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ABSTRACT.—We assessed short-term variability and long-term change in the composition of the littoral fish community in Spirit Lake, Iowa. Fish were sampled in several locations at night with large beach seines during spring, summer and fall of 1995–1998. Long-term changes were inferred from comparison with a similar study conducted over 70 y earlier in Spirit Lake. We found 26 species in the littoral zone. The number of species per sample ranged from 4 to 18, averaging 11.8. The average number of species per sample was higher at stations with greater vegetation density. A distinct seasonal pattern was evident in the number of species collected per sample in most years, increasing steadily from spring to fall. Patterns of variability within our 1995–1998 study period suggest that: (1) numerous samples are necessary to adequately characterize a littoral fish community, (2) sampling should be done when vegetation and young-of-year densities are highest and (3) sampling during a single year is inadequate to reveal the full community. The number of native species has declined by approximately 25% over the last 70 y. A coincident decline in littoral vegetation and associated habitat changes during the same period are likely causes of the long-term community change.

INTRODUCTION

Community composition is a fundamental characteristic of ecological and environmental assessments (Krebs, 1999). Changes in community composition can be short-term, reflecting life-cycle or migratory responses to regular seasonal changes in habitat and physical conditions, as well as long-term, reflecting invasions and extirpations in response to habitat degradation and environmental changes (Morin, 1999). Sampling over multiple years is necessary to establish the repeatability of seasonal changes within years. Demonstrating long-term changes is more difficult since the temporal scale of interest is usually longer than the duration of most studies (Magnuson *et al.*, 1994). Inferring long-term changes typically relies on comparisons of contemporary studies with historical data.

The littoral zone fish community is an important component of freshwater lakes (Northcote, 1988). Abundance is often greater than in other areas of the lake, and in many lakes littoral species comprise the majority or even all of the lake-wide fish community (*e.g.*, Keast and Harker, 1977; Werner *et al.*, 1977). Littoral zone habitat and food resources are more diverse than in the pelagic zone, and are often crucial for spawning, feeding and avoiding

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predation (Keast and Harker, 1977; Savino and Stein, 1982; Wiley *et al.*, 1984; Carpenter and Lodge, 1986; Rasmussen, 1988). Because of the importance of littoral species to the overall fish communities and fisheries in lakes, changes in the composition of the littoral community can have significant implications for lake ecosystems (Simon, 1998), and could potentially affect energy flow, food web interactions and fishery yields from the entire system.

Spirit Lake, Iowa, supports one of Iowa's most important natural lake fisheries, which has attracted anglers and commercial fishers for over a century (Hofsommer, 1975). Walleye (*Stizostedion vitreum*) stocking dates back to the late 1800s, and fishery research and management has occurred for several decades (Rose, 1949; Larscheid, 1997). Angling pressure is high for 10 mo of the year with up to a dozen targeted species. In addition to angler harvest, common carp (*Cyprinus carpio*), bigmouth buffalo (*Ictiobus cyprinellus*) and freshwater drum (*Aplodinotus grunniens*) are harvested commercially.

The purpose of this study was to assess short-term variability and long-term change in the composition of the littoral fish community in Spirit Lake. Our specific objectives were to: (1) characterize the current community, (2) quantify seasonal, yearly and among-station variation in the littoral community as revealed by replicated sampling, and (3) assess change in the community over the last 70 y.

METHODS

Study site.—Spirit Lake (43°28′N, 95°06′W) is located near the Iowa-Minnesota border in northwest Iowa. Iowa's largest natural lake, Spirit Lake has a surface area of 2229 ha, a maximum depth of 7 m, a mean depth of 5 m and is eutrophic (Bachmann *et al.*, 1995). Ice cover occurs from early December to early April, and summer water temperatures peak in July and August at 24–26 C with no thermal stratification. Changes in numerical abundance and biomass of littoral zone fishes during the same period as this study are detailed in Pierce, Sexton *et al.*, (*in press*).

We defined the littoral zone as extending from the shore to a depth of 3 m, which is the approximate extent of submerged vegetation in most years. The littoral zone occupies roughly 14% of the lake surface area. The bottom in the littoral zone is gently sloping, and the substrate consists of various mixtures of sand, gravel and cobble, with sporadic clusters of boulders. Submerged vegetation is essentially nonexistent in early spring, but by early fall is dense in a few areas (<20% of littoral zone) while sparse or nonexistent in others. Most of the shoreline is privately owned and developed with cottages and docks, and land use in the drainage basin is primarily agricultural. Emergent vegetation is rare, occurring only in the few remaining undeveloped areas.

Sampling.—We sampled in July and September 1995, May, July and September 1996 and 1997, and monthly from June through September 1998. All sampling was done at night, which has been shown to reveal more species than daytime sampling (Pierce, Corcoran *et al.*, (*in press*). Because of private cottages and docks along most of the shoreline, we used eight fixed sampling stations. Four of these stations were in areas with relatively dense submerged vegetation in early fall, and the other four were in areas where submerged vegetation was either sparse or nonexistent in early fall. We attempted to sample each station once during a 4–5 d period near the new moon phase of each month; fewer than eight stations were sampled in some months. During each sampling period stations were sampled in haphazard order, with wind conditions often dictating the stations sampled on a particular night.

We used 6 mm (bar) mesh, lampara-style, beach seines (Hayes *et al.*, 1996) for all samples. Seine dimensions were as follows: 133 × 4 m in September 1995 and all of 1996 and 1997, 333 × 4 m in July 1995 and 152 × 4 m in all of 1998. Seines had weighted bottom lines and floats along the top lines, and were deployed from a boat in a semicircle extending out from the shoreline. Seines were pulled to shore from both ends simultaneously. Areas sampled were 0.28 ha (133 m seine), 1.76 ha (333 m seine) and 0.37 ha (152 m seine). Captured fish were identified and counted in the field and released alive.

Historical data.—Long-term changes in the littoral zone fish community were inferred from comparison of our cumulative species list with data collected over 70 y earlier in Spirit Lake by Larrabee (1926). Larrabee made an unspecified number of collections by seine, angling and inspection of angler creels in Spirit Lake during the summers of 1921–1925. Details regarding the collecting dates, seine dimensions, mesh size, number of seine hauls and other methods were not reported. However, Larrabee did report sampling at three stations which roughly match three of our stations.

Statistical analyses.—Short-term variation in the number of species collected in our 1995–1998 samples was tested by ANOVA, using untransformed data in SAS (SAS Institute Inc., 1988). We used a repeated measures split-plot ANOVA because the same eight stations were sampled throughout the study (Maceina *et al.*, 1994).

RESULTS

Current community.—From 89 samples and over 166,000 fish collected over a 4 y period (1995–1998), we found 26 species in the littoral zone of Spirit Lake (Table 1). Two of these species are known to be introduced, either unintentionally (common carp) or by intentional stocking (muskellunge [*Esox masquinongy*]). Two species, yellow perch (*Perca flavescens*) and walleye, were found in every sample. Eleven species, including bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), spottail shiner (*Notropis hudsonius*), largemouth bass (*Micropterus salmoides*), black bullhead (*Ameiurus melas*), logperch (*Percina caprodes*), smallmouth bass (*Micropterus dolomieu*), common carp and freshwater drum in addition to yellow perch and walleye, were present in 70% or more of our samples.

Short-term variability.—The average number of species per sample was 11.8, but there was considerable variation among samples (Fig. 1). The number of species in individual samples ranged from 4 to 18. The number of species varied significantly among stations ($P < 0.001$). The four stations with relatively dense submerged vegetation averaged between 12 and 14 species per sample, whereas the four stations where vegetation was either sparse or nonexistent averaged between 9 and 12 species per sample.

A consistent seasonal pattern was evident in the number of species collected per sample in 1996, 97 and 98, with the number of species increasing steadily from spring to fall (Fig. 1). This pattern was not seen in 1995, however, when July and September samples contained similar numbers of species. This inconsistency in the seasonal pattern among years resulted in a significant year by month interaction ($P < 0.013$).

The number of species collected each year ranged from 19 in 1995 to 23 in 1996 and 1998. The cumulative number of species collected was 19 in 1995, 24 by 1996, 25 by 1997 and 26 by 1998.

Long-term changes.—Our intensive collections over 4 y revealed a total of 26 species, compared with 34 species reported by Larrabee (1926) from collections in the early 1920s (Table 1). The 24 native species we found is a 25% decline from the 32 native species reported by Larrabee. Of the two introduced species we found, Larrabee's collections included common carp, but not muskellunge. Common carp were introduced to North America in the late 1800s (Cooper, 1987) and have become widespread. Muskellunge were introduced to Spirit Lake in the 1970s and are sustained by annual stocking. Larrabee listed an additional introduced species, lake trout (*Salvelinus namaycush*), that had been stocked

TABLE 1.—Long-term change in the littoral zone fish community in Spirit Lake, Iowa. Species' origin determined according to Larrabee (1926) and Harlan and Speaker (1987). Species listed as native are native to the region, not necessarily to Spirit Lake

Species	Common name	Origin[1]	Study/years of collection[2] Larrabee (1926)/ 1921–1925	This study/ 1995–1998	1995–1998 Rank abundance
Perca flavescens	Yellow perch	N	P	P	1
Lepomis macrochirus	Bluegill	N	P	P	2
Stizostedion vitreum	Walleye	N	P	P	3
Pomoxis nigromaculatus	Black crappie	N	P	P	4
Notropis hudsonius	Spottail shiner	N	P	P	5
Micropterus salmoides	Largemouth bass	N	P	P	6
Ameiurus melas	Black bullhead	N	P	P	7
Percina caprodes	Logperch	N	P	P	8
Micropterus dolomieu	Smallmouth bass	N	P	P	9
Cyprinus carpio	Common carp	I	P	P	10
Notemigonus crysoleucas	Golden shiner	N	P	P	11
Aplodinotus grunniens	Freshwater drum	N	P	P	12
Etheostoma nigrum	Johnny darter	N	P	P	13
Ictiobus cyprinellus	Bigmouth buffalo	N	P	P	14
Lepomis gibbosus	Pumpkinseed	N	P	P	15
Morone chrysops	White bass	N	P	P	16
Esox lucius	Northern pike	N	P	P	17
Lepisosteus platostomus	Shortnose gar	N	P	P	18
Noturus gyrinus	Tadpole madtom	N	NF	P	19
Lepomis cyanellus	Green sunfish	N	P	P	20
Esox masquinongy	Muskellunge	I	NF	P	21
Notropis atherinoides	Emerald shiner	N	NF	P	22
Lepisosteus osseus	Longnose gar	N	P	P	23
Catostomus commersoni	White sucker	N	P	P	24
Pimephales notatus	Bluntnose minnow	N	P	P	25
Etheostoma exile	Iowa darter	N	P	P	26
Salvelinus namaycush	Lake trout	I	R	NF	
Ictiobus bubalus	Smallmouth buffalo	N	P	NF	
Pimephales vigilax	Bullhead minnow	N	P	NF	
Ameiurus natalis	Yellow bullhead	N	P	?[3]	
Ameiurus nebulosus	Brown bullhead	N	P	NF	
Fundulus diaphanus	Banded killifish	N	P	NF	
Percopsis omiscomaycus	Trout-perch	N	P	NF	
Pomoxis annularis	White crappie	N	P	NF	
Ambloplites rupestris	Rock bass	N	P	NF	
Stizostedion canadense	Sauger	N	P	NF	
Ictalurus punctatus	Channel catfish	N	?[4]	NF	
Number of native species			32	24	
Total number of species			34	26	

[1] Abbreviations: N = native, I = introduced

[2] Abbreviations: P = present, NF = not found, R = relict

[3] A few individuals caught by Dept. of Natural Resources personnel near wetland outflow April, 1995

[4] Reported by anglers but not collected in survey. Occasional stocking by Dept. of Natural Resources and periodic reports by anglers indicate sporadic presence since the 1920s

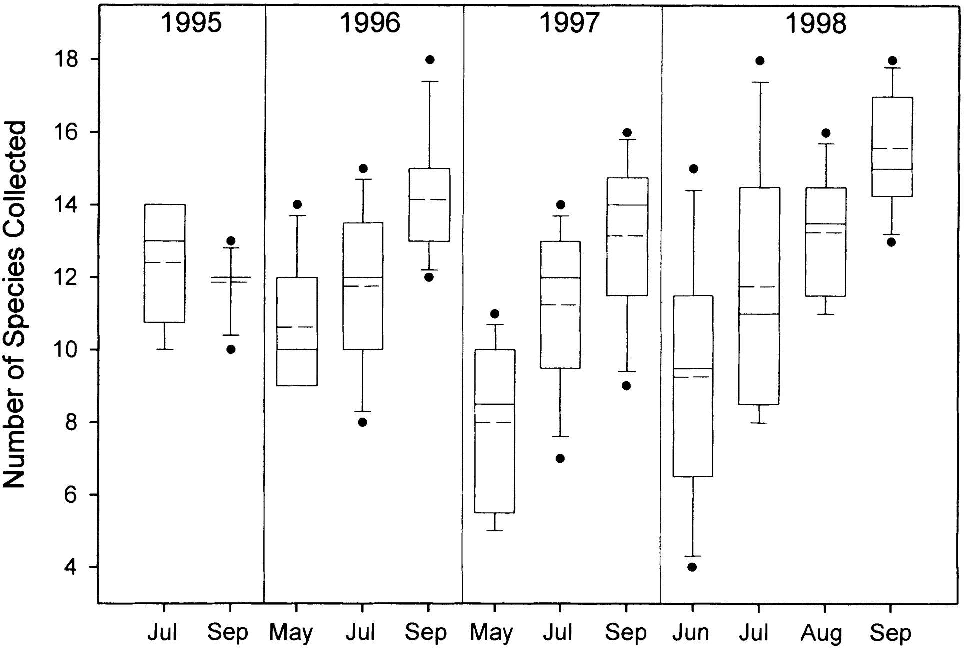

FIG. 1.—Variability in the number of species collected in the littoral zone of Spirit Lake, Iowa, 1995–98. Boxes encompass inter-quartile ranges, solid lines within boxes represent medians, dashed lines within boxes represent means, vertical lines above and below boxes extend to 90th and 10th percentiles, respectively, and dots indicate individual values beyond 90th and 10th percentiles

as adults earlier and possibly remained as a small relict population. No lake trout were collected by Larrabee, but occasional catches were reported by anglers at the time.

DISCUSSION

The 26 species we collected in Spirit Lake is roughly twice the typical number documented in other lakes relative to lake surface area. Published species-area relationships predict 12 to 16 fish species in a lake the size of Spirit Lake (Eadie and Keast, 1984; Matuszek and Beggs, 1988; Jackson and Harvey, 1989; Pierce *et al.*, 1994). Zoogeographic differences no doubt account for some of this discrepancy. Spirit Lake lies in the Mississippi River drainage, which is known to harbor a more diverse fish fauna than either the St. Lawrence River or Hudson Bay drainages, where most of the lakes featured in the above-mentioned studies are found (Hocutt and Wiley, 1986). Early fish surveys in other lakes near Spirit Lake report 40 and 36 species in East and West Okoboji lakes, respectively (Larrabee, 1926), both of which are connected to Spirit Lake during floods, and 43 species in Clear Lake (Bailey and Harrison, 1945), located roughly 140 km east of Spirit Lake and in the same major zoogeographic region.

We are confident that the 26 species we collected in the littoral zone is a reasonably accurate estimate of the current species community in Spirit Lake for five reasons: (1) seines captured more species than any of the five other gears used in Magnuson *et al.*'s (1994) study, (2) we sampled over 33 ha of surface area and identified more than 166,000 specimens during a 4 y period, (3) the cumulative number of species increased by only one species in each of the last two years of collecting, (4) Spirit Lake is relatively shallow (maximum depth 7 m) and is not known to support pelagic fishes that would likely be missed by littoral sampling gear and (5) intensive offshore bottom trawling conducted in 1998 as part of another study revealed no additional species (Pelham, 2000). Of course, the true number of species is perhaps impossible to determine, as rare species can elude even exhaustive sampling efforts in a large natural lake (Magnuson *et al.*, 1994). A study focusing on young-of-the-year fishes in Spirit Lake conducted ten years before ours recorded 21 species, including two species that were absent from our collections, yellow bullhead (*Ameiurus natalis*) and banded killifish (*Fundulus diaphanus*) (Bryan and Scarnecchia, 1992). It is not known whether these absences from our collections represent sampling error or real extirpations.

Comparison of our cumulative species list for Spirit Lake with individual samples illustrates some important implications for the sampling effort required to accurately estimate community composition. Our mean number of species per sample, 11.8, was 45% of the cumulative total species richness. Our samples containing the most species, with 18, only contained 69% of the total. These single-sample percentages of the total compare reasonably well with the mean of 61% reported by Pierce *et al.* (1994), supporting their contention that despite sampling large areas, numerous samples are required to detect the presence of rarer species. The combined evidence to date suggests that a single deployment of a large seine (*i.e.*, >100 m long) might be expected to reveal roughly half the species present in a littoral zone community.

Our results also demonstrate the potential influence of seasonal timing of sampling on estimates of community composition (Fig. 1). The seasonal increases in number of species collected per sample in 1996–1998 suggest that to maximize chances of recording all species present, sampling should occur in the late summer or fall. This period corresponds with maximal abundance of young-of-the-year of many species in the littoral zone, at sizes where they are effectively sampled by a seine. Bryan and Scarnecchia (1992) documented a similar pattern of seasonal increase in the number of species sampled in the littoral zone of Spirit Lake.

With multiple samples and stratifying those samples over several months, we obtained yearly total numbers of species ranging from 73 to 88% of our overall 4 y total. Had the study only been conducted in 1995 and 1997, the two years with the lowest numbers of species collected, the total species list would have been 85% of what we obtained in four years of sampling. In contrast, had the study only been conducted in 1996 and 1998, the two years with the highest numbers of species collected, the total species list would have been 96% of what we obtained in four years of sampling. These scenarios suggest that to approach a reasonably complete picture of community composition, at least two and possibly three years of sampling is required. Magnuson *et al.* (1994) have also recommended against inferring species richness from a single year of sampling.

A recent study (Hatzenbeler *et al.*, 2000) in northern Wisconsin lakes demonstrated a seasonal pattern in the number of species that differed from ours, with the exception of our 1995 pattern. The seasonal pattern they documented should be interpreted cautiously, however, since they only sampled during a single year (1996). They reported greatest species richness in summer (mid-July to mid-August), with fewer species recorded during spring (May to early June) and fall (September to early October). Although this seasonal pattern differed from the steady seasonal increase we documented in 1996–98, their explanation is consistent with our qualitative observations in Spirit Lake. The seasonal increases and subsequent declines in number of species in Wisconsin lakes coincided with a similar pattern in the density of submerged and floating vegetation. In contrast, although we lack quantitative data, we observed a steady seasonal increase in density of littoral vegetation in Spirit Lake, with greatest density appearing to occur in September. Spirit Lake lies 2–3° south of the northern Wisconsin lakes, perhaps explaining its apparent lag in seasonal decline of littoral vegetation compared to the more northerly lakes. Regardless of the seasonal sequence or controlling mechanism, the combined evidence to date suggests that the number of species collected differs seasonally. To maximize the number of species collected, sampling should occur during periods of maximal vegetation density as well as when young-of-the-year fishes are present and vulnerable to sampling gear.

Comparison of the fish community we documented with the survey conducted over 70 y ago by Larrabee (1926) revealed a 25% decline in the number of native species found, from 32 in the 1920s, to the 24 native species we identified in the mid 1990s (Table 1). Because of uncertainties about Larrabee's sampling intensity and seasonality as well as other problems with quantifying community change over time (Magnuson *et al.*, 1994), this should be viewed as an approximate estimate of the decline. Potential reasons for this decline are many, including commercial and recreational exploitation (Roberts, 1997), introduction of exotic species (Li and Moyle, 1999), rough-fish removal (Wiley and Wydoski, 1999), deteriorating water quality resulting from intensive agricultural land use and residential shoreline development (Gianessi *et al.*, 1986; Edmondson, 1991) and associated habitat changes such as reduction of coarse woody debris (Christensen *et al.*, 1996) and vegetation (Bryan and Scarnecchia, 1992) in the littoral zone. Sigler (1948) reported dense and diverse beds of submerged littoral vegetation occurring along roughly 80% of the shoreline of Spirit Lake in the mid 1940s. Bryan and Scarnecchia (1992) reported that littoral vegetation had declined to only about 10% of the shoreline in Spirit Lake by the late 1980s, and that abundance and number of species of young-of-the-year fishes were reduced in areas without vegetation. Our qualitative observations of vegetation density and extent confirm Bryan and Scarnecchia's assessment. Littoral vegetation enhances abundance and productivity of many species by providing necessary spawning habitat, harboring abundant and diverse invertebrate prey, and providing cover (Keast and Harker, 1977; Keast *et al.*, 1978; Savino and Stein, 1982; Wiley *et al.*, 1984; Carpenter and Lodge, 1986; Rasmussen, 1988). Based on the established importance of littoral vegetation for fishes and the documented decline of littoral vegetation in Spirit Lake, it seems reasonable to speculate that this is a factor contributing to the long-term decline in the number of species in Spirit Lake. Reductions in habitat and water quality associated with similar watershed and shoreline land use changes have been implicated in declines of other littoral fish communities (Clady, 1976; Lyons, 1989). Ironically, a long-term decline in number of littoral zone fish species in Lake Mendota, Wisconsin was attributed in part to an *increase* in vegetation abundance, although in this case the increase was due to introduction of the exotic Eurasian watermilfoil, *Myriophyllum spicatum* (Lyons, 1989).

The two native species we found that were absent from Larrabee's collections, emerald shiner (*Notropis atherinoides*) and tadpole madtom (*Noturus gyrinus*), are small-bodied species that may have simply been missed in the earlier survey. Both were among the rarer species in our study. Because of the popularity of recreational fishing in Spirit Lake and the existence of several live bait dealers in the area, bait bucket transfer (Litvak and Mandrak, 1993; Ludwig and Leitch, 1996) is also a possible explanation for the appearance of these species since the earlier survey.

Natural species turnover through periodic colonization and extirpation is yet another potential explanation for the appearance and disappearance of species over time (Magnuson *et al.*, 1994). Spirit Lake is at the upstream end of a chain of lakes, and although movement of fish into Spirit Lake from downstream lakes is normally impeded by a spillway, periodic floods make upstream fish passage into Spirit Lake possible. In addition, Spirit Lake has permanent connections with several extensive wetland areas. These areas could serve as a source pool of species for periodic colonization. Species that naturally occur in low abundance face a variety of perils, both natural and anthropogenic, that could result in extirpation (Meffe *et al.*, 1997). Magnuson *et al.* (1994) suggest that some level of species turnover occurs in lake fish communities, but the mechanisms for these colonizations and extirpations are often unclear. In addition, they acknowledge that turnover is difficult to separate from potential sampling error.

A significant portion of the native littoral fish community appears to have been extirpated from Spirit Lake over the last 75 y, and similar declines have been recorded in other lakes where historical collections were available for comparison with recent studies (Clady, 1976; Lyons, 1989). There are many possible causes for these declines, but habitat deterioration is a likely factor. Our results suggest that to halt and perhaps reverse these declines, further habitat changes should be avoided, and efforts to restore original habitat conditions should be undertaken.

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