

## LAKES AS ISLANDS: THE DISTRIBUTIONAL ECOLOGY OF TWO AQUATIC PLANTS, *LEMNA MINOR* L. AND *L. TRISULCA* L.<sup>1</sup>

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**Abstract.** Groups of lakes can be considered archipelagos, and island biogeographic theory can be used to explain the distribution of aquatics within them. Two species of duckweed, *Lemna minor* and *Lemna trisulca*, were studied as examples. Both are found in southern Ontario, but *L. minor* occurs much more frequently than *L. trisulca*. It is this difference the experiments were designed to explain.

Colonization capability of each species was defined as its ability to: (1) withstand desiccation, (2) quickly populate a new habitat, and (3) inhibit the other species competitively. *Lemna minor* was clearly far superior to *L. trisulca* in abilities (1) and (2), and in (3) it was judged superior or equal to *L. trisulca*.

Wherever *L. minor* and *L. trisulca* are still colonizing recently deglaciated habitats, superior colonization capability alone can explain the more frequent occurrence of *L. minor*.

Southern Ontario lakes may already have reached equilibrium, where the rate of species colonization is balanced by the rate of species extinction. Increases in summer pH above 8 occur, and as both species die above this point, pH could be the major cause of mortality. The observed frequencies of occurrence could therefore be the result of a balance between different rates of colonization and approximately equal rates of extinction.

**Key words:** Aquatics; biogeography; Canada; competition; distribution; duckweed; islands; lakes; Lemnaceae; Lemna; reproductive rate.

### INTRODUCTION

Savile (1956) noted: "Many aquatic plants . . . occur sporadically over wide areas, being plentiful in one lake or group of lakes, but absent from others within a few miles. Their distribution shows no clear pattern explainable by river systems or topography. Although they are unexplainably absent from some bodies of water, a number of these plants have circumboreal or occasionally nearly world-wide distribution."

Since ponds are islands of water surrounded by land, it seems reasonable to extend island biogeographic theory (MacArthur and Wilson 1967) to explain such distributions. The total geographic range or world range of any plant species invariably contains large areas unsuited to that species, but this is especially true for aquatics, which live in small islands of water surrounded by large hostile terrestrial areas.

MacArthur and Wilson (1967) theorized that the number of species on an island (and the presence or absence of any single species) is the result of a balance between rates of colonization and rates of extinction. Also, certain mainland species occur more frequently than others on islands (MacArthur 1972).

Those found most frequently must have superior abilities to colonize and persist.

The chances of extinction are highest in the colonization phase (Fig. 1). Successful colonization depends upon at least three characteristics of the species concerned:

- 1) Ability to disperse. The species must first be able to spread to a new habitat. One species has an advantage if it can disperse successfully more frequently than another.

- 2) Ability to multiply and spread in the new habitat. The larger and more widespread the colonizing population, the smaller the likelihood of extinction.

- 3) Ability to compete with established species. MacArthur (1972) shows that, in theory, the greater the coefficient of competition encountered by colonists, the greater are the chances of extinction. Hence, a newly arrived species is much less likely to colonize successfully if a close competitor is already present.

At first, island biogeographic theory was supported largely by data from birds and plants on oceanic islands. More recently it has been applied to a wide range of situations: mice on islands (Crowell 1973), insects on islands (Simberloff and Wilson 1969, 1970, Wilson and Simberloff 1969), birds (Vuilleumier 1970) and mammals (Brown 1971a) on mountains, cave faunas (Culver 1970, Vuilleumier

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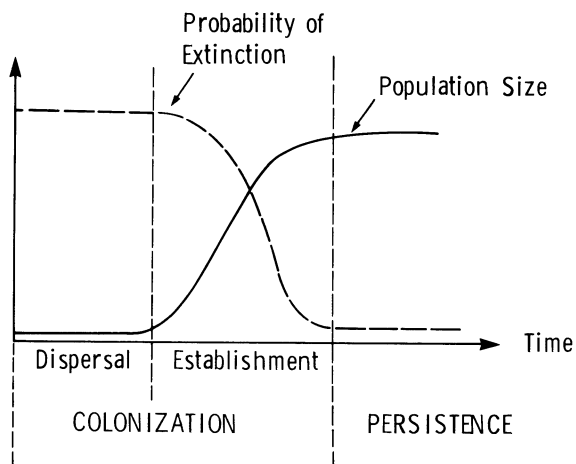


FIG. 1. The stages of archipelago survival, and the probabilities of extinction associated with each.

1973), macroinvertebrates on floating artificial substrates (Dickson and Cairns 1972), and protozoans on both artificial plastic (Cairns et al. 1969) and glass (Patrick 1967) substrates. Simberloff (1974) provides an excellent review of these studies.

With specific reference to colonization processes, Maguire (1963) stressed the similarities of lakes and islands. In addition to reviewing early work he carried out a detailed study on the dispersal of small aquatic organisms away from two bodies of water. Talling (1951) emphasized that the element of chance plays a very important role in determining the species composition of ponds. Hutchison (1961) discussed co-existence of phytoplankton species in lakes, having observed that a great many species can apparently co-exist in a largely homogeneous environment. More recently, Cairns et al. (1969) and Dickson and Cairns (1972) illustrated the dynamic aspect of species composition in aquatic protozoan communities. Daborn (1974), working with small aquatic organisms in an aestival pond, noted several instances of an immigrant species apparently replacing an already established species as lake conditions changed.

Lakes are also islands for fish populations. Lowe-McConnell's (1969) review showed that the African Great Lakes have served as evolutionary islands; the isolation of each lake has permitted the development of sizeable numbers of endemic species and genera of cichlid fishes. Brown (1971*b*) studied endemism in desert pupfish (*Cyprinodon* spp.) in the Death Valley region of the United States, where fish species are restricted to scattered small springs and streams.

With respect to aquatic vascular plants, Darwin (1859) commented on their wide geographical distributions, and dealt in detail with possible dispersal mechanisms. Later, Godwin (1923) stressed that

chance plays a strong role in determining pond floras, and that plant ecologists too often assume that each given species grows in every area which is suitable. Savile (1956) reviewed some factors pertaining to the distribution of aquatics and again emphasized the importance of long-distance dispersal mechanisms.

It seems clear that dispersal rates of vascular plants (and of many small aquatic organisms) are much higher than in fish; thus, with the former it is probable that the dynamics of inter-island dispersal and colonization, rather than the simple occurrence of long-term island isolation, will be of most interest in explaining species distributions. This study experimentally examines precisely that: the role of dispersal and colonization in determining the distributions of two aquatic vascular plants.

*Lemna minor* and *L. trisulca* are two aquatics which display the characteristics of distribution mentioned by Savile (1956), sporadic local distribution and wide geographic range. A survey of ponds in the Toronto, Ontario, Can. area revealed the sporadic nature of their distribution. Many of the ponds surveyed had no duckweed; 20 had *L. minor* alone, but none had only *L. trisulca*. There were two ponds with both species present. This is similar to the situation Jacobs (1947) found while working with duckweeds in Minnesota. However, in spite of this scattered local distribution both species exhibit a wide geographic range. In North America, both range from the Arctic southward to Mexico. They also co-occur in Eurasia and Australia. *Lemna minor* is found in South America and New Zealand and *L. trisulca* in southern India and the East Indies (Hultén 1968).

In an attempt to explain the observed frequencies of occurrence of *L. minor* and *L. trisulca*, their relative colonization capabilities (defined as the sum of the above mentioned abilities) were evaluated.

## DISPERSAL

### *Rationale*

Since flowering is an extremely rare occurrence in *Lemna* (Hillman 1961), few seeds are produced; instead, vegetative reproduction is the primary method of population increase. Therefore, dispersal by means of vegetative parts will be much more significant than dispersal by seeds. Jacobs (1947) states that the latter is undoubtedly negligible for *Spirodela polyrhiza*, a close relative. Transportation of these vegetative parts by waterfowl seems most likely. Jacobs (1947) reports that *L. minor* plants were found on migrating ducks, but also observed that muskrats are important carriers. It follows from the above discussion that the relative dispersal abilities of *Lemna* species will depend primarily on the tolerances of their laminae to drying.

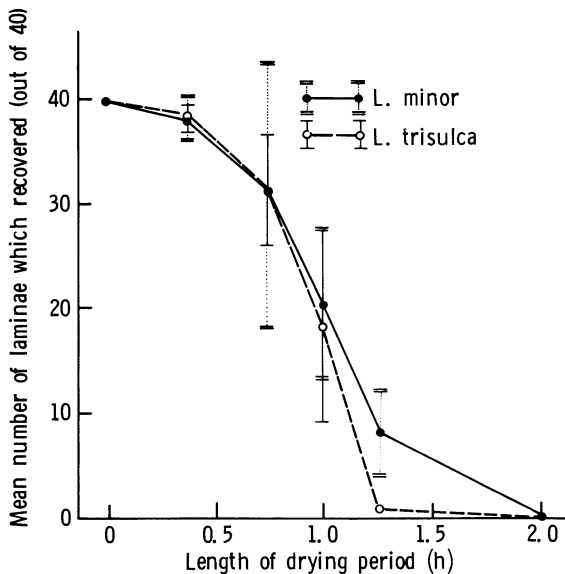


FIG. 2. The response of *Lemna minor* and *Lemna trisulca* to desiccation. Means of  $n = 6$  replicates are shown for each species, except for  $1\frac{1}{4}$  h where  $n = 4$  for *L. trisulca*. 95% confidence limits indicated.

#### Method

In order to test the tolerance of laminae to desiccation, specimens were dried on hardware mesh at room conditions ( $25^{\circ}\text{C}$ , relative humidity = 70%) for the time periods indicated in Fig. 2. Six replicates of 40 laminae were dried for each time period. After drying, the laminae were returned to their growth solution.

All specimens wilted during drying, but some recovered when returned to the solution. Those that recovered did so within 12 h. The number of survivors was counted after 24 h. Reproduction was minimal within this period. New laminae were easily recognized and were not counted.

Two replicates of *L. trisulca* from  $1\frac{1}{4}$  h had to be discarded because the drying screens had trapped excess water in spite of attempts to standardize by blotting.

#### Results and interpretation

As Fig. 2 shows, both species exhibited the same response to drying, but *L. trisulca* tended to suffer higher mortality. A  $t$ -test was performed for each time interval. There was a significant difference ( $p < 0.01$ ) after  $1\frac{1}{4}$  h drying.

At this point it is also worth noting that *L. trisulca* tends to grow a distance from shore, usually submerged, whereas *L. minor* floats on the surface and is often stranded on the shoreline by waves or retreating water. Therefore, it is reasonable to assume that, due to this difference in growth habits, dis-

persal by waterfowl and other agents is more likely to occur with *L. minor* than with *L. trisulca*. Even if chances of survival during dispersal were approximately equal, *L. minor* would have a higher probability of being picked up and carried from one habitat to another. Evaluation of dispersal ability shows that  $L. minor > L. trisulca$ .

#### COLONIZATION

##### Rationale

When a colonist propagule arrives in a new habitat, growth (in size) and multiplication (in number of individuals) are clearly essential for successful establishment. For example, Crowell (1973) demonstrated with mice that the species with the greatest rate of increase was the most widely distributed on offshore islands in Maine. The probability of extinction decreases with increasing population size. Many possibilities exist for the elimination of duckweed immigrants; they are eaten by ducks and other water birds, fish, and muskrats (Jacobs 1947).

A comparison of the potential population growth rates of the two species should result in some measure of their relative colonizing abilities. Potential rate of increase,  $r$ , was measured under the following conditions: (1) low density (minimal intraspecific competition), (2) no interspecific competition, (3) complete nutrient solution, (4) ample light, and (5) pH well within the limits (Hicks 1932) of both species.

##### Method

The two species were cultured in complete nutrient stock at initial densities of approximately 1 lamina/4  $\text{cm}^2$  surface area. Six replicates of 20 laminae for each species were grown for 3 wk. Laminae were counted two times a week. Each time, surplus laminae (total number minus 20) were removed at random to prevent overcrowding and the nutrient solution was changed. Reproduction (number of surplus laminae) was also recorded each time. A bank of fluorescent lights provided illumination; a cycle of 16 h illumination followed by 8 h darkness was used.

##### Results and interpretation

The rate of reproduction of *L. minor* (0.164/individual per day) was more than  $6\times$  that of *L. trisulca* (0.024/individual per day), a highly significant result ( $p \ll 0.0001$ ). This would dramatically affect their abilities to colonize. To illustrate this, potential maximum population size was predicted (Table 1) for a 10-wk period, using the experimentally derived  $r$  values and assuming that one colonist propagule started the population of each species. This table shows that after 5 wk a single colonist lamina

TABLE 1. A comparison of potentially attainable population size and dispersion over a 10-wk period beginning with the arrival of 1 colonist lamina of either *Lemna minor* or *Lemna trisulca*. Potentially attainable population size calculated from experimentally derived  $r$  values

Week	<i>L. minor</i>		<i>L. trisulca</i>	
	Population size	No. of clusters (mean cluster size = 4)	Population size	No. of clusters (mean cluster size $\geq 4$ )
0	1.0	1.0	1.0	1.0
1	2.9	1.0	1.2	1.0
2	8.4	2.1	1.4	1.0
3	24.3	6.1	1.7	1.0
4	70.3	17.6	1.9	1.0
5	203.4	50.9	2.3	1.0
6	588.9	147.2	2.7	1.0
7	1,704.3	426.2	3.2	1.0
8	4,935.9	1,234.0	3.8	1.0
9	14,290.0	3,572.5	4.5	1.0
10	41,371.7	10,342.9	5.3	1.0

of *L. minor* could theoretically have produced 202 daughter laminae, whereas *L. trisulca*, during the same time period could have produced only 1.

Dispersion within the new habitat would also reduce the chances of a single disastrous event eliminating the entire newly-established population. *Lemna minor* would not only produce more laminae, but these would be more likely to disperse; clusters of more than four laminae are uncommon in the field. *Lemna trisulca* would not only produce few laminae, but they would likely remain attached, localizing the entire initial population; mats of dozens of interconnected individuals occur in the field. Table 1 shows these differences in dispersion as well. Evaluation of ability to establish shows clearly that *L. minor* > *L. trisulca*.

#### INTRAGENERIC COMPETITION

##### Rationale

The greater the competition an immigrant species faces, the less probable successful colonization becomes (MacArthur 1972).

It is intuitively obvious that closely related species, when compared to unrelated species, are more likely to have similar resource requirements. Therefore, one might anticipate that congeneric species would be particularly likely to compete intensely with each other. This is supported by many of the competitive exclusion studies in the literature, e.g., congeneric pocket gophers (Miller 1967), chipmunks (Sheppard 1971), and salamanders (Jaeger 1970).

The intensity of congeneric competition is also illustrated by the biogeographic phenomenon of character displacement. Brown and Wilson (1956) give examples of pairs of congeneric species which are similar to virtually indistinguishable except in the zone of sympatry, where their characters become

strongly divergent. In addition, the checkerboard distribution patterns of pairs of congeners is cited by MacArthur (1972) as evidence that either one or the other, but not both, species can survive on any given island. However, Simberloff (1974) has challenged this last piece of evidence, pointing out that due to similarities in generic and familial dispersal rates, islands in fact tend to have slightly more congeneric pairs than one would predict assuming purely random colonization.

With respect to *L. minor* and *L. trisulca*, intrageneric competition for space would not appear to be significant since *L. minor* spreads out on the water surface while *L. trisulca* remains largely submerged. Due to this vertical separation, the competition for nutrients would likely be less significant than the direct competition which occurs for light.

Some of the observed ponds had a solid cover of *L. minor* several centimeters deep. While *L. minor* could spread over the surface to shade *L. trisulca*, the submerged *L. trisulca* could not possibly shade *L. minor*. Therefore, competition for light is unidirectional.

##### Method

The apparatus I used allowed competition for light without competition for other factors. The shading mat of *L. minor* was grown in a glass dish placed on top of the culture dish containing the test species. The shading mat had a surface density of 40 laminae/cm<sup>2</sup> and was several laminae thick, not counting the dead lower layers. This is similar to the dense natural situations observed. Air holes around the top of the culture dish permitted gaseous exchange and reduced greenhouse effect. The control culture dishes were covered by a glass dish containing only nutrient solution. Six replicates of 20 laminae for each species were counted two times a week, and maintained for 3 wk. The effect of shading was measured by comparing mean increase in number of laminae in shaded dishes for each time interval to the mean increase of the controls.

##### Results and interpretation

Figure 3 shows that *L. minor* inhibits its own growth rate more than the growth of *L. trisulca*. Reproduction for *L. trisulca* remained fairly constant with time at  $\approx 70\%$  of the control rate, whereas *L. minor* showed a sharp and continual decrease in reproduction. After 24 days (not shown in Fig. 3) the shaded *L. minor* actually exhibited a negative growth rate.

This is a clear example of intraspecific competition limiting the population size of one species and thereby permitting the survival of another.

It appears then that these two *Lemna* species can coexist. *Lemna minor* will form a mat covering the

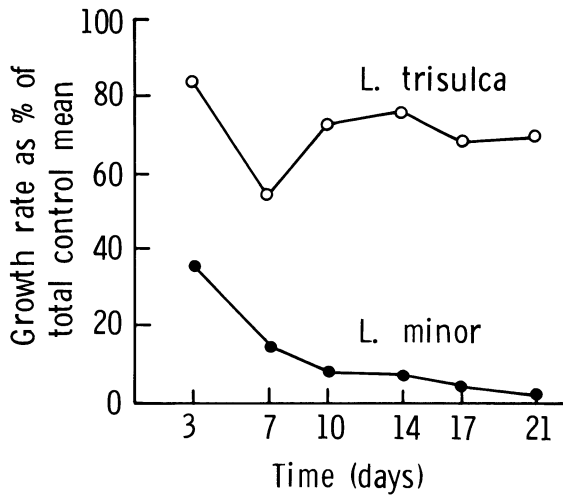


FIG. 3. Responses of both *Lemna minor* and *Lemna trisulca* to shading by *L. minor*. Shaded growth rate expressed as percentage of control growth rate. Mean of 6 replicates.

surface; this mat will grow thicker until it reaches a state of dynamic equilibrium, where the death rate of individuals on the bottom is matched by the reproductive rate of the upper layers. Under these conditions, *L. trisulca* can still reproduce.

However, while a population of *L. minor* cannot competitively eliminate a population of *L. trisulca*, it can reduce the chances of *L. trisulca* successfully colonizing. A *L. trisulca* propagule arriving in a pond already populated with *L. minor* will suffer some reduction in growth rate,  $\approx 30\%$  according to this experiment. (As Fig. 3 shows, *L. trisulca*, when shaded by *L. minor*, grows at about 70% of its control rate.) The colonization phase (the period of high extinction probability) of *L. trisulca*, previously shown to be long, therefore will be further lengthened. Many areas do not develop thick mats of *L. minor*, but it is reasonable to assume that thinner mats of *L. minor* will still affect, although to a lesser degree, the growth rate, and therefore, the chances of colonization of *L. trisulca*.

Lastly, it is significant to note that *L. minor* does indeed have a higher probability of arriving first. It is highly probable that *L. trisulca* will indeed disperse to a lake already colonized by *L. minor*. In this case, the advantage does indeed lie with the species arriving first, as MacArthur and Wilson (1967) theorized. (But note that if *L. trisulca* arrives first MacArthur and Wilson's generalization does not necessarily hold.) Evaluation of competitive ability shows that  $L. minor \geq L. trisulca$ .

#### DISCUSSION

It should now be possible to determine which species is the better colonist. Table 2 summarizes

TABLE 2. An assessment of the relative colonization abilities of *Lemna minor* and *Lemna trisulca*

Factor	Assessment
Dispersal	$L. minor > L. trisulca$
Colonization	$L. minor > L. trisulca$
Competition	$L. minor \geq L. trisulca$

the results of the experiments, and shows that *L. minor* displays greater colonization capability than *L. trisulca*. This can account for the different observed frequencies of occurrence in either one of two ways:

1) Where the two species are still in the process of colonizing a new area it is obvious that *L. minor* will occur more frequently. Since much of southern Ontario has been ice-free for only about 12,000 yr (Douglas 1970, Fig. XII-15), it could be considered a relatively new area, geologically.

Despite the observed difference in local frequencies of occurrence, the total geographic distributions of the two species in North America are similar. These two observations are not contradictory. It is not that *L. trisulca* will not colonize, but simply that it has a lower probability of successful colonization than *L. minor*. Both species could have been carried to the physical limits of their respective ranges by migrating waterfowl, but with *L. trisulca* more sparsely distributed and still filling in the gaps.

2) Local equilibrium may already have been achieved. That is, the number of lakes occupied by each species has reached a constant level, and colonization of an additional lake by a species is balanced by its extinction from another.

Changing physical conditions may be one mechanism of extinction. Even short unsuitable periods could eliminate a species, with time lag occurring before recolonization. This would result in a discontinuous distribution of the species concerned.

For example, Hicks (1932) demonstrated that the Lemnaceae are very sensitive to pH. The tolerance ranges of the two species under consideration are similar, and both have an upper limit near pH 8. While most duckweeds can survive unfavourable periods by forming turions (Jacobs 1947, McLay 1974), Hicks (1932) records that both *L. minor* and *L. trisulca* simply died at pH greater than 8. Wile and McCombie (1972) found a mean summer pH near this value of 8 for 24 small lakes in southern Ontario. Although the mean pH was 8, fluctuations above (and below) this critical level likely occurred. Fluctuations higher than pH 8 could be a major cause of extinction if they involved the entire lake. (If pH changes did not involve the entire lake, extinction might not occur. McLay [1974] found sig-

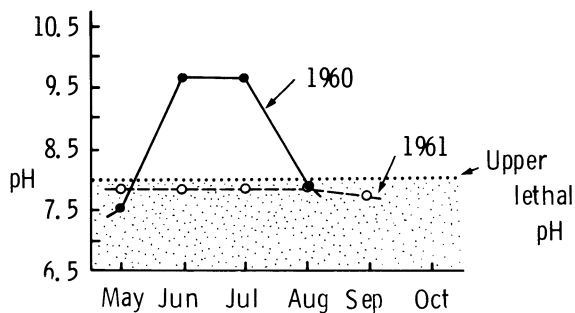


FIG. 4. Changes in pH over two summers for Heart Lake, Ontario (from data in Stocek and McCrimmon 1965).

nificant changes in pH from one part of a lake to another. However, this complication does not alter the possibility of extinction due to changes in lake pH.)

Figure 4 shows changes in pH over two summers for Heart Lake, Ontario. One might speculate (bearing in mind within lake variation) that the high summer pH in 1960 eliminated *Lemna*, while in 1961 suitable conditions returned.

Thus, although extinction is most likely to occur early in colonization, it always remains a possibility (Fig. 1). Successful colonization does not guarantee persistence, as MacArthur and Wilson (1967) pointed out.

The differences in the observed frequencies of occurrence of *L. minor* and *L. trisulca* may result from an equilibrium between extinction rates (which are possibly due to pH changes) and the relative colonization rates (proportional to the colonization capabilities) of the two species concerned. Figure 5 shows a simple model of the situation, which in this example would result in *L. minor* occurring about three times as frequently as *L. trisulca*. It is assumed in the model that all lakes hold equal probabilities for colonization or extinction. Thus, if only 1 out of 10 lakes has *L. minor*, the probability that a dispersed propagule will arrive in a new lake rather than one already colonized is 0.9. Conversely, by the time 9 out of 10 lakes have *L. minor*, the probability that it will disperse to an unpopulated lake is only 0.1. Therefore, the rate of colonization decreases as the percentage occupation increases. Furthermore, if a given number of lakes per annum become physically unsuitable, it follows that the greater the percent occupancy, the higher will be the extinction rate.

I conclude that island biogeographic theory can, with respect to *L. minor* and *L. trisulca*, account admirably for the aquatic plant distributional peculiarity described by Savile (1956), i.e., sporadic occurrence to absence locally, in spite of a wide

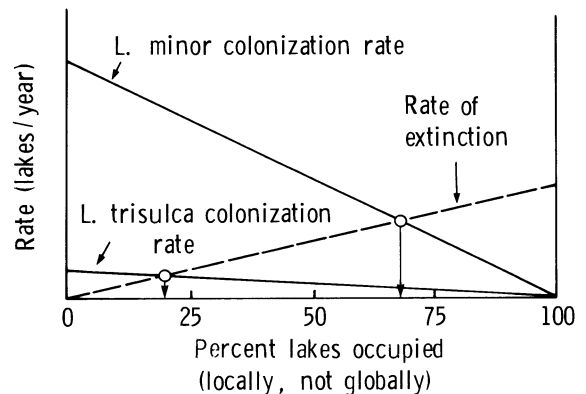


FIG. 5. Simple model of equilibrium situation, where different colonization capabilities of *Lemna minor* and *Lemna trisulca* result in different frequencies of occurrence. Equal chances of extinction in all lakes is assumed, but this is not essential to the theory. In this example, *L. minor* occurs three times as frequently as *L. trisulca*.

overall geographic distribution. The local frequencies of occurrence of many aquatic species with smaller geographic ranges can no doubt often be explained in a similar way. The island biogeographic element is superimposed upon the distributional patterns already determined by the physical requirements of a particular species.

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