from the primordia to the posterior edge of the otolith. For each population, a standard L_T and O_R relationship was determined by linear regression using fish collected during all study years (sample sizes for each population were 160–198 fish). Using the standard L_T and O_R intercepts for each population, the L_T-at-age was backcalculated for each fish by the Fraser-Lee method (Bagenal & Tesch, 1978). The mean backcalculated L_T for each age (years) was then determined, as was the instantaneous growth rates g, $g = [\ln(L_T \text{ at age } x + 1) - \ln(L_T \text{ at age } x)]$ between consecutive ages for each sex to quantify age-specific growth patterns in each population. Instantaneous growth rates between age 0 and age 1 year were calculated using mean size-at-hatch (5·44 mm L_T) for L_T at age 0 years (Grant & Tonn, 2002).

As a measure of body condition, the relationship (slopes) between body mass (M_B) and L_T for males and females was examined for each lake pooled across years, and the trend for each sex compared to test for differences in body condition across populations. The proportion of mature fish at each age was determined for each sex and compared across populations. To examine trends in the allocation of energy to gonads for each sex, the relationship between M_B and gonad mass (M_G) was compared by pooling data among years for either males or females and testing for differences among populations.

REPRODUCTIVE ACTIVITY

During the breeding season, reproductively active males establish territories around the underside of structures, including introduced nesting substrata, and subsequently fertilize and care for the eggs that are laid on the structure by females (Wynne-Edwards, 1932; Andrews & Flickinger, 1974; Benoit & Carlson, 1977). Reproductive activity was monitored from 1996 to 1998 by deploying 12–16 floating fence boards (100 × 4·5 cm) anchored to bricks along the shoreline of each lake as nesting substrata (Danylchuk & Tonn, 2001). Nestboards were placed in groups of three to four in the north, south, east and west ends of each lake, with nestboards in each group *c.* 20 m apart. To estimate the initiation of spawning in each lake, nestboards were checked every 2–3 days for the presence of eggs beginning just after ice-out. Following the initiation of spawning, nestboards were checked *c.* every 7–10 days, recording the number of nests on each nestboard, and assessing egg development. From these observations, peak spawning activity and duration of the reproductive season was estimated for each population in each year. Peak spawning was noted as the date with the highest mean number of nests per board for each population. The duration of the spawning season was estimated by determining the number of days between the initiation of spawning and the date of the last survey when eggs were present on nestboards. Monitoring the nestboards ceased when no nests were present for two consecutive sampling periods.

Because water temperature can affect the initiation of reproduction (Ridgway *et al.*, 1991), a temperature data logger (Hobo 8K, Onset Computer Corporation, Pocasset, MA, U.S.A.) was deployed in each lake shortly after ice-out in each year. Loggers were set in *c.* 30 cm of water at the north end of each lake. Water temperature was recorded hourly throughout the open water season, and the thermal regime of each lake in each year was characterized by calculating cumulative degree-days $\geq 15°$ C, based on mean daily temperatures; 15° C is the approximate mean minimum water temperature at the initiation of spawning activity (Andrews & Flickinger, 1974). From these data, the mean cumulative degree-days at initiation of spawning was determined for each population to test whether population-level differences in the initiation of spawning activity was related to lake-specific differences in thermal regime.

DATA ANALYSES

Data were tested for normality and homogeneity of variance with Shapiro-Wilk and Bartlett tests, respectively (Sokal & Rohlf, 1995). Backcalculated L_T at age 3 years ($\log_{10}$), L_T, M_B and M_G ($\log_{10} x + 1$), and proportion mature (arcsine square root) were transformed to meet the assumptions of parametric statistics (*t*-test, ANOVA, ANCOVA). Non-parametric statistics (Mann–Whitney *U*-test, Kruskal-Wallis test) were used when these assumptions could not be satisfied. Data compared using ANCOVA were first tested for parallelism of slopes, and if this assumption could not be met (even using transformed data) subsets of the populations within common, but limited ranges of the independent variables (*i.e.* L_T and M_B) were compared among lakes. For all tests, differences among variables were considered marginally significant if $0{\cdot}1 \geq P > 0{\cdot}05$ and significant if $P \geq 0{\cdot}05$. Statistical analyses were performed using Statistica '99 for the PC (StatSoft Inc., Tulsa, OK, U.S.A.) and Minitab 11 (Minitab Inc., State College, PA, U.S.A.).

RESULTS

AGE, GROWTH AND BODY CONDITION

Maximum age of fathead minnows was highest (5+ years) in the two more stable populations, SCL100 and SCL20, and lowest (3+ years) in the most disturbed and variable population, SCL800 (Fig. 1). The only difference in longevity between sexes occurred in SCL800, where males lived 1 year less than females. Because of relatively large variation, size-at-age did not differ between sexes (*t*-test or Mann–Whitney *U*, d.f. = 6 $P > 0{\cdot}1$) except for age 5 year fish in SCL 20 and SCL100, and age 2 year fish in SCL800; in these cases, males were larger than females (*t*-test, d.f. = 2–6, $P < 0{\cdot}05$). Given these few differences, the backcalculated size-at-age for both sexes was subsequently combined to examine general trends for the four populations.

Maximum size and size-at-age displayed the opposite pattern relative to longevity: fathead minnows in SCL800, the most disturbed and variable population,

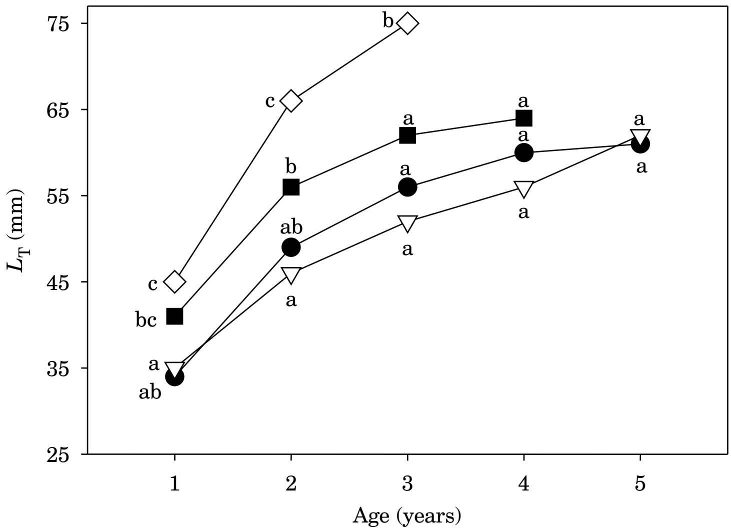

FIG. 1. Mean backcalculated total lengths at age for fathead minnows in the four study lakes [SCL 100 (▽), SCL20 (●), SCL 200 (■) and SCL800 (◇)]. Lower case letters indicate significant differences ($P < 0{\cdot}05$) across populations for a given age (Mann–Whitney *U* or Tukey's HSD).

had the fastest growth and achieved the greatest mean L_T (75 mm), followed by fish in SCL200, SCL20 and SCL100 (Fig. 1). Mean L_T-at-age was significantly different across populations for ages 1+, 2+ and 3+ years (Kruskal-Wallis or ANOVA, d.f. = 3,12, $P < 0{\cdot}05$). Fish of these ages in the two more stable populations, SCL20 and SCL100, were smaller than fish in SCL800 (Mann–Whitney *U* or Tukey's HSD, $P < 0{\cdot}05$). Fish in SCL100 were also smaller at ages 1+ and 2+ years than similar-aged fish in SCL200 (Mann–Whitney *U*, $P < 0{\cdot}05$). In turn, age 2+ and 3+ year fish in SCL200 were smaller than fish of comparable ages in SCL800 (Mann–Whitney *U*, $P < 0{\cdot}05$).

For both sexes, age-specific growth rates differed among populations between age 0 and 3 years (ANOVA or Kruskal-Wallis, $P < 0{\cdot}05$; Fig. 2). During their first year of life, fathead minnows in SCL200 and SCL800 grew faster than conspecifics in the more stable SCL20 and SCL100 (Mann–Whitney *U*, $P < 0{\cdot}05$). These differences were maintained in the next year for males (Tukey's HSD, $P < 0{\cdot}05$), however, females differed only between SCL800 and SCL100, with those in the former growing faster than those in the latter (Tukey's HSD, $P < 0{\cdot}05$). Between age 2 and 3 years, males and females in SCL20 and SCL200 grew faster than those in SCL100 (Mann–Whitney *U*, $P < 0{\cdot}05$); faster growth for these age-classes also occurred for females in SCL800 when compared to females in SCL100 (Mann–Whitney *U*, $P < 0{\cdot}05$).

Body mass ($\log_{10} M_B$) at a given L_T ($\log_{10} L_T$) differed among populations for both males and females (Fig. 3, ANCOVA, $P < 0{\cdot}01$). Males and females from SCL800 were significantly heavier at a given $\log_{10}L_T$ than males and females from SCL20, SCL100 and SCL200 (Tukey's HSD, $P < 0{\cdot}05$). In addition, males and females from SCL200 were heavier at a given $\log_{10}L_T$ than females than females in SCL20 and SCL100 (Tukey's HSD, $P < 0{\cdot}05$).

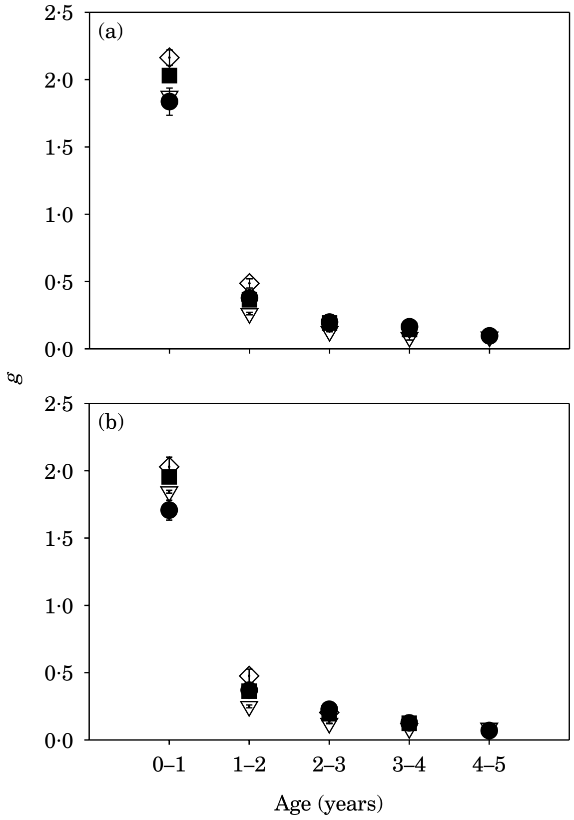

FIG. 2. Mean ± S.E. age-specific instantaneous growth rates for (a) male and (b) female fathead minnows in the four study lakes [SCL 100 (▽), SCL20 (●), SCL 200 (■) and SCL800 (◇)].

REPRODUCTIVE TRAITS

Seventy five per cent or more of age 1 year males in the more disturbed and variable SCL200 and SCL800 populations were mature, whereas this degree of maturity was not documented until age 3 years in SCL100 and age 4 years in SCL20 (Table II). Differences in maturity were less pronounced for females, nevertheless the percentages of females at age 2 years that were mature in SCL200 and SCL800 were slightly higher than in SCL20 (Table II).

Slopes of the relationship between gonad mass [$\log_{10}(M_G + 1)$] and body mass [$\log_{10}(M_B + 1)$] for mature males and females differed among populations. To facilitate a comparison, a common subset of M_B was selected (1·50–3·00 g for both males and females), allowing for the assumptions of parallel slopes to be met. For the narrower subset of M_B, the relationship between M_G and M_B differed significantly among the four study populations (Fig. 4; ANCOVA, $P < 0{\cdot}0001$). For males, M_G from SCL 800 and SCL200 were significantly greater than M_G from SCL 20 and SCL100 (Tukey's HSD, $P < 0{\cdot}05$). Similarly, M_G of females from SCL800 and SCL200 was significantly greater than M_G of females from SCL20 and SCL100 (Tukey's HSD, $P < 0{\cdot}05$), and M_G of females from SCL800 was also greater than females from SCL200 Tukey's HSD, $P < 0{\cdot}05$).

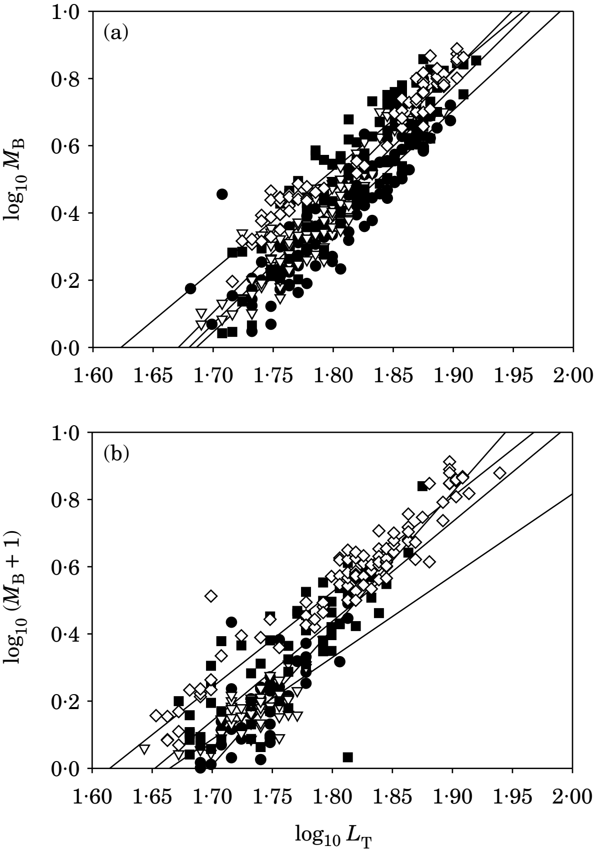

FIG. 3. Relationship between body mass and total length for (a) male and (b) female fathead minnows in the four study lakes [SCL20 (●), SCL 100 (▽), SCL 200 (■) and SCL800 (◇)]. The curves were fitted by: (a) SCL 20 $y = -5{\cdot}57 + 3{\cdot}30\,x$, SCL 100 $y = -5{\cdot}92 + 3{\cdot}52$, SCL 200 $y = -6{\cdot}01 + 3{\cdot}60x$ and SCL 800 $y = -4{\cdot}85 + 2{\cdot}99x$; (b) SCL 20 $y = -6{\cdot}89 + 4{\cdot}06\,x$, SCL 100 $y = -4{\cdot}05 + 2{\cdot}43\,x$, SCL 200 $y = -4{\cdot}89 + 2{\cdot}96x$ and SCL 800 $y = -4{\cdot}57 + 2{\cdot}83x$.

Based on the monitored nestboards, nesting activity began between mid-May and early-June (Table III). Initiation of spawning activity differed marginally among populations (two-way ANOVA, d.f. = 3, 8, $P < 0{\cdot}1$), with fathead minnows in SCL200 and SCL800 initiating spawning activity 1–2 weeks earlier than conspecifics in the more stable SCL20 and SCL100 populations. Similarly, cumulative degree-days $\geq 15°$ C needed to initiate spawning also differed marginally among lakes, with spawning activity in SCL200 and SCL800 beginning after fewer cumulative degree-days than in SCL20 and SCL100 (ANOVA, d.f. = 3,8, $P < 0{\cdot}1$). Although spawning activity appeared to peak earlier in SCL200 and SCL 800 (Table III), differences among populations were not significant (ANOVA, d.f. = 3,8, $P > 0{\cdot}1$), probably due to high variation among years. The duration of spawning activity also did not differ among populations (ANOVA, d.f. = 3, 8, $P > 0{\cdot}1$).

TABLE II. Mean ± S.E. percentage of males and females of age that were mature in a given lake over a 4 year period. Samples sizes in parentheses refer to the number of years fish at each age were collected for a given lake

Males Lake	Age (years) 1	2	3	4	5
SCL100		0 ± 0	100 ± 0	88 ± 8	100 ± 0
	$(n = 0)$	$(n = 1)$	$(n = 2)$	$(n = 4)$	$(n = 4)$
SCL20		54 ± 0	57 ± 20	79 ± 11	98 ± 3
	$(n = 0)$	$(n = 1)$	$(n = 3)$	$(n = 3)$	$(n = 3)$
SCL200	100 ± 0	100 ± 0	93 ± 8	100 ± 0	
	$(n = 2)$	$(n = 4)$	$(n = 4)$	$(n = 2)$	$(n = 0)$
SCL800	75 ± 18	100 ± 0			
	$(n = 2)$	$(n = 3)$	$(n = 0)$	$(n = 0)$	$(n = 0)$
Females Lake					
SCL100			90 ± 10	97 ± 3	100 ± 0
	$(n = 0)$	$(n = 0)$	$(n = 3)$	$(n = 3)$	$(n = 3)$
SCL20		80 ± 0	100 ± 0	83 ± 18	70 ± 30
	$(n = 0)$	$(n = 1)$	$(n = 2)$	$(n = 4)$	$(n = 2)$
SCL200	100 ± 0	100 ± 0	89 ± 10	100 ± 0	
	$(n = 1)$	$(n = 4)$	$(n = 2)$	$(n = 2)$	$(n = 0)$
SCL800	100 ± 0	100 ± 0	100 ± 0		
	$(n = 1)$	$(n = 3)$	$(n = 2)$	$(n = 0)$	$(n = 0)$

DISCUSSION

Life-history traits of fathead minnow varied among populations, and differences were related to the incidence of natural disturbance and its demographic effects. Fathead minnows in lakes prone to frequent and severe winterkills were shorter lived, exhibited faster growth rates, grew to a larger body size at age, allocated a greater proportion of their body mass to gonad development and tended to mature earlier compared to fathead minnows in more stable lakes. In addition, spawning activity began and peaked earlier in the season in lakes with more frequent or severe winterkills.

As a natural disturbance, winterkill directly removes individuals from a population; not surprisingly, fathead minnow densities in lakes prone to frequent or severe winterkill were lower and more variable than those in lakes less subject to this disturbance (Danylchuk & Tonn, 2003). In turn, population density, through its effects on per capita resource availability, could influence opportunities for the uptake of energy that can then be allocated to the competing ends of maintenance, growth and current reproduction (Murnyak *et al.*, 1984; Deacon & Keast, 1987). For example, Deacon & Keast (1987) found that pumpkinseed grew to a large body size and had higher reproductive output in a lake with lower population density and higher prey availability than did conspecifics inhabiting a lake with higher population density and lower prey availability. Although a

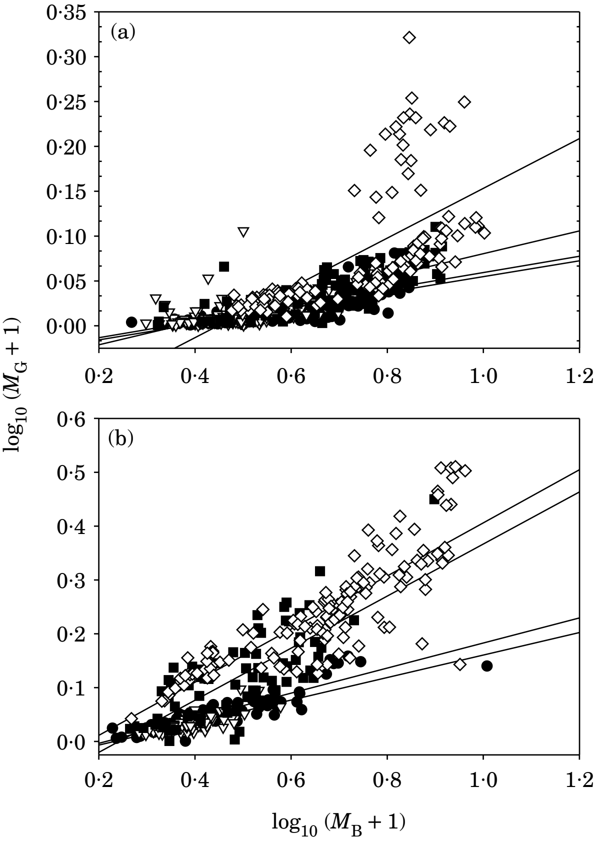

FIG. 4. Relationship between gonad mass and body mass for (a) male and (b) female fathead minnows in the four study lakes [SCL20 (●), SCL 100 (▽), SCL 200 (■) and SCL800 (◇)]. The curves were fitted by: (a) SCL 20 $y = -0{\cdot}033 + 0{\cdot}088x$, SCL 100 $y = -0{\cdot}031 + 0{\cdot}091x$, SCL 200 $y = -0{\cdot}047 + 0{\cdot}127x$ and SCL 800 $y = -0{\cdot}124 + 0{\cdot}277x$; (b) SCL 20 $y = -0{\cdot}050 + 0{\cdot}233x$, SCL 100 $y = -0{\cdot}049 + 0{\cdot}209x$, SCL 200 $y = -0{\cdot}117 + 0{\cdot}484$ and SCL 800 $y = -0{\cdot}086 + 0{\cdot}494x$.

concomitant increase in both growth and reproduction seems contrary to the idea of trading-off energy among life-history traits, differences in growth among the fathead minnow populations were largely established within the first year of life, prior to fish reaching maturity, indicating that differences were probably related more to per capita resource availability than a trade-off of energy between growth and current reproduction. Moreover, costs of allocating resources from one trait to another may only be incurred when energetic resources are limited (Schultz & Warner, 1991). In the present study, food resources may not have been limited in lakes prone to winterkill because of lower population density and higher invertebrate biomass (Prepas *et al.*, 2001), allowing greater allocation of energy to both growth and reproduction by fathead minnows.

In conjunction with higher per capita resource availability, differences in first-year growth rates could also be linked indirectly to densities through the timing of reproduction. Seasonal timing of reproduction in fishes can be positively

TABLE III. Indicators of reproductive activity (mean ± S.E.; range in parentheses) for fathead minnow populations inhabiting the four study lakes from 1996 to 1998. CDD, cumulative degree-days $\geq 15°$ C. Also given are the lake-effect results of two-way (lake-by-year) ANOVAS

Lake	Julian day at first reproduction	CDD at first reproduction (degree-days)	Julian day at peak reproduction	Duration of spawning season (days)
SCL100	158 ± 8	24·7 ± 0·9	174 ± 14	69 ± 4
	(142–169)	(22·9–26·2)	(146–193)	(63–76)
SCL20	155 ± 4	29·2 ± 11·4	168 ± 10	51 ± 9
	(146–161)	(9·8–49·4)	(162–188)	(34–56)
SCL200	147 ± 8	14·7 ± 2·3	160 ± 7	63 ± 8
	(132–157)	(10·1–17·1)	(146–168)	(55–79)
SCL800	142 ± 8	6·3 ± 3·5	161 ± 10	61 ± 10
	(132–157)	(1·8–13·3)	(146–180)	(49–80)
$F_{(3,8)}$	3·71	3·32	0·88	1·30
P	<0·1	<0·1	>0·1	>0·1

size-dependent (Ridgway *et al.*, 1991; Danylchuk & Fox, 1994, 1996). The larger body size of fathead minnows inhabiting lakes prone to winterkill may therefore have allowed an allocation of energy to reproduction earlier in the season relative to smaller fish inhabiting more stable lakes. In turn, spawning early in the season could contribute to the larger body sizes of YOY in winterkill lakes by providing offspring more time to accumulate energy, especially if competition for food resources within a cohort is low (Post *et al.*, 1999).

The timing of reproduction within an individual's lifetime could also be affected by the susceptibility to winterkill through its influence on lifespan. Individuals from populations with relatively different lifespans should have different ages at maturity, to increase the likelihood of contributing young to the next generation and maximize parental fitness (Stearns, 1992; Gunderson, 1997). The trend of younger ages at maturity observed for populations more prone to winterkill is probably related to reduced lifespan associated with this disturbance (Fox & Keast, 1991). A similar response in age at maturity has been linked to predator-induced mortality (Reznick, 1996), however, the major predators in the current study lakes are piscivorous birds, such as the common loon *Gavia immer* (Brunnich), which were present on all four lakes.

In spite of the close proximity of the four lakes and their generally similar limnological characteristics, the frequency and severity of winterkill among the four populations varied, which then had concomitant effects on life-history traits. The observed differences in life-history traits are probably related to both density effects and micro-evolutionary selection that influences the trade-off of energetic resources throughout the course of an individual's lifetime (Stearns, 1992; Van Winkle *et al.*, 1993). Because the extent of winter hypoxia varies dramatically and unpredictably from year to year, the evolution of more flexible, plastic phenotypes can also result (Stearns, 1992; Belk, 1995; Baker & Foster, 2002).

The ability of fathead minnow populations to persist in highly variable and unpredictable environments, not only in the boreal forest but throughout their wide geographic range (Scott & Crossman, 1973; Sublette *et al.*, 1990), suggests that selection has favoured the evolution of phenotypic plasticity (Stearns, 1992). Empirical studies that compare and contrast the expression of life-history traits among populations exposed to different, and varying, environmental conditions are critical to identify the phenotypic traits that are variable and probably contribute to the success of these populations. Manipulative studies, including common garden and transplant experiments (Fox, 1994; Belk, 1995), should subsequently be performed to examine the extent to which the observed variation in life-history traits is attributable to phenotypic plasticity and genetic differentiation (Belk, 1995; Danylchuk & Tonn, 2001).

The authors acknowledge the generous support for the TROLS project from NSERC, Alberta-Pacific Forest Industries, Weyerhaeuser Canada Ltd, Alberta Environmental Protection, Manning Diversified Forest Products, Syncrude Canada Ltd, Alberta Economic Development and Tourism, Ainsworth Lumber Co. Ltd, Employment Canada, NRC, NWRI, R.L. & L. Environmental Services, CS Resources, and the University of Alberta. Additional support for our research was received from the Biodiversity Grants Program (Department of Biological Sciences, University of Alberta and Alberta Conservation Association), and grants from the Canadian Circumpolar Institute (AJD), Alberta Sports, Recreation, Parks, and Wildlife Foundation (AJD), and NSERC (WMT). Thanks to S. Teige, C. Decker, G. Sandland, R. Dillon, J. Haag, L. Turner, K. Field, S. Reedyk, N. Scott and W. Zyla, who assisted in the field, and to N. Carmosini, M. Serediak and K. Aos for logistical support. The manuscript benefited from constructive criticisms of J.J. Magnuson, N. Stacey and C. Paszkowski, and statistical advice from R. Moses. Preparation of this manuscript was completed while the first author was employed by The Island School and Cape Eleuthera Institute.

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