

# Indirect effects of fish winterkills on amphibian populations in boreal lakes

**B.R. Eaton, W.M. Tonn, C.A. Paszkowski, A.J. Danylchuk, and S.M. Boss**

**Abstract:** We exploited fish winterkills in small, boreal Alberta lakes to determine if anuran amphibians respond to large but natural changes in fish densities. Eight large declines in fish abundance occurred in seven lakes over a 5 year period, while major increases in fish abundance, reflecting recovery after winterkill, were recorded 5 times. Summer pitfall trapping of young-of-the-year (YOY) Wood Frogs (*Rana sylvatica* LeConte, 1825) and Boreal (*Bufo boreas boreas* Baird and Girard, 1852) and Canadian (*Bufo hemiophrys* Cope, 1886) toads indicated that frog abundance responded consistently to such large changes in fish abundance, but especially if fish communities were dominated by small-bodied species (sticklebacks and minnows). As well, changes in YOY Wood Frog and fish abundance were negatively correlated; YOY Wood Frogs were as much as 7.7 times more abundant after winterkills than in non-winterkill years. These increases in metamorphs did not result from an increased immigration of breeding adults to winterkill lakes, suggesting instead that larval survival was greater. Higher abundance of YOY Wood Frogs and toads was associated with smaller body size at metamorphosis. Despite this apparent reduction in individual growth, abundance of juvenile frogs remained significantly elevated 1 year after winterkill. In contrast to Wood Frogs, YOY toads tended to respond positively to recoveries of small-fish populations. Because anuran amphibians can respond to fish winterkill, and because winterkill is a frequent natural disturbance, small fish-bearing lakes can serve as important breeding habitat for amphibians in Alberta's boreal forest.

**Résumé :** Nous avons utilisé les mortalités massives de poissons en hiver dans de petits lacs boréaux de l'Alberta pour vérifier si les amphibiens anoures réagissent aux changements importants mais naturels de densité des poissons. Il y a eu huit déclin d'abondance majeurs des poissons dans sept lacs au cours d'une période de 5 ans, alors qu'il s'est produit des accroissements importants de l'abondance des poissons à 5 reprises, en récupération de la mortalité hivernale. Les captures dans des pièges à fosse en été de jeunes de l'année (YOY) de la grenouille sylvestre (*Rana sylvatica* LeConte, 1825), du crapaud boréal (*Bufo boreas boreas* Baird et Girard, 1852) et du crapaud du Canada (*Bufo hemiophrys* Cope, 1886) indiquent que l'abondance des anoures réagit de façon uniforme à ces grands changements d'abondance des poissons, mais particulièrement lorsque les communautés de poissons sont dominées par des espèces de petite taille (épinoches et cyprins). De plus, il y a une corrélation négative entre les changements d'abondance des YOY de la grenouille sylvestre et ceux des poissons; les YOY de la grenouille sylvestre sont jusqu'à 7,7 fois plus nombreux après les années de mortalité hivernale que les années sans mortalité hivernale. Cette augmentation du nombre d'anoures métamorphosés ne résulte pas d'un accroissement du nombre d'adultes reproducteurs dans les lacs à mortalité hivernale, ce qui laisse croire que la survie y est meilleure. L'abondance accrue de jeunes YOY de la grenouille sylvestre et des crapauds est associée à des tailles plus petites à la métamorphose. Malgré cette réduction apparente de la croissance individuelle, l'abondance des jeunes anoures demeure significativement élevée 1 année après la mortalité hivernale. Au contraire des grenouilles sylvestres, les jeunes crapauds de l'année ont tendance à réagir positivement à la récupération des populations de petits poissons. Puisque les amphibiens anoures peuvent réagir aux mortalités hivernales de poissons et que cette mortalité est une perturbation naturelle fréquente, les petits lacs qui contiennent des poissons peuvent servir d'habitats de reproduction importants pour les amphibiens dans la forêt boréale de l'Alberta.

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## Introduction

Natural disturbances play important roles in ecology, affecting life history, population genetics, structure, and dynamics, assemblage structure, and ecosystem energetics (Pickett and White 1985). For residents of small north-temperate lakes, the development of under-ice hypoxia and resulting mortality (winterkill) is a major natural disturbance (Magnuson et al. 1989). Because the rate and extent of winter oxygen depletion among lakes within a region are primarily associated with productivity and depth (Greenbank 1945; Mathias and Barica 1980), lakes will differ in their propensity to become hypoxic. Combined with a generally observed pattern that smaller fish species (and individuals) have more effective adaptations and (or) greater tolerances against under-ice hypoxia (Casselman and Harvey 1975; Klinger et al. 1982), these among-lake differences often lead to local fish assemblages being dominated either by large-bodied species, including fish piscivores, or by small-bodied species that are more tolerant of hypoxia but vulnerable to predation (Harvey 1981; Robinson 1989; Robinson and Tonn 1989). Nevertheless, both large and small fishes are susceptible to winter hypoxia (e.g., Casselman and Harvey 1975; Danylchuk and Tonn 2003). And, because the extent of oxygen depletion within a lake is influenced by factors such as duration of ice cover, depth of snow, and water levels (Greenbank 1945; Danylchuk and Tonn 2003), winterkill events can be unpredictable.

This unpredictability, and the under-ice (and out of sight) nature of the disturbance, has impeded our ability to examine the ecological effects of winterkill. Effects are best known for fish, and have included changes to population structure and dynamics (Danylchuk and Tonn 2003), distribution and behavior (Magnuson and Karlan 1970; Magnuson et al. 1985), life history (Fox and Keast 1991; Danylchuk and Tonn 2006), and assemblage structure (Tonn and Magnuson 1982). A few studies, however, have shown that the disturbance can have broader influences on lake ecosystems; by suddenly and often drastically reducing the number of fish predators, their prey can benefit indirectly. Such studies have examined these indirect effects on smaller fishes (Tonn and Paszkowski 1986), macroinvertebrates (Tonn et al. 2004), and zooplankton and water clarity (Mittelbach et al. 1995; Zimmer et al. 2001). Could other taxa, e.g., amphibians, also be affected indirectly by winterkill?

Short-term and (or) small spatial-scale experiments, as well as landscape-level distribution patterns, indicate that the ecology of pond-breeding amphibians is shaped largely by a combination of habitat permanence and aquatic predators, including the presence or absence of fish (e.g., Wellborn et al. 1996; Hamer et al. 2002; Babbitt et al. 2003). Large-scale surveys indicate that some amphibians are typically excluded from systems containing predatory fish (Hecnar and M'Closkey 1997), and fish introductions can extirpate native amphibians (Knapp et al. 2001; Dunham et al. 2004), even across entire landscapes that still contain some fishless lakes (Pilliod and Peterson 2001). Such studies, however, frequently focus on fish vs. fishless systems, including situations created by introductions of exotic fish predators into previously fishless systems. Winterkill, in contrast, provides an opportunity to examine effects of sudden and unpredict-

able changes in native fish densities on amphibians. Can amphibian populations respond to fish winterkill, e.g., by attracting breeding adults or increasing survival of larvae?

A unique opportunity to examine this question arose in the course of an extensive study (the Terrestrial and Riparian Organisms, Lakes, and Streams (TROLS) program; see Prepas et al. 2001; Hannon et al. 2002) involving fish, amphibians, and water quality in 12 lakes on the Boreal Plains of Alberta over a 5 year period. Lakes in this region are naturally productive and relatively shallow, and when combined with long boreal winters, are subject to under-ice oxygen depletion (Mathias and Barica 1980; Danylchuk and Tonn 2003). Indeed, significant winterkill events, defined here by a decline in fish abundance from one survey to the next of >63% (see the section Statistical analyses below), were documented in seven lakes during the study; we also observed substantial recoveries in five of these lakes (Danylchuk and Tonn 2003; Tonn et al. 2004; W.M. Tonn, unpublished data). Annual surveys gave us the serendipitous ability to examine how such large changes in fish density affected anuran amphibians. Here, we examine these data to address the following questions. (i) Is the abundance of recently emerged young-of-the-year (YOY) anuran amphibians related to fish density, i.e., does amphibian recruitment respond to winterkill? (ii) Does fish assemblage type, i.e., lakes dominated by large piscivores vs. small-bodied species, influence the amphibian response? (iii) Is the amphibian response (if any) due to an increased immigration of breeding adults to a lake following winterkill or to an increased survival of tadpoles? (iv) Does the amphibian response (altered numbers of YOY) affect traits of the emerging metamorphs (e.g., size) and numbers of yearlings in the year following a winterkill, i.e., do fish winterkills have the potential to shape local anuran populations?

## Materials and methods

### Study systems

The study lakes were a subset of 12 lakes that were the focus of the aforementioned TROLS project (Prepas et al. 2001; Hannon et al. 2002). The 7 lakes (LLB20, LLB200, LLB800, SCL200, SCL800, SPH100, SPH800) were located in three roadless regions within the aspen-dominated mixed-wood forest of northern Alberta (Lac La Biche (LLB; 55.2°N, 111.7°W), South Calling Lake (SCL; 55.1°N, 113.7°W), and South Pelican Hills (SPH; 55.3°N, 113.7°W)). Access to all lakes was limited to all-terrain vehicles. Study lakes were moderately small ( $72 \pm 10$  ha; mean  $\pm$  SE), shallow ( $4.4 \pm 0.9$  m maximum depth), and naturally eutrophic ( $65 \pm 11$   $\mu$ g/L of total phosphorus) (see Prepas et al. 2001). Fish assemblages in three lakes were dominated by the large-bodied piscivores northern pike (*Esox lucius* L., 1758) and yellow perch (*Perca flavescens* (Mitchill, 1814)), whereas four lakes lacked piscivores but contained small-bodied fish assemblages, comprising combinations of fathead minnow (*Pimephales promelas* Rafinesque, 1820), brook stickleback (*Culaea inconstans* (Kirtland, 1840)), and finescale dace (*Phoxinus neogaeus* Cope, 1867) (Tonn et al. 2003). Amphibian species consisted of the Wood Frog (*Rana sylvatica* LeConte, 1825), Boreal Toad (*Bufo boreas boreas* Baird and Girard, 1852), and Canadian Toad (*Bufo hemiophrys* Cope,

1886). The Boreal Chorus Frog (*Pseudacris maculata* (Agassiz, 1850)) was also present but was not included in the analyses because it could not be monitored reliably (Stevens and Paszkowski 2005).

Fish were monitored annually from 1995 to 1999, although a few lakes were not sampled in 1997 and (or) 1999. After initial surveys determined fish assemblage type, fish abundance in lakes dominated by piscivorous and small-bodied fish was estimated using gillnets and minnow traps, respectively. Gillnets were benthic survey nets of 14 panels, 3 m × 1.5 m each, with square mesh sizes ranging from 6 to 75 mm (Lundgrens Fiskredskap, Stockholm, Sweden); minnow traps were standard Gee traps with 6 mm wire mesh (Nylon Net Company, Memphis, Tennessee). Gear was set overnight (ca. 18 h) at random locations stratified by depth. Fish captured in gill nets were weighed and measured (total length); fish captured in minnow traps were simply counted. Abundance estimates in piscivorous lakes were standardized as biomass per unit effort (BPUE: kg of fish captured·net<sup>-1</sup>·h<sup>-1</sup>), because individuals of these species vary greatly in body size and predatory impact. The small-bodied fishes captured in minnow traps vary little in body size, therefore, catch per unit effort (CPUE: number of fish captured·trap<sup>-1</sup>·h<sup>-1</sup>) is an appropriate index of abundance (Danylchuk 2003). Gillnetting effort averaged 218 net·h·lake<sup>-1</sup>·year<sup>-1</sup> (range: 69–346) and minnow trapping averaged 2717 trap·h·lake<sup>-1</sup>·year<sup>-1</sup> (range: 146–7609); effort was adjusted by lake size.

Amphibians were also sampled annually from 1995 to 1999, although the two SPH lakes were not sampled in 1995 and only SCL lakes were sampled in 1999. Amphibians were sampled around each lake with two grids (160 m × 100 m) of pitfall traps and drift-fences. Each grid contained three lines of traps that paralleled the lakeshore. One line was located at the edge of the untreed riparian zone, while the second and third were located 50 and 100 m upslope from the first, respectively. Each line contained five sets of three pitfall traps joined by two 5 m lengths of plastic drift fence to form a “V”, with the open side facing the lake (Heyer et al. 1994). A pitfall trap consisted of a metal can (25.5 cm deep, 15.5 cm diameter) buried to its rim with a plastic funnel (10 cm diameter opening) inside the can. Upright sticks placed in traps provided escape routes for small mammals. Pitfall traps were checked approximately every 2 days; captured amphibians were identified, measured (snout-to-urostyle length, SUL), weighed, marked, and released. Trapping sessions lasted 5–8 days·lake<sup>-1</sup> (typically 7 days·lake<sup>-1</sup>). Trapping effort averaged 560 trap·nights·lake<sup>-1</sup>·year<sup>-1</sup> (range: 299–1533). Captures were standardized as the number of new individuals captured / 100 trap·nights. Spring trapping (12 May – 18 July) targeted adult amphibians as potential breeders (≥40 mm SUL; Berven 1990; Leclair et al. 2000) and yearlings (≤30 mm; B.R. Eaton and C.A. Paszkowski, unpublished data), whereas metamorphs (YOY, ≤27 mm SUL; B.R. Eaton and C.A. Paszkowski, unpublished data) were the focus of late-summer trapping, 20 July – 2 September, mostly in August. Collection and handling procedures for both fish and amphibians were in accordance with guidelines from the Canadian Council on Animal Care; protocols were reviewed and approved by the BioSciences Animal Policy and Welfare Committee at the University of Alberta.

## Statistical analyses

Abundance estimates (BPUE or CPUE) of each fish species were combined to determine a lake's total fish abundance within each year. Data from both *Bufo* species were also combined because they are ecologically similar and study sites included both sympatric and allopatric populations (Eaton et al. 1999; Russell and Bauer 2000). Abundance estimates (CPUE) of newly metamorphosed YOY amphibians were determined separately for YOY Wood Frog and toads, but sufficient data from spring surveys of adults and yearlings existed only for Wood Frog.

To standardize changes in abundance at a lake over time, we calculated an index of population change (IPC) for fish and YOY amphibians using the formula  $IPC = \ln(N_{t+1}/N_t)$ , where  $N_t$  and  $N_{t+1}$  are estimated abundance in years  $t$  and  $t + 1$ , respectively (Cooper et al. 1990; Osenberg et al. 1997; Tonn et al. 2004). IPCs were usually calculated using data from consecutive years; when a group was not sampled for a given lake-year (e.g., fish in three lakes in 1997), IPCs were calculated from the closest 2 years for which data were available for both fish and amphibians (e.g., 1996 and 1998). In years where no fish or YOY amphibians were captured at a lake, but were previously and subsequently captured at the same site, a value of 0.001 was assigned to indicate low abundance and to avoid dividing by zero in the analyses. Because relatively small increases and decreases in fish abundance would not likely affect amphibian populations, we used  $|IPC| > 1.0$  to identify lake-year pairs having proportionately large changes in fish densities (caused by winterkill or recovery from winterkill).

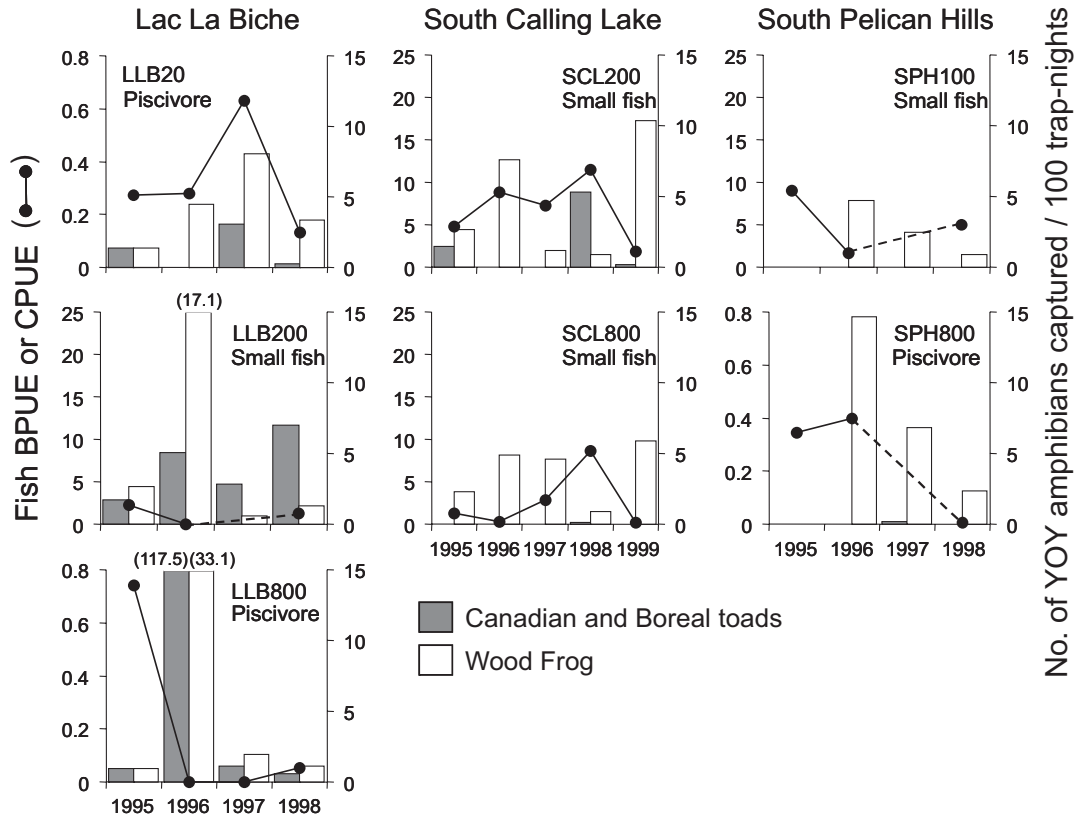
Concordance of changes in fish and YOY amphibian abundance (Wood Frog and toads separately) was quantified by totaling the number of cases in which corresponding fish and YOY amphibian IPCs had the same or opposite signs, reflecting population changes of fish and amphibians in the same or opposite directions (Tonn et al. 2004). These totals were compared with a binomial distribution that assumed equal likelihood for parallel or opposite changes. Comparisons were done for all lake-year pairs, for lake-year pairs when fish  $|IPC| > 1$ , and separately for the three lakes containing piscivorous fish and four lakes with small-bodied fish. We also compared the  $\log(x + 1)$ -transformed CPUE of amphibians (summer YOY, spring adults, following spring yearlings) from lake-years associated with fish winterkills vs. non-winterkill lake-years using Student's  $t$  tests.

Differences in production and recruitment of YOY amphibians could, in turn, affect the sizes of metamorphs that emerge from their natal lakes (e.g., Smith 1983). To test for a relation between the size of YOY metamorphs and their abundance, we regressed mean SUL against log-transformed YOY abundance (CPUE). Analyses were performed separately for Wood Frog and Canadian Toad, as data on Boreal Toad were too sparse. Even so, we used data from all 12 TROLS lakes (Prepas et al. 2001) to increase sample sizes, resulting in 43 lake-years for Wood Frog and 14 lake-years for Canadian Toad.

## Results

Combined fish abundances ranged from relatively stable to very variable (Danylchuk and Tonn 2003). Eight dramatic

**Fig. 1.** Abundance of fish and young-of-the-year (YOY) Wood Frog (*Rana sylvatica*) and toads (Boreal, *Bufo boreas boreas*, and Canadian, *Bufo hemiophrys*, toads combined) from the seven study lakes in three regions of boreal Alberta. Fish communities are classified as being dominated by larger, piscivorous species or by small species. Abundance estimates for fish are in biomass per unit effort (BPUE, kg·h<sup>-1</sup>; piscivores) or catch per unit effort (CPUE, number of fish captured·h<sup>-1</sup>; small fish); amphibian estimates are in CPUE (numbers / 100 trap-nights). Amphibians were not sampled at the SPH lakes in 1995; fish were not sampled in 1997 at LLB200 or the SPH lakes.



year-to-year decreases in fish abundance (fish  $IPC < -1$ ), known or suspected to be caused by under-ice hypoxia, occurred in seven different lakes during the course of this study. Such decreases, often resulting in fish abundance estimates approaching zero (Fig. 1), were recorded for four lakes after the long winter of 1995–1996 (>7 months of ice cover), for one lake in each of 1996–1997 and 1997–1998, and for two lakes in 1998–1999, the winter with the deepest snow cover during the study (Danylchuk and Tonn 2003). Strong increases in fish abundance ( $IPC > 1$ ) were also recorded 5 times, typically within 1–2 years following a suspected winterkill (Fig. 1).

A total of 18 and 13 lake-year pairs were available from the seven lakes for IPC analyses of YOY Wood Frogs and toads, respectively. Across all of these lake-year pairs, YOY Wood Frog ( $P = 0.12$ ) and toad ( $P = 0.50$ ) abundance did not respond consistently to changes in abundance of fish (binomial probabilities). However, when analyses were restricted to lake-year pairs associated with fish winterkill or recovery ( $|IPC_{fish}| > 1$ ), changes in the abundance of YOY Wood Frogs were in the opposite direction to changes in fish abundance in 83% of the cases (binomial probability,  $n = 12$ ,  $P = 0.02$ ). Indeed, CPUEs of Wood Frog metamorphs were 2.5 times higher after winterkills than during non-winterkill years across all regions and lakes (8.2 vs. 3.3 frogs / 100 trap-nights;  $t_{[26]} = -3.28$ ,  $P = 0.003$ ) and as much as 7.7 times

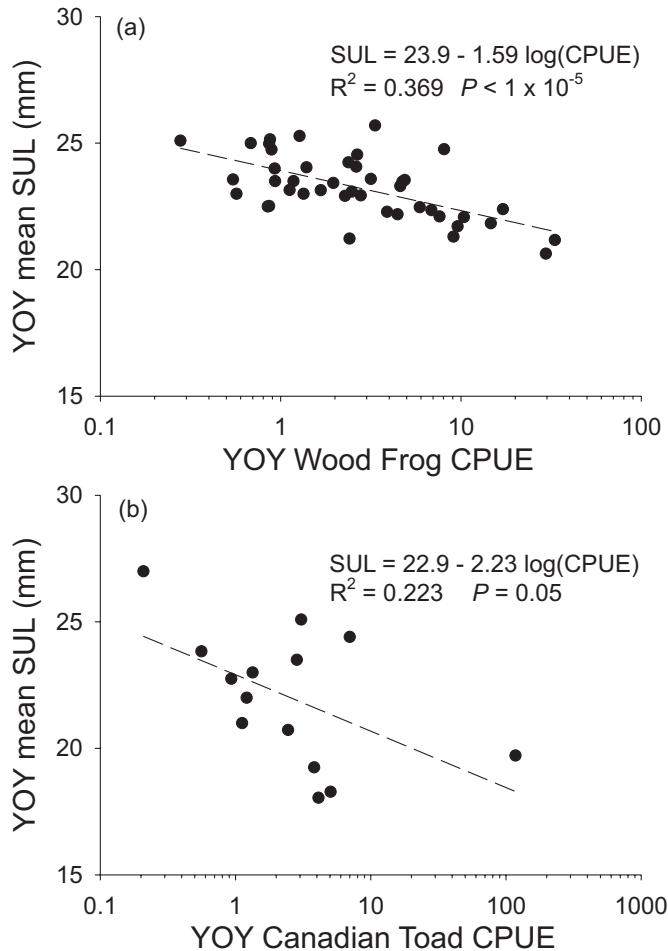
higher at an individual lake. In contrast, YOY toads were inconsistent in their response to fish winterkills or winterkill recoveries, changing in the opposite direction to fish in only 38% of cases (binomial probability,  $n = 8$ ,  $P = 0.36$ ), despite a singularly dramatic increase following the 1996 winterkill of northern pike and yellow perch in LLB800 (Fig. 1).

Interestingly, recruitment responses of Wood Frog to large changes in the abundance of fish were strongly dependent on the type of fish assemblage present. Abundance of YOY Wood Frogs responded in the opposite direction to fish in all eight cases when the fish assemblage was dominated by small-bodied species (binomial probability,  $P = 0.004$ ), but in only two of four cases involving piscivorous fish (binomial probability,  $P = 0.69$ ). In contrast, changes in the abundance of YOY toads were in the same direction as changes in small-bodied fishes in four of five cases (binomial probability,  $P = 0.19$ ). This contrasting response of Wood Frog and the two toad species to changes in small-fish densities was itself significant (Fisher's exact test,  $P = 0.007$ ). YOY toad abundance was in the opposite direction to piscivorous fish in two of three cases (binomial probability,  $P = 0.50$ ).

The increased recruitment of YOY Wood Frogs following winterkill did not appear to result from an increased immigration of breeding adults to such lakes. The abundance of adult (breeding) Wood Frogs in spring was only slightly higher at lakes following winterkill (0.94 frogs / 100 trap-



**Fig. 2.** Relationships between the mean snout-to-urostyle length (SUL) and abundance (catch per unit effort, CPUE) for young-of-year (YOY) (a) Wood Frog and (b) Canadian Toad at 12 (Wood Frog) and 4 (Canadian Toad) lakes in the Boreal Plains of Alberta, Canada, 1995–1999. Each point represents a lake-year. Note the log scales.



nights) than in non-winterkill years (0.61 frogs / 100 trap-nights;  $t_{[12]} = -1.07$ ,  $P = 0.31$ ). A qualitative assessment of toad data similarly suggested no trend.

A strong negative relation existed between mean SUL and abundance of YOY Wood Frog ( $R^2 = 0.37$ ,  $F_{[1,41]} = 25.67$ ,  $P < 0.001$ ; Fig. 2a). This relationship translated into a 25% difference in mean Wood Frog length between the minimum and the maximum abundances (25.7 vs. 20.6 mm, respectively). A similarly negative relation was observed between SUL of YOY Canadian Toads and their CPUE ( $R^2 = 0.22$ ,  $F_{[1,12]} = 4.72$ ,  $P = 0.05$ ; Fig. 2b).

Despite the smaller sizes of YOY frogs, increases in their abundance following winterkill of fish translated subsequently into higher abundances of 1 year old frogs (SUL  $\leq 30$  mm) the following spring in the LLB region, the only region for which we had sufficient data. The abundance of 1 year old Wood Frogs in the spring 1 year after a winterkill event (4.1 frogs / 100 trap-nights) was almost 4 times greater than their abundance in non-winterkill lake-years (1.1 frogs / 100 trap-nights;  $t_{[4]} = -5.20$ ,  $P = 0.007$ ).

## Discussion

In many forested ecoregions, ponds are generally fish-free and numerous, e.g., of the waterbodies  $>0.1$  ha in the 500 km<sup>2</sup> South Calling Lake region, 37% are  $<1$  ha (Eaton 2004). As a result, ponds often offer very promising breeding habitat for frogs and toads (Wellborn et al. 1996). In the semi-arid Boreal Plains ecoregion, however, such ponds will frequently dry prior to larval metamorphosis or may even hold no water at all during drought years (B. Eaton, personal observation). In contrast, small lakes (ca. 1–100 ha) offer physically more dependable habitats, but typically contain fish, so can be associated with significant predation risk (Hopey and Petranks 1994; Wellborn et al. 1996; Baber and Babbitt 2003). But because fish winterkills are not uncommon for small lakes in this landscape (Danylchuk and Tonn 2003), the resulting reduction in predation by fish may keep such systems profitable as breeding habitat for anuran amphibians, if they can respond to fish winterkill with a subsequent increase in recruitment of YOY.

The development of winter hypoxia varies among lakes as a function of lake productivity, depth (Barica and Mathias 1979), and landscape-level factors (Danylchuk and Tonn 2003). Differences among lakes in the frequency and severity of winterkills, and differences among species in their tolerances to hypoxia and predation, contribute to the occurrence of different fish communities in boreal Alberta (Robinson and Tonn 1989; Tonn et al. 2003) and elsewhere (Harvey 1981; Tonn and Magnuson 1982). As well, winter hypoxia results in frequent, and often severe, reductions in fish populations of both small-fish and piscivore-dominated communities (Danylchuk and Tonn 2003; Tonn et al. 2004).

Although the probability of a winterkill in any given lake-year is related to factors such as water level, length of the ice-covered period, and thickness and quality of the ice and snow (Greenbank 1945; Cooper and Washburn 1949; Danylchuk and Tonn 2003), fish winterkills are not easily predicted by limnologists, nor likely by amphibians. The anuran species in our study are disconnected from lakes in winter, since all three complete their larval development in a single summer and hibernate in the surrounding terrestrial landscape (Russell and Bauer 2000). Therefore, recruitment responses following fish winterkills would likely reflect 1 of 2 scenarios: (1) each spring, adult amphibians assess sites for the presence and density of fish and breed preferentially in water bodies that have no or low fish populations (Resetarits and Wilbur 1989; Hopey and Petranks 1994; Binckley and Resetarits 2002, 2003), or (2) amphibians breed in lakes indiscriminately (Laurila and Aho 1997), but mortality of larvae is dependent on densities of the resident fish populations.

Many amphibians show high philopatry, with adults returning to breed at the same, usually natal, site every year (Berven 1990; Marsh and Trenham 2001). As well, Wood Frogs, the most abundant of the three species in our study, breed synchronously over short time periods in early spring, shortly after ice out (Petranks and Thomas 1995), giving female Wood Frogs little time to sample multiple potential breeding sites before ovipositing. Both of these traits would work to limit the ability of adults to assess lakes for the presence and density of fish. These factors, combined with

the presence of at least some YOY frogs at all lakes in every year, tend to support the second scenario, that amphibians breed in the study lakes regardless of the presence of fish. Indeed, we found no evidence of increased numbers of adult Wood Frogs during spring at lakes that had just experienced a winterkill. Successful recruitment into the population, however, may primarily occur following winterkills that substantially decrease populations of the resident fish.

Large changes in fish abundance caused by winterkill did affect recruitment of YOY Wood Frogs (and occasionally, sometimes spectacularly, recruitment of toads), but effects depended on the fish community composition. Wood Frogs responded consistently to large changes in the abundance of small-bodied fishes, i.e., increases in the recruitment of YOY frogs regularly followed small-fish winterkills, but showed no consistent response to winterkill in piscivore-dominated communities. Toads also showed a recruitment response to small-fish winterkills, but their response was the reverse of the pattern observed in Wood Frogs; recruitment of toads tended to decrease following winterkills but increase when fish populations recovered.

Pond experiments demonstrate that fathead minnow and brook stickleback can have significant predatory impacts on Wood Frog, but not Boreal Toad, larvae (Eaton 2004). Toad larvae appear to be less palatable to fish predators (Formanowicz and Brodie 1982) and thus their survival is more often unaffected by the presence of predatory fish (e.g., Baber and Babbitt 2003). Because adults appear safe from predation by small minnows and sticklebacks, breeding Wood Frogs can persist within a region at sufficient densities to capitalize on occasional winterkills in small fish-bearing lakes. Direct release from predation can thus provide a mechanism explaining increases in Wood Frog recruitment following winterkills in small-fish lakes. Why toads respond in parallel to small-fish populations is less clear, but may involve indirect interactions that are mediated by these fishes. The earlier hatching and larger Wood Frog larvae can eat toad eggs and larvae (Petranka et al. 1994), thereby suppressing toad populations in years with high Wood Frog recruitment. As well, high densities of ranid tadpoles, such as those occurring after winterkills of small fish, can reduce growth and survival of *Bufo* tadpoles (Griffiths 1991). Another hypothesis would suggest that small-bodied fishes can depress the abundance of invertebrate predators that can be effective predators on the smaller toad tadpoles (Smith et al. 1999; Zimmer et al. 2000; Adams et al. 2003). These hypotheses are not mutually exclusive.

Results from piscivore lakes were inconclusive, owing in part to small sample sizes. Nevertheless, a piscivore lake (LLB800) provided the most dramatic anuran response that we observed, when Wood Frog and toad recruitment both increased by 36 times and 126 times, respectively, in the summer (1996) following a virtually complete winterkill of northern pike and yellow perch. Northern pike, in particular, are known predators of Wood Frog larvae and adults (Venturelli and Tonn 2005). The high pre-winterkill densities of the large-bodied fishes in this lake appear to have suppressed populations of large invertebrate predators and eliminated small-bodied fishes (Tonn et al. 2003, 2004), so the winterkill may have provided anurans with a temporary refuge from predation from all three groups. Effects of winter-

kill of large predatory fishes may thus depend on both the severity of the disturbance and the nature of the pre-winterkill food web, resulting in greater variability in anuran response.

Although YOY frogs were as much as 7.7 times more abundant at our study lakes following winterkills than in non-winterkill years, the increases in recruitment likely came at a cost of reduced growth, given the negative relationship between YOY abundance and size. To the extent that abundance and size of metamorphs reflect densities and growth of larvae, this relationship is consistent with density-dependent growth of amphibian larvae that has been documented in the field (e.g., Smith 1983), in mesocosms (Loman 2001), and in the laboratory (Martinez et al. 1996). Nevertheless, although reduced growth may sometimes be related to subsequent reduced survival of metamorphs (e.g., Beck and Congdon 1999; Morey and Reznick 2001), increased abundance of young Wood Frogs persisted a year after winterkill into the following spring.

Thus, in years following winterkill, an important but understudied natural disturbance of boreal lake ecosystems, small fish-bearing lakes may serve as sources of juvenile Wood Frogs that disperse to establish or augment populations in ponds. When fish abundance is high, the same lakes may be temporary population sinks for Wood Frog, but sources for toads. We thus propose that native fish populations and winterkill influence the structure and dynamics of anuran metapopulations on the boreal landscape. Unlike the almost uniformly negative and sometimes catastrophic effects of non-native fish on naïve amphibian populations, however, Boreal Plains amphibians can persist in the region's smaller, fish-bearing lakes because of this unpredictable but frequent natural disturbance. The management of native, as well as introduced, fish stocks should therefore be integrated into conservation strategies for boreal amphibians (Semlitsch 2000).

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