Stephen A. Forbes, Antecedent Wetland Ecologist?

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ABSTRACT

Stephen A. Forbes (1844-1930) was an American entomologist/zoologist who was born, raised and largely educated in northern Illinois. He spent most of his professional career as the director of the Illinois Natural History Survey and as a faculty member and administrator at the University of Illinois. Early in his scientific career, he studied fish and bird diets by examining the stomach contents of these animals. In 1887, he published his most famous and influential paper, "The lake as a microcosm," which contains one of the earliest formulations of what came to be called the ecosystem. In this paper, Forbes describes a hypothetical isolated, small lake as being a microcosm that is in equilibrium. This equilibrium is the result of trophic interactions among the organisms in the microcosm that limit the sizes of both predator and prey populations. Forbes believed that natural selection was responsible for limiting the reproductive capacities of predators and prey. Although energy transfer among trophic levels is not the main focus of his paper, Forbes postulated that food (energy) is one of the main factors structuring ecosystems, but he did not explicitly discuss the energetics of his lake microcosm. Forbes' microcosm is based on his studies of the shallow portions of small, glacial lakes in northern Illinois that were dominated by aquatic plants. Today his microcosm would be classified as a palustrine or lacustrine wetland.

STEPHEN ALFRED FORBES

Stephen Alfred Forbes (1844-1930; Figure 1) was a major figure in the development of ecology, especially animal ecology, in the United States during the last quarter of the nineteenth and first quarter of the twentieth century (Kingsland 1985; van der Valk 2011). He was an entomologist interested in insect pests of crops and diseases of insects, but he also did research on fish and birds. He pioneered the use of stomach contents to work out food webs in both aquatic and terrestrial systems. Much of his research was done in response to crop pest issues facing farmers in Illinois. His research career started in the mid-1870s when he decided to try to solve the "Bird Question." Were birds beneficial to farmers or not? Birds ate insects that damaged crops, but birds also ate some kinds of crops, particularly grains. It was trying to answer this question that got Forbes looking at stomach contents of birds as a way to figure out what they were eating. Throughout his career Forbes advocated that ecologists should emphasize research that would benefit farmers, fishermen, hunters, etc. who ultimately supported their research (Forbes 1915, 1922).

FIGURE 1. Stephen Alfred Forbes (1844-1930). From Howard (1932).

Forbes was born, raised, and mostly educated in northern Illinois. He spent the Civil War in the Union Army fighting in southern states (Mississippi, Alabama and Tennessee). After the war, he studied medicine in Chicago, but never finished medical school. Instead he got interested in natural history

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and eventually became the curator of the Illinois State Natural History Society Museum and an instructor of zoology at Illinois State Normal University. He then helped establish the Illinois State Laboratory of Natural History and became its first director. Forbes had a distinguished career are both a researcher and administrator: Illinois State Entomologist, professor of zoology and entomology at the University of Illinois, and Dean of the College of Science at the University of Illinois. He served as president of a number of scientific societies, including the Ecological Society of America, and was elected a member of the National Academy of Sciences. For a detailed account of Forbes' life and times, see Howard (1932) and especially Croker (2001), and for an evaluation of his scientific career, Lovely (1995).

Most of his scientific publications deal with some aspect of applied entomology. During his lifetime, he published nearly 400 books and papers (see Lovely 1995), of which only 33 deal with aquatic topics, primarily fish and their foods. At first glance, Forbes does not seem to have ever studied wetlands. Not one of his aquatic papers has any term like bog, marsh or swamp, in the title. The closest that you get is an 1884 paper, "Destruction of fish food by bladderwort (*Utricularia*)." This is a half-page note describing the invertebrates found in some *Utricularia* bladders. He includes the same information in "The lake as microcosm" (Forbes 1887).

THE LAKE AS A MICROCOSM

Stephen A. Forbes is best known today as the author of "The lake as a microcosm," which was a paper he delivered to members of the Peoria Scientific Association on February 25, 1887 and that was published in the their Bulletin (Forbes 1887).[2] This talk and resulting paper are based on research that he and his colleagues conducted starting in the mid-1870s that focused on the food of Illinois fishes (Forbes 1880b). Because of its significance for the development of the ecosystem concept (Odum 1968; Hagen 1992; Golley 1993; Hansson et al. 2013), a great deal has been written about this paper (Bocking 1990; Lovely 1995; Schneider 2000; Croker 2001; and numerous papers cited by them). It is considered to be a classic paper in the history of ecology. An excerpt from it was included in Kormondy's *Readings in Ecology* (1965) in the section on The Concept of the Ecosystem. This was an early and influential compilation of the most important papers in the development of ecology. The entire 1925 reprinted version of the paper is included in Real and Brown (1991) *Foundations of Ecology: Classic Papers with Commentaries*. It is the first paper in this volume in the section called Foundational Papers.

2 He also gave this talk as a commencement address at the University of Indiana that same year (Croker 2001).

Today, only the concluding pages of this classic paper are of general interest. In them, Forbes outlines his beliefs that the organisms in the lake microcosm are part of a *community of interest* and that predator-prey interactions have evolved so that the lake microcosm is in equilibrium. Although Forbes showed that food webs were an important link among species at different trophic levels in his idealized lake microcosm, his emphasis is not on ecosystem energetics, but on demonstrating that species interactions result in community or assemblage stability. Nevertheless, this paper is seen as a pioneering exploration of ecosystem energetics (Odum 1968; Hagen 1992; Golley 1993; Hansson et al. 2013). This is not, however, the central focus of the paper. Forbes wanted to show that the struggle for existence that Darwin proposed as a major mechanism for natural selection would result in an adjustment of reproductive rates for both predators and prey and that this would result in stable population sizes of all the components of the microcosm. The results of this balanced mortality is that primeval, natural communities or assemblages are in equilibrium, unless disrupted for some reason, especially by man. This is an idea that Forbes had previously developed in more detail in an 1880 paper, "On some interactions of organisms" (Forbes 1880a).

Forbes had also introduced his concept of a microcosm in another paper published in 1880: "The food of fishes" (Forbes 1880b). "For a clear conception of the general and intricate interdependence of the different forms of organic life upon the earth, one can not [sic] do better than to study thoroughly the life of a permanent body of fresh water, -- a river or smaller stream, or better then these, a lake. The animals of such a body of water are, as a whole, curiously *isolated*, -- closely related among themselves in all their interests, but so far independent of the life of the land about them that if every terrestrial plant and animal were annihilated it would doubtless be long before the general multitude of the inhabitants of the lake or stream would feel the effects of this event in any important way." (Forbes 1880b, p. 19). "Consequently, one finds in a single body of water a far more complete and independent equilibrium of organic life and activity than in any equal body of land. It forms a little world within itself, -- a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on a small scale as to bring it easily within the mental grasp." (Forbes 1880b, p. 19). "Nowhere can one see more clearly illustrated what may be called the *sensibility* of such an organic complex, -- expressed by the fact that whatever affects any species belonging to it, must speedily have its influence of some sort upon the whole assemblage." (Forbes 1880b, p. 19). These quotes are from Forbes' earlier papers on the "The food of fishes." Virtually the same arguments and language are used to justify why a lake is an ideal system for examining what is responsible for the stability of natural (organic) assemblages in “The lake as a microcosm.” In fact, in “The lake as a microcosm” Forbes was recycling much of what he had already published in 1880 in “The food of fishes” and “On some interactions of organisms.”

In both his 1880b and 1887 papers, Forbes never adequately defines what he means by a microcosm. It seems to be just an isolated piece or part of the natural world with clear boundaries that is isolated from the rest of nature. Because such situations are rare, as Forbes himself makes clear, this makes it a concept of rather limited utility. If most of the world cannot be easily divided into different microcosms, including all terrestrial communities and most other aquatic communities, how do these non-microcosms differ from microcosms? Forbes in “The lake as a microcosm” seems to be explaining the exception, not the rule. Nevertheless, Forbes does stress that all pieces or parts of nature need to be studied as a unit, and this became a central tenet in ecology (Croker 2001).

Exactly what kind of lakes did Forbes have in mind? Forbes is very specific about the answer to this question. In the “The lake as a microcosm” Forbes describes in considerable detail the small lakes of northern Illinois and their flora and fauna that he used as the basis for his idealized lake microcosm. Forbes (1887) distinguishes two broad classes of small lakes, which he refers to as “fluviatile” lakes, i.e., those associated with rivers and their floodplains, and “water-shed” [sic] lakes, i.e., those small lakes not associated with rivers.

Forbes describes fluviatile lakes as highly dynamic because they are regularly flooded by overflowing rivers. “Enough has been said to illustrate the general idea that the life of waters subject to periodical expansions of considerable duration, is peculiarly unstable and fluctuating; -- that each species swings, pendulum-like, but irregularly, between a highest and a lowest point, and that this fluctuation affects the different classes successively, in the order of their dependence upon each other for food.” (p. 539; *note that all page numbers that follow are for the 1925 reprint of the 1887 paper*). Forbes then switches to water-shed lakes, which according to him are the much more stable lakes.

Water-shed lakes in northern Illinois are found on “a nearly level plateau with slight irregularities of the surface, many of these will probably be imperfectly drained and the accumulating water will form either marshes or lakes, according to the depth of the depression.” (p. 539). These

FIGURE 2. Postcard of Fox Lake, circa 1910. Reprinted with the permission of the Lake County Forest Preserve Dunn Museum.

lakes were glacial in origin and formed in depressions in glacial till. Forbes used his studies of specific lakes (Fox, Long, Cedar, and Deep) in northeastern Illinois (Lake County) and nearby Geneva Lake in southeastern Wisconsin to develop his ideal lake microcosm. The field work on these lakes was done between 1880 and 1882 (Croker 2001). These lakes, as described by Forbes (1887), are small, but they do differ in size and depth. Most of them have "marshy" vegetation along the margins and their basins generally were not very deep, although they usually had one or more deeper spots. For example, the northern and eastern basins of Fox Lake (Figures 2 and 3) "were visibly shallow – covered with weeds and feeding water-fowl…" (p. 541). Forbes' estimate that most of the lake is less than 2 fathoms deep (ca. 3.6 m), but he did find a small deep area of 5 fathoms (9 m). Most of the other lakes had comparable deep areas: 11.5 m for Long Lake; 8.3 m for Cedar Lake (much of the lake, however, was much shallower and "full of water plants"); 9.5 m for Deep Lake; while Geneva Lake was the exception at 41 m.

Forbes spends most the paper describing the vegetation and animal communities of these small lakes. "… so clogged with weeds that a boat can scarcely be pushed through the mass; when, lifting a handful of the latter he finds them covered with shells and alive with small crustaceans; and then, dragging a towing net for few minutes, finds it lined with myriads of diatoms and other microscopic Algae, and with multitudes of Entomostraca [an old term for some orders of Crustacea], he is likely to infer that these waters are everywhere swarming with life." (p. 542). He goes on to describe the vegetation and its associated fish fauna in more detail. "Among the weeds and the lily-pads upon the shallows and around the margins, the *Potamogeton*, *Myriophyllum*, *Ceratophyllum*, *Anacharis* and *Chara*, and the common *Nelumbium* [*Nelumbo*, Figure 3] – among these fishes chiefly swim and lurk, by far the commonest being barbaric bream or "pumpkin seed" of northern Illinois, splendid with its green and scarlet and purple and orange. Little less abundant is the common perch (*Perca lutea*), in the larger lakes – in the largest outnumbering bream itself." (p. 542). There were also game fish, including black or large-mouth bass (most common), pickerel, gar, and dog fish. He notes that the fish fauna of these small lakes is very different from that of Lake Michigan ("burbot, white fish, trout, lake herring or cisco, etc.)" (p. 543). The water in these small, shallow lakes is much too warm in the summer to support the cold-water fish found in Lake Michigan. The invertebrate fauna (bivalves, insects, worms, Crusta-

FIGURE 3. Postcard of an American lotus (Nelumbo lutea Willd.) bed in Fox Lake in the early twentieth century. Reprinted with the permission of the Lake County Forest Preserve Dunn Museum.

cea, and Entomostraca, primarily cladocera, ostracods, and copepods) of small lakes is also described and sometimes compared with the invertebrate fauna of Lake Michigan, which Forbes had also studied (Forbes 1882).

Forbes notes that "The system, of aquatic animal life rests essentially upon the vegetable world, although perhaps less strictly than does the terrestrial system, and in a large and deep lake vegetation is much less abundant than in a narrower and shallower one, not only relatively to the amount of water but also to the area of the bottom. From this deficiency of plant life results a deficiency of food for Entomostraca, whether of algae, of Protozoa, or of higher forms, and hence, of course, a smaller number of the Entomostraca themselves, and these with more slender bodies, suitable for more rapid locomotion and wider range." (p.546). Forbes' pioneering work on food of fishes (Forbes 1880b) had demonstrated that Entomostraca are a key component of lake food chains for fish, especially young fish, of nearly all species. "…the marshes and shallower lakes are the favorite breeding grounds of fishes, which migrate to them in spawning time if possible, and it is from the Entomostraca found here that most young fishes get their earliest food supplies …." (p. 547).

Having set the scene, Forbes then goes on to consider some of the interactions among animals in these lakes with a focus on black or large-mouth bass. The emphasis is on the food eaten by bass, especially young bass, and on bass competitors and predators. "…all our young fishes except the Catostomidae feed at first almost wholly on Entomostraca, so that the little bass finds himself at the very beginning of his life engaged in a scramble for food with all the other little fishes in the lake. In fact, not only young fishes but a multitude of other animals as well, especially insects and the larger Crustacea, feed upon these Entomostraca, so that the competitors of the bass are not confined to members of its own class. Even mollusks, while they do not directly compete with it do so indirectly, for they appropriate myriads of the microscopic forms upon which the Entomostraca largely depend for food. But the enemies of the bass do not all attack it by appropriating its food supplies, for many devour the little fish itself. A great variety of predaceous fishes, turtles, water-snakes, wading and diving birds, and even bugs of gigantic dimensions destroy it on the slightest opportunity. It is in fact hardly too much to say that fishes which reach maturity are relatively as rare as centenarians among human kind." (p. 548).

Not only are other fish species and other animals competitors of the bass for Entomostraca, but so are some plants. "As an illustration of the remote and unsuspected rivalries which reveal themselves on a careful study of such a situation, we may take the relations of fishes to the bladderwort-—a flowering plant which fills many acres of the water in the shallow lakes of northern Illinois. Upon the leaves of this species are found little bladders—several hundred to each plant—which when closely examined are seen to be tiny traps for the capture of Entomostraca and other minute animals. The plant usually has no roots, but lives entirely upon the animal food obtained through these little bladders." (p. 548). Forbes then goes on to discuss the results of his studies of the content of *Utricularia* bladders: they contained mostly Entomostraca.

Finally, in the last two pages Forbes gets to the take-home messages of his paper. (1) <u>Natural assemblages like his lake microcosm are in equilibrium</u>. "Perhaps no phenomenon of life in such a situation is more remarkable than the steady balance of organic nature, which holds each species within the limits of a uniform average number, year after year, although each one is always doing its best to break across boundaries on every side. The reproductive rate is usually enormous and the struggle for existence is correspondingly severe. Every animal within these bounds has its enemies, and Nature seems to have taxed her skill and ingenuity to the utmost to furnish these enemies with contrivances for the destruction of their prey in myriads. For every defensive device with which she has armed an animal, she has invented a still more effective apparatus of destruction and bestowed it upon some foe, thus striving with unending pertinacity to outwit herself; and yet life does not perish in the lake, nor even oscillate to any considerable degree, but on the contrary the little community secluded here is as prosperous as if its state were one of profound and perpetual peace. Although every species has to fight its way inch by inch from the egg to maturity, yet no species is exterminated, but each is maintained at a regular average number which we shall find good reason to believe is the greatest for which there is, year after year, a sufficient supply of food." (p. 549).

Forbes continues "It is a self-evident proposition that a species can not [sic] maintain itself continuously, year after year, unless its birth-rate at least equals its death-rate. If it is preyed upon by another species, it must produce regularly an excess of individuals for destruction, or else it must certainly dwindle and disappear. On the other hand, the dependent species evidently must not appropriate, on an average, any more than the surplus and excess of individuals upon which it preys, for if it does so it will continuously diminish its own food supply, and thus indirectly but surely exterminate itself. The interests of both parties will therefore be best served by an adjustment of their respective rates of multiplication such that the species devoured shall furnish an excess of numbers to supply the wants of the devourer, and that the latter shall confine its appropriations to the excess thus furnished. We thus see that there is really a close community of interest between these two seemingly deadly foes." (p. 549).

(2) Natural selection is the mechanism responsible for the equilibrium of natural assemblages as exemplified by small lakes. "And next we note that this common interest is promoted by the process of natural selection; for it is the great office of this process to eliminate the unfit. If two species standing to each other in the relation of hunter and prey are or become badly adjusted in respect to their rates of increase, so that the one preyed upon is kept very far below the normal number which might find food, even if they do not presently obliterate each other the pair are placed at a disadvantage in the battle for life, and must suffer accordingly. Just as certainly as the thrifty business man who lives within his income will finally dispossess his shiftless competitor who can never pay his debts, the well-adjusted aquatic animal will in time crowd out its poorly-adjusted competitors for food and for the various goods of life. Consequently we may believe that in the long run and as a general rule those species which have survived, are those which have reached a fairly close adjustment in this particular.' (pp. 549-550).

Forbes summarizes his discussion about the equilibrium that he thinks characterizes natural assemblages: "Two ideas are thus seen to be sufficient to explain the order evolved from this seeming chaos; the first that of a general community of interests among all the classes of organic beings here assembled, and the second that of the beneficent power of natural selection which compels such adjustments of the rates of destruction and of multiplication of the various species as shall best promote this common interest." (p. 550).

Forbes was not the first early ecologist to postulate that natural, undisturbed communities or assemblages are in equilibrium because of interactions among their component species. Earlier Möbius had come to a similar conclusion based on his studies of oyster beds (van der Valk 2017). Many historians of ecology have pointed out the similarity of the Forbes' lake microcosm and Möbius biocönose (e.g., Bocking 1990; Lovely 1995; Croker 2001; van der Valk 2011). Möbius published his paper on oyster beds in 1877 and an English translation was published in 1883 (Rice 1983) in a fisheries publication that Forbes was known to read. Forbes, however, had developed his basic ideas about the stability of natural assemblages by 1880 in a paper entitled "On some interactions of organisms" (Forbes 1880a). In fact, he points to this earlier paper for a "fuller statement" about his position in the 1925 version of "The lake as a microcosm." How much Forbes' thinking was influenced by Möbius will probably never be known for certain (Lovely 1995; Croker 2001). Forbes does not cite Möbius in his 1887 paper or in the 1925 reprint of it or in any of his earlier publications like "The food of fishes" (Forbes 1880b). The idea that natural assemblages were inherently stable, the balance of nature as it was called at that time, was common in the nineteenth century among naturalists and early ecologists (Egerton 1973). It is not surprising that Forbes and Möbius held similar views. It should be noted, however, they believed that very different mechanisms were responsible for assemblages being in equilibrium. Forbes held that it was mechanisms regulating food supplies while Möbius emphasized competition for space. Forbes, however, made a more compelling and detailed case for his view that primeval, natural assemblages are in equilibrium as a result of trophic interactions in his 1880 paper "On some interactions of organisms" (Forbes 1880a). Ironically, this paper is largely forgotten today.

LAKES OR WETLANDS?

It is clear from reading Forbes' papers that the small "lakes" on which he modeled his idealized "microcosm" were really wetlands as defined by Cowardin et al. (1979). Based on his descriptions of them (mostly shallow, dominated by aquatic plants; see Figures 2 and 3) and their fauna, they were either large palustrine wetlands or in some cases wide lacustrine wetlands associated with small lakes. In fact, most large palustrine wetlands in the Upper Midwest are called lakes. There was no other term to describe them during the nineteenth century when this area was first settled.

Forbs seems to have been attracted to these wetlands because of their obvious high production of both plants and animals. His brief descriptions of deep water areas in lakes are mostly negative in tone: "singularly barren of both plant and animal life" and "as simple and scanty as … a desert" (Forbes 1925, p. 542). The fluviatile lakes, undoubtedly also wetlands, are too prone to disturbances, which disrupt the "harmony of interactions among organic groups" (Forbes 1880a, p. 5). The lake microcosm for Forbes seems to represent a glimpse into the primeval condition of the natural world that is free from human disturbances. It "presents a settled harmony of interaction among organic groups which is in strong contrast with the many serious maladjustments of plants and animals found in countries occupied by man." (Forbes 1880a, p. 5). Because these wetlands are well delimited and highly isolated systems with clear boundaries like giant fishbowls or wading pools full of "organic life," Forbes finds it easier to comprehend their overall organization and workings.

It is the aquatic plants in these wetlands which give them a three-dimensional structure that seems to make them attractive to Forbes. The structure created by this dense vegetation made it easier for him to envision the various food webs and the interactions among the animals that affect a specific organism in a food web. The aquatic plants also made these lakes appear to be more stable. In larger and deeper lakes not dominated by aquatic plants, a variety of currents continuously alters the distribution and abundance of organisms at a variety of time scales. The food webs of Forbes' wetlands are static, rather than dynamic. Forbes ignores seasonal and interannual changes in them. This makes it easier to comprehend and describe their food webs. At the time that the paper was written, Forbes and his colleagues had only sampled small Illinois lakes for a couple of years and only in October. This may go a long way to explain why Forbes believed these wetlands to be such stable entities.

Although Forbes did not realize it, he was studying the food webs of wetlands, which he viewed as being in some kind of primeval conditions and as yet unaffected by man. This was not true of the uplands of northern Illinois which in Forbes' time had been largely converted to farmland. Forbes thus was an antecedent wetland ecologist, a scientist whose work was influential in the development of wetland ecology, but who did not consider himself to be a wetland ecologists (van der Valk 2017). The same features of wetlands (isolation, high productivity, and stability) that attracted Forbes to wetlands seem also to have played a role in later studies of ecosystem energetics. Forbes never quantified food (energy) flows within wetlands from trophic level to trophic level. This would be done by the next generation of ecologists working in wetlands: Raymond Lindeman (1942) at Cedar Creek Bog, Minnesota, and Howard Odum (1957) at Silver Springs, Florida. Starting with Forbes, wetlands have played a major role in the development of ecosystem ecology. ■

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