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DENSITY COMPENSATION IN *UMBRA-PERCA* FISH ASSEMBLAGES OF NORTHERN WISCONSIN LAKES[1]

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Abstract. Small, shallow seepage lakes in northern Wisconsin that have both low winter oxygen concentrations and low pH possess depauperate fish assemblages containing primarily or exclusively central mudminnows, *Umbra limi*, and yellow perch, *Perca flavescens*. Six times during three years I determined the total densities of fish in five lakes by mark-recapture and catch-per-effort methods. The richness of the fish assemblages in these lakes varied from one to three species in a nested pattern. While seasonal variations in density occurred within and among lakes due to variations of growth, mortality, and recruitment, total densities overall were independent of species richness. This pattern, called complete density compensation, suggests that total densities are expressions of the lakes' similar abilities to support fish and that the species interact rather than being independent. An intense negative correlation between perch and mudminnow densities was found, suggesting a strong interspecific population dominance of perch over mudminnows. There was also indirect evidence that both competition (exploitation and interference) and predation by perch regulate mudminnow populations when the species co-occur. Because these assemblages were unpredictably variable in time and space, conclusions from single censuses would have been unreliable. An exercise simulating single seasonal censuses from each richness class showed that less than one-half of such single censuses would have produced the pattern of complete compensation that was observed in the field study. In general, my results support the idea that the relative importance of the factors that determine community structure, or even the factors themselves, can differ not only from assemblage to assemblage at any one time, but even from season to season or year to year within a single assemblage.

Key words: density compensation; fish assemblages; interspecific interactions; mark-recapture; natural experiment; Perca flavescens; *severe environment; spatial and temporal heterogeneity;* Umbra limi; *Wisconsin.*

INTRODUCTION

Direct assessment of the effects of interspecific interactions on communities is often difficult under natural field conditions. As a result, ecologists frequently use indirect methods to evaluate the importance of competition and predation in structuring multispecies assemblages. Park (1948) suggested that the direction and intensity of interactions can be measured by comparing the population performance of each species alone with its performance in the presence of other species, under similar environmental conditions. Park's discussion originally pertained to laboratory competition experiments, but subsequently this approach has been applied to a variety of field manipulations (e.g., Grant 1969, Wilbur 1972, Werner and Hall 1976, Dunham 1980) and natural experiments (e.g., Diamond 1970*a*, *b*, Yeaton 1974, Case 1975). For example, insular habitats can provide changes in the biotic environment at otherwise similar sites, analogous to the manipulative experiments suggested by Park (1948).

One way that the natural experiment approach has been used to assess biotic interactions is in studies that compare the total densities of guilds at sites having different numbers of species; such studies ask: do the species remaining at species-poor sites increase in population size and compensate for the absence of the species present at richer sites? Like Park's laboratory experiments, these density compensation studies (MacArthur et al. 1972) can empirically indicate the presence and direction of interspecific interactions, measure the intensity of their population effects, and help begin to identify the mechanisms of interaction and to assess their roles in determining community structure.

Except for a brief analysis of fish surveys by Carlander (1955), Crowell (1962) was apparently the first to measure quantitatively the relationship between total faunal density and species richness. He found that the density of the bird fauna in Bermuda, comprising 10 species, was at least as great as in comparable habitats on the North American mainland that supported 20–30 species. Crowell (1962) believed that the total densities of the faunas were expressions of the habitats' carrying capacities rather than the faunas' richness, suggesting that the populations were not independent but interacted. Since Crowell's pioneering study, total densities have been compared between species-rich and species-poor insular sites for assemblages of insects (Janzen 1973, Faeth and Simberloff 1981, Lawton 1982, Southwood et al. 1982), lizards (Case 1975) and, in

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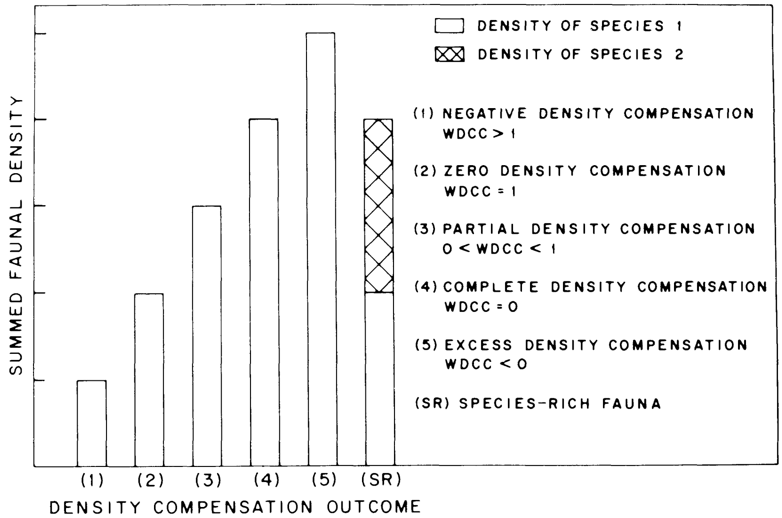

FIG. 1. Graphical illustration of the five possible degrees of density compensation. The summed faunal densities of species-poor sites (cases 1–5, consisting only of species 1) are compared to the summed density of the species-rich site (case SR; consisting of species 1 and species 2). Wright's Density Compensation Coefficient (WDCC; see Methods: Data Analyses) for each of the five outcomes is given.

more than a dozen studies, birds (see references in the review by Wright 1980; also Martin 1981, Vassallo and Rice 1981, Bongiorno 1982).

In this paper I compare the total densities of fish in five small seepage lakes in northern Wisconsin to assess the effects of interspecific interactions in structuring the fish assemblages of these lakes. The assemblages varied in richness from one to three breeding populations, in a nested pattern. Two lakes contained only central mudminnows (*Umbra limi*), two lakes contained mudminnows and yellow perch (*Perca flavescens*), and one lake contained mudminnows, perch, and golden shiners (*Notemigonus chrysoleucas*). The comparisons involved six seasonal whole-lake censuses of each assemblage, conducted from May through October over a 3-yr period.

Degrees of density compensation

In a comparison of population densities of species-poor sites to those of species-rich sites, five outcomes are possible (modified from Wright 1980; see Fig. 1):

1) Population density per species is greater at species-rich sites than at species-poor sites (negative density compensation). Diamond (1970*b*) suggested that "an intrinsic inefficiency of small-island populations," caused by impoverished gene pools, reduced selection pressures, and/or low endemism, could result in negative density compensation.

2) Population density per species is constant and independent of species richness (zero density compensation). As discussed by Wright (1980), niche theory predicts that when fundamental niches no longer overlap, e.g., in depauperate assemblages, the population densities of each species will be at their maxima and thus will remain constant at sites with an even lower species richness. This pattern might also result when a community is taxonomically defined but is composed of noninteracting members of different guilds (Lawton 1982; S. J. Wright, *personal communication*). Thus, the null hypothesis that no interspecific interaction occurs predicts zero compensation.

3) Population densities of each species are greater at species-poor sites than at species-rich sites but these increased densities do not completely make up for the absence of populations. As a result, summed faunal densities are greater at species-rich sites (partial density compensation). If exploitation competition is the primary structuring mechanism in the communities, maximum community efficiencies, and presumably maximum community densities, should occur at the species-rich sites (Wright 1980).

4) Average population density per species is greater at species-poor sites and the increased densities fully compensate for the loss of some populations from the species-rich sites. Thus, total faunal densities are constant and independent of species richness (complete density compensation). This pattern might be produced when several different mechanisms contribute to community structure, e.g., exploitation competition among some species and predation among others (S. J. Wright, *personal communication*) and/or when the total densities of the assemblages are functions of the similar carrying capacities of the similar sites (Crowell 1962).

5) Population density per species and total faunal density are greater at species-poor sites than at species-rich sites (excess density compensation or density overcompensation). This pattern might result when

predation, interference competition, or resource overexploitation is the primary structuring mechanism in the assemblage (Case et al. 1979, Wright 1980).

Wright's (1980) density compensation coefficient (WDCC; see Methods: Data Analyses) provides a standard estimate of the extent of density compensation, in terms of these five possible outcomes (Fig. 1).

Density compensation as a natural experiment

Density compensation studies possess both the advantages and the disadvantages inherent to natural experiments (Diamond 1978, Abbott 1980, Wiley and Cruz 1980). Because the spatial and temporal scales appropriate to most community ecology studies prohibit the use of direct manipulations, one must rely on naturally occurring differences in the experimental variable (the richness of the assemblages) to evaluate the predictions (the five possible outcomes described above, with zero density compensation being the null hypothesis). While these a priori predictions allow for less ambiguous interpretations of outcomes than do simple correlational studies, the lack of direct manipulation and randomization, as well as the possible existence of several independent processes influencing faunal densities, requires a special awareness of alternative hypotheses (Wiley and Cruz 1980).

In addition to the mechanisms of interspecific interactions discussed above, several other factors can affect the extent of density compensation among sites. The degree to which total faunal densities at species-poor sites approach the levels at species-rich sites can depend on the "appropriateness" of the habitats available at the former sites to the species present there (Diamond 1970*b*, MacArthur et al. 1972, Yeaton 1974, Wright 1980). Appropriate habitat for a species is defined to be the habitat(s) in which it is found at species-rich sites. In a multiple regression analysis of avifauna density compensation studies, Wright (1980) found that habitat appropriateness accounted for a larger proportion of the variance in total density than did the number of species, although both factors were significant (and independent). Area alone might not be the most meaningful parameter to use in determining density; a measure of a particular portion of the available habitat, such as length of habitat edge, might be more appropriate (Ranney et al. 1981). Naturally, if the distribution and abundance of resources are markedly different among sites, the extent of density compensation can be altered regardless of the mechanisms structuring the assemblages. The fauna under consideration should consist of a single guild, or should include species in predator-prey relationships or otherwise involved in overlapping food webs and thus with a potential for interaction (Wright 1980, Martin 1981). Finally, comparisons involving densities of individuals may be misleading if the distributions of body sizes differ significantly among the faunas; e.g., large species are often underrepresented in depauperate faunas. Comparisons of biomass densities or production are generally more biologically meaningful.

Reliable and unambiguous density compensation studies must also use spatial and temporal scales appropriate to the assemblages under investigation. Many density compensation studies have compared the faunal density at a single site on a species-poor island with the density at a single site on a species-rich island or mainland (reviewed by Wright 1980 for avifaunal studies). Rarely have multiple sites or islands with the same species richness been censused to assess spatial variability, even though population and community structures are known to differ on relatively small spatial scales in "uniform" habitats (Wiens and Rotenberry 1980, Wright and Faaborg, cited in Wright 1980). Furthermore, many density compensation studies involve either a single census or multiple censuses during a single season or year and are thus unable to detect seasonal or annual variations in population densities. These studies must assume that either the faunas are in equilibrium, or, if variable, that the variations are synchronous or are buried by the overall patterns in density (Wiens 1981). In light of analyses by Wright (1980), Wiens (1981), and others, these assumptions are not always justified in comparative community studies. The reliability of density compensation studies would be enhanced if several sites were compared over several seasons and years.

Advantages of the present study

The nested fish assemblages of my study lakes presented an opportunity to assess the presence, direction, and intensity of interspecific interactions. Modifying Park's (1948) suggestion, I compared the performance (total density) of assemblages consisting of mudminnows alone with assemblages having one or two additional populations. Competition (both exploitation and interference) and predation are potentially important interactions among these species. Varying degrees of overlap in diet, use of space, and activity times occur among the three species. Mudminnows (typically <120 mm total length) and similarly-sized perch have, in particular, similar generalist diets, while with increasing size larger perch (>115 mm) increasingly attempt piscivory and ultimately (>135 mm) become partially piscivorous (Keast 1978, 1979, Tonn 1983, Paszkowski 1984). Because a combination of interactions potentially influences these assemblages, and in the absence of prior knowledge about the relative importance of the various types of interactions, I predicted that complete density compensation (outcome 4; see Fig. 1) would occur in *Umbra-Perca* assemblages.

Studying a series of five lakes that included multiple one- and two-species lakes enabled me to examine the effect of the experimental variable, species richness, on total densities and also to document differences between lakes of the same richness. Similarly, seasonal and annual differences in total densities within and among lakes could be measured and compared to the effects of species richness. I expected that measurements of population densities during six periods over three years, along with other natural history observations, would contribute insights into the nature of the population and assemblage dynamics of these assemblages, and that multiple censuses in time and space would also increase the reliability of any conclusions concerning the presence and intensity of interspecific interactions.

Methods

Fish assemblages and study lakes

The *Umbra-Perca* fish assemblages studied here are a subset of the *Umbra*-cyprinid assemblage type of the Northern Highlands Lake District of Wisconsin and Michigan, USA (Tonn and Magnuson 1982, Rahel 1984). These assemblages occur in shallow, dystrophic seepage lakes where other assemblage types are apparently excluded due to severe environmental conditions. Low pH, a lack of suitable spawning substrata, frequent or irregular low levels of dissolved oxygen in winter, and an absence of refuges or recolonization routes do not appear to exclude these tolerant species but do prevent populations of other fishes from becoming established (Tonn and Magnuson 1982, Rahel 1984).

The five study lakes (Table 1) are located in Vilas and Oneida counties, Wisconsin. The lakes are similar in habitat characteristics; all are small (<8 ha), shallow (<7 m), dystrophic seepage lakes dominated by soft organic bottom material and floating bog-mat shorelines. They are all bordered by second-growth forest lands and relatively isolated, except for Jude, which has a county road next to it. With the exceptions of a few casts by a single fisherman at Jude and my trapping of a few isolated individuals from bait-bucket releases in Jude, Camp 2, and Lake 33-13, I have not observed exploitation of the fish populations during six years of research on these lakes. Thus, these fish assemblages exist in very similar, simple habitats under natural, unexploited conditions.

Density measurements

Censuses of each population were made in six sampling periods during three years (Table 2) by multiple, Petersen-type mark-recapture and also catch-per-unit-effort methods (Ricker 1975). A population is defined here as all trappable individuals (see below) of a successfully reproducing species in a lake. Pearl dace (*Semotilus margarita*), which had been present in moderate numbers in Camp 2 in 1978 (Tonn and Magnuson 1982), were represented by only a very few large individuals by 1980, and no young were ever observed during the 1980–1982 study period. As a result, these few nonreproducing individuals were not considered a population and ignored for the purposes of this study. Separate estimates were made of yearling perch in Jude during the 1981c census and in Junnie during the 1981c and 1982b periods.

Fish were captured using minnow traps (20–40 per lake; 6 × 6 mm mesh) and small fyke nets (2–5 per lake; 5 × 5 mm mesh). Approximate minimum trappable sizes (Total length, TL) for each species during the study with these mesh sizes were as follows: 40 mm for mudminnows, 55 mm for perch, 80 mm for golden shiners. These sizes roughly correspond to late young-of-the-year or yearling fishes in Wisconsin (Becker 1983). The two sets of gear were differentially selective with regard to species. Even smaller individuals of golden shiners and larger sizes of both shiners and yellow perch generally avoided the minnow traps, while mudminnows of all sizes were taken equally well in both nets and traps. With this combination of gear, approximately equal sampling effort, in terms of net- and trap-days, was made in all lakes within a census

Table 1. Location, environmental and habitat characteristics, and fish assemblages of the five northern Wisconsin study lakes. Data are from Rahel (1984) and the present study.

Lake	Location	Water source	Total area (ha)	Shore-line (m)	Conductivity* (μS)	Alkalinity (as $CaCO_3$, mg/L)	pH	Winter 1981 oxygen (mg/L)	Bottom substrates	Maximum depth (m)	Proportion of area >3 m depth	Adjusted area (ha)	Fish species
33-13	46°05′N 89°37′W	seepage	2.9	800	12	5.0	6.4	2.2	organic	4.24	0.225	2.25	central mudminnow
6-7	46°04′N 89°36′W	seepage	2.0	620	9	0.0	5.2	0.8	organic	2.01	0.0	2.0	central mudminnow
Jude	46°05′N 89°37′W	seepage	2.9	625	15	0.5	5.7	2.1	organic	3.70	0.062	2.72	central mudminnow, yellow perch
Junnie	45°43′N 89°37′W	seepage	7.1	1500	19	0.0	4.5	4.1	organic	7.00	0.323	4.80	central mudminnow, yellow perch
Camp 2	46°05′N 89°06′W	seepage	6.2	980	16	2.0	5.9	1.4	organic, sand	1.66	0.0	6.2	central mudminnow, yellow perch, golden shiner

* At 25°C.

TABLE 2. Sampling schedule for each lake for the six census periods.

Census period	Dates	Sampling sequence (and no. daily estimates)
1980	10 July to 28 October	Camp 2 (8), Junnie (12), 33-13 (13), Jude (9), 6-7 (9)
1981a	6 May to 30 June	Jude (7), 33-13 (8), Camp 2 (5), Junnie (6), 6-7 (7)
1981b	3 July to 29 August	Jude (7), 33-13 (7), Camp 2 (5), Junnie (5), 6-7 (8)
1981c	2 September to 24 October	Jude (8), 33-13 (8), Camp 2 (6), Junnie (7), 6-7 (7)
1982a	8 June to 2 August	6-7 (10), Junnie (9), Jude (8), 33-13 (10), Camp 2 (7)
1982b	17 August to 18 October	6-7 (9), Junnie (9), Jude (9), 33-13 (9), Camp 2 (9)

period; some adjustments were made among periods due to time and equipment-use constraints. Based on other sampling in these and similar nearby lakes using larger fyke nets, trammel nets, angling, and electroshocking, there appeared to be no maximum trappable sizes; also, the combination of gear used probably did not underrepresent larger size classes of the three species in the study lakes (W. M. Tonn, *personal observation*; J. Lyons, *personal communication*). Maximum sizes (TL) during the study period were 138 mm for mudminnows, 341 mm for perch, and 170 mm for golden shiners. Examples of size-frequency distributions are given in the Appendix.

Traps (set in pairs) and nets were set on the lake bottoms at random locations, determined by overlaying a numbered grid on a map of each lake and using a random numbers table. In each census period the traps and nets were checked daily and new random locations were selected for each day of sampling. Fish were transferred from a net or trap into a 60-L cooler tank containing ≈1 mg/L of antibiotic drugs (Furan-2 [Aquarium Pharmaceuticals, Perkasie, Pennsylvania, USA]). One by one, fish were removed from the cooler by a vinyl-gloved person and each was given a partial pelvic fin-clip with dissecting scissors. The number of previously marked (recaptured) fish, as well as the number of newly marked fish, was tallied for each trap and net. Which pelvic fin was clipped was alternated in successive seasons; fins typically grew back completely, or nearly so, between two seasons, and new clips could be identified easily. Fish were generally returned to the lake at the site of capture. Census periods for each lake consisted of 5–13 daily estimates (Table 2).

Independent daily population estimates were made from the mark-recapture data using the Petersen method (Ricker 1975). These estimates were calculated as follows:

$$P = \frac{(M + 1)(C + 1)}{R + 1},$$

where P = estimated population size
M = number of marked fish
C = number of fish in the daily sample examined for marks
R = number of recaptured marked fish in the daily sample.

Only estimates where $R \geq 3$ were used, because of a possibility of statistical bias when $R < 3$ (Ricker 1975). By the end of each sampling period, R was typically at least 10% of C, and frequently was much larger. Except in analyses involving a single lake or single census period, where the daily estimates themselves were used, the population estimates for each census period were determined by taking the means of the $\log_{10}$-transformed daily estimates, and the differences between each day's independent estimate and the mean provided an estimate of sampling error. Although this procedure treats a series of unequally reliable estimates as though they were equally reliable, it provides an estimate of error based on observed (rather than theoretical) variability. Furthermore, this method is not as sensitive to violations of its underlying assumptions as are other techniques (Seber 1973, Ricker 1975).

Catches of mudminnows in Junnie and Camp 2, and also in Jude during 1982, were too small to permit reliable estimates by the mark-recapture technique; fewer than the minimum of three recaptures were obtained on at least three days during the census period. For these populations, I used a catch-per-unit-effort approach. A least squares regression equation was calculated using the mean minnow-trap catches and the mean adjusted densities (see below) from all of the available census-period mark-recapture estimates of mudminnow populations:

$$\begin{aligned}&\log(\text{mean adjusted density})\\&\quad = 2.456 + 1.856\{\log[(\text{fish/trap pair}) + 1]\};\\&\quad r^2 = 0.88, \quad N = 15, \quad P < .01.\end{aligned}$$

Using this regression and the catch-per-unit-effort data, I calculated the missing mudminnow population densities.

The total size of the fish assemblage in each lake for each census period was determined by summing the component species' population estimates. Simple summed assemblage densities could then be calculated by dividing summed population estimates by total lake area. However, during a separate study of the spatial distribution of the fishes, where the sampling gear was set just under the surface and in midwater as well as on the bottom, I observed that when the gear was set where the water column was >3 m, the number of fish caught declined dramatically. This suggested that the central, benthic and pelagic portions of the lakes where the water column was >3 m represented inappropriate habitat for the populations considered here. Larval or young-of-the-year fish, too small to be caught by my sampling methods, feed on zooplankton and may use the pelagic portion of this region. Indeed, combining surface, midwater, and bottom catches, numbers of fish in the distribution study were significantly less than would be expected where the water column was >3 m, based on the proportion of gear set at these locations (for mudminnows: $\chi^2 = 88.3$, df = 1, $P < .001$; for perch: $\chi^2 = 25.9$, df = 1, $P < .001$). This might have complicated comparisons of total faunal densities because the five lakes had different proportions of this inappropriate habitat (Table 1). Therefore, I subtracted the portion of a lake where the water column was >3 m from its total area and the densities reported here were obtained by dividing the population estimates by the areas of the lakes where the depth was ≤3 m (Table 1). In other lake types, sampling with minnow traps and fyke nets where the water column is >3 m has been done without diminished success (W. M. Tonn, *personal observation*). However, for skeptics, the data were also analyzed using the total surface areas of the lakes. With one exception (reported below), results of statistical tests from the two methods of calculating densities were similar, and all conclusions concerning the extent of density compensation were unaffected.

For several days during most censuses, all individuals from the catches of several nets and traps were weighed to the nearest 0.01 g (live, wet mass). From these data, mass-frequency distributions, using 0.3 g intervals, were determined for each population. Masses were not measured during the 1980 census period in Lakes 33-13, Junnie, and Camp 2. Mass-frequency distributions that were obtained temporally closest to the 1980 samplings for each population in each of these lakes were substituted. For all of these populations except golden shiners, distributions measured during the course of another study in February 1981 were substituted; for the golden shiner population in Camp 2 the mass-frequency distribution from the 1981a census was used. Overwinter growth is minimal in these lakes (W. M. Tonn, *personal observation*). Where mudminnow catches were too small (Junnie, Camp 2), the distribution from the Jude population of the same census period was substituted. While among-lake differences in mudminnow sizes exist, they are minor among the three lakes with perch (Tonn 1983), and since mudminnows made up a small proportion of the total biomass in Junnie and Camp 2 (Tonn 1983), errors due to small differences in size distributions should be unimportant in total biomass calculations. Sample sizes of all census-period mass distributions averaged 428 ± 250 individuals ($\bar{x}$ ± SD) for mudminnow populations (N = 18 distributions), 297 ± 128 individuals for perch (N = 18 distributions), and 68 ± 28 individuals for the golden shiner population (N = 5 distributions). Examples of mass-frequency distributions for each species are presented in the Appendix. Census-period mass-frequency distributions were combined with the population estimates and densities for that period to obtain daily and seasonal population biomass estimates and densities. Values for component populations were then summed to determine the total fish biomass and biomass density for each lake.

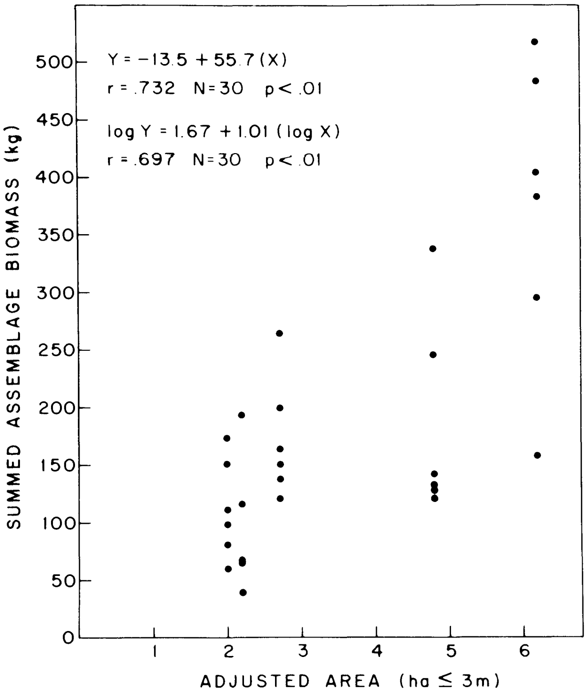

FIG. 2. Summed fish assemblage biomass vs. adjusted lake area. Each data point represents the mean of the daily estimates from one lake during one census period. The slope (1.01) of the log-log regression is not significantly different from 1 and the intercept (−13.5) of the arithmetic regression does not differ significantly from 0, indicating that the relationship is directly proportional.

Data analyses

Summed biomass estimates and densities were $\log_{10}$-transformed before all analyses unless otherwise noted. Least squares linear regressions were used to analyze the relationships between summed biomass and area, using the means of the daily estimates from each census period in each lake (Ryan et al. 1976). To examine the hypothesis that faunal abundance increases in direct proportion with area, as suggested by May (1975) and Diamond and Mayr (1976) and supported by avifaunal data of Martin (1981), both the power (log-log) and the arithmetic functions of the biomass–area relationship were analyzed. The exponent (slope) of the power (log-log) function should equal 1 while the intercept of the arithmetic relationship should equal 0 for a directly proportional relationship (Martin 1981). The importance of an edge effect to summed fish biomass was also examined through regression (Dixon and Brown 1979), using the shoreline length of each lake (Table 1) as a measure of habitat edge. One-way analyses of variance (ANOVA) were used to examine differences in summed biomass densities, calculated from both total lake area and area adjusted for inappropriate habitat, among species richness classes and lakes for all censuses, among lakes and richness classes for each census period, and among census periods for each lake (Ryan et al. 1976, Dixon and Brown 1979).

To determine the extent of density compensation, in terms of the five possible outcomes (Fig. 1), Wright's (1980) density compensation coefficient (WDCC) was calculated for the summed biomass densities, using the census period estimates from all lakes. This coefficient is obtained by dividing the slope of the observed relation between the number of species and the summed densities at all sites being compared, by the ratio of the summed density to the number of species at the most species-rich site (Wright 1980).

RESULTS

Abundance-area relations

Lake area was much more strongly correlated with fish abundance than was length of shoreline (habitat edge). Using the lake means for each census period ($N = 5$ lakes × 6 census periods = 30 censuses), summed fish biomass was significantly correlated with adjusted area ($r = 0.705$) and also with total area ($r = 0.533$; $P < .01$ for both), but was unrelated to edge length ($r = 0.266$, $P > .05$).

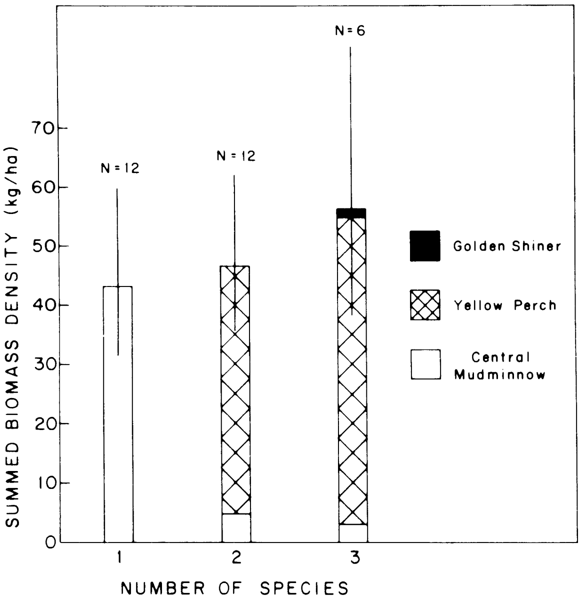

FIG. 3. Summed fish assemblage (and individual population) biomass densities for the three species-richness classes (lakes in each class combined). Histograms represent seasonal means and 95% confidence intervals of the summed densities. N's refer to the number of censuses (from a single lake in a single census period) in each species-richness class.

The data for total fish biomass support the hypothesis that the abundance of a fauna increases in direct proportion with area (Fig. 2). Using the seasonal estimates, the slope of the biomass–adjusted area power function (1.01) did not differ significantly from 1.0 ($t = 0.051$, df = 28, $P > .90$), while the intercept of the arithmetic relationship (-13.5) did not differ significantly from 0 ($t = -0.35$, df = 28, $P > .50$). Thus, summed biomass densities remained constant for increasing area; the slope of the regression equation of biomass density on adjusted area (0.055) was not significantly different from 0 ($t = 1.12$, df = 28, $P > .20$). Similar results were obtained when total lake areas were used rather than adjusted areas.

Extent of density compensation

General patterns.—Because the species differ so much in body size, it is more meaningful to compare fish biomass densities than densities of individuals. Using seasonal means for each lake and combining lakes within species-richness classes, summed assemblage biomass densities did not differ significantly among the richness classes across all sampling periods (for adjusted areas: $F_{2,27} = 0.65$, $P > .50$, Fig. 3; for total areas: $F = 1.31$, $P > .25$). The slope of the relation between the number of species and the summed densities in all five lakes (0.055), and thus the density compensation coefficient (0.094), did not differ significantly from 0 ($t = 1.12$, df = 28, $P > .20$), indicating complete fish biomass density compensation among the species-richness classes (outcome 4; see Introduction and Fig. 1). Again, similar results were obtained when total lake areas were used (slope = 0.072, WDCC = 0.123, $P > .20$). Specifically, mudminnow biomass densities declined dramatically when other species were present in the assemblages (Fig. 3).

Summed assemblage biomass densities did vary among lakes and species-richness classes within a sampling period and among sampling periods within the same lake (Table 3, Figs. 4 and 5). However, as I discuss below, patterns in the variation support the general conclusion of complete density compensation.

Seasonal patterns.—Summed biomass densities differed among the six census periods for each lake (ANOVAs: $P < .001$; Fig. 4). Despite some discrepancies, there appeared to be a basic, underlying pattern to the seasonal variation in four of the five lakes. In general, densities were highest in the fall (1980, 1981c, 1982b samplings), reflecting individual growth over the summer and recruitment of young to my sampling gear by fall. Although mortality occurred throughout the year, the long time lag (7–9 mo) between fall and spring samplings, combined with minimal individual growth over winter (W. M. Tonn, *personal observation*), resulted in particularly noticeable drops in total biomass density between 1980 and 1981a and between 1981c

TABLE 3. Mean total fish biomass densities in lakes of the three species-richness classes for each census period, and results of Tukey multiple comparison tests (means connected by an underline are not significantly different at the .05 level).

Census period	Mean total biomass densities (kg/ha) Species-richness classes		
1980	25.4 3-species lake	49.2 2-species lakes	86.1 1-species lakes
1981a	34.1 2-species lakes	36.8 1-species lakes	61.8 3-species lake
1981b	29.6 1-species lakes	50.7 2-species lakes	78.0 3-species lake
1981c	34.4 1-species lakes	47.5 3-species lake	71.6 2-species lakes
1982a	34.2 1-species lakes	39.7 2-species lakes	83.4 3-species lake
1982b	38.2 2-species lakes	53.3 1-species lakes	65.2 3-species lake

and 1982a censuses. This seasonal pattern was best illustrated in Lake 6-7 (Fig. 4). Only in Camp 2 was this pattern not observed, although differences among sampling periods did occur (Fig. 4).

In addition to this general seasonal change, there appeared to be fluctuations in mortality and in the recruitment of yearlings for populations in most lakes, based on an examination of population estimates and size-frequency data (Appendix). These fluctuations, in combination with variations in growth, could have accounted for low biomass densities in individual lakes during individual fall sampling periods. Low recruitment appeared to occur in three of the study populations at least once each during the 1980–1982 period (Lake 33-13: 1981c; Jude perch: 1982b; Junnie perch: 1980, 1982b), and to a lesser extent in a fourth (Lake 6-7: 1981c) (Appendix). The level of recruitment in Camp 2 was less clear, although, based on the size-frequency data, it appeared to be low in all three years. Occurrence of low recruitment was both unpredictable within a lake and asynchronous among lakes. As a result, biomass densities differed significantly among the species-richness classes within each of the census periods, but the direction of these differences varied from period to period (Table 3).

Using only data from the three fall sampling periods, to control for seasonal variation, I found no significant differences in summed biomass density among the three species-richness classes ($F_{2,12} = 0.21$, $P > .75$). To control for both annual and seasonal fluctuations, I compared the classes using daily estimates of fish biomass for each lake obtained during that lake's period of maximum biomass density (see Lawton 1982 for a similar analysis). This analysis compared estimates of maximum carrying capacity; there were no significant differences among the species-richness classes ($F_{2,42} = 0.04$, $P > .95$). Neither the slope of the regression of summed biomass density on species richness (-0.008) nor the WDCC (-0.012) differed significantly from 0 ($t = -0.29$, df = 43, $P > .50$), indicating complete density compensation. Similar relationships were obtained using total lake areas.

Patterns among the lakes.—The five lakes did not differ significantly in their summed biomass densities during this study, using adjusted lake areas ($F_{4,25} = 2.31$, $P > .05$; Fig. 5). This result supports the supposition that the five lakes are similar in their habitat characteristics and their abilities to support fish assemblages, and also strengthens the conclusion of complete density compensation. That the individual lakes differed when total lake area was used in calculating densities ($F_{4,25} = 6.02$, $P < .01$) could be the result of the differences in the extent and frequency of short-term fluctuations in recruitment during 1980–1982, or could illustrate that misleading results can be obtained when inappropriate habitat is included in analyses, as dis-

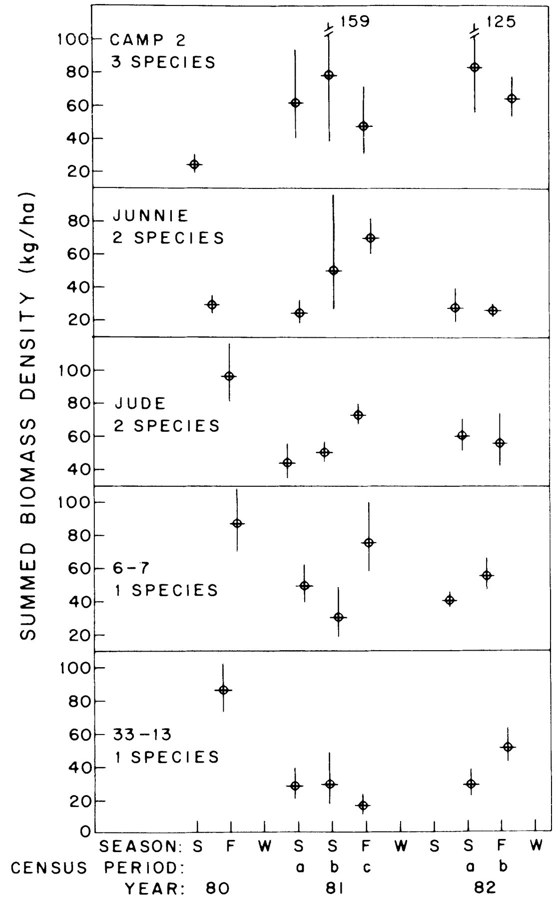

FIG. 4. Census-period means and 95% confidence intervals from the daily independent estimates of summed fish assemblage biomass density for each of the five study lakes. Sample sizes (number of daily estimates) are given in Table 2.

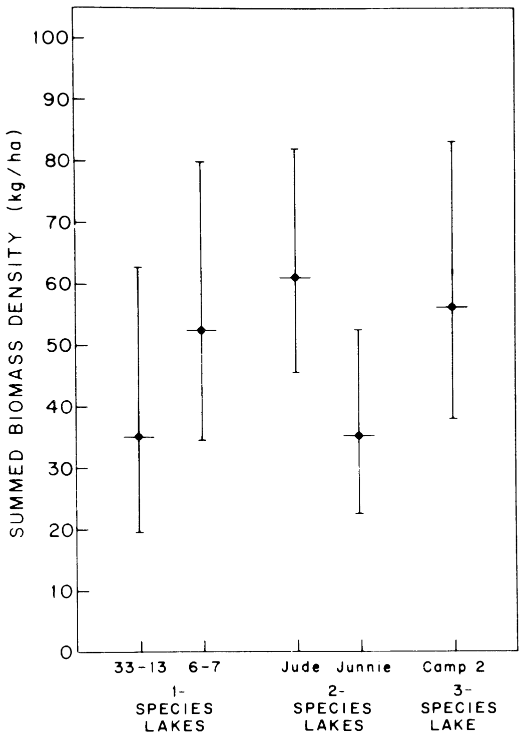

FIG. 5. Summed fish assemblage biomass densities for the five study lakes. Horizontal lines and vertical bars represent means and 95% confidence intervals, respectively, of the six seasonal estimates.

cussed above in Introduction: Density Compensation as a Natural Experiment (see also Wright 1980).

There were significant differences ($P < .01$) among lakes within any one census period, although the pattern was never identical across periods, reflecting the unpredictable, asynchronous population fluctuations. With seasonal differences controlled for, there were no significant annual fluctuations in summed biomass density among the lakes; a comparison of the three fall sampling periods revealed no significant differences ($F_{4,10} = 1.12, P > .25$). Also, no differences were found among the five lakes when the maximum observed biomass densities were compared ($F_{4,40} = 1.26$, $P > .30$). Once again, a similar result was obtained when total lake areas were used in the density calculations. Thus, it appears that all of the lakes had similar fish standing crop maxima during the 3-yr study period. This also supports the conclusion that the lakes are similar and that complete density compensation occurs in *Umbra-Perca* assemblages.

Finally, rank correlations of summed biomass densities (from both adjusted and total areas) with the nine quantitative environmental and habitat characteristics of the five lakes listed in Table 1 were not significant ($P > .05$). These results also support the assumption of similar habitats in the lakes and suggest that the natural environmental variation among the lakes does not systematically affect assemblage densities; thus, these results also tend to support the conclusions regarding the extent of density compensation.

Importance of multiple sites and censuses

To evaluate the contribution of multiple census periods and lakes to the conclusion concerning the extent of density compensation, I conducted a simulation exercise, similar to that of Wiens (1981), that determined the WDCC's that might have been obtained if only a single seasonal census from each richness class had been conducted. Single values of the mean census-period biomass estimates were randomly selected, one each from a one-species, a two-species, and the three-species lake, and the corresponding WDCC was calculated. A series of 1000 iterations of this randomized selection procedure of actual censuses yielded a frequency distribution of WDCC values (Fig. 6). This distribution depicts the probability that a given WDCC value would be obtained by randomly conducting a trio of single censuses. It also indicates the probability of arriving at the conclusions expressed here concerning the overall extent of density compensation had only one trio of single seasonal censuses been conducted.

To evaluate the results of this simulation exercise, it is necessary to determine the proportion of the iterations whose WDCC's can be considered not to differ from 0, the value for complete density compensation (Fig. 1). It is possible to pick an interval about 0 and conclude that any iteration whose WDCC falls within that interval is not different from 0; those WDCC's greater than the upper limit of the interval (but <1) would indicate partial density compensation, while

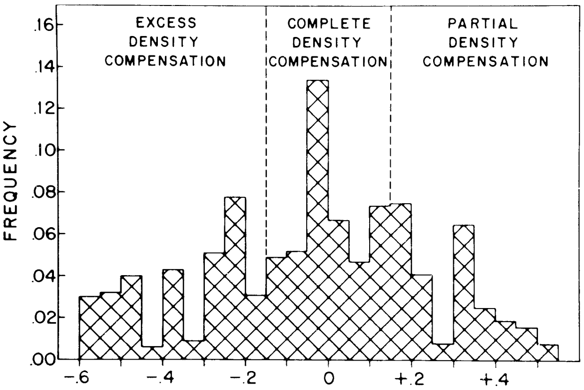

FIG. 6. Frequency distribution of Wright's Density Compensation Coefficient (WDCC) from the simulation exercise. Single values of the mean census-period estimate of summed fish biomass density were randomly selected, one each from a one-species, a two-species, and a three-species lake from the field study, and the compensation coefficient was computed for this trio (see Methods: Data Analyses). The random selection of single-census trios was repeated 1000 times to produce the distribution. A qualitative confidence interval about 0 delineates iterations that indicate excess, complete, and partial density compensation.

those WDCC's less than the lower limit of the interval would indicate excess compensation. Based on all of the seasonal field estimates of biomass density made during this study, I was able to calculate an actual 95% confidence interval for the resulting WDCC (0.094, see Extent of Density Compensation: General Patterns, above). This 95% confidence interval ranged over 0.34 WDCC units. Using this actual 95% confidence interval calculated from the field data as a framework, I arbitrarily chose for the simulation iterations a qualitative confidence interval about 0 to range from −0.15 to +0.15, giving an interval of 0.30 WDCC units. When this confidence interval is applied, only 42% of the single-census trios in the simulation produce the pattern of complete compensation that was observed in the field study (Fig. 6). In contrast, 32% indicate excess compensation and 26% indicate partial compensation.

DISCUSSION

A major goal of community ecology is to identify and assign relative importance to the processes responsible for the structure of an assemblage. Regarding the role of interspecific interactions, one must first establish whether species interact and, if so, to what extent these interactions affect the populations comprising the assemblage. Density compensation studies can empirically present the results of interspecific interactions and suggest their direction and intensity by comparing the population and faunal densities at sites differing in their faunal richness.

Before interpreting the results of a density compensation study with respect to interspecific interactions, one must consider alternative factors that can affect the abundance of species at different sites, but cannot be directly controlled in the natural experiment. One such factor is the appropriateness of the habitats available in the species-poor sites to the species (Diamond 1970*b*, MacArthur et al. 1972, Wright 1980). As discussed earlier, the five small lakes in this study are quite similar in their simple habitat characteristics. The one clear difference is in the proportion of the lakes where the water column is deeper than 3 m. This was shown to be inappropriate habitat for the populations of both mudminnows and perch studied here. This factor was corrected for by using area of appropriate habitat in the data analysis; however, even uncorrected (total area) data gave similar results regarding the extent of density compensation, and differed only with regard to whether the individual lakes, not the species-richness classes, had similar total densities over the 1980–1982 period.

Another factor that can affect faunal densities, the distributions and abundances of resources, is rarely measured directly in density compensation studies, and mine was no exception. However, several limnological characteristics known to be related to productivity (e.g., conductivity, alkalinity) were very similar among the lakes (Table 1) and were not correlated with total densities. Qualitative sampling of benthic, littoral, and planktonic invertebrates also revealed no major differences (W. Tonn, *personal observation*). The assumption that resources for fish production were similar across lakes was also supported by the facts that the five lakes did not differ in biomass density in the three fall sampling periods or in maximum biomass density, and that total fish biomass increased in direct proportion to the area of appropriate habitat (and to total lake area).

The assumption that the fish species in the assemblages are members of the same or overlapping food webs has been discussed previously. Other animals in these lakes may overlap in food resources (e.g., odonates, notonectids, *Belostoma, Notophthalmus*) or be occasional predators on larval or young-of-year fish (e.g., Hirudinea, *Dytiscus*) or even adults (*Chelydra, Chrysemys*). However, compared to the fish, these populations appear to have small biomass densities (W. M. Tonn, *personal observation*) and I assume that they have negligible effects on fish populations.

Finally, because my comparisons involve fish biomass rather than numbers of individuals, they avoid the confounding factor of body size differences. While measures of production or estimates of bioenergetic consumption may be ecologically more important, standing crop biomass data are sufficient approximations when necessary production or bioenergetic data are unavailable (Carlander 1955, Hall et al. 1970).

Dominance of perch over mudminnows

I found no evidence for an intrinsic inefficiency of mudminnow-only assemblages, when compared to the multispecies assemblages. Biomass densities per species are not less in the single-species, mudminnow-only lakes than in the multispecies lakes (Fig. 3). Furthermore, biomass density per species was not independent of species richness, even in these depauperate assemblages. As a result, zero density compensation (outcome 2 in Fig. 1), the predicted outcome of the null hypothesis that no interspecific interactions occur, can also be rejected.

The density of mudminnows was strongly and negatively related to the presence of other species, especially perch (Fig. 3). A strong dominance (sensu Svärdson 1976) of perch populations over mudminnows is clearly suggested. Total biomass densities did not differ between the mudminnow-only assemblages and those containing perch, yet densities of mudminnows declined dramatically when in the presence of perch, averaging about $\frac{1}{10}$ of their densities when alone. My data on golden shiners are insufficient for an analysis of interactions between golden shiners and perch or mudminnows; thus, my analysis has concentrated on the mudminnow-perch relationship.

Evidence of the strong interaction between mudminnows and perch is provided by sequential population fluctuations of the two species in Jude Lake. Low dissolved-oxygen levels during the winter of 1980 caused a severe winterkill of perch (Tonn 1983; L. Radloff, *personal communication*). The mudminnow population responded dramatically with a successful recruitment, such that they composed >63% (61kg/ha) of the total assemblage biomass in the 1980 census. By the next fall (the 1981c census), the perch population had recovered, increasing from 35 kg/ha to 65 kg/ha, while the mudminnow population plummeted to 7 kg/ha, composing <10% of the total assemblage biomass.

Svärdson (1976; see also Skud 1982) indicated that populations of dominant species in fish assemblages are regulated mainly by abiotic factors or intraspecific interactions, while subordinate species are affected predominantly by interspecific competition or predation. This may occur in *Umbra-Perca* assemblages, where perch populations are altered by winterkill and variation in year-class strength (which is presumably caused by intraspecific competition, cannibalism, and/or abiotic factors). Indirect evidence that both competition and predation by perch regulate mudminnow populations is presented below.

Many freshwater fishes are generalists in diet and habitats, and have flexible, indeterminate growth and high reproductive potential. Perch are one of several intermediate-sized generalists in north-temperate lakes, such as sunfish (*Lepomis* spp.), bullheads (*Ictalurus* spp.) and the roach (*Rutilus rutilus*), that frequently dominate fish assemblages, presumably through competition for food (Carlander 1955, Svärdson 1976, Werner 1977, Keast 1979, Werner and Hall 1979, Persson 1983). For example, an accidental introduction of yellow perch into an Ontario lake drastically reduced the growth rate of three salmonid species and the survival rate of brook trout through competition for food (Fraser 1978). The biomass density of the three salmonids declined sharply following the introduction of perch.

Both perch and mudminnows are generalized in their diet, taking a wide variety of benthic, littoral, and, especially as young-of-year, planktonic invertebrates (Jones 1973, Keast 1978, 1979, W. M. Tonn, *personal observation*). Experimental studies measuring the foraging rates of both species from four types of foraging sites reveal similar generalist patterns within the species, but perch are much more efficient than mudminnows at feeding from all foraging sites (Paszkowski 1984). When the two species forage together, mudminnows shift their feeding to the sites where the perch were least efficient when foraging alone.

While exploitation competition may play a role in the *Umbra-Perca* assemblages, especially among young fish, the overall density compensation coefficient, 0.094, indicates that complete compensation occurs. This outcome is beyond the level of compensation predicted by niche theory if exploitation competition is assumed to be the primary structuring mechanism (Case et al. 1979, Wright 1980).

Both interference competition and predation are known to be important and interrelated regulators of fish populations. As with exploitation competition, the evidence for interference and predation is indirect in this compensation study. Small species, or young of larger forms, are typically found only in the most dense macrophyte cover (Werner et al. 1977). This suggests that the threat of predation can provide a strong constraint on growth and survival of small fish, particularly in lakes where cover is limited or provides a poorer resource base (Werner et al. 1983). In four of my five study lakes (Camp 2 is the exception), macrophytes are extremely sparse. Limited cover is provided by the overhanging bog mat, consisting of *Sphagnum* moss and stems of ericaceous plants. In Jude Lake, where perch are present, the concentration of mudminnows in inshore minnow traps (<2 m from shore) vs. offshore traps (>10 m from shore), was greater than in Lake 33-13, a mudminnow-only lake ($\chi^2 = 4.71$, df = 1, $P < .05$; data from September 1982 and May 1983; all traps were set at depths ≤3 m; W. Tonn, *personal observation*).

While the observed difference in concentration may be attributable to exploitation competition, this shift away from open-water habitat is contrary to the findings from laboratory foraging experiments (Paszkowski 1984). Furthermore, a similar shift to inshore traps occurred within Jude, from the 1981a census to 1982, corresponding to a shift in the size distribution of the perch population. During the 1981a census, the perch population was dominated by smaller fish (115–125 mm TL), which are more likely to overlap in diet with mudminnows but are too small to pose a significant predation threat (Keast 1978, Tonn 1983). By 1982, a significant proportion of the perch were large enough (>135 mm) to be piscivorous on adult mudminnows, and mudminnows were caught exclusively in inshore traps, near the refuge of the bog mat. Reduced feeding and altered activity by mudminnows as a direct response to active foraging by perch has been observed in laboratory experiments (Paszkowski 1984, W. M. Tonn, *personal observation*).

The rapid increase of mudminnow biomass in Jude Lake following the winterkill of perch in 1980, the equally rapid decrease in 1981 following the recovery of perch, and the maintenance of low densities in 1982 (to levels similar to those before the winterkill and to those in Junnie and Camp 2) suggest that predation plays a significant role in the mudminnow-perch interaction. The rapidity with which mudminnow populations respond is comparable to that observed for perch by Gammon and Hasler (1965) following an introduction of the piscivorous muskellunge. The maintenance of a small population of mudminnows in all three lakes with perch (mudminnow densities were 8.5, 2.2, and 3.0% of perch densities in Jude, Junnie, and Camp 2, respectively, during the 1982b census) also suggests a similarity with the perch-musky interaction in the two nearby lakes studied by Gammon and Hasler (1965) and Schmitz and Hetfeld (1965). Schmitz and Hetfeld attributed the survival, successful reproduction, and maintenance of a small perch population to the fact that predators could not eliminate all perch and left a minimum population determined by perch body size, with a density reflecting the amount of cover that served as a refuge. The maintenance of prey or subdominant populations by spatial (or temporal) refuges is a common phenomenon in a wide variety of ecological systems (e.g., Andrewartha and Birch 1954, Thomson and Lehner 1976, Woodin 1978). The role of size in the mudminnow-perch interaction will be reported elsewhere.

Spatial and temporal heterogeneity

The overall biomass density differences among the five study lakes were not significant (using lake areas corrected for inappropriate habitat) and did not appear to be related to the assemblage richness nor to inherent differences in the lakes' abilities to support fish. All of the lakes showed seasonal variation in density due to patterns of growth, mortality, and recruitment. The lakes also showed annual differences due to exceptionally strong or weak recruitment. However, they differed in the extent, timing and frequency of population fluctuations during the 3-yr study period.

Large fluctuations in recruitment are common among fish populations. While they are especially well documented among commercially important marine species (Cushing 1975), these fluctuations also commonly occur in lake populations (e.g., Alm 1951, Le Cren 1955, Koonce et al. 1977 for European and yellow perch). The causes of these large variations, and whether density-dependent or density-independent factors are more important, are still unclear. My study was not designed to examine these questions; however, years of strong and weak recruitment were not synchronized among the study lakes, which would have suggested weather-related phenomena, nor were similar density-related patterns seen among the lakes. At the scale of my study, recruitment fluctuations appear to be unpredictable in a given lake and year.

Because these fish assemblages were variable but unpredictable in their variability, any conclusions regarding the extent of density compensation would have been unreliable had only a single set of three censuses (one for each species-richness class) been taken. Biomass density showed significant variation within a single lake and the correlation between summed biomass density and species richness even changed from positive to negative during a single year and from year to year. The simulation exercise of Fig. 6 shows that less than one-half of the single-census trios would have led to the conclusion that total assemblage biomass density is not related to species richness, the relationship supported by the entire set of censuses, by comparisons among the three fall census periods, and by the comparison among the lakes' maximum densities.

Most studies of density compensation compare a single species-rich site with a single species-poor site, during a single season or year (reviewed by Wright 1980). One potential problem with this approach is the assumption that the populations either are at a stable equilibrium or fluctuate in parallel (Wiens 1981). The assumption that the two sites in such a study differ only with respect to the treatment variable, species richness, at the time of the study becomes critical. My results, and those of Wiens (1981), clearly show that the first assumption is likely to be incorrect. I believe that my lakes are at least as similar as the sites used in other compensation studies, and may be as similar as possible in a natural experiment in that they did not differ in their observed capacities to support fish during the study (Fig. 5). However, their independent and unpredictable fluctuations in population sizes demonstrate the need to increase the number of sites in the comparison, in order to determine the general, overall effects of species richness on faunal density (see also Wright 1980). Finally, most compensation studies involve large numbers of species, so that the effects of important interspecific interactions, if present, are often hard to isolate.

Both stochastic factors (at the scale of my study), in the form of unpredictable winterkills and recruitment fluctuations, and deterministic mechanisms, in the form of exploitation and interference competition and predation, may play important roles in determining population densities within *Umbra-Perca* assemblages. The relative importance of these processes appears to shift in time and space. Other multiyear, multisite studies (e.g., Dayton 1971, Sousa 1979, Wiens and Rotenberry 1979) suggest that many assemblages are structured by a heterogeneous mixture of both biotic and abiotic mechanisms. That a single, constant process (e.g., chance or competition) structures an assemblage is a simplistic view too often the result of using inappropriate temporal and spatial scales.

Density compensation studies such as mine are not designed to directly identify the mechanisms of interaction nor measure their relative importance. Compensation studies can suggest the presence and direction of an interspecific interaction (e.g., the dominance of perch over mudminnows) and can indicate the intensity of the interaction by measuring its effect, the densities of the species in different assemblages. With this information, and other natural history knowledge gained during a compensation study, some mechanisms may be excluded or their role minimized; more importantly, meaningful hypotheses may be developed about the mechanisms of interaction (Tonn 1983). Combining the natural experiments of multiyear, multisite compensation studies with other approaches can ultimately lead to a detailed understanding of the factors determining the structure of species assemblages.

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APPENDIX

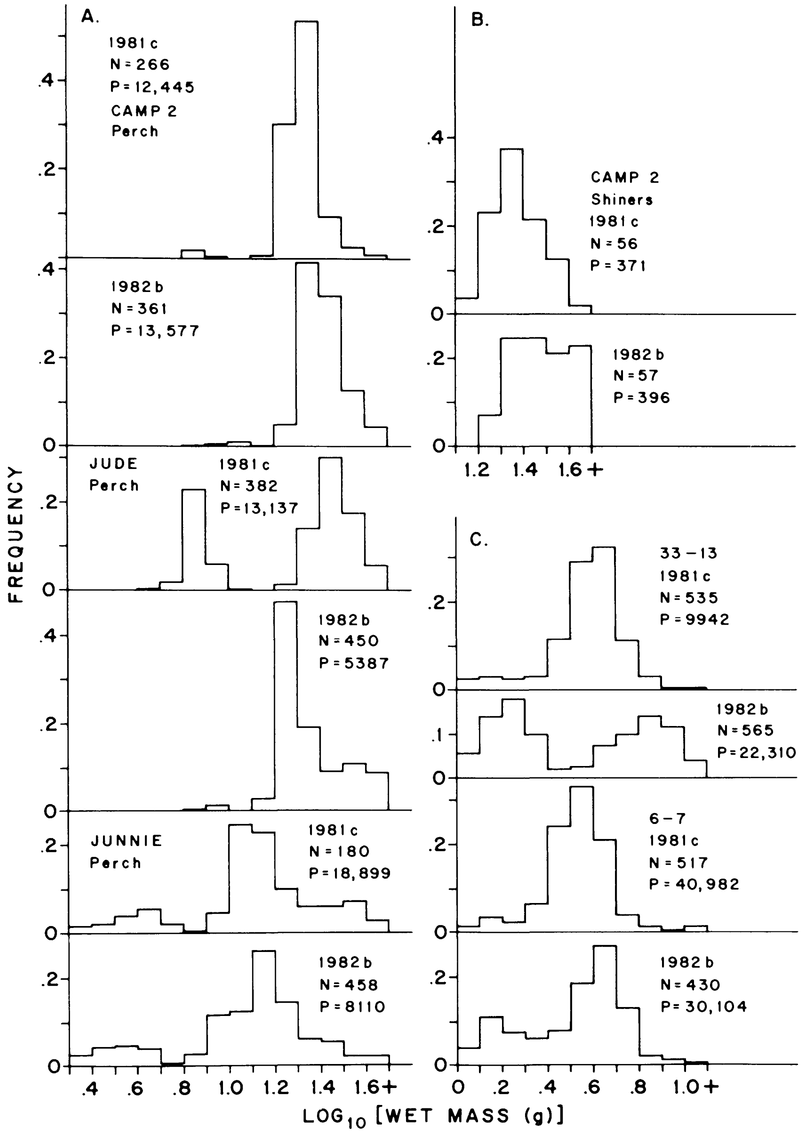

FIG. A1. Examples of mass frequency distributions, number of fish measured (N), and population estimates (P) from the 1981c and 1982b census periods for (A) yellow perch, (B) golden shiners, and (C) central mudminnows.