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Lake size, Aquatic Macrophytes, and Largemouth Bass Abundance in Florida Lakes: A reply

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We thank the Journal of Aquatic Plant Management for stretching the size limit set for their papers and allowing us to list all the data we used in the paper titled "Largemouth bass abundance and aquatic vegetation in Florida Lakes: An Empirical Analysis." Our intention was to allow everyone the ability to use and interpret the data using their own insights, as Maceina (1996) has already done. Thus, one of our objectives has already been met. We feel the process of making data easily available to other researchers is healthy for science and should be incorporated more often in other Journals as well as gray literature.

We also thank Maceina (1996) for trying to support the hypothesis we put forward that aquatic macrophyte abundance may be more important to largemouth bass populations in large than small lakes. A major problem with Maceina's analysis, however, is that the data he used from Hoyer and Canfield (1996) was designed to examine the relationships among largemouth bass populations, aquatic macrophyte abundance and lake trophic status but not lake size. The lakes were selected along a lake trophic gradient from oligotrophic to hypereutrophic and within each trophic category lakes were selected that had macrophyte coverage ranging from <10% to over 75%. Splitting the data set at 54 ha as Maceina (1996) did, yielded two data sets that do not cover the whole ranges of lake trophic states.

The lakes with surface areas above and below 54 ha have significantly different trophic state variables (Table 1), with the small lakes tending toward oligotrophic systems and large lakes tending toward hypereutrophic systems. The third data set Maceina used with lakes greater than 116 ha also average hypereutrophic. Thus, any relationships described by Maceina (1996) should be used with the knowledge that they were developed on subsets of data from lakes that do not incorporate the whole range of lake trophic states, which can lead to erroneous conclusion when extrapolating relationships to real world populations of lakes.

As one example, Maceina (1996) suggests that the approach of incorporating phosphorus and nitrogen sequestered in plants to those in the water column allowed Hoyer and Canfield (1996) to have a true analysis of trophic state associations, but mask the influence of aquatic plants on largemouth bass population characteristics. He suggests that in the lakes greater than 54 and 116 ha, the relations between adjusted chlorophyll *a* and largemouth bass population characteristics were either non-existent or much weaker than those described by PAC or PVI alone. We believe that Maceina's (1996) findings are simply because of the scale of analysis (Duarte and Kalff 1990) and that the lake greater than 54 and 116 ha were all nutrient rich systems yielding a small range of lake trophic states to show any relations. Several studies, using a wide range of lakes, have shown the importance of lake trophic status to fish standing crop and yield (Oglesby 1977; Jones and Hoyer 1982) and largemouth bass standing crop and yield (Hoyer et al. 1985; Ploskey et al. 1986). Thus, Maceina's (1996) suggestion is a good example of the danger in splitting Hoyer and Canfield's (1996) data by lake size.

While we feel the data set from Hoyer and Canfield (1996) is not the proper one to unravel the relations among largemouth bass population characteristic and lake size, we do believe that lake size is important to the functioning of lake systems. It has long been suggested that lake size and morphology determine in part the general productivity of lakes (Rawson 1939), with large deep lakes being less productive than small shallow lakes. The importance of the littoral zone to overall lake production along a lake size gradient has also been addressed. Rounsefell (1946) suggested that area of fertile shallow water, which is generally much less in proportion to total area in the larger lakes than in smaller ones, as indicated by differences in length of shoreline. Thus, a circular lake of 503 acres has a shoreline of 3.14 miles, or 0.00624 miles per acre, while one of 50,200 acres has a shoreline of only 31.42 miles, or 0.000626 miles per acre, or about one-tenth as much shoreline per acre. Rounsefell (1946) concluded that the shallow, fertile areas usually are relatively much less extensive in the larger lakes. Other investigators also suggest that the sources of organic matter from the littoral zone play a major role in the metabolism of many lakes, especially small lakes with a decreasing importance in large lakes (Wetzel 1973; Sculthorpe 1967).

How aquatic macrophytes affect these generalities about large and small lakes will be determined by the quantity and distribution of aquatic plants in a lake. The most important environmental factors affecting the abundance of aquatic macrophytes in lakes have been identified as general water chemistry (Beal 1977; Kadono 1982; Hoyer et al. 1996), lake trophic characteristics (Spence 1967; Hutchinson 1975), substrate characteristics (Pearshall 1920; Barko et al. 1986), light availability (Canfield et al. 1985), prevailing winds (Duarte and Kalff 1986) and lake morphology (Pearshall 1917; Duarte and Kalff 1986). These factors can work independently and in combination, varying with the scale of analysis (Duarte and Kalff 1990). The factors also suggest that lakes can be divided into four general groups, small and large shal-

TABLE 1. AVERAGE VALUES FOR LAKES TROPHIC STATE VARIABLE FOR LAKES <54 HA, >54 HA, AND >116 HA. THE STANDARD ERROR OF THE MEAN IS RECORDED IN PARENTHESES. THE DATA ARE FROM HOYER AND CANFIELD (1996).

Trophic State Variables	Lakes <54 ha (n = 27)	Lakes >54 ha (n = 32)	Lakes >116 ha (n = 17)
Total phosphorus (μg/L)	16 (4)	91 (35)	44 (11)
Total nitrogen (μg/L)	570 (70)	1250 (160	1470 (260)
Chlorophyll *a* (μg/L)	10 (3)	44 (10)	44 (14)
Secchi depth (m)	2.5 (0.3)	1.4 (0.2)	1.3 (0.2)
Adjusted chlorophyll *a* (μg/L)	27 (6)	67 (15)	88 (24)

low lakes with abundant aquatic macrophytes, and small and large deep lakes with sparse aquatic macrophytes. This results from the littoral zone of lakes being inversely related to basin slope, depth, and to the degree of regularity of the shoreline.

When lakes are shallow and the above factors are favorable for aquatic macrophyte growth, lake coverage can be substantial in lakes with small or large surface areas. As aquatic macrophytes fill the water column of a lake, studies have shown significant relations between aquatic macrophyte abundance and lake water chemistry (Canfield et al. 1983), phytoplankton population structure and biomass levels (Landers 1982), sediment resuspension and wave action, periphyton and invertebrate populations (Cattaneo and Kalff 1980), fish growth, abundance, and population structure (Wiley et al 1984; Canfield and Hoyer 1992); angler utilization of fish populations (Colle et al. 1987); aquatic bird abundance and species composition (Hoyer and Canfield 1994) and may other limnological processes (Hutchinson 1975). The magnitudes of these relations are generally in proportion to the abundance of aquatic macrophytes.

In small and large deep lakes there is less littoral area for aquatic macrophyte growth than in shallow lakes. The importance of aquatic macrophytes to the overall functioning of these lakes decreases proportionately as lakes get larger and deeper (Rounsefell 1946; Tilzer and Serruya 1990). In some cases, however, small areas of littoral habitats may play a limiting factor for the reproduction or recruitment of some aquatic organisms in large lakes but not the overall production of the organisms. Gasith (1991) used Lake Kinneret (170 km^2) as an example, where year class strengths of a dominant pelagic fish (*Mirogrex terraesanctae*) were related to the availability of specialized littoral habitat.

Shallow lakes can also have limited littoral zone with low aquatic macrophyte abundances because of natural circumstances or lake management activities (e.g., aquatic macrophyte control with herbicides, biocontrol, or mechanical harvesting). The proportion of shoreline habitat to whole lake area in shallow lakes, without aquatic macrophytes, also decreases as lake surface area increases (Gasith 1991). This is where we hypothesize that in shallow Florida large lakes, without aquatic macrophytes, shoreline habitat is not enough for successful largemouth bass recruitment. In these lakes aquatic macrophytes can increase the recruitment of largemouth bass to the carrying capacity of the lake system. If this hypothesis is correct, the next step is to define the lake size where aquatic macrophytes are needed to supplement shoreline habitats.

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