Winterkill cascade: indirect effects of a natural disturbance on littoral macroinvertebrates in boreal lakes

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Abstract. Natural disturbances can provide insights into mechanisms organizing communities by perturbing systems at larger scales and more realistic intensities than can often be achieved otherwise. We took advantage of 2 winterkills of fish, a common disturbance of small lakes on the Boreal Plains of northern Alberta (Canada), to assess the effects of sudden, large reductions in fish densities on littoral macroinvertebrate assemblages. Winterkill nearly eliminated the native fish assemblages (dominated by northern pike, *Esox lucius*, and yellow perch, *Perca flavescens*) in the 2 lakes, whereas 2 nearby lakes with similar fish assemblages were unaffected and served as references. Environmental characteristics of both winterkill and reference lakes changed little from year to year. Uni- and multivariate analyses of macroinvertebrates revealed some inherent among-lake differences; however, strong and parallel changes in the invertebrate assemblages occurred only in the 2 winterkill lakes, congruent with the winterkills of fish. Decreases in fish biomass were generally accompanied by increases in macroinvertebrate density, particularly among taxa (e.g., amphipods, leeches, chironomids) commonly eaten by the native fish. As a result, analyses of matrix concordance and variance partitioning showed variation in macroinvertebrate assemblages was related to both temporal changes in fish density and environmental differences among lakes but that the fish and environmental matrices were not strongly concordant. Our serendipitous study of community-level disturbance revealed that winterkill-induced reductions of fish densities can have strong, cascading effects on littoral macroinvertebrates in these boreal lakes.

Key words: macroinvertebrate communities, fish predation, multivariate analysis, Boreal Plains, Alberta, natural disturbances, winterkill.

Winterkill is a natural disturbance of fish populations in north-temperate and boreal regions, resulting from oxygen depletion in ice-covered lakes (Greenbank 1945). Shallow, productive lakes, which predominate on the Boreal Plains of western Canada, are more susceptible than deeper, less productive ones (Mathias and Barica 1980). In addition to often drastic decreases in fish abundance, winterkill contributes to distinct and predictable differences in the composition of fish assemblages among lakes (Tonn and Magnuson 1982, Robinson and Tonn 1989, Paszkowski and Tonn 2000). In any given lake, however, there can be considerable and unpredictable year-to-year variation in the extent

of oxygen depletion as a result of climatic factors such as length of ice cover and amount of snow (Greenbank 1945, Danylchuk and Tonn 2003). Climatic variability on the Boreal Plains also leads to changes in water yield, which can affect access of fish to stream refuges and thus exacerbate or moderate effects of oxygen depletion on fish assemblages (Magnuson et al. 1998, Danylchuk and Tonn 2003). Despite its unpredictability, winterkill is a common and significant disturbance that can quickly reduce fish biomass in a lake by 50 to 90% or more (Danylchuk and Tonn 2003).

Basic effects of winterkill on fish assemblages are known, but our understanding of its role in shaping lake ecosystems more broadly has been limited by its unpredictability. Winterkill can also directly impact invertebrates, producing declines in abundance that parallel those of fish (Hoffsten 2003). Alternatively, winterkill could affect invertebrates indirectly, via a release from predation by fishes. Such an indirect effect would result in increased invertebrate abundance in response to decreases in their fish

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TABLE 1. Seasonal mean (May–August) environmental characteristics of the 4 study lakes during the study years 1995 to 1997. Data are from Langlois (2000), Prepas et al. (2001), and EEP and WMT (unpublished data). L = Lac La Biche area, S = South Pelican Hills area.

Study lake	Surface area (ha)	Total P (μg/L)	Dissolved inorganic N (μg/L)	Dissolved organic C (mg/L)	Conduct-ivity (μS/cm)	Maximum depth (m)	Water residence time (y)	Macro-phyte dry mass (g/m²)[a]	Catchment area (ha)
L20	62	54	109	12	254	5.5	0.1	77	575
L800	75	50	48	12	147	7.1	6.6	2	473
S20	157	24	28	10	215	8.2	5.2	145	1002
S800	65	50	20	12	260	3.7	0.9	58	619

[a] Measured in 1997 only

predators. Examples of zooplankton responses to natural disturbances of their fish predators have been documented (Hall and Ehlinger 1989, Vanni et al. 1990) but we are unaware of studies documenting similar responses of benthic macroinvertebrates. As a cause of major declines in fish populations in lake ecosystems, however, winterkills can provide opportunities to study cascading foodweb responses at scales not possible with planned but smaller-scale experiments (Carpenter 1996, Schindler 1998, Zimmer et al. 2001).

Impacts of fish on macroinvertebrates remain controversial (Thorp 1986). A number of comparative, multilake studies suggest effects are significant (e.g., Dermott 1988, Wong et al. 1998, Zimmer et al. 2000), and whole-lake fish removals and introductions also indicate that predation by fish can affect macroinvertebrate assemblages (Ball and Hayne 1952, Post and Cucin 1984, Zimmer et al. 2001). Mesocosm experiments, however, often conclude that fish impacts are limited (Thorp and Bergey 1981, Pierce and Hinrichs 1997, Cobb and Watzin 1998). Some of the discrepancies among studies is suggested to result from stronger predator effects when fish are added to a previously fishless system, compared to effects of changes in fish densities on coexisting macroinvertebrates (McPeek 1990, Wellborn et al. 1996). Winterkills can thus offer a valuable test of top-down effects in natural fish–invertebrate communities.

The chance to study the effects of winterkill on fish and macroinvertebrates arose serendipitously during a large-scale (5-y, 12-lake) study of forest harvesting effects on lakes in the boreal forest of northern Alberta (Prepas et al. 2001). Although not all components of the lake ecosystems could be sampled in all lakes or all years, we documented severe winterkills of fish in 2 lakes, and partial recovery of fish populations in 1, for which we had nearly complete and largely concurrent sampling of fish, littoral macrobenthos, and environmental characteristics. Two nearby lakes with similar fish assemblages did not experience winterkill and served as reference lakes. We examine the responses of littoral macroinvertebrates to these natural disturbances of fish to determine if direct or indirect effects predominate, and thereby assess whether fish are important in shaping macroinvertebrate assemblage structure in Boreal Plains lakes.

Methods

Study area and lakes

The 4 unnamed study lakes (designated as L20, L800, S20, and S800) are located in 2 roadless areas of northern Alberta's Boreal Mixedwood ecoregion (Rowe 1972), Lac La Biche (L) (ca lat 55°N, long 112°W) and South Pelican Hills (S) (ca lat 55°N, long 114°W). The lakes are typically ice-covered from November through April, are relatively small and shallow and, based on total P (TP) levels, range from mesotrophic to eutrophic (Wetzel 1983; Table 1). Each lake has at least 1 impermanent inlet or outlet stream; whether these streams provide functional connections during a particular year is dependant on climatic conditions. The lakes are accessible by all-terrain vehicles only and their catchments are largely undeveloped, although shortly before our study (1994), 6% of the forest within 800 m of L800 was harvested and 26 to 28% of the catchments of L20 and S20 were har-

vested in the winter of 1996 to 1997 (Prepas et al. 2001).

During the 4-y study period (1995–1998), severe winterkills of fish occurred twice, in L800 in early 1996, and in S800 in 1997. In non-winterkill years, the 4 lakes had similar fish communities, dominated by northern pike (*Esox lucius* (L.)) and yellow perch (*Perca flavescens* (Mitchell)). The diets of both perch and pike are often dominated numerically by macroinvertebrates in these and other boreal Alberta lakes (Chapman et al. 1989, Beaudoin et al. 1999, 2001). Low numbers of white sucker (*Catostomus commersoni* (Lacépède)) also occurred, somewhat irregularly, in all 4 lakes. The only other species of fish caught, irregularly and in very small numbers, were cisco (*Coregonus artedi* Lesueur) in L20 and brook stickleback (*Culaea inconstans* (Kirtland)) in S800.

Fish sampling

Fish were sampled in all lakes with monofilament bottom-set gillnets (42 × 1.5 m, with fourteen 3-m wide panels of 6.25–75 mm square mesh) set overnight from July to August of 1995, 1996, and 1998. Fishing effort (6–18 net-nights) was adjusted for lake size (area, depth) and concentrated in shallower depths (<3 m) based on standardized Nordic procedures (Appelberg 2000). All captured fish were identified to species, measured (total length [TL], ±1 mm), and up to 200 individuals/species/sample were also weighed (wet mass, ±1 g). Catches were subsequently converted to biomass-per-unit-effort (BPUE, as g net^{-1} h^{-1}). Biomass of fish that were measured but not weighed was estimated from population-specific mass–length regressions (WMT, unpublished data).

Environmental sampling

Environmental data were based on seasonal means for each lake in each year from euphotic-zone water samples collected every ~3 wk (May–August) from 1995 to 1997; regional climate data (Environment Canada, values determined from Slave Lake, Fort McMurray, Athabasca, and Cold Lake, weighted according to a lake's distance from each station) contributed to calculations of water residence time (see Prepas et al. 2001). Catchment area, surface area, and macrophyte abundance were determined from

map and air-photo analyses, bathymetric measurements, and Ekman grab samples, respectively (Langlois 2000, Prepas et al. 2001). These 3 variables were used as general descriptors of the study lakes and, as such, were only measured once, with the same value being used for all lake-years. Macrophyte abundance was based on mean dry mass of plants collected from 3 sets of four 232-cm^2 Ekman grab samples, collected along the 1-, 2-, and 3-m depth contours (*n* = 12 grabs per lake) in September 1997 (Langlois 2000).

Invertebrate sampling

The large scale of the full 12-lake study, in which the current study was embedded, limited the number of invertebrate samples that could be collected and processed in each lake. L800 and S20 were sampled from 1995 to 1997, and S800 and L20 from 1996 to 1997. Benthic macroinvertebrates were collected from littoral sediments in all lakes during a standard mid-summer period (late July to early August), and sampling was also standardized to a single depth zone and a common habitat type. Samples were collected from around the lake at 4 (1995) or 6 (1996–1997) haphazardly chosen (but approximately evenly distributed) mid-littoral (1.5–3 m) sites characterized by soft sediments that were locally free of macrophytes. For all 4 lakes, Sorensen's Similarity coefficients were uniformly high (0.85–0.92) between the summer 1996 invertebrate samples and extra grab samples taken in spring 1996, suggesting that our sampling, although limited, was characterizing the assemblages adequately.

Samples were collected with a 232-cm^2 Ekman grab, fitted with a 0.5-mm mesh top-screen; contents were sieved in the field through a 0.2-mm Nitex bag and preserved in 4% formalin. In the laboratory, samples were sieved through 4-, 1-, and 0.25-mm meshes. The smaller size fractions from samples with abundant fine detritus were centrifuged and floated in sugar solution to facilitate separation of invertebrates from detritus (Cromar and Williams 1991). Macroinvertebrates were removed from samples and identified to family (or lower) under a dissecting microscope using Clifford (1991). Counts were subsequently converted to densities (individuals/m^2). Analyses were

TABLE 2. Summary of types of data collected in the 4 study lakes from 1995 to 1998. F = fish data, I = invertebrate data, E = environmental data. For some analyses, the 1998 fish data were matched with 1997 invertebrate and environmental data (see Methods). Bold text indicates lake-years in which winterkill occurred.

Lake	1995	1996	1997	1998
L20	F	F, I, E	I, E	F
L800	F, I, E	**F, I, E**	I, E	F
S20	F, I, E	F, I, E	I, E	F
S800	F	F, I, E	**I, E**	F

based on mean densities of the 4 or 6 samples taken in each lake each year.

Analyses focused on 9 aggregate taxa that were abundant, known to be sensitive to fish predation (e.g., Zimmer et al. 2001), or common in the diets of resident fish (Beaudoin et al. 1999, 2001): Ceratopogonidae, Chaoboridae, Chironomidae, *Gammarus*, Hirudinea, *Hyalella*, Sphaeriidae, Trichoptera, and ''other'' (consisting mainly of various worms, mites, and snails; Langlois 2000). Different taxonomic levels were used because of different levels of abundance and potential to show a response to fish winterkills. For example, the irregular presence of uncommon groups can adversely affect multivariate analyses (Gauch 1982), so individual caddisfly and leech families (Langlois 2000) were each combined into composite taxa. In contrast, *Hyalella* and *Gammarus* were often analyzed separately because they were abundant in both the benthos and fish diets, and because Zimmer et al. (2000, 2001) reported differential responses by these genera to fish predation.

Data analyses

Analyses focused on 10 lake-years that encompassed pre- and post-winterkill periods in L800 and S800, and contemporary data from reference lakes L20 and S20 (Table 2). Because fish data were not collected in 1997, 1998 data were substituted for all lakes. Qualitative fish sampling in 1997 (WMT, unpublished data) and related observations of the lake ecosystems in 1997 and 1998 (B. Eaton and C. Paszkowski, University of Alberta, personal communication) indicated that the 1998 fish data generally reflected 1997 conditions in all 4 lakes.

Community-level responses.—Patterns of temporal coherence between total fish abundance (summed BPUE) and densities of invertebrates were assessed by comparing the direction of change between fish and invertebrate abundance (increase or decrease) between consecutive years for each lake. A negative relationship between the abundance of fish and a macroinvertebrate taxon should produce opposite directions of change, e.g., when fish decrease that invertebrate taxon should increase. This hypothesis was tested using the 9 composite macroinvertebrate taxa by tabulating the number of invertebrate changes that were of the same or opposite sign as the corresponding fish change, and results were compared to the binomial distribution (assuming a 50% probability that the 2 had the same sign). As noted above, the 1998 fish data were paired with 1997 invertebrate data to provide 10 lake-years with complete data sets (Table 2).

A standardized index of population change (IPC) was calculated for the fish data to distinguish between periods associated with proportionately large changes in fish densities (caused by winterkill or recovery therefrom) versus the small, noncatastrophic changes of reference lakes:

$$IPC = \ln (N_{t+1}/N_t)$$

where N_t and N_{t+1} are the total fish BPUE in a given and subsequent year, respectively, in a given lake (see Cooper et al. 1990, Osenberg et al. 1997). To avoid division by 0, fish BPUE for L800 in 1996, following winterkill, was arbitrarily assigned a value of 0.1.

Invertebrate assemblage patterns were summarized by principal components analysis (PCA), after preliminary analyses (using detrended correspondence analysis) showed the primary gradient length to be <2 SD units, indicating linear relationships across the environmental gradient (ter Braak 1987). Excessive and redundant variables in multivariate analyses reduce stability, reliability, and interpretability of solutions (King and Jackson 1999), so 2 groups (Chaoboridae and ''other'') were dropped from the final analysis. These groups contributed little to the explanatory power of a preliminary ordination and were correlated with other taxa.

For community-level analyses of the littoral macroinvertebrate responses, site scores from ordination analyses were compared between

winterkill and reference lakes (see also Wiens et al. 2001). If the invertebrate assemblages were affected by winterkill, then postdisturbance site scores for winterkill lakes should diverge from predisturbance positions, relative to changes observed at reference sites. Subsequently, if fish populations show some recovery following a winterkill, then site scores should change again, moving towards the predisturbance positions.

Linking invertebrate responses to fish and environment.—A PCA was performed on environmental data from the 10 focal lake-years in which invertebrate sampling was conducted to summarize general environmental patterns within and among lakes (Table 2). The environmental PCA was limited to TP, dissolved inorganic N (DIN), dissolved organic C (DOC), conductivity, maximum depth, catchment area (CA), water residence time (WRT), and macrophyte biomass following examination of a correlation matrix among environmental variables.

Patterns in invertebrate assemblages in reference and disturbed lakes were compared to patterns in fish populations and environmental characteristics. Concordance of the macroinvertebrate assemblages with both the environmental patterns and fish assemblages was assessed via Mantel tests, using Euclidian distance (PC-ORD version 3.2, MjM Software, Gleneden Beach, Oregon). Environmental and invertebrate matrices comprised the sample (i.e., lake-year) scores from the first 3 principal components of the aforementioned PCAs; fish data consisted of the log-transformed BPUEs of the 3 primary component species (pike, perch, sucker). Significance of the computed Mantel statistic was determined by Monte Carlo permutation tests (9999 runs).

Variance in the invertebrate data was partitioned into components that could be explained by environment, fish, and their interactions to assess the relative importance of the biotic and abiotic environment in structuring macroinvertebrate assemblages. Partitioning was based on the method of Borcard et al. (1992), which uses a series of partial redundancy analyses (RDAs). To insure that the fish and environmental data sets consisted of an equal number of variables (see Borcard et al. 1992), scores were used for the first 3 components of the environmental PCA and the BPUE of the 3 fish species, together with the densities of invertebrates for each of the lake-years.

All ordinations were based on correlation matrices using either PC-ORD (PCAs) or CANOCO (C. J. F. ter Braak and P. Smilauer. 1998. CANOCO reference manual and user's guide to Canoco for Windows, version 4, Microcomputer Power, Ithaca, New York) (RDAs). Environmental data (except pH), invertebrate densities, and fish BPUE were transformed (log $(x + 1)$) prior to analyses.

Taxon-specific responses.—Changes in the densities of the 9 individual invertebrate groups were also compared between consecutive years in winterkill vs reference lakes with 1-tailed *t*-tests. For the winterkill lakes, change in density = (density post-winterkill)−(density pre-winterkill) ($n = 2$); for reference lakes, change in density = (density in year x)−(density in year $x - 1$) ($n = 3$). A significance level of $p < 0.1$ was used for the *t*-tests, given the unplanned nature of the study (and resulting low replication), and the composite nature of some invertebrate groups.

Results

Fish

Temporal patterns of fish BPUE in S20 and L20 (reference lakes) were characterized by relatively similar, stable assemblages, with high densities of pike and moderate densities of perch (Fig. 1). In contrast, densities in L800 and S800 displayed strong temporal patterns indicative of severe winterkills. The fish assemblage in L800 was decimated between the 1995 and 1996 surveys, and hundreds of dead fish were observed at ice-out in the spring of 1996 (K. Field, University of Alberta, personal communication). Some fish were subsequently caught during qualitative sampling in 1997 (WMT, unpublished data) and, by the 1998 survey, the pike and perch populations in L800 had begun to recover (Fig. 1). Water levels in the inlet and outlet streams of L800 were high in 1997, so it is possible that immigration, along with growth and reproduction of a remnant population, contributed to the recovery. Similarly, S800 went from high densities of perch and moderate densities of pike during the 1996 survey to low levels of pike and a virtual absence of perch during the 1998 survey. Independent lines of evidence, particularly increased catches of new metamorphs of anurans whose tadpole larvae are
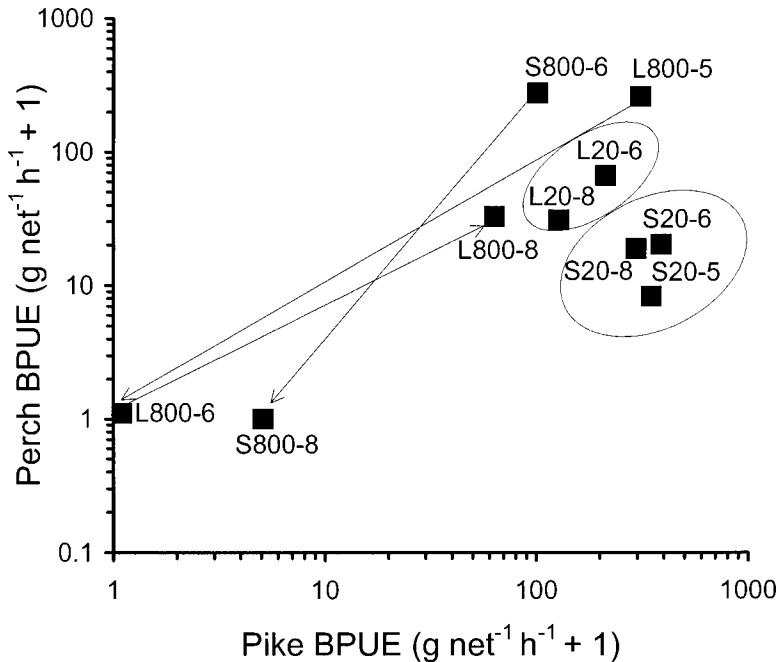
FIG. 1. Abundance of northern pike and yellow perch in the 4 study lakes (reference: L20 and S20; winterkill: L800 and S800) during the study period (1995–1998), as biomass-per-unit-effort (BPUE) in gillnet catches. Encircled groups represent individual reference lakes among years; arrows show direction and extent of change before and after winterkills in L800 and S800. Note log-scale of the axes. Numbers following lake identities are study years: 5 = 1995, 6 = 1996, and 8 = 1998.

TABLE 3. Principal components (PC) analysis of lake environments.

| | PC axes | | |
	1	2	3
Eigenvalue	3.89	2.68	1.05
% of variance	48.7	33.5	13.2
	Eigenvectors		
Variable	1	2	3
Total P	−0.46	0.23	−0.04
Dissolved inorganic N	−0.24	0.08	−0.82
Dissolved organic C	−0.47	0.03	0.21
Conductivity	0.23	0.53	0.03
Maximum depth	0.18	−0.49	−0.46
Water residence time	0.06	−0.56	0.24
Macrophyte dry mass	0.41	0.33	−0.11
Catchment area	0.50	−0.01	−0.03

sensitive to fish predation (B. Eaton and C. Paszkowski, personal communication), indicated that the winterkill in S800 occurred in early 1997.

The IPC, using total fish BPUE, also distinguished reference and winterkill lakes. Changes in BPUE between consecutive surveys in L20 and S20 were all small (|IPC| < 0.4). In contrast, winterkills in S800 and L800, and the 1996 to 1998 recovery in L800, were characterized by IPC values an order of magnitude larger (|IPC| ≥ 4).

Lake environments

The first 2 axes of the environmental PCA explained 49% and 34% of the variance, respectively (Table 3), and sorted the 10 lake-years into 3 distinct clusters (Fig. 2). These clusters were primarily defined by among-lake similarities and differences. The 1st PC separated S20 from the other 3 lakes as a result of its lower TP and DOC and larger catchment area and macrophyte density (Table 3, Fig. 2). L20 and S800
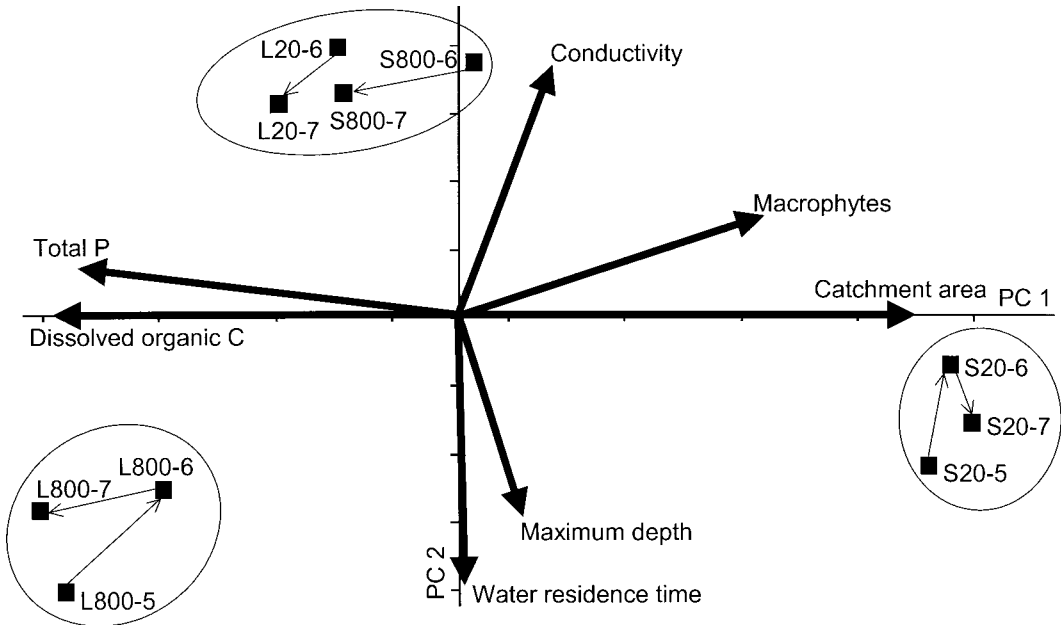
FIG. 2. Principal component analysis joint plot of the 4 study lake environments (1995–1997). Lakes are classified as reference or winterkill as in Fig. 1. Thicker arrows indicate the direction and strength of the relationships between a given environmental variable and axes 1 and 2; dissolved inorganic N had a very short vector and is not shown. Thin arrows indicate within-lake temporal changes in environmental conditions; parallel movements on the ordination indicate parallel changes in environmental traits among lakes. Lake-years assorted themselves into the 3 encircled groups. Numbers following lake identities are study years: 5 = 1995, 6 = 1996, and 7 = 1997.

were differentiated from L800 on the 2nd PC as a result of the latter's lower conductivity, greater depth, and higher water residence time (Table 3, Fig. 2). Among-year variation was relatively minor and largely consistent among lakes, as indicated by parallel shifts in position.

Macroinvertebrates

Only 52% of year-to-year changes in density of the 9 invertebrate groups were opposite in sign to the corresponding change in total fish BPUE when those fish changes were minor ($|IPC| < 0.4$), i.e., in the reference lakes ($n = 27$, $p > 0.5$). However, the proportion of invertebrate changes that were opposite in sign to fish increased to 67% ($n = 27$, $p = 0.06$) in lakes and years associated with winterkill (or recovery), when changes in fish BPUE were substantial ($|IPC| \geq 4$).

The PCA of littoral invertebrate assemblages also revealed strong and parallel changes in composition in L800 and S800 that were tem-

porally coherent with the fish winterkills (Fig. 3). Compared to the pre-winterkill year of 1996, S800 increased greatly on PC2 in 1997, and to a lesser extent on PC1, with PC2 reflecting increased densities of leeches, and PC1 indicating an increase in amphipods (Table 4, Appendix). A parallel shift in L800 following its winterkill (1996) reflected similar increases in leeches and amphipods. A subsequent shift in 1997, when fish populations had begun to recover, reflected decreases in amphipods. In contrast, changes in the 2 reference lakes were relatively minor or did not parallel the trajectories of the winterkill lakes. All 3 lake-years of S20 were grouped at one end of the 1st PC axis (Fig. 3), reflecting moderately high densities of amphipods and trichopterans (Table 4, Appendix). As well, L20 had low scores on PC2, indicating consistently low densities of leeches; a shift to the left in 1997 reflected an increase in chironomids and a decrease in *Gammarus*, *Hyalella*, and Trichoptera (Table 4, Appendix).
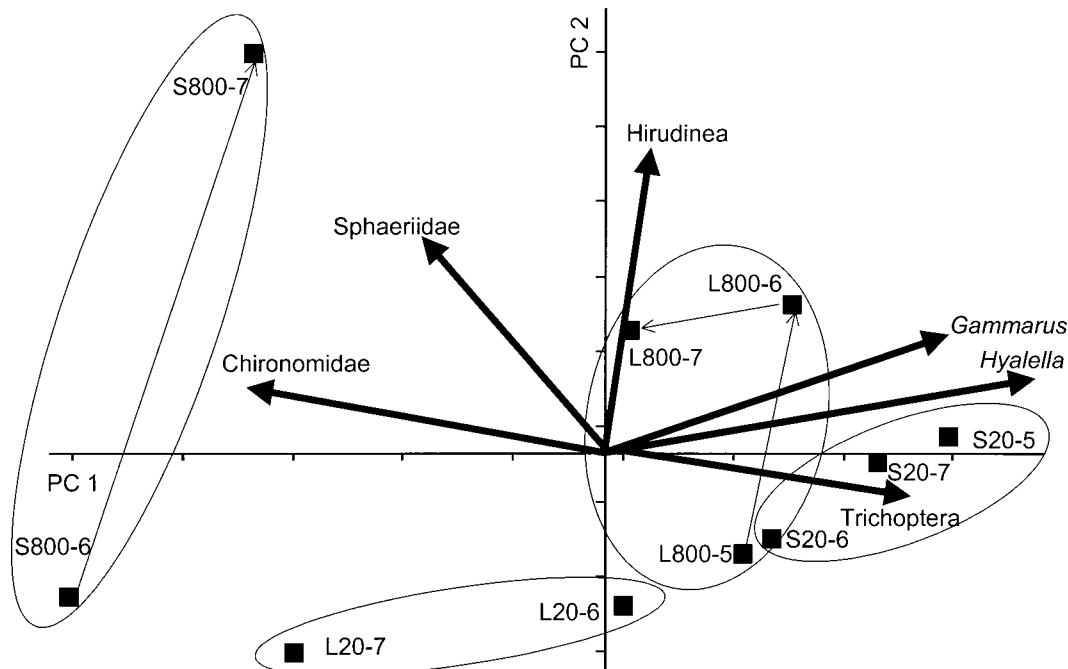
Partial RDAs revealed that, of the explained

Fig. 3.   Principal component analysis joint plot of macroinvertebrate assemblages in the 4 study lakes during the study period (1995–1997). Lakes are classified as reference or winterkill as in Fig. 1. Scores for each lake are enclosed with an oval. Thicker arrows indicate the direction and strength of the relationships between a given invertebrate group and axes 1 and 2; Ceratopogonidae had a very short vector and is not shown. Thin arrows indicate within-lake temporal changes after fish winterkills in L800 and S800. Numbers following lake identities as in Fig. 2.

Table 4.   Principal components (PC) analysis of macroinvertebrate densities.

	PC axes		
	1	2	3
Eigenvalue	2.54	2.04	1.53
% of variance	36.3	29.2	21.8
	Eigenvectors		
Taxa	1	2	3
Gammarus	0.45	0.36	−0.34
Hyalella	0.51	0.28	0.28
Chironomidae	−0.46	0.27	−0.06
Hirudinea	0.16	0.57	−0.35
Trichoptera	0.42	−0.22	0.43
Ceratopogonidae	−0.07	0.34	0.65
Sphaeriidae	−0.34	0.48	0.27

variation in the invertebrate data (= 84.5%), considerable proportions could be ascribed to both the fish (33% of explained variation) and environmental characteristics of the lakes (47%). These results are consistent with the combination of among-lake differences in environmental characteristics and among-year changes associated with fish winterkills, and are also consistent with the tests of concordance among data sets. Invertebrate assemblages were significantly concordant with both the lake environment ($p = 0.012$) and the fish assemblages ($p = 0.042$). Lake environments and fish assemblages, however, were not concordant ($p = 0.223$).

Density changes of individual taxa supported and helped clarify the community-level responses. As a group, the 4 invertebrate taxa that are common prey of perch and pike in these lakes (*Gammarus*, *Hyalella*, leeches, and chironomids; Beaudoin et al. 1999, 2001, Venturelli 2004) responded consistently to the large changes in fish BPUE associated with winterkill. In-
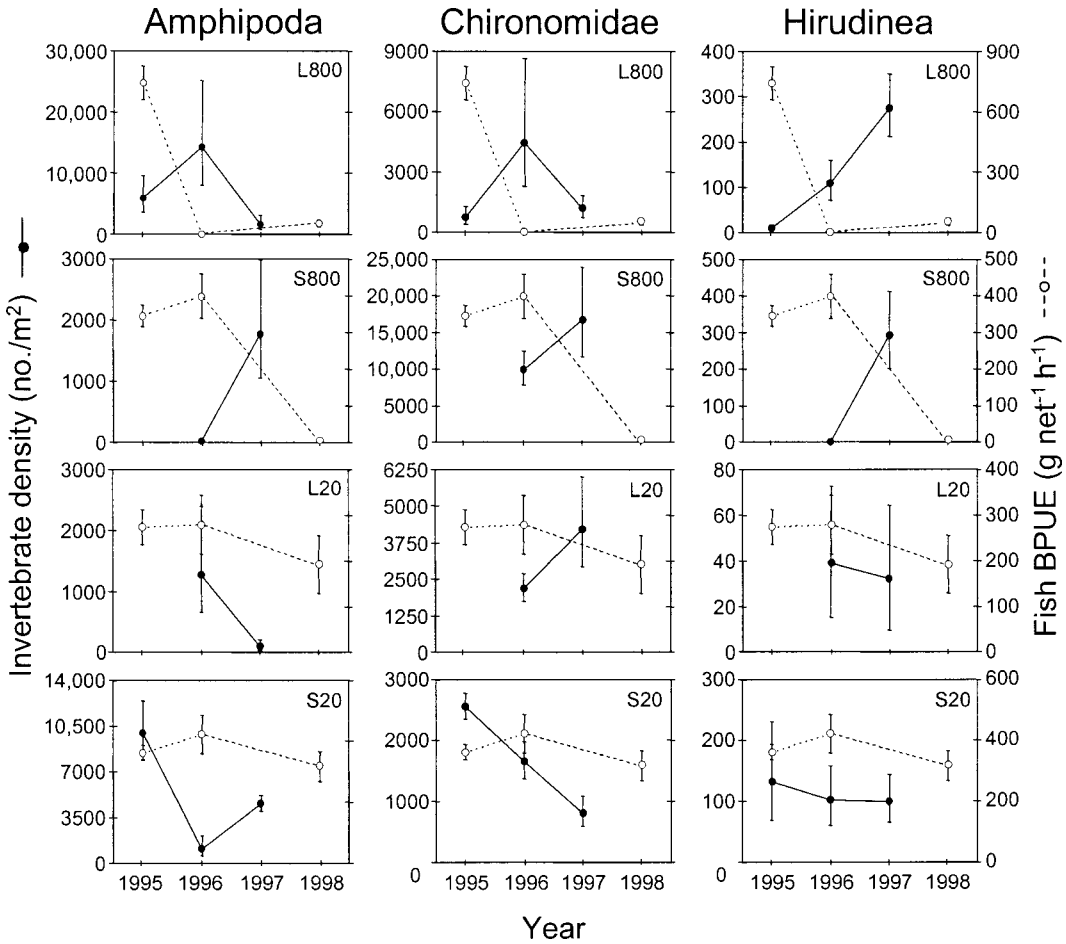
FIG. 4. Fish biomass-per-unit-effort (BPUE) (right y-axes) and densities (left y-axes) of amphipods, chironomids, and leeches in the 4 study lakes from 1995 to 1998. Lakes are classified as reference or winterkill as in Fig. 1. Patterns for total macroinvertebrates (not shown) paralleled amphipods in each lake. Values are back-transformed means (± 1 SE). Note that axes differ among lakes and taxa.

deed, 92% of year-to-year changes in density for these taxa were opposite in sign to the corresponding changes in total fish BPUE when $|IPC| \geq 4$ ($n = 12$, $p = 0.003$); the corresponding figure when $|IPC| < 4$ was only 58% ($n = 12$, $p = 0.39$).

Univariate responses to winterkill were consistent with these results. Changes in invertebrate densities were greater in winterkill lake-years than in reference lake-years for Amphipoda (*Gammarus* and *Hyalella* combined), Hirudinea, and Chironomidae (Fig. 4), as well as for total macroinvertebrates (*t*-tests, all $p < 0.10$) (see Appendix). Density changes in the reference lakes, even for the winterkill-responsive

groups (Fig. 4), were independent and unrelated to fish densities. Densities of the remaining taxa (Sphaeriidae, Ceratopogonidae, Trichoptera, Chaoboridae, and "other") sometimes, but not consistently, increased in winterkill lake-years (all $p > 0.1$; Appendix).

Discussion

Winterkill caused dramatic changes in the densities of fish in 2 of our study lakes. These disturbances, when linked with limited temporal variation in other features of the study lakes' environments and the availability of nearby reference lakes, provided a serendipitous whole-

lake natural experiment that facilitated an examination of top-down effects of fish predation on littoral macroinvertebrates. Furthermore, winterkills altered the abundances of the lakes' native fish populations, so responses by invertebrates should provide stronger, more natural evidence of top-down effects than would responses to the experimental introduction of nonnative fishes (McPeek 1980, Thorp 1986, Wellborn et al. 1996).

Community-level responses

Macroinvertebrate assemblage structure changed dramatically, and with parallel trajectories, in L800 (1995–1996) and S800 (1996–1997), coincident with the winterkills in those lakes. However, invertebrate assemblages in both L20 and S20 displayed moderate consistency over the same time period in the absence of winterkill. The temporal variation that did occur in our reference lakes was not concordant, i.e., each assemblage varied independently, and the trajectories in ordination space were perpendicular to the disturbance-driven responses in the 2 winterkill lakes. As a result of these contrasting patterns, the invertebrate assemblages were significantly concordant with the winterkill-driven patterns in the fish assemblages.

Taxon-specific responses

Our analyses indicated that, when fish densities decreased, macroinvertebrate taxa that are common prey of the fish in these lakes (amphipods, leeches, and chironomids) increased. Amphipods, in particular, are important prey of fish in our study lakes (Beaudoin et al. 1999, 2001), and are sometimes consumed by the hundreds by a single pike (WMT, personal observation). Hanson and Butler (1994) also found amphipods to be the group most responsive to fish removal, and suggested that the large size and active nature of amphipods made them vulnerable to fish predation. Interestingly, Zimmer et al. (2000, 2001) found that *Hyalella*, but not *Gammarus*, was responsive to the absence or experimental removal of fathead minnows, a trend not evident in our data. The similarity in response of both amphipod taxa in our study and in Hanson and Butler (1994) may reflect the larger gapes of the fishes in these studies, relative to the fathead minnow studied by Zimmer

et al. (2000, 2001). Leeches are similarly large, active, and likely vulnerable invertebrates, and are readily consumed by pike in boreal Alberta lakes (Venturelli 2004). Chironomids are important prey of juvenile perch (Venturelli 2004), and are responsive to altered predation pressure from fish (Goyke and Hershey 1992, Karjalainen et al. 1999).

Life-history characteristics of these macroinvertebrates may also have contributed to their strong responses. Amphipods and leeches both complete their life cycles in lakes and, thus, both adult survivorship and juvenile recruitment can respond to fish winterkill. Amphipods mate shortly after ice-out in boreal lakes; young-of-the-year hatch ~3 wk later and mature over the course of the summer (Clifford 1991, Wen 1992). They are, thus, well suited to take advantage of winterkill-induced reductions in fish density in spring; breeding adults become much less vulnerable to fish predation and their offspring are introduced into a benign biotic environment. Likewise, chironomids in Alberta lakes are typically uni- or multivoltine (Clifford 1991), and should exhibit relatively short response times to reduced predation pressure. Taxa that did not respond strongly to the fish winterkills may have been lacking in one or more of these size, behavioral, or life-history traits, although it is also possible that the coarse taxonomic resolution required for some groups obscured responses at lower taxonomic levels (McPeek 1990).

Alternatives to predation?

Winterkill conditions can also directly affect macroinvertebrates (Lindeman 1942, Kolar and Rahel 1993) to produce fish–invertebrate concordance (Hoffsten 2003). Such direct mortality effects, however, would result in changes in the densities of fish and invertebrates that were in the same direction, which is the opposite of what we observed. Conversely, the decomposition of fish carcasses following winterkill could lead to an increase in macroinvertebrates independent of a predation effect because of nutrients recycled back into the system (e.g., Wipfli et al. 1998, but see Zimmer et al. 2001). That chlorophyll and P levels in L800 and S800 were not exceptionally elevated in the summers following the winterkills (Prepas et al. 2001) suggests that such a bottom-up effect did not occur.

Minor temporal changes in limnology within the lakes were observed, but appeared to reflect regional, e.g., climatic, variability that affected winterkill and reference lakes alike. For example, decreases in water residence times in L800 and S20 from 1995 to 1996 were consistent with a 32% increase in May to July precipitation between those 2 years (EEP and WMT, unpublished data). The lack of concordance between the fish and environmental ordinations indicated further that winterkill was a biotic disturbance that did not strongly affect other ecosystem characteristics; therefore, macroinvertebrate responses appear attributable to changes in fish populations caused by winterkill.

Winterkill: a natural disturbance and natural experiment

We worked with unpredictable natural disturbances, so our study design was largely unplanned. As a result, our sample sizes (numbers of lake-years) were limited, which may have reduced our ability to detect significant changes in abundance of some taxa with traditional univariate statistics. We were nevertheless able to detect several taxon-specific changes in density, as well as consistent changes at the community level, revealing changes in assemblage structure brought about by releases from fish predation as a result of winterkills of fish. Whole-system studies are powerful approaches to examining the effects of unpredictable disturbances that are not amenable to well-replicated but smaller-scale studies (Schindler 1998, Wiens et al. 2001, Zimmer et al. 2001). Small-scale, intensive studies can be helpful in understanding how various factors can interact with fish predation, e.g., structural heterogeneity (Crowder and Cooper 1982), omnivory (Diehl 1992), and seasonality (Gilinsky 1984). Such studies, however, may not reliably represent the complete array of conditions and processes that occur in whole systems, such as predator and prey behavior or life history and, thus, may be unable to capture all of the relevant ecological interactions (Carpenter 1996).

Winterkill is a natural disturbance that has strong effects on lake food webs and deserves greater consideration as an important agent structuring northern lake communities (Tonn and Magnuson 1982, Mittelbach et al. 1995, Danylchuk and Tonn 2003). Exactly how important will likely depend on such factors as its frequency, intensity, and selectivity (by size or species), and the relationship between the rates of response by invertebrates and the rates of recovery of fish populations.

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APPENDIX. Average densities (no./m²) of benthic macroinvertebrates collected in the 4 study lakes from 1995 to 1997. Shown are back-transformed averages (±1 SE). Numbers following lake identities are study years: 5 = 1995, 6 = 1996, and 7 = 1997. L = Lac La Biche area, S = South Pelican Hills area.

Study lake	Gammaridae	Hyalellidae	Chironomidae	Chaoboridae	Hirudinea	Trichoptera
L20-6	257.3	727.7	2171.1	15.0	39.1	52.6
	(113, 534)	(301, 1685)	(1746, 2697)	(5, 28)	(15, 73)	(24, 93)
L20-7	41.2	57.7	4188.1	58.1	32.0	5.3
	(10, 90)	(13, 139)	(2921, 5996)	(21, 117)	(9, 64)	(0, 11)
L800-5	44.4	5824.3	731.0	33.5	8.2	199.8
	(0, 135)	(3600, 9408)	(404, 1297)	(9, 69)	(0, 18)	(80, 437)
L800-6	981.6	13,287.1	4447.8	5.3	108.8	52.6
	(490, 1926)	(7623, 23,136)	(2283, 8629)	(0, 11)	(71, 159)	(29, 84)
L800-7	427.6	831.9	1160.1	594.5	273.5	11.2
	(281, 640)	(328, 2020)	(737, 1813)	(446, 788)	(212, 350)	(4, 20)
S20-5	1047.1	8625.9	2549.6	13.6	131.6	174.5
	(630, 1724)	(7040, 10,567)	(2350, 2766)	(0, 32)	(69, 230)	(69, 380)
S20-6	682.7	526.7	1645.2	73.9	101.2	89.9
	(479, 965)	(257, 1038)	(1366, 1980)	(47, 109)	(61, 157)	(55, 138)
S20-7	1429.2	3323.2	797.2	17.9	99.2	30.1
	(1150, 1773)	(2824, 3909)	(587, 1078)	(5, 34)	(66, 143)	(14, 51)
S800-6	0.0	26.7	9832.8	0.0	0.0	22.1
	(0, 0)	(13, 44)	(7803, 12,388)	(0, 0)	(0, 0)	(5, 45)
S800-7	455.3	1049.0	16,702.6	37.3	291.4	0.0
	(270, 750)	(572, 1897)	(11,647, 23,944)	(15, 68)	(202, 413)	(0, 0)

Study lake	Ceratopogonidae	Sphaeriidae	Other	Total
L20-6	26.7	412.7	3108.3	9628.0
	(8, 53)	(213, 769)	(1978, 4871)	(7005, 13,228)
L20-7	17.9	425.3	2698.3	8680.7
	(5, 34)	(275, 645)	(1882, 3860)	(6584, 11,441)
L800-5	1039.4	1073.1	907.4	12,340.4
	(499, 2118)	(828, 1387)	(637, 1285)	(8900, 17,105)
L800-6	620.0	533.8	734.2	21,108.6
	(355, 1062)	(341, 824)	(445, 1196)	(11,913, 37,375)
L800-7	166.4	971.4	696.1	7307.5
	(109, 245)	(677, 1385)	(523, 922)	(5470, 9756)
S20-5	17.9	616.0	351.7	14,294.2
	(0, 43)	(421, 894)	(180, 656)	(11,729, 17,418)
S20-6	46.4	387.6	185.8	4715.1
	(25, 75)	(324, 462)	(98, 330)	(4118, 5399)
S20-7	30.1	496.6	579.8	7502.7
	(14, 51)	(34, 729)	(494, 680)	(6757, 8330)
S800-6	137.1	1360.2	386.7	12,291.2
	(101, 182)	(923, 1996)	(279, 530)	(9893, 15,268)
S800-7	475.3	4975.0	756.6	28,024.3
	(344, 652)	(4287, 5772)	(608, 939)	(21,638, 36,292)