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MORPHOEDAPHIC AND BIOGEOGRAPHIC ANALYSIS OF CRAYFISH DISTRIBUTION IN NORTHERN WISCONSIN

Gregory M. Capelli and John J. Magnuson

ABSTRACT

We surveyed crayfish distribution and abundance among 67 lakes in the Vilas County area of northern Wisconsin, and then used multiple regression to analyze the relationship between our results and various physical, chemical, and biological variables. The region is dominated by *Orconectes rusticus, O. propinquus,* and *O. virilis,* but *Cambarus diogenes, Procambarus acutus,* and *O. immunis* are also present; only *O. virilis* was previously documented from the area. No single variable or combination of variables fully explained variations in crayfish distributions. However, substrate, calcium level, geographic isolation as related to colonization opportunity, and lake size appear to be of general importance. Continuing introductions and competitive exclusion are also probably significant, resulting in a dynamic situation involving an interaction of multiple controlling factors.

Although crayfish (Decapoda, Cambaridae) are a common component of lake and stream communities throughout most of the United States, relatively little is known about the mechanisms that determine species composition and abundance. In many areas species composition has changed significantly during the past few decades (Penn and Fitzpatrick, 1963; Schwartz *et al.,* 1963; Hobbs and Walton, 1966; Crocker and Barr, 1968; Capelli, 1982). Physical-chemical factors, competition for food, interspecific aggressive interactions, and predation have been suggested as important (Bovbjerg, 1952, 1970; Eberly, 1960; Penn and Fitzpatrick, 1963; Stein, 1976; Berrill, 1978). Introductions by fishermen using crayfish as bait may be responsible for initiating many such changes (Crocker and Barr, 1968; Berrill, 1978).

The general question of what determines species composition (both numbers and kind) in a community is central to ecology. During the past 20 years much of the theoretical work on determinants of species composition has been developed from the study of islands (MacArthur and Wilson, 1963, 1967; Rusterholtz and Howe, 1979). Barbour and Brown (1974) and Magnuson (1976) suggested that island biogeographic theories may apply in some degree to lakes, which like islands tend to be small, geologically recent, and isolated from other similar habitats. In this study we examined the relationship of crayfish species composition and abundance to physical and chemical factors, abundance of other crayfish species, and biogeographic factors, such as lake size, geographic isolation, and human use, in 67 lakes in the Vilas County area of northern Wisconsin. These waters exhibit a great range of physical, chemical, and biological characteristics, and are located in three major drainage systems: the Lake Superior system flowing north, the Flambeau-Chippewa River system flowing southwest to the Mississippi River, and the Wisconsin River system flowing south, also to the Mississippi (Fig. 1).

Because the glacial drift of the area is low in calcium and other soluble materials (Black *et al.,* 1963), lakes generally have low alkalinity and low to moderate productivity. The majority are small seepage lakes of kettle origin, with no inlet or outlet, but numerous drainage lakes also occur. Drainage lakes tend to have higher levels of calcium and other dissolved materials, as well as higher overall productivity. Drainage lakes also provide better colonization opportunities. The major crayfish species in the area are restricted continuously to water and have no obvious natural way of colonizing a seepage lake.

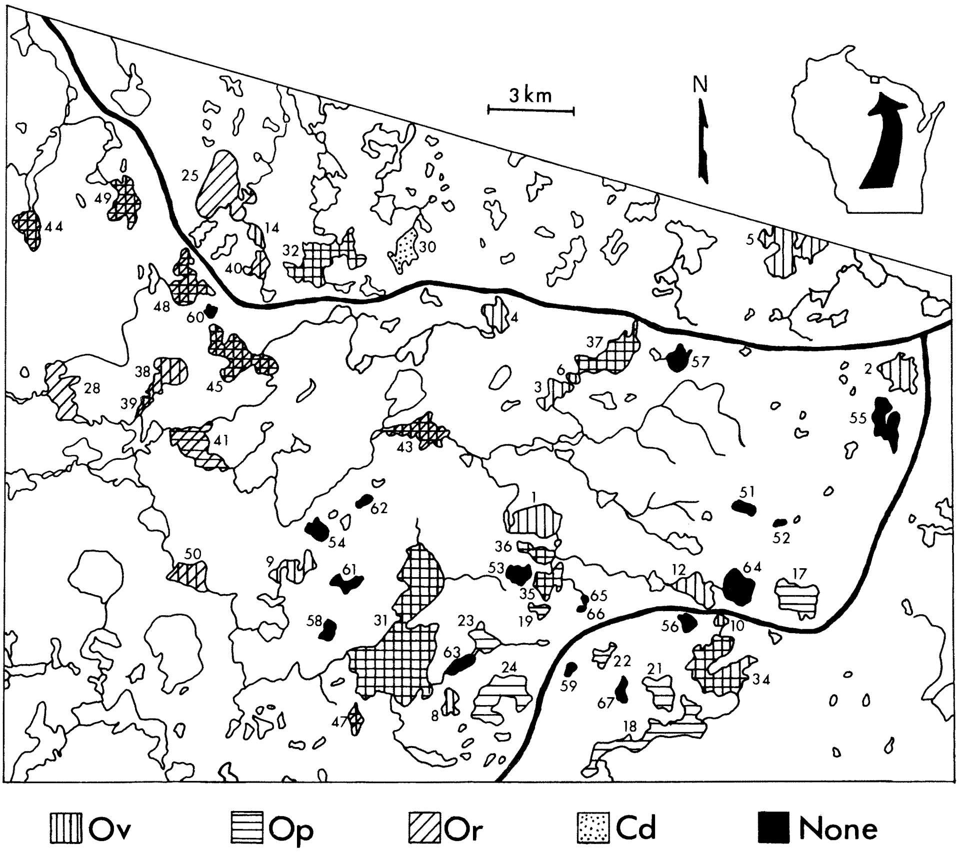

Fig. 1. A selected portion of the Vilas County, Wisconsin, study area showing crayfish species composition in sample lakes. Lake numbers correspond to those used in Appendix. Dark lines indicate major drainage basins: Lake Superior to the north, Flambeau-Chippewa Rivers to the west and southwest, and Wisconsin River to the south. Ov = *O. virilis*, Op = *O. propinquus*, Or = *O. rusticus*, Cd = *C. diogenes*. (Note: not all sample lakes occur in this area.)

General Methods, Variables, and Data Sources

Sampling was conducted from 1972 through 1977, during the period from late June through mid-September. Lakes ranged in size from 6–1,548 ha, and were chosen to provide a wide variety of physical, chemical, and biological characteristics. To sample crayfish populations in each lake, we used 15–18 wire-mesh minnow traps (openings enlarged to 3.5 cm diameter at each end) baited with 120 g beef liver. Traps were placed at depths of 1–3 m, spaced approximately 100 m apart, and left for 24 h. In larger lakes only a fraction of the total shoreline was sampled and results reported here do not completely preclude the possibility of a different species composition in an unsampled part of a given lake. This method is also obviously selective for species living in lakes proper, rather than semiterrestrial forms living along lake margins or in other wet areas.

Trap catches are independent of temperature within the range (17–23°C) occurring during our sampling (Capelli, 1975). However, traps are strongly selective for adult males, which typically comprise 80–100% of the catch (Capelli, 1975). All results are reported as mean number of adult males/trap, which provides a relative index to crayfish abundance. Males were classified as adults on the basis of either a form I condition or a carapace length of at least 20 mm during periods when adults were in form II. (In all crayfish of the family Cambaridae, adult males alternate via molts between two recognizable morphological forms known as form I and form II. The most conspicuous differences involve the anatomy of the gonopod. Mating occurs only in form I, which can therefore be used as a sign of sexual maturity. For the three *Orconectes* species of major importance in the work reported

Table 1. Summary of variables for the 67 study lakes in Wisconsin. See text for explanation of units not indicated below.

Variable	Mean	Range
Area (km^2)	2.0	0.06–15.5
Mean Depth (m)	4.5	0.5–14.5
Perimeter Length (km)	8.7	1.0–30.7
Shoreline Development Factor	1.9	1.0–4.5
Fetch (km)	1.4	0.3–5.4
Secchi Disc (m)	3.7	1.1–9.3
Substrate	3	1.0–4
pH	7.4	6.0–9.3
Conductivity (μmhos)	70	15–160
Calcium (mg/l Ca^{+2})	8.3	0.9–27.6
MEI (as $Ca^{+2}/\bar{z}$)	27.0	2.5–196.8
Human Activity	51	1–225
Geographic Isolation	55	1–121

here, form I is first achieved at a carapace length of about 20 mm, after which form II occurs only for about a 1-month period each year during midsummer.)

To check the reliability of trap catches of adult males as an index to species composition and abundance, 13 lakes sampled by traps were also searched and sampled by divers using SCUBA in the same areas where traps had been placed and in 2–4 other areas. In addition to random collecting by hand in these areas, direct estimates of crayfish density and biomass were made in four lakes by using 1 m^2 sampling rings placed randomly on the bottom.

The following variables were included in the analysis:

a) Morphometric variables: area, depth, perimeter length, shoreline development factor, fetch. Fetch was measured from west to east (the direction of the prevailing winds) on 1:24,000 scale topographic maps; other data were taken from Black *et al.* (1963).

b) Other physical variables: Secchi disc depth, substrate. Secchi disc data were taken from Black *et al.* (1963). Substrate in each sampling area was categorized with regard to its shelter potential as follows: 1) probably unsuitable, consisting mostly of silt or muck of varying depth with no firm support, 2) poor, mostly sand-gravel (<16 mm particle size) providing little shelter, 3) mixture of sand-gravel areas with cobble-pebble areas (≈16–256 mm particle size), and 4) good, mostly cobble-pebble with little or no sand-gravel areas. For data analysis substrate categories were assigned numerical values of 1, 2, 3, 4, respectively.

c) Chemical variables: pH, conductivity, calcium. Data for pH and conductivity were taken from Black *et al.* (1963). Calcium was determined using either an atomic absorption spectrophotometer or standard titrametric procedures (Taras *et al.*, 1971); all results are expressed as mg/l Ca^{+2}.

d) Morphoedaphic index. MEI (total dissolved solids/mean depth) or its correlates have been shown to predict accurately the productivity of fish and some benthic invertebrates (Ryder, 1965; Ryder *et al.*, 1974; Johnson, 1974). We estimated mean depth of all lakes from $\bar{z} = 0.41\ z_{max}$ (Koshinsky, 1970; Cole, 1975) and used calcium concentration/mean depth as our MEI.

e) Variables related to colonization probability: human activity, geographic isolation. Assuming that the probability of crayfish introductions by humans is a function of the amount of human activity on the lake, we developed an index to human use as follows: each house = 1, each resort = 5, primitive public access only = 1, unimproved or difficult boat landing = 5, improved boat landing = 10. Values ranged from 1 for a lake with no houses or resorts and only primitive access to 225 for a highly developed lake with several convenient access points. Weightings and the resulting totals are arbitrary but probably provide a reasonable index to relative use of the lakes.

Presumably the further upstream a drainage lake is in a watershed, the more difficult it has been for crayfish to colonize it by natural means since the retreat of the glaciers approximately 8,000 years ago. Seepage lakes, which have no connection to surface drainage systems, are presumably even more difficult to colonize, with the degree of difficulty perhaps depending in part on distance from the nearest drainage water. Within each of the three main drainage systems (Fig. 1), drainage lakes were classified as downstream, intermediate, or upstream on the basis of distance from a common downstream point. Geographic isolation values of 1, 11, and 20, respectively, were assigned to them. Seepage lakes were classified on the basis of distance from the nearest drainage water and were assigned values of 101 (<0.5 km), 111 (0.6–1.0 km), and 121 (>1.0 km), reflecting our assumption that a gap in surface water connections poses a much greater hindrance to colonization than does a long distance via connecting streams.

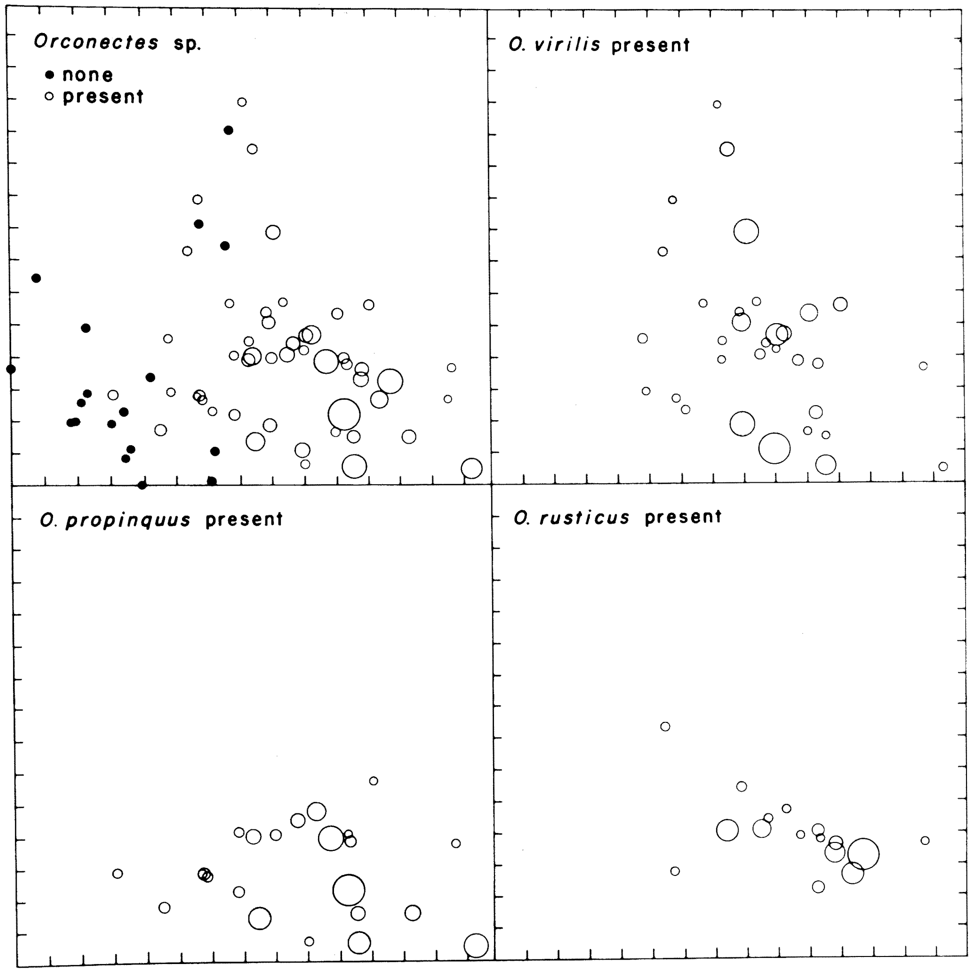

Fig. 2. Ordination of the 67 sample lakes from the Vilas County, Wisconsin, area on the basis of the variables used in this study. Axes represent "similarity," i.e., lakes falling close together are generally similar in regard to the variables used in the analysis, and those more distant are less similar. Circle diameters indicate relative abundance of crayfish in each lake.

f) Crayfish abundance. The abundances of individual crayfish species, singly or in combination expressed as number of adult males/trap, were included among the independent variables in some analyses.

The range and mean values of variables used, other than those describing crayfish abundance, are summarized in Table 1.

Results

Species Composition and Abundance

Fifty of the 67 lakes sampled contained crayfish: *Orconectes virilis* (Hagen), *O. propinquus* (Girard), *O. rusticus* (Girard), *O. immunis* (Hagen), *Cambarus diogenes* (Girard), and *Procambarus acutus* (Girard) (see Appendix). Abundance varied greatly with mean numbers of adult males/trap ranging from 0.1–29.7 in lakes with crayfish. *Orconectes propinquus, O. rusticus,* and *O. virilis* were the most abundant, occurring in all possible species combinations and in all three major drainage systems (Fig. 1, Appendix). However, species generally tended to be isolated from each other. Of the 51 lakes with crayfish, 30 contained only one species. In lakes with at least two species, one was usually several times more abundant than the other(s).

In all 13 lakes sampled by divers, including three with no crayfish, species composition results corresponded exactly to those based on traps. In these lakes divers also sampled two to four areas in addition to those sampled by traps; therefore our trap catch data appear to reflect accurately species composition of whole lakes. In the four lakes (Laura, Escanaba, Nebish, Trout) in which direct estimates of total population biomass were made, results correlated strongly with trap catches of adult males ($r = +0.97$, $P < 0.05$), indicating that trap catches are also a reliable estimate of relative abundance.

As a general aid to determining whether there were significant differences among lakes occupied by crayfish, we ordinated all lakes on the basis of the variables listed in Table 1. All data were converted to relative values within a common range, to adjust for the large differences in variable magnitude. Coefficients of similarity were calculated as 2w/(a + b) (Bray and Curtis, 1957) and endpoints were chosen for a two-dimensional ordination using a regression method developed by Beals (in press). The result (Fig. 2) is a plot which locates lakes along a two-dimensional coordinate system in which both axes represent units of "similarity." Lakes falling close together were generally similar in regard to the chosen variables; those farther apart were less similar. Relative crayfish abundance in each lake is depicted by the diameter of the circle used to locate the lake.

No precise interpretation can be attached to such an ordination because location within the ordination is determined by many different kinds of variables, some of which have been artibrarily quantified or are self-correlated to varying degrees. However, certain general patterns emerge (Fig. 2). Lakes without crayfish are clustered toward the lower left portion of the ordination, probably reflecting their tendency to be near the extreme with regard to many different variables: size related (small), geographic isolation (high), human activity (low), dissolved materials and pH (low), substrate (fair to poor). The three dominant species of the area, *O. virilis, O. propinquus,* and *O. rusticus,* do not clearly segregate in the plots, suggesting a general overlap among species in the characteristics of the lakes they occupy. This is consistent with previous reports that all three prefer similar habitats of clear, well-oxygenated water with firm substrates.

The remainder of our analysis, except as noted, will be confined to specific variables and the three dominant *Orconectes* species.

Crayfish Abundance in Relation to Specific Environmental Variables

The relationships among crayfish abundance and other variables were analyzed using stepwise multiple regression with untransformed data, semilog transformed data (i.e., only crayfish abundance converted to log form), and log-log transformed data. Generally, the semilog and log-log transformations produced higher coefficients of determination (R^2 values, which indicate the fractional amount of variation in crayfish abundance accounted for by given variables) than did untransformed data. All results reported here are based on the log-log transformed data.

Correlation coefficients indicated that many variables were significantly ($P < 0.05$) related to each other, as well as to crayfish abundance. Most size-related

Table 2. Relation of crayfish catch/trap to selected variables (calcium, substrate, perimeter, geographic isolation, human activity) among all lakes and lakes with crayfish. Results are from stepwise multiple regression with all data converted to log form. Abbreviations: Op = *Orconectes propinquus*, Or = *O. rusticus*, Ov = *O. virilis*.

Data set	Dependent variable catch/trap	Independent variables	Coefficient of determination (R^2) Cumulative	Coefficient of determination (R^2) Total corrected	Regression coefficient	Intercept
All lakes (N = 67)	All species	Calcium	0.34		0.4792	
Abiotic variables		Substrate	0.52		1.6333	
		Geographic isolation	0.56		−0.1850	
		Perimeter	0.59	0.56	0.3787	−0.9181
	O. virilis	Calcium	0.20		0.3996	
		Substrate	0.28	0.26	0.7189	−0.6188
	O. propinquus	Substrate	0.19		1.2234	
		Perimeter	0.26	0.24	0.4697	−0.8689
	O. rusticus	Geographic isolation	0.24		−0.2288	
		Human activity	0.28	0.26	0.1563	0.2534
Crayfish lakes (N = 49)	All species	Substrate	0.32		2.8393	
Abiotic variables		Geographic isolation	0.43		−0.2266	
		Perimeter	0.49	0.45	0.4551	−1.1533
	O. virilis	Substrate	0.13		1.4499	
		Calcium	0.23	0.20	0.5219	−1.1492
	O. propinquus	Substrate	0.28	0.26	3.203	−1.5660
	O. rusticus	Geographic isolation	0.21		−0.2491	
		Human activity	0.27	0.24	0.2657	0.0926
Crayfish lakes (N = 49)	*O. virilis*	Substrate	0.13		2.0590	
All variables		Op + Or	0.26		−0.2552	
		Calcium	0.37	0.33	0.5488	−1.4051
	O. propinquus	Substrate	0.28		3.0335	
		Or + Ov	0.37	0.34	−0.3808	−1.7940
	O. rusticus	Geographic isolation	0.21		−0.2491	
		Human activity	0.27	0.24	0.2657	0.0926

Table 3. Median and range from first through third quartiles for five variables for various lake sets. Calcium units are mg/l as Ca^{+2}; perimeter is expressed in km. See text for explanation of other units.

Lake set	Number of lakes	Substrate	Geographic isolation	Calcium	Human activity	Perimeter
With crayfish	49	3 (3–4)	20 (11–101)	10.2 (6.3–12.8)	50 (22–87)	8.7 (5.3–14.5)
Without *Orconectes* sp.	18	3 (1–3)	101 (101–121)	1.6 (1.2–3.2)	11 (3–21)	3.7 (1.9–5.3)
With *O. virilis*	35	3 (3–4)	20 (11–20)	10.5 (7.2–14.4)	45 (23–81)	8.2 (5.3–11.9)
With *O. propinquus*	23	3 (3–4)	20 (11–101)	9.2 (5.2–11.1)	55 (17–87)	10.3 (6.4–15.9)
With *O. rusticus*	17	3 (3–3)	1 (1–20)	11.9 (10.1–14.8)	71 (35–110)	10.5 (6.9–13.8)

variables (area, depth, fetch, perimeter length) were strongly positively self-correlated, as were those related to chemistry (calcium, pH, conductivity). Human activity was also strongly positively correlated with size-related variables. Many individual variables correlated significantly ($P < 0.05$) with abundances of individual species or species combinations for all lakes and for crayfish lakes only. The five variables which showed the highest correlation values for at least some species or species combinations were chosen for further analysis involving stepwise multiple regression: calcium, substrate, perimeter length, geographic isolation, and human activity. To assess the importance of variables related to MEI, we determined R^2 and regression values for calcium/mean depth and for calcium + mean depth. In some analyses, abundances of individual species and species groups were also included among the independent variables.

R^2 values from stepwise multiple regression and other data for all crayfish species combined, as well as for individual species, are summarized in Table 2.

The first analysis included all lakes, but crayfish abundance was analyzed only in relation to the five selected variables listed previously. For total crayfish abundance the order of importance of the variables was calcium, substrate, geographic isolation (negatively related to crayfish abundance), and perimeter. These four variables accounted for about 56% of the variation in total crayfish abundance. Among individual species, variables differed in importance. For example, human activity was a significant variable for *O. rusticus,* but was not significant for the other two species.

The second analysis included only lakes that contained crayfish. For this set calcium was no longer significantly related to total crayfish abundance and was of reduced importance to *O. virilis* abundance. Substrate assumed greater importance, ranking first for total crayfish abundance, and for abundance of *O. virilis* and *O. propinquus.* For *O. rusticus,* geographic isolation and human activity retained greatest significance.

The third analysis included only lakes with crayfish, but also included the abundances of crayfish species among the independent variables. There was a significant inverse relationship between the total abundance of other crayfish and the abundances of *O. virilis* and *O. propinquus,* although substrate retained greatest importance for these two species. The abundance of other species did not contribute significantly to the observed variation in *O. rusticus* abundance.

The median and first through third quartile values for the five selected non-crayfish variables for various lake sets are summarized in Table 3. Compared to lakes with crayfish, lakes lacking crayfish tended to be lower in calcium and human activity, more isolated in the watershed (i.e., further upstream or with connections only via seepage), and smaller. Poorest substrates (consisting of muck, with an assigned value of 1), were found only in non-crayfish lakes. However, many non-

Table 4. A comparison between multiple linear regression using calcium (Ca) and mean depth ($\bar{z}$) and a morphoedaphic index using the same variables (Ca/$\bar{z}$) as predictors of crayfish abundance.

		log Y = a + b log Ca + c log $\bar{z}$					log Y = a + b log(Ca/$\bar{z}$)			
Data set	Index to abundance	R^2	P	a	b	c	R^2	P	a	b
Crayfish lakes	catch/trap	0.21	0.01	−0.595	0.608	0.938	0.00	0.27		
Crayfish lakes	perimeter × catch/trap	0.33	0.01	−1.14	1.09	2.07	0.04	0.08	1.852	−0.726
All lakes	perimeter × catch/trap	0.58	0.01	−1.77	1.74	1.92	0.00	0.53		

crayfish lakes had substrates similar to those in crayfish lakes. Lakes with *O. rusticus* tended to be lower in the watershed and higher in human activity than those with other species.

The relation of total crayfish abundance to calcium and mean depth, the variables involved in our analysis of MEI, is shown in Table 4. In two of the analyses crayfish abundance was multiplied by perimeter length to approximate a relative index to total population size. In all cases both calcium and mean depth were positively related to crayfish abundance, which is contrary to the generally expected negative relation with mean depth when MEI is a good predictor of productivity or abundance. Thus, calcium + mean depth was significantly related to crayfish abundance, but calcium/mean depth (a correlate of MEI) was not.

The variables for which we could obtain data account for a relatively small portion of the total variation in crayfish abundance. Probably the most important variable for which no direct data are available is food supply. Crayfish are generally scavengers on the benthic community (Capelli, 1980). In the littoral zones where crayfish are most abundant, allochthonous inputs of organic plant material may represent a significant but variable food source either for crayfish directly or for their prey. Presumably such input is reflected to some degree by the dissolved solids in the water, a variable which was included in our analysis. However, the relation between dissolved materials and crayfish production is apparently not strong (see below).

Fish, as well as a variety of other organisms, may feed significantly on crayfish (Penn, 1950; Stein, 1975). Fish abundance should correlate well with some variables used in our analyses, but adequate data are not available to relate crayfish abundance directly to predation.

Discussion

Environmental Variables

Calcium.—Crayfish exoskeletons contain relatively large amounts of calcium (17–40% dry weight, McWhinnie *et al.*, 1972), which suggests that low levels of calcium may limit crayfish survival and production. During molt processes crayfish retain some calcium in gastroliths deposited on the anterior portion of the stomach, but a substantial amount is lost to the environment and must be reabsorbed after ecdysis (McWhinnie, 1962; McWhinnie *et al.*, 1969). Intermolt crayfish also exchange calcium continuously with the environment (McWhinnie, 1962).

Rhoades (1962) suggested but did not document that the mineral content of certain Ohio waters, as determined by the presence or absence of limestone substrate, influenced the distribution of *O. propinquus* and *O. rusticus*. De la Bretonne *et al.* (1969) found a positive correlation between water hardness (at Ca^{+2} levels of 4–60 ppm) and production in an experimental study of the southern species *P. clarkii* (Girard). At 4 ppm, survival of *P. clarkii* was only 9% of that at higher levels, and many individuals remained poorly calcified. Despite the large amount of research on molting processes in crayfish (McWhinnie, 1962; McWhinnie *et al.*, 1969; McWhinnie *et al.*, 1972; Stevenson, 1972; Armitage *et al.*, 1973), the work on *P. clarkii* provides the only information on minimum calcium levels necessary for exoskeleton formation.

Our data suggest that the *Orconectes* species in northern Wisconsin require a minimum Ca^{+2} level of about 2.5 ppm. Above this minimum level, calcium is not related to abundance. The lowest calcium level in any lake with *Orconectes* was 2.6 ppm (Frank Lake, #22 in Fig. 1 and Appendix). Among lakes with no crayfish but with suitable substrates (rated "2" or higher, #51–62 in Appendix) only two exceeded 2.5 ppm: Jean (#52, 2.6 ppm) and Dorothy Dunn (#51, 3.4 ppm). Levels of calcium in other non-crayfish lakes with suitable substrates ranged from 0.9–2.1 ppm (Fig. 3).

The existence of a minimum or threshold calcium level is consistent with the results of our multiple regression analyses. Calcium accounted for a significant amount of variation in total crayfish abundance for all lakes combined ($r = +0.54$; $P < 0.01$) but was not significant when lakes without crayfish were eliminated from the analysis ($r = +0.17$; $P > 0.05$) (Table 2). However, calcium level accounted for a significant proportion of the observed variability in *O. virilis* abundance (Table 2) in lakes with crayfish and thus should not be totally discounted.

The presence of *C. diogenes* and absence of *Orconectes* species in Lynx Lake (#30), a drainage lake with a calcium level of only 1.8 ppm, suggests that species may differ regarding minimum calcium requirements. *C. diogenes* is a burrowing, semiterrestrial species not continuously restricted to open water on either a daily or seasonal basis. The fact that Lynx Lake is a drainage lake with a natural connection to other waterways that contain crayfish suggests that calcium level, and not lack of colonization opportunity, has prevented *Orconectes* from invading.

The determination of the relationship between crayfish abundance and calcium levels is complicated by the fact that all lakes with suitable substrates but lacking crayfish are seepage lakes with low or moderate human activity. The two non-crayfish lakes with calcium levels exceeding 2.5 ppm and with suitable substrates (Dorothy Dunn and Jean Lakes) have difficult access and low human activity values (=10 for both). The absence of crayfish in these two lakes may simply reflect a lack of colonization opportunity via either natural routes or human introduction. Lack of colonization opportunity cannot be ruled out as a factor in other seepage lakes lacking crayfish. However, the fact that eight seepage lakes sampled contained crayfish (#2, 13, 17, 19, 21, 22, 24, 27) verifies that such lakes can be colonized. Among seepage lakes with suitable substrates, crayfish were present in a significantly higher proportion of lakes with calcium levels exceeding 2.5 ppm than in lakes with calcium levels below 2.5 ppm ($P < 0.01$, Fisher test). Although seepage lakes without crayfish are, on the average, lower in human activity than those with crayfish, there is substantial overlap for this variable among the two types of lakes (Fig. 3). Thus, there is no compelling evidence that lack of colonization opportunity due to low human activity is an adequate general explanation for the absence of crayfish in these lakes.

Substrate.—Capelli (1975) found a large difference in the density of *O. propinquus* between contiguous areas of sand-gravel and cobble-pebble substrate in Trout Lake (#31) and suggested that the difference was related not only to shelter po-

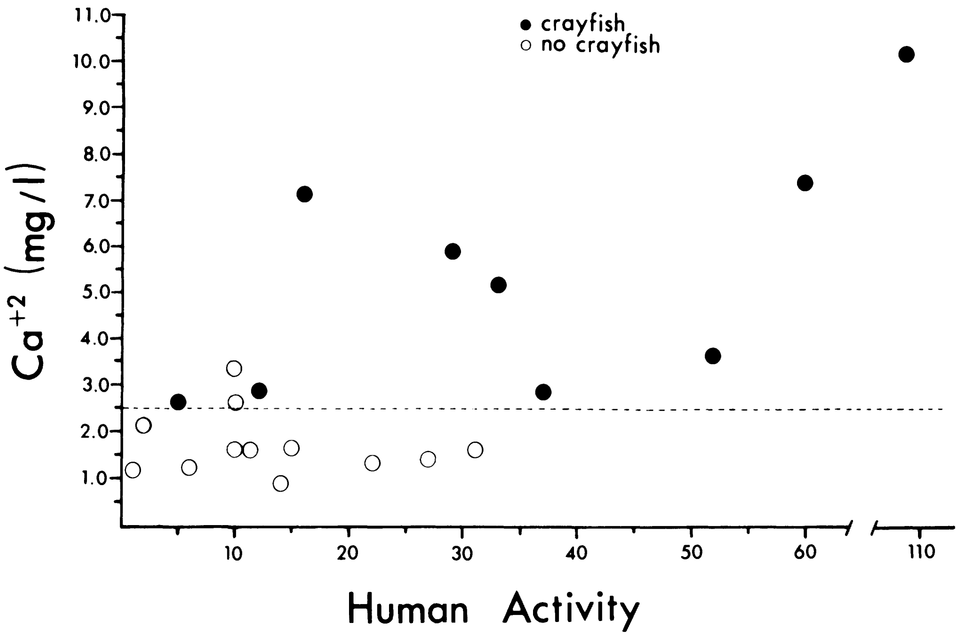

Fig. 3. Calcium and human activity values for lakes lacking crayfish but with suitable substrates.

tential but to a better-developed food supply in areas with larger substrate particles. Stein (1975) demonstrated that the shelter provided by substrate is important for predator avoidance in *O. propinquus.* Shelter is probably also important in preventing cannibalism of females with eggs and of individuals undergoing molt. Our analyses suggest that substrate is the single most important variable related to total crayfish abundance (Table 2).

Correlation coefficients for substrate with total crayfish abundance and for substrate with *O. propinquus* and *O. virilis* abundances were higher than those for any other variables for all lakes combined as well as for crayfish lakes ($r >$ $+0.35$ in all cases, $P < 0.01$). For *O. rusticus,* however, correlations between substrate and abundance were low and not significant ($r = 0.01$ for all lakes, -0.13 for crayfish lakes). These results are consistent with our general observations, based on direct collection and underwater surveys, that *O. rusticus,* unlike the other species, is commonly abundant on open sand as well as in areas with more shelter and appears to survive better than the other species in areas with reduced shelter.

The ability of crayfish to avoid predators increases with increasing body size and hence the need for shelter decreases. However, in laboratory studies (Capelli and Munjal, 1982; plus unpublished data) even relatively large adults (30 mm carapace length) of all three species showed a strong preference for shelter and avoided unsheltered areas regardless of food availability or life history stages. *O. rusticus* was consistently more aggressive than *O. virilis* and *O. propinquus,* and was able to outcompete the other species for limited shelter. The greater aggressiveness of *O. rusticus* may be important in defense against predators as well as in interspecific competition, and may therefore increase the probability of survival in unsheltered areas. Moreover, the mandible of *O. rusticus,* which is often used to scrape food directly from the substrate, is distinctly different from the mandibles of *O. virilis* and *O. propinquus* (Capelli and Capelli, 1980). The difference in mandible shape suggests that differences in either feeding mechanisms or ability to utilize certain items could be involved in increased ability to survive in open areas.

Morphoedaphic Index (MEI) and Size-Related Variables.—A positive relation between abundance and MEI implies a positive relation between abundance and dissolved solids and a negative relation between abundance and depth. In a review of the relations between benthic productivity (or standing crop) and dissolved solids, depth, and MEI, Johnson (1974) found that dissolved solids generally showed either a positive relation or no relation to productivity. Mean depth variously showed a positive or negative relation or no relation. However, for three different lake sets highly significant correlations between benthic productivity and MEI occurred. For these sets, the data appear to apply to the total benthic community including a significant chironomid component distributed throughout profundal regions. The negative influence of depth on productivity in profundal regions is presumably based on reduced temperature and food supply.

For organisms such as crayfish, which are restricted primarily to littoral and near-littoral areas, lake depth is probably not directly relevant. The strong positive correlation ($r = +0.46$, $P < 0.01$) that we found between crayfish abundance and mean depth probably reflects the fact that mean depth and crayfish abundance are strongly positively correlated with size-related variables such as perimeter and fetch. Lakes with large fetches and increased wave action tend to have rockier shorelines with substrates of cobble-pebble rather than silt or sand-gravel. Thus lake depth probably has no direct relation to crayfish abundance. The absence of a negative relation between depth and abundance precludes the use of MEI as an indicator of crayfish abundance.

Biogeographic Considerations

Among the six crayfish species we found, only *O. virilis* had been reported by Creaser (1932) from the Vilas County area. The semiterrestrial *C. diogenes* was probably also present at that time, but occurrences of the other four species constitute significant extensions of their known ranges.

O. propinquus occurred in the eastern and southern parts of Wisconsin to within 110 km of Vilas County. At its closest proximity, in the eastern part of the state, however, it was limited to the Lake Michigan drainage, which includes only one of our sample lakes (Butternut, #29). Its nearest occurrence via natural water routes (Wisconsin River or other streams in the Mississippi River drainage) was at least 300 km to the south. *O. immunis* and *P. acutus* were known only from southern Wisconsin, with the nearest records to Vilas County approximately 260 km for *O. immunis* and 340 km for *P. acutus*. The presence of *O. rusticus* had not been documented previously in Wisconsin; nearest records were from northern Illinois and southern Michigan, approximately 500 km to the south (Creaser, 1931, 1932).

Circumstantial evidence strongly suggests that the species composition of many of the lakes has in fact changed during the past several decades. Creaser (1932) did not sample the area extensively and his exact records are no longer extant, but his published distribution maps suggest that he sampled Lac Vieux Desert (#15), Trout Lake (#31), and Island Lake (#41) or one of the lakes in the Manitowish River flowage just west of Island Lake. Although Lac Vieux Desert still contains only *O. virilis,* it would be impossible to collect today in Trout Lake without encountering *O. propinquus,* or in Island or neighboring lakes without encountering *O. rusticus.* Moreover, Creaser sampled central Wisconsin extensively (>100 sites) and found only *O. virilis* and *C. diogenes.* It is extremely unlikely that large but disjunct populations of other species occurred in Vilas County at that time.

Human Activity.—Nothing is known of the time required for colonization of the Vilas County area from the south via natural waterways, or of the present distribution of crayfish in the rest of the state. We believe, however, that the apparent changes were at least initiated as a result of introductions by humans. The highly restricted distributions of *O. immunis* and *P. acutus* among our study lakes suggest that these species have not invaded the area by any recent general range extension. The significant relationship between *O. rusticus* abundance and human activity also suggests the importance of introductions. We have recently discovered an isolated population of *O. rusticus* in a small area of Trout Lake, in the immediate vicinity of a campground/boat launch area. During the past 10 years we have sampled this area extensively and until recently had found no evidence of *O. rusticus.* We have little doubt that its appearance is the result of an introduction by humans. Crocker and Barr (1968) and Berrill (1978) suggested that the occurrence of *O. rusticus* in some Ontario waters was the result of introductions by fishermen. Vilas County is a major tourist area heavily fished by individuals from southern Wisconsin and northern Illinois.

Only *O. rusticus* abundance exhibited a strong, significant relationship to human activities ($r = +0.40$, $P < 0.01$). This finding is consistent with our belief that this species is the newest invader in the area and has probably been introduced by humans. Although human activity was expected to relate primarily to presence-absence, the general relation to total abundance probably reflects introduction at an earlier date with a longer time for population expansion in lakes with high human activity. For *O. propinquus* the correlation between human activity and abundance was lower than that for *O. rusticus* ($r = +0.23$, $P = 0.06$), and for *O. virilis* no correlation was apparent ($r = 0.00$). These results are consistent with our belief that human introductions are more important in influencing the present distribution of *O. rusticus,* which has had less time to expand naturally in the area, than they are for the other species. The relation between *O. propinquus* and human activity is consistent with our belief that it too was probably introduced, but at an earlier date than *O. rusticus.* Because of a longer time for natural expansion within the area, this species would be expected to show less association with human activity. *O. virilis* has apparently been in the area long enough so that its present distribution is uninfluenced by human activity.

Geographic Isolation.—For islands, isolation is an important determinant of the likelihood of colonization by new species. Less isolated islands should have a greater likelihood of being encountered by new species. Relative isolation of an island can often be reasonably determined because the most likely mode of colonization can be surmised (flight, drift in ocean currents, etc.) and the distance to the nearest similar habitat easily determined. For lakes, isolation is more difficult to determine and quantify. Variations in distance between seepage lakes may be irrelevant if the organisms in question are incapable of significant survival outside their normal habitat. Drainage lakes may be connected by waterways that are continuously variable in the degree to which they allow the survival and movement of a given species. Furthermore, little is known about likely colonization mechanisms for many aquatic organisms, even for those that have managed to cross substantial barriers.

Among individual species, geographic isolation was important only to *O. rusticus* abundance ($r = -0.24$, $P < 0.05$); its contribution to variation in total crayfish abundance (Table 2) probably reflects the importance of *O. rusticus* in total crayfish abundance. The greater restriction of *O. rusticus* within the drainage systems of the area is consistent with the belief that it has not been in the area as long as the other species and has had less time to colonize via natural means. The negative relation of *O. rusticus* abundance to geographic isolation (i.e., the tendency for *O. rusticus* to occur in the downstream portions of the drainage systems) suggests that some of the invasion into the area may have occurred via natural means from the south and west (Fig. 1). However, many lakes in these areas also have high human activity values compared with lakes upstream. The lower correlations between geographic isolation and *O. propinquus* abundance ($r = -0.22$) and *O. virilis* abundance ($r = -0.18$), although not significant at the 0.05 level, are consistent with the belief that *O. virilis* has been in the area longer than the other two species and has had time to colonize more remote lakes. *O. propinquus* has had less time to colonize lakes and *O. rusticus* the least.

Lake Size.—An important determinant of species richness on islands is size (MacArthur and Wilson, 1963, 1967; May, 1975; Rusterholtz and Howe, 1979). Larger islands should have a greater likelihood of being encountered by new species and should likely provide greater habitat diversity. In lakes, size may be related less directly to colonization probability because even those of widely varying size have at most one outlet, the most likely colonization route for many organisms (Magnuson, 1976). Nonetheless, Barbour and Brown (1974) found a significant relation between surface area and number of fish species in a sample of 70 lakes from around the world.

Using regression analyses we examined the relation between the number of crayfish species and lake size. Both surface area and perimeter were tested. For all lakes combined, both surface area and perimeter accounted for a significant proportion of the variation in crayfish species number, but R^2 values were relatively low (surface area, $R^2 = 0.23$; perimeter, $R^2 = 0.25$). For lakes with crayfish, neither index to size was significantly related to species number. Thus, our data suggest that small lakes are less likely to contain crayfish than are large lakes, but that size does not otherwise influence species number.

Interspecific Competition.—Our data suggest that the absence of a relation between lake size and species number in lakes with crayfish is a result of competitive exclusion. Species tend to be isolated on a lake-to-lake basis with almost all lakes containing monospecific populations or populations dominated by one species (Appendix). Our observations and those of others (Crocker and Barr, 1968) indicate that general habitat requirements of the three *Orconectes* species are similar. Niches of the three species apparently overlap broadly, although specific information about some important niche components such as food habits is not adequate to determine the degree of overlap. The presumed increase in habitat diversity in a larger lake, which should allow more species to coexist, becomes irrelevant if species are not capable of using that diversity. Conversely, the three *Orconectes* species may be capable of greater resource partitioning, but these capabilities are not realized in our study area because of the relative similarity of habitats in lakes with crayfish.

Previously, the evidence that competitive exclusion is actually occurring was based on distribution patterns and was therefore mostly circumstantial. It suggested that *O. propinquus* is able to displace *O. virilis,* and that *O. rusticus* can displace both other species. Recent resampling of several lakes has confirmed this displacement pattern. For example, data reported here for Papoose Lake (#48) were taken in 1975 when the order of numerical abundance was *O. propinquus, O. rusticus, O. virilis* in a ratio of approximately 12:2:1 (Appendix). Resampling the same area in 1979 indicated that *O. rusticus* outnumbered *O. propinquus* by 5:1, and no *O. virilis* were present. In 1980, only *O. rusticus* was found. Rates of change within lakes are highly variable, however; for a fuller discussion and data on other lakes see Capelli (1982).

There was a significant negative relation between abundance of both *O. virilis* and *O. propinquus* and the abundance of other crayfish species (Table 2). Abundance of *O. rusticus,* however, was not significantly related to the abundance of other species. The exact mechanisms by which *O. rusticus* is subject to less interference from other species are not known, but could be related to a variety of niche components, such as the ability to survive on a wider range of substrate types and possible differences in feeding habits as discussed previously. Moreover, *O. rusticus* young hatch about two weeks earlier than those of the other species, thereby gaining a size advantage that may be important in shelter procurement and predator avoidance (Lorman, 1980). Laboratory studies have shown that *O. rusticus* is clearly more aggressive than *O. virilis* and *O. propinquus,* can outcompete the others for certain limited resources, and may interfere with the successful reproduction of the other species (Capelli and Munjal, 1982; plus unpublished data).

Summary and Conclusions

Orconectes propinquus, O. rusticus, and the "native" *O. virilis* are the dominant crayfish species in northern Wisconsin. Their distribution patterns are determined by an interaction of multiple physical-chemical factors as well as biological factors such as species introductions and competitive exclusion.

No single variable or combination of variables fully explained variation in crayfish abundance. Calcium level, lake size, substrate, and geographic isolation appear to be of general importance; crayfish probably require a minimum calcium level of about 2.5 ppm, are generally most abundant in larger lakes and on rocky substrates providing good shelter, and are probably absent in some lakes because of a lack of colonization opportunity due to the lake's isolation. Some variation among species exists; for example, *O. rusticus* appears to be less dependent than the others on shelter and its present distribution is more strongly influenced by variables related to colonization opportunity. In light of apparent continued displacements, particularly of *O. virilis* and *O. propinquus* by *O. rusticus,* competitive exclusion of some kind should be considered a major determinant of distribution patterns. Since it is unlikely that distribution will stabilize in the foreseeable future, assessment of the factors controlling distribution by use of environmental correlates will remain complex and difficult.

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Appendix. Crayfish species composition and abundance for 67 lakes in the Vilas County, Wisconsin, area. Lakes are arranged by species composition; within the same category, lakes are listed in decreasing order of crayfish abundance. In multispecies lakes, species are listed in order of numerical dominance. See text for explanation of substrate types. Abbreviations: Ov = *O. virilis*, Op = *O. propinquus*, Or = *O. rusticus*, Oi = *O. immunis*, Cd = *C. diogenes*, Pa = *P. acutus*. Locations of lakes with duplicate names and those not in Vilas County are described in footnotes.

Lake	Species	Mean number adult males/trap	Ca^{+2} (ppm)	Substrate
1. White Sand[1]	Ov	11.6	7.2	4
2. Forest	Ov	7.9	7.3	4
3. Fishtrap	Ov	6.9	12.4	3
4. Wildcat	Ov	5.3	24.4	4
5. Big[2]	Ov	4.6	14.4	3
6. Rush	Ov	3.6	14.7	3
7. Erickson	Ov	0.6	7.6	3
8. Little John	Ov	0.4	11.6	3
9. Upper Gresham	Ov	0.4	10.3	2
10. Little Star[3]	Ov	0.2	7.6	2
11. South Twin	Ov	0.2	10.8	2
12. Ballard	Ov	0.1	6.1	2
13. Snipe	Ov	0.1	2.9	3
14. Averill	Ov	0.1	17.0	2
15. Lac Vieux Desert	Ov	0.1	9.2	3
16. Black Oak	Ov	0.1	6.8	2
17. Laura	Op	15.6	5.9	4
18. Plum	Op	9.5	11.0	4
19. Nebish	Op	4.8	2.8	3
20. Little Spider	Op	4.7	10.2	3

Appendix. Continued.

Lake	Species	Mean number adult males/trap	Ca^{+2} (ppm)	Substrate
21. Razorback	Op	3.3	3.6	3
22. Frank	Op	2.2	2.6	2
23. Upper Allequash	Op	1.6	9.2	3
24. Big Muskellunge	Op	0.6	5.2	4
25. Presque Isle	Or	25.3	19.2	3
26. Crescent[4]	Or	15.0	10.2	3
27. Oneida[5]	Or	13.2	10.0	3
28. Rest	Or	12.6	11.9	2
29. Butternut[6]	Or	8.1	—	2
30. Lynx[7]	Cd	0.5	1.8	3
31. Trout	Op, Ov	19.9, 0.9	10.5	4
32. Crab	Op, Ov	17.4, 5.7	5.6	4
33. Circle Lilly	Op, Ov	7.4, 0.1	10.5	4
34. Star	Op, Ov	6.7, 0.3	7.2	4
35. Escanaba	Op, Ov	4.1, 0.1	4.6	4
36. Lost Canoe	Op, Ov	1.8, 0.1	4.8	3
37. High	Ov, Op	3.5, 0.4	27.6	3
38. Clear	Or, Ov	9.8, 1.0	12.8	3
39. Fawn	Or, Ov	1.5, 0.8	11.0	3
40. Van Vliet	Ov, Or	8.7, 0.5	14.8	3
41. Island	Or, Op	3.8, 0.2	13.2	3
42. Whitefish	Ov, Pa	0.4, 0.1	4.9	2
43. Boulder	Op, Ov, Or	20.8, 1.5, 0.1	8.9	4
44. South Turtle	Op, Ov, Or	12.1, 3.8, 1.6	11.1	3
45. Big[2]	Op, Ov, Or	2.8, 1.2, 0.1	19.2	3
46. North Twin	Op, Ov, Or	1.2, 0.2, 0.1	10.8	2
47. Sparkling	Op, Ov, Or	1.1, 0.3, 0.1	7.2	3
48. Papoose	Op, Or, Ov	29.7, 4.8, 2.4	14.9	4
49. Birch	Op, Or, Ov	7.3, 1.0, 0.6	14.8	3
50. Wild Rice	Or, Ov, Oi	2.2, 0.4, 0.2	12.8	3
51. Dorothy Dunn	None	0	3.4	3
52. Jean	None	0	2.6	2
53. Pallette	None	0	2.1	3
54. Jag	None	0	1.8	3
55. Lac du Lune	None	0	1.6	3
56. Lone Tree	None	0	1.6	2
57. Jute	None	0	1.5	4
58. Diamond	None	0	1.4	3
59. Starrett	None	0	1.3	4
60. Anne[8]	None	0	1.2	2
61. Day	None	0	1.2	4
62. Street	None	0	0.9	3
63. Lower Allequash	None	0	9.2	1
64. Irving	None	0	7.5	1
65. Mystery	None	0	1.0	1
66. Spruce[9]	None	0	1.2	1
67. Aurora	None	0	7.5	1

[1] Located at Township 42 North (T42N), Range 7 East (R7E).
[2] Lake #5 is located at T43N, R8E; lake #45 is located at T42N, R6E.
[3] Located at T41N, R8E.
[4] Located in Oneida County at T36N, R8E.
[5] Located in Oneida County.
[6] Located in Forest County.
[7] Located at T43N, R7E.
[8] Located at T43N, R6E.
[9] Located at T41N, R7E.