

THE DISTRIBUTION OF DUCKWEED *LEMNA PERPUSILLA*
IN A SMALL SOUTHERN CALIFORNIA LAKE:
AN EXPERIMENTAL APPROACH¹

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Abstract. The duckweed *Lemna perpusilla* in a small, alkaline lake was studied during 1970 and a map of its distribution was prepared. Duckweed, the only floating, unrooted higher aquatic plant present, was distributed around most of the edge of the lake but its density was extremely patchy.

Experiments were made involving manipulation of the duckweed density, modification of its distribution, and measurement of the factors which experiments suggested were significant influences on its pattern of abundance. Attention was particularly focused on the importance of other plants in molding the duckweed pattern.

Duckweed was absent from the central area of the lake primarily because there was nothing to prevent the plants from being transported by waves generated by the prevailing winds from the southwest. Growth on water taken from the center of the lake was poor compared to growth on water from near the shore. Duckweed can exist in the *Potamogeton* zone at a much higher density, and the low density does not result from grazing by animals. Growth of plants exchanged between this zone and a zone nearer the shore was depressed in the *Potamogeton* zone and stimulated in the other. Several experiments suggested that the lowered growth rate was attributable to the higher pH of the water, probably produced by the photosynthesis of other aquatic plants. Where it was dense enough, duckweed was able to overcome this effect by shading the plants beneath. It can be reasoned, from the structure of plants that retain their progeny inserted in the reproductive pockets, that the average ability per frond to produce further progeny is thereby impaired. Also, plants broken up into single fronds produced progeny at a faster rate than unbroken plants.

Dense patches of duckweed occurred among the *Scirpus* plants and along the edge of the shore. Duckweed growth was more rapid on mud than on water but plants transplanted to selected places around the lakeshore did not reveal any differences in the ability of the mud to support their growth. Dense populations were associated with breaks in the dense cover of *Scirpus* stems, which reduced the light intensity beneath them by 80%–90%. Comparison of growth of plants on mud in situ, in shaded and unshaded areas, indicates that these openings in the cover are responsible for allowing dense populations to develop. Development of dense patches along the unshaded shore of the lake was limited by their inability to grow fast enough to keep pace with the receding water and hence appeared only where the slope was steep. Most dense patches were eventually stranded on the mud and died, drastically reducing the density because very few new plants (growing from turions or seeds) could be recovered when water was added to dried mud. Therefore the patches must be built up again the following summer. Traditional methods of distribution study would not detect the two distinct causes of patchiness of duckweed in this lake.

Key words: Distribution; experimental ecology; inhibition; lakes; Lemnaceae; patchiness; population; reproductive rate; shading; stranding.

INTRODUCTION

The spatial distribution of both plants and animals has received considerable attention from ecologists. In some cases a distribution reflects interactions between species in the same area so if one species were removed the distribution of another would change; in other cases some species appear to be independent. This paper is concerned with the actions of several species of aquatic plants and other factors influencing the distribution of the duckweed *Lemna perpusilla* Torr. in a small lake.

To explain local distribution is to answer the question "Why is this plant not distributed uniformly throughout this area?"—in other words to account for the horizontal differentiation (Whittaker 1967) of the species. Non-uniformity in distribution implies the presence of factors preventing the attainment of an even distribution since it can be assumed that sufficient time has been available for uniformity to be achieved given the current ability to reproduce. A satisfactory explanation must be scientific—derived independently of the observations, able to make predictions that can be compared with the observed distribution, and capable of further testing. An experimental approach to the study of distribution

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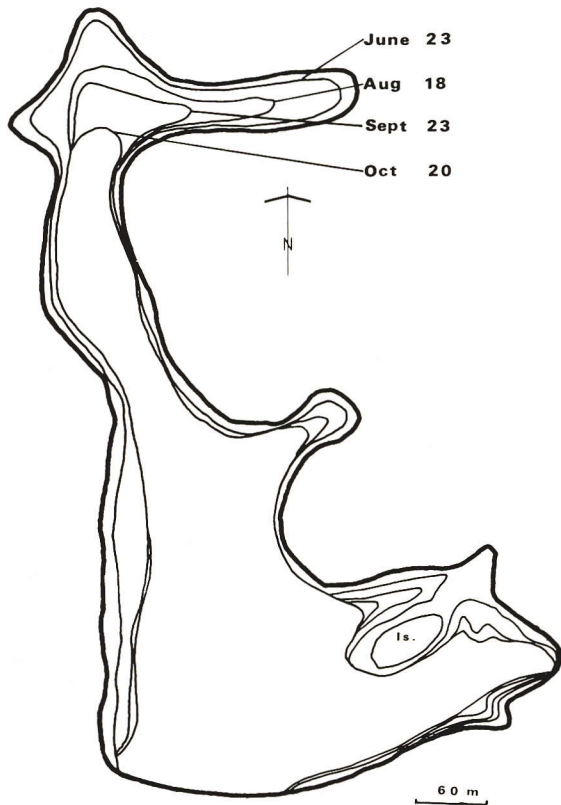


FIG. 1. Map of Lake Los Carneros showing the successive shore lines during summer 1970. The map is taken from U.S. Geological Survey Map, AMS 2052 NE/4 Series U895. Dates on which the water levels were recorded are shown on the map.

has been adopted by few ecologists but they have dealt with a wide range of different organisms, e.g., Blackman and Rutter (1950) (the bluebell *Scilla non-scripta*), Oosting and Billings (1942) (sand dune vegetation), Connell (1961) and Foster (1971) (barnacles).

Unlike the intertidal distribution of marine animals for example, the clumped pattern of duckweed distribution in Lake Los Carneros is apparently unique. It is not known whether most duckweed shares this kind of distribution, although Sculthorpe (1967: 12) notes the patchiness of free-floating plants, being abundant "... in suitably sheltered places." For the most part the ecology of duckweeds has not been closely investigated, extensive field studies having been undertaken on only two occasions in North America by Jacobs (1947) and Landolt (1957). Miscellaneous observations of duckweed natural history are scattered but the general life history features are summarized by Arber (1920). All aspects of the study of duckweeds have been reviewed extensively by Hillman (1961).

METHODS

Duckweed population densities in the lake were measured by two different methods. In areas where the duckweed was very sparse I counted the number of fronds in a floating wooden frame (50×50 cm), and where the duckweed was very dense I took samples by lifting a small mesh-covered wire frame (2×2 cm) up through the layer of plants. Duckweed plants were exceedingly tangled and any plants not lying on the frame were discarded. Since they differ in size the frequency of plants with different numbers of fronds attached to a common parent was recorded. Buds that were less than half the size of their parent were not recorded. I measured the wet weight of plants by briefly placing them on absorbent paper to remove excess water and then quickly weighing them.

For many experiments I removed plants from the lake and grew them in the laboratory using a constant set of conditions, referred to subsequently as "standard conditions." These plants were grown in either 8-oz glass jars or plastic cups or 50×20 mm disposable petri dishes in a water bath at a constant temperature of 25°C and beneath a bank of fluorescent tubes at 5380 lux (500 foot-candles) continuous illumination. The plants were grown on various solutions but the only artificial medium used was 10% Hutner's Medium (Hutner 1953) recommended by Hillman (1961). I measured all light intensities with a Weston Illumination Meter (model 756).

LAKE LOS CARNEROS

The duckweed grows in Lake Los Carneros, a small, shallow lake (14.2 ha) that was formed by damming a small stream near the town of Goleta, California. Prior to 1885 (approx.) a small duckpond used to water stock was present and until 1920 the level was raised several times by additions to the earthen dam at the south end, so the lake did not reach its present size and shape until this time (Tompkins 1966). There are no records of the distribution of vegetation and so the present conditions can only be assumed to have prevailed since some time after 1920. Rainfall in this area is normally restricted to November–March; the nearby airport has an annual average rainfall of 17 in (43 cm) (Goleta Watershed Report 1968). There is no constant overflow from the lake; its level increases during the winter months from rainfall and decreases during the summer months from evaporation. The successive water levels during May–November 1970 are shown in Fig. 1, and margins of the lake which moved the greatest distance indicate where the shore has the smallest slope. When the lake is full there is a small island in the southeast corner. The lake has an alkaline pH (mean 8.32) but the pH varies in

different parts and inflowing water has a pH of only 7.40. The mean conductivity ratio of the water is 0.021, substantially lower than that of inflowing water (0.031).

As far as is known there is only one species of duckweed in the lake, *Lemna perpusilla* Torr.; the other conspicuous aquatic plants are *Potamogeton pectinatus* L. and *Rhizoclonium* sp. The most common plants around the edge of the lake are *Scirpus californicus* (C. A. Mey) Steud., *Polygonum coccineum* Muhl., *Salix* sp., and a few *Typha latifolia* L. *Scirpus* borders the whole edge of the lake except along the dam wall, and *Potamogeton* fills the northern half of the lake and forms a margin in deeper water beside the *Scirpus* along the rest of the shore (Fig. 2). The *Potamogeton* does not grow beneath the *Scirpus*, which seems to exclude the pond weed from shallower waters. Duckweed occurs in among the *Scirpus* and *Potamogeton* stems and on mud along the lake shore.

Several species of waterfowl are resident and breeding in the lake during the summer months, including the American Coot (*Fulica americana*), Ruddy Duck (*Oxyura jamaicensis*) and an unidentified grebe, but none of these birds consume duckweed. Near the end of August migrating ducks began to arrive: Mallard (*Anas platyrhynchos*), shoveller (*Spatula clypeata*), Cinnamon Teal (*A. cyanoptera*), Pintail (*A. acuta*), Blue-winged Teal (*A. discors*), Canvasback (*Aythya valisineria*), goldeneye (*Bucephala* sp.?), and scaup (*Aythya* sp.?). These birds consumed *Potamogeton* and, from dense areas, some *Lemna*, although sparse areas seemed relatively unaffected. Migratory ducks are not considered important factors in duckweed distribution because they modified it after the pattern of dense and sparse areas had been established.

THE STRUCTURE OF DUCKWEED PLANTS

The fronds of *Lemna perpusilla* are thin, oval, and up to 3 mm long by 2 mm wide. If a root is present it is borne near the pointed end of the frond. Arranged on either side of the root base are two reproductive pockets that open on the sides of the frond, and from these the daughter fronds or flowers are produced. Several generations of fronds may remain connected together via the reproductive pockets; I recorded plants of up to nine fronds. The average length of roots varied from 0.8 to 2.0 cm, but only 50%–75% of the fronds had roots.

THE DISTRIBUTION OF *LEMNA* IN LAKE LOS CARNEROS

The duckweed is distributed around most of the shore of the lake except for the southern shoreline, which is the wall of the dam. A map of the distribution was prepared from observations and measure-

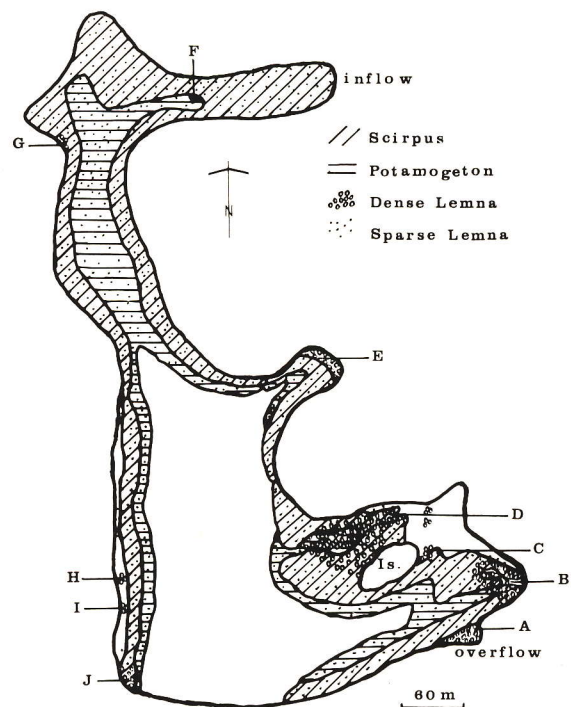


FIG. 2. The distribution of *Lemna perpusilla* in relation to the major aquatic plants *Scirpus californicus*, *Potamogeton pectinatus* in Lake Los Carneros during summer 1970. Dense patches of duckweed are labeled A–J.

ments taken along the shore and from a boat (Fig. 2). Along most of the shore duckweed was uncommon but in a few areas it was extremely abundant forming dense mats covering many square meters. Samples taken throughout the lake showed that in these mats the average density was 48.23 fronds/cm² (SE = 4.38, N = 18) but only 0.057 fronds/cm² (SE = 0.006, N = 14) in sparse areas. This difference in density was maintained throughout the summer; the dense areas expanded but the sparse areas, despite their low density, remained thinly populated. Plants from the two areas differed significantly in size ($p < .01$, t -test) with only 1.76 (SE = .05) fronds per plant in dense areas but 2.99 (SE = .06) fronds per plant in the sparse areas. The frequency of plants of different sizes (Fig. 3) shows that larger plants were more common in the sparse areas.

The area occupied by the patches of duckweed (Fig. 2) was the maximum area and, although the nuclei of the patches were all present in the spring, not all were present at the same time because some died out as the water receded during the summer. The vegetation in Lake Los Carneros shows the familiar pattern of lake zonation (Sculthorpe 1967). A generalized profile of the lakeshore (Fig. 4) shows four distinct zones: (1) the shore zone at the lake edge which is largely vacant mud invaded by ter-

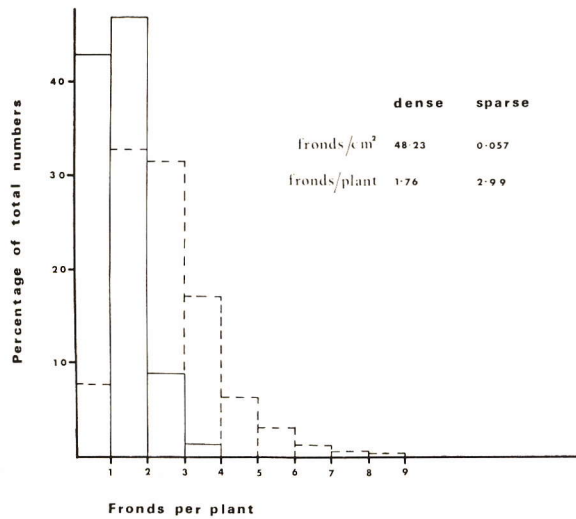


FIG. 3. The frequency of *L. perpusilla* plants in Lake Los Carneros with different numbers of fronds in dense areas (solid line) and sparse areas (broken line).

restrial plants as the water level falls, (2) a zone of emergent *Scirpus* plants, (3) a zone of submerged *Potamogeton*, and (4) the lake itself or central zone. Duckweed was present in all but the last zone; dense patches occurred only in the shore and *Scirpus* zones but in the late summer spread over *Potamogeton* at a few places. The width of the zones varied in all parts of the lake since it was largely determined by the slope of the shore. Where the slope was steep the shore zone was absent because *Scirpus* grows right up to the highest level, and where the lake was shallow the water was mostly filled with the *Potamogeton* zone (Fig. 2). The lake was studied from April to November 1970.

RESULTS

The absence of Lemna from the central area of the lake

The reason for the absence of *Lemna* from the open water of the lake seems obvious. Since duckweed is not a rooted plant it is very susceptible to transport by wind-produced waves. With the prevail-

TABLE 1. Comparison of the growth of duckweed on water from the different parts of the lake. Initial number of fronds = 10; results are the number of fronds present after 16 days. Numbers in parentheses are SE of the mean

Source of water	Source of plants	
	Sparse area	Dense area
Central zone	19.33 (0.95)	25.17 (0.54)
<i>Potamogeton</i> zone	17.83 (1.14)	24.67 (1.09)
<i>Scirpus</i> zone	40.17 (2.1)	40.17 (1.17)
Shore zone	31.50 (1.65)	45.00 (3.75)

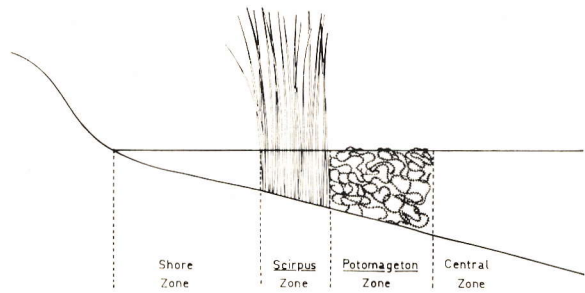


FIG. 4. A generalized profile of the lake, divided into four zones.

ing wind from the southwest, it seems likely that any plants accidentally leaving the shore population would tend to move northeast. To check for the ability of waves to transport duckweed, I released some 30–40 g (wet weight) from a boat at the south end of the lake on 12 August 1970, when a light wind was blowing from the southwest, producing waves up to 10 cm high in the center of the lake. As expected the plants were gradually transported shorewards in the direction of the prevailing wind.

The low density of Lemna in the Potamogeton zone of the lake

Scattered fronds of *Lemna* occurred throughout the *Potamogeton* stems at a density of only 0.057 fronds/cm² and the plants were larger, with higher numbers of fronds than plants from dense areas. The causes of this low density may have been either that the growth rate was depressed and the duckweed could not grow fast enough to reach a high density during summer, or the growth rate was normal but plants were removed or lost from the zone as fast as they were produced and only a small stock of residents persisted. The growth of duckweed on water in the laboratory differed depending upon which part of the lake the water came from. Table 1 shows that fewer fronds were produced on water from the central and *Potamogeton* zones than on water from the *Scirpus* and shore zones where dense duckweed developed. To check whether the growth rate differed under natural conditions I exchanged duckweed plants between an enclosure in the *Potamogeton* zone and one in the shore zone (in the southeast corner of the lake). Resident duckweed was cleared from wire netting cages and selected plants were grown at low density (0.03 fronds/cm²) in floating frames to which were attached plastic bags to protect the plants from removal by animals such as fish or ducks. The results (Table 2) show that the sparse area plants were stimulated when transferred to the dense area and the dense area plants were suppressed when transferred to the sparse area. Since the experimental plants had been protected from loss,

TABLE 2. The effect on the growth of duckweed in the lake, of transferring plants from the shore zone to the *Potamogeton* zone and vice versa. Initial number of fronds = 20/square and the data show the number of fronds per square after 7 days

a) Plants from the shore zone grown in the <i>Potamogeton</i> zone		
	Control	Treatment
Mean no. of fronds	61.2	47.0**
No. of replicates	9	16
SE	2.49	2.68
Ratio treatm./control—0.77		
b) Plants from the <i>Potamogeton</i> zone grown in the shore zone		
	Control	Treatment
Mean no. of fronds	40.4	61.0**
No. of replicates	16	10
SE	1.82	3.84
Ratio treatm./control—1.51		

** Significantly different at the .01 level (*t*-test).

the difference in growth was probably due to some inhibitory factor in the water in the *Potamogeton* zone.

Because the major difference between the wire netting enclosures was the presence of *Potamogeton*, it was a natural suspect as the inhibitor of duckweed growth. The effect of this plant may be to alter the quality of water by removing essential nutrients or to release some substance into the water analogous to the volatile growth inhibitors discovered by Muller et al. (1964) on *Salvia* shrubs.

Some early research on the ecology of duckweeds (Hicks 1932) suggests that they are particularly sensitive to the pH of the water. Although Hicks did not work with *Lemna perpusilla* he grew seven other species of duckweed in Ohio in artificial buffered solutions and found that while they had a wide range of tolerance, growth above a pH of 8 was very poor and some species did not grow at all. Therefore I compared the pH of water samples from the enclosure in the *Potamogeton* zone with that of water from the shore zone enclosure (Table 3). Water from the sparse area had a pH greater than 8 (pH = 8.23) and from the dense area less than 8 (pH = 7.69). This difference is highly significant and in the light

TABLE 3. Comparison of pH of water samples from areas of sparse and dense duckweed in the southeast corner of Lake Los Carneros. (1100 h, 25 September 1970)

	Sparse area	Dense area
Mean pH	8.23**	7.69
Range	(8.15–8.4)	(7.55–7.9)
SE	0.024	0.028

** Significantly different at the .01 level (*t*-test).

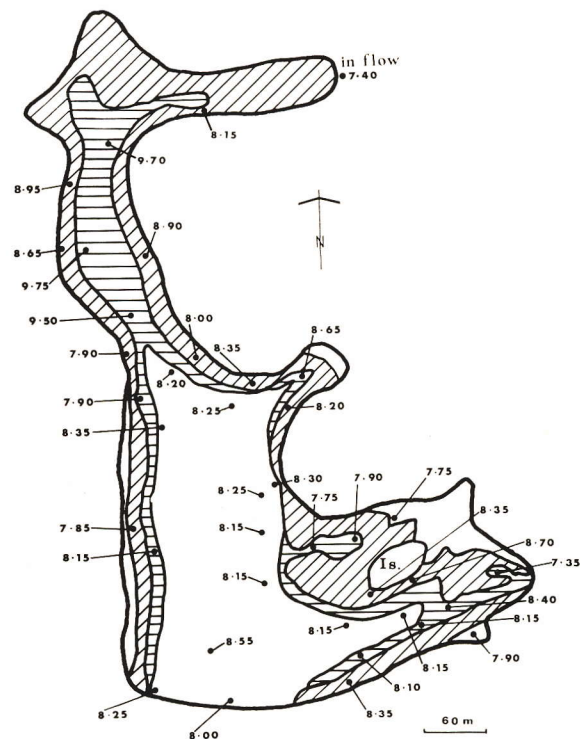


FIG. 5. The distribution of pH of the water in Lake Los Carneros on 21 September 1970, 1100–1300 hours. The mean pH for the whole lake is 8.32 (7.35–9.70). Aquatic plants are represented by cross-hatched areas (see Fig. 2).

of the work of Hicks it may be an important factor in the inhibition of duckweed growth. To see if this difference in pH was present throughout the lake, I took water samples and noted the density of duckweed associated with them (Fig. 5). (Water samples were taken over a period of 2 h during which the pH could have changed, but this could not have biased the results because their collection followed no particular pattern.) When the pH values were grouped into those from sparse and those from dense areas, the mean pH in the sparse areas was found to be 8.50 (SE = 0.12) and in dense areas 7.74 (SE = 0.08); this difference is highly significant ($p = 0.01$, *t*-test). The average pH in the *Potamogeton* zone was 8.70.

The higher pH of the water from the bed of lakeweed was probably a consequence of the large quantity of weed present whose photosynthesis would have used up HCO_3^- ions (Ruttner 1963: 68), increasing the pH. A unique situation in the southeast corner of Lake Los Carneros allowed this idea to be tested. During the summer a front of dense duckweed spread out from the shore zone to cover a small bed of *Potamogeton*. If the lakeweed was responsible for elevating the pH as a result of photosynthesis

TABLE 4. The effect of rinsing water from the *Potamogeton* zone through dense duckweed, upon the growth of duckweed on the treated water. (Initial number of duckweed fronds = 10, number of days growth = 12; 25 g wet wt of dense duckweed per 1000 ml of water was used for rinsing)

	Control	Treatment
Mean no. of fronds	28.7	29.3
Range	(24-34)	(24-34)
No. of replicates	6	6
SE	1.96	1.78

No significant differences (*t*-test).

then shading by the duckweed should result in the reduction of the pH and the production of conditions more suitable for its own growth. Therefore water samples were taken from the shaded and unshaded *Potamogeton*, and their pH was measured. In the unshaded area the mean pH was 8.32 (SE = 0.09) but beneath the *Lemna* it was only 7.18 (SE = 0.11). Ganning and Wulff (1970) found that a dense cover of *Lemna minor* on a rock pool allowed only 0.9% of the light to pass through and totally suppressed photosynthetic activity beneath.

It appears that when duckweed becomes very dense it can overcome the growth inhibition that seems to be associated with the water pH. Provided that high pH causes the inhibition, the results can be interpreted in a reasonable way. But it may be that some other factor was causing the inhibition and thus the shade produced by the duckweed was irrelevant. Therefore water from among the *Potamogeton* stems was washed through a mass of duckweed several times to see if this improved duckweed growth on the water. When grown under laboratory conditions there was no difference between treated and control containers (Table 4). Consequently, this alternative hypothesis must be rejected. Another alternative, which has not been investigated, is the possibility of nutrient competition between *Lemna* and *Potamogeton*; the evidence presented for the effect of pH could equally well support this idea. Shading by *Lemna* could suppress photosynthesis by *Potamogeton* and improve its own potential for growth either by lowering the pH or stopping the uptake of nutrients.

One additional contribution to the low growth rate of duckweed results from the way in which the duckweed reproduces. Daughter fronds are produced from two reproductive pockets and may remain connected to the parent, thereby effectively blocking the production of further progeny by that pocket. As a result, plants in the *Potamogeton* zone should grow more slowly, because they are larger than plants in other areas (Fig. 3). If the fronds break off as soon as they are formed then the total number of vacant pockets in a population is simply twice the number of fronds. But if the fronds remain attached, the number of vacant pockets per plant is only one more

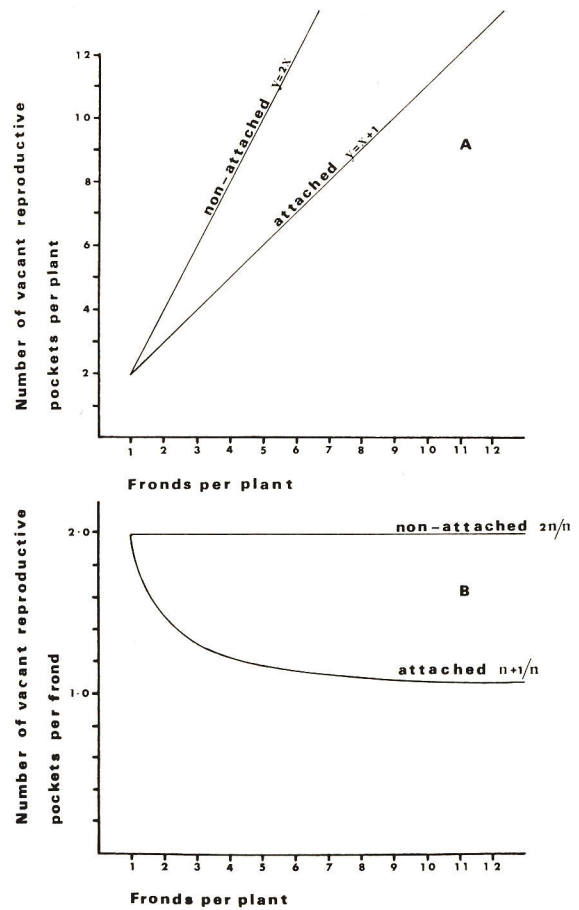


FIG. 6. A—the relationship between potential numbers of progeny-producing pockets and the size of the plant for populations in which fronds remain attached to the parent plant and for those in which progeny break off before reproducing themselves. B—the average number of vacant reproductive pockets per frond for different-sized plants in non-attached and attached populations.

than the number of fronds composing the plant, regardless of plant size. Therefore the number of vacant pockets per frond and hence the reproductive potential of the plant, is much lower on larger plants (Fig. 6A, B). If the total number of fronds in a population is T and the number of fronds per plant is F then there will be T/F plants in the population. Since the number of vacant reproductive pockets per plant is $F + 1$ then the ratio

$$(F_1 + 1) T/F_1 / (F_2 + 1) T/F_2$$

will always be greater than 1.0 when $F_1 < F_2$. Therefore plants in the shore zone (1.76 fronds per plant) should produce 1.18 times as many progeny as plants in the *Potamogeton* zone (2.99 fronds per plant).

To test for this effect of plant size, I compared the growth of plants broken into single fronds with growth of unbroken plants. In all cases the growth of single fronds was greater than that of

TABLE 5. The effect of breaking up the duckweed plants on the number of fronds produced

a) Plants grown on Hutner's medium						
	<i>Potamogeton</i> plants			Shore plants		
	Unbroken	Broken	Ratio	Unbroken	Broken	Ratio
No. of replicates	10	7		10	9	
Mean increase in no. of fronds	5.05	7.14	1.41	8.5	9.44	1.11
Range	(3.4-6.8)	(5-10)		(5.5-12.5)	(3-15)	
Mean no. of initial fronds per plant	5.1	1.0		2.0	1.0	
Expected ratio			1.67			1.33
b) Plants grown on lake water						
No. of replicates	10	10		10	10	
Mean increase in no. of fronds	3.3	5.7	1.73	2.98	4.1	1.38
Range	(2-3.8)	(3-11)		(1.3-6.5)	(3-7)	
Mean no. of initial fronds per plant	4.4	1.0		2.0	1.0	
Expected ratio			1.63			1.33

unbroken plants from the same area (Table 5). The ratios of number of fronds produced were close to the expected ratios calculated from the above expression. The difference in plant size in the lake clearly influences the growth of duckweed, but the reasons for the larger size of plants in the *Potamogeton* zone are not clear. It may be that frequent contact and forces generated between plants in the dense duckweed of the shore zone reduce plant size. Nutritive factors may also be involved; Hillman (1961) notes that plants with many fronds are produced under certain conditions when sugars are present in the media.

The second possibility, that duckweed may have been kept at a low density by removal, was tested by floating wooden frames (25 × 25 cm) stocked with high densities of duckweed inside wire netting cages, placed at intervals around the lake and left for 3-4 wk. The cages were placed in the lake at the edge of the *Scirpus* in among lakeweed at the points shown in Fig. 7 between 14 August and 5 October 1970. At the end of this period I measured the amount of duckweed remaining but found no significant differences between the amount of duckweed in the experimental enclosures and that in the control (a naturally dense area in the *Scirpus* zone). The low density in the enclosure midway along the eastern shore was due to accidental loss. The purpose of the experiment was not to measure the growth rate but simply to observe the fate of dense duckweed in an area that had only a sparse distribution of resident plants. Since the initial density in all cages was the same, the absence of any difference between the experimental cages and the control cage indicates that duckweed is equally able to persist in both areas. There does not therefore seem to be any animal removing duckweed from the *Potamogeton* zone or any toxic factor that could kill the plants and be responsible for the low density. Resident ducks in

the lake were never observed eating duckweed in this zone.

In addition to *Potamogeton* the most common aquatic plant in this zone is a filamentous algae *Rhizoclonium* sp. but it is also common in the *Scirpus* and shore zones where duckweed can reach high densities, and so it could not be responsible for any differences in duckweed growth between the two zones. A number of experiments have been completed that confirm the unimportance of *Rhizoclonium* sp. in influencing the growth rate of *Lemna* even when the density of the algae is increased beyond its natural level in Lake Los Carneros. The only role that the filamentous algae might play is in forming a barrier influencing the pattern of spread of *Lemna* when the algae forms large, floating, bubble-filled mats at the surface. Other experiments have also shown that *Rhizoclonium* sp. might be able to compress patches of duckweed plants when a floating mat of filaments expands. Evidently the resistance to compression is much greater for the algae than it is for the more loosely knit duckweed population.

The occurrence of dense areas of duckweed in the Scirpus zone

In most areas of the lake where *Scirpus* grows *Lemna* is even less common than in the *Potamogeton* zone, but in a few places it is exceedingly dense. Although *Potamogeton* acts to some extent as a buffer, the tall (2 m) *Scirpus* stems are the major stabilizing influence on waves, serving to protect the shore from direct action and the duckweed from being dispersed. A factor which may be important was the gradual decrease in lake level during the summer, which stranded the duckweed on the mud for many months. Differences in the ability of the mud to support duckweed growth were perhaps associated with the occurrence of these patches. Placing duckweed on lake mud had a dramatic effect

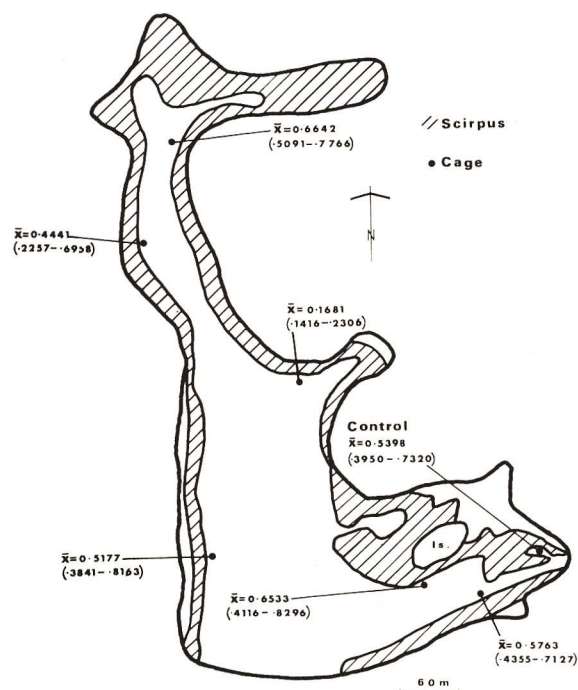


FIG. 7. The quantity of duckweed surviving transfer to different parts of the lake. The mean (based on eight samples) and range of wet weight of duckweed (g) in cages in the water around the edge of the lake is shown.

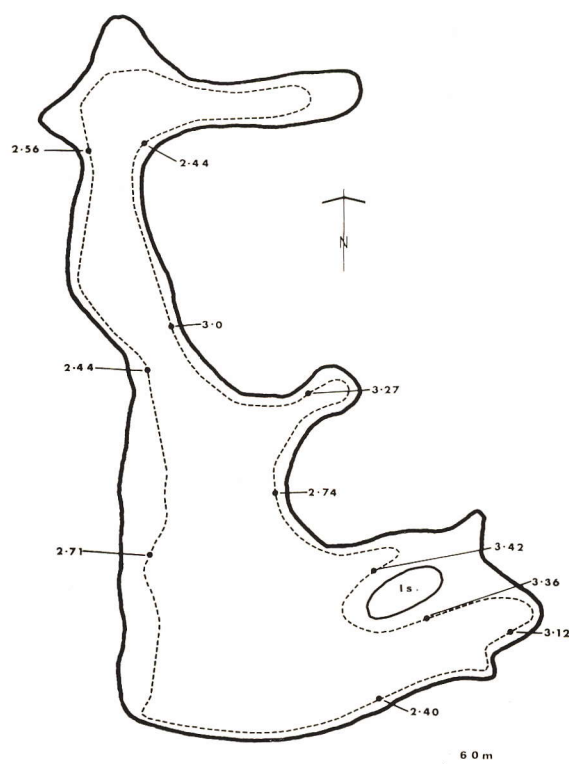


FIG. 8. Growth of *L. perpusilla* on mud beneath *Scirpus* stems around the edge of Lake Los Carneros 24 September-6 October 1970. Initial number of fronds per plant was two and the results show the average number of fronds per plant after 2 wk. Broken line indicates the water level at this time.

upon its growth. Duckweed plants with two fronds grown under laboratory conditions for 14 days on lake water and lake mud produced three times as many fronds on mud as on water (Table 6). Vigorous growth of other duckweeds (*Spirodela* spp.) on mud has been reported by McCann (1942), and Arber (1920) has cultivated *Lemna minor* on mud for periods up to 22 mo.

To test for differences in the growth of *Lemna* on mud, I transferred selected plants to several places around the edge of the lake. At 11 places the resident duckweed beneath the *Scirpus* stems was cleared from an area of mud (30 x 30 cm) beside the water, and 20-25 plants, each with two fronds were placed on the mud and left for 2 wk. The results (Fig. 8) show no consistent differences, growth on mud in areas of dense duckweed being no different from growth

in sparse areas (3.09 and 2.72 fronds per plant respectively). The growth rate was remarkably low compared to that in the laboratory: 1.4 as opposed to 9.8 fronds produced per plant in 2 wk (Table 7), but differences in the quality of mud do not appear to influence the development of dense patches.

All the patches of dense duckweed in the *Scirpus* zone are associated with breaks in the cover of *Scirpus* stems, and the poor growth of duckweed on the mud beneath *Scirpus* stems suggested that it may have resulted from the low light intensity. The tall *Scirpus* stems had an average density of 36.8 stems/m² (12 m² samples) and formed a dense overhead cover. The light intensity above and below the stems was measured during July 1970, and although the

TABLE 6. Comparison of growth of duckweed on mud and water under standard laboratory conditions (length of experiment 14 days)

	Mud	Lake water
Mean increase in no. of fronds (final no./initial no.)	9.75**	3.17
SE	0.646	0.289
No. of replicates	22	17
Roots per frond	0.434	—

** Significantly different at .01 level (*t*-test).

TABLE 7. Comparison of growth of duckweed on mud in the laboratory and in the lake

	Laboratory	Lake
Mean increase in no. of fronds	9.75	1.39**
SE	0.646	0.12
No. of replicates	22	143

** Significantly different at the .01 level (*t*-test).

TABLE 8. The effect of *Scirpus* stems on the amount of light reaching mud. (Measurements of light intensity made 1-7 July 1970 along eastern edge of the lake)

No. of measurements	29
Mean percentage reduction	87.49
Range	(41.0-99.2)
SE	2.86

intensity was very patchy the average reduction was 87.5% (Table 8). Testing for the effect of shading did not prove simple because of interference with the experiment, but fortunately natural circumstances provided a simple comparison. As the lake level fell duckweed plants were stranded, and where the slope of the shore was the same in two areas the plants at some level must have been stranded at the same time. Therefore the effect of shading could be detected by measuring the number of fronds per "colony" in shaded and unshaded, low-density areas. The only sources of variability are the effect of the mud (shown in Fig. 8 to be fairly uniform) and the initial number of fronds per plant, which will at least be the same in shaded and unshaded areas. When the sizes of colonies in two adjacent areas 1-2 m apart were measured on 9 October 1970, the difference in plant-size was very significant (Table 9): the average size of shaded plants was only one-fifth of that in the unshaded area. The results confirm the importance of the association of duckweed patches with lack of *Scirpus* cover and it is significant that all unshaded openings are filled with dense duckweed.

The continued production of fronds in open areas can push plants at the margin out of the sunlight into the shade of *Scirpus*, but at the same time there must be a buildup in the density to the point where the forces resulting from multiplication can be transmitted to the perimeter of the patch. It seems likely that the growth of patches might be limited by a negative density-dependent effect upon the growth rate. A decrease in the growth rate might result from the submergence and shading of a large proportion of the population as the mat thickens or from nutrient depletion of the water or both of these causes acting together. To examine the effects of density on duckweed growth I grew plants in small petri dishes on Hutner's medium under laboratory conditions. The initial number of fronds varied from 1 to 400 per

TABLE 9. Comparison of sizes of shaded and unshaded duckweed colonies stranded on the mud

	Unshaded	Shaded
Mean no. of fronds per colony	21.56	4.60**
No. of colonies measured	40	92
Range	(12-32)	(2-10)
SE	0.77	0.18

** Significant at the .01 level (*t*-test).

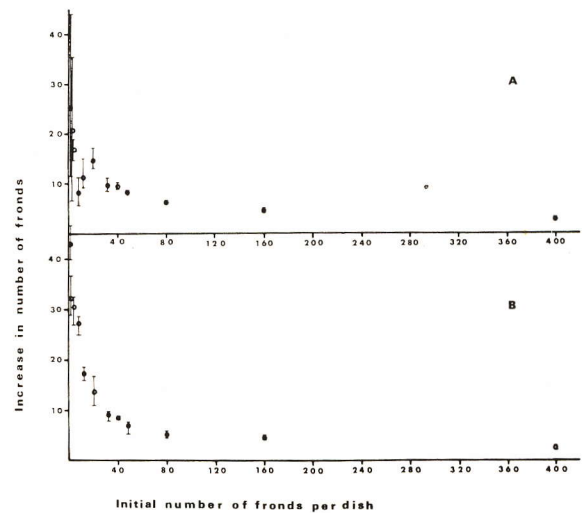


FIG. 9. The effect of density upon the growth rate of *L. perpusilla*. The ratio of the final to the initial numbers of fronds is plotted against initial density of fronds per petri dish. A—growth of plants from a sparse area. B—growth of plants from a dense area of duckweed. The mean and range is given for each density.

dish (0.05-20.4/cm²) and each density was replicated three times. Growth was measured after 14 days. The rate of growth declined rapidly at first but as density increased further it changed very little (Fig. 9). Both nutrient depletion and shading were probably operating in this experiment, but only at higher densities could shading be effective. Plants from sparse areas (Fig. 9A) responded differently at low density than plants from dense areas (Fig. 9B). It is difficult to apply this negative growth rate relationship to the field, where nutrients are probably regenerated, but the results support the idea that it should decline with increasing density.

The presence of only a small number of dense patches of duckweed in the shore zone

The results of previous sections have suggested that duckweed growth may be very sensitive to pH changes and to the presence of shade. In the shore zone both of these factors favor the growth of duckweed and yet only a few patches were present. This zone is restricted because *Scirpus* plants grow to virtually the highest water level and for the most part *Lemna* was uncommon, but when it did occur it was very dense.

A likely explanation for the lack of duckweed seems to be associated with the falling water level during the summer, when the inflow to the lake is exceeded by evaporation losses and the level falls uniformly (0.5 cm/day, SE = .06). The result is that the duckweed growing around the edge of the lake is stranded on the mud. Where the slope of the

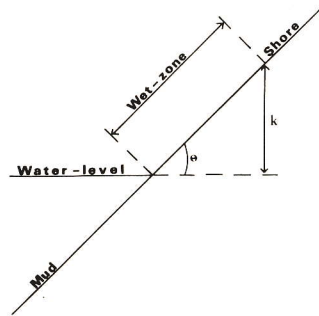
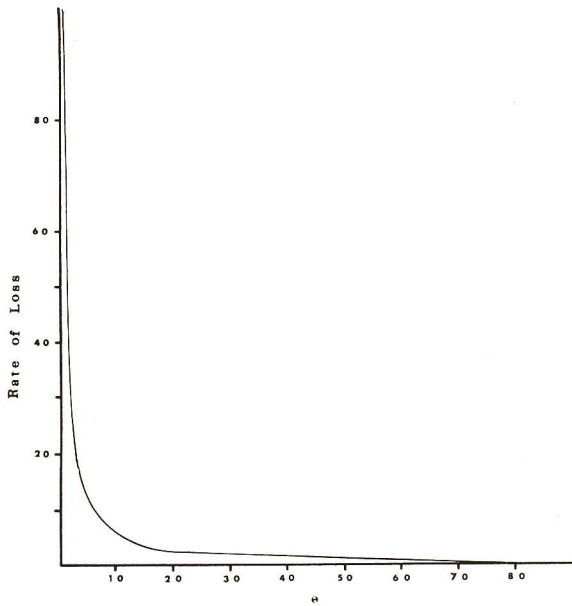


FIG. 10. The relationship between the rate of loss of duckweed from the population due to stranding (cotangent of θ) and the slope of the shore (θ). The relationship of the zone of wet mud to θ and the water level is also shown in the lower half of the figure.

shore (θ) is small the edge of the water moves rapidly and where it is large the water moves more slowly; consequently the rate of stranding(s) of the plants is related to the slope (Fig. 10) according to

$$ds/dt = a \cot \theta.$$

where a is the rate of fall of the water level. Therefore it may be that the duckweed is able to survive and form dense patches only where the rate of loss is substantially less than the rate at which the population expands into new areas. If the hypothesis is correct, sparse or vacant areas should be associated with gently sloping shore and dense areas with steep shores.

The rate of expansion of the population depends upon the rate of multiplication. One could reasonably expect this to depend at least upon the population size, so population growth would tend to be exponential, provided that it was unimpeded and the average

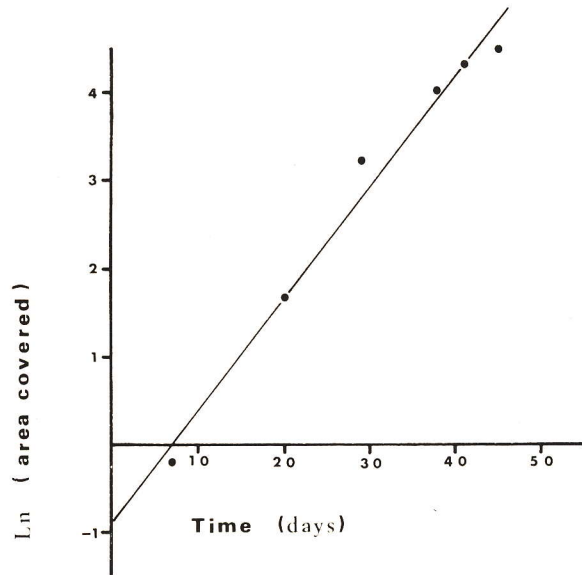


FIG. 11. The expansion of a patch of *L. perpusilla* across an unshaded water surface. The natural logarithm of the area covered is plotted against time and the equation of the line is $y = 0.86 + 0.1257 X$ (correlation coefficient = 0.96).

plant size did not change drastically. Therefore if the reproductive forces are transmitted uniformly by the floating mass, then the front of duckweed should move away from the shore at a rate proportional to the distance (W) from the shore already covered, i.e.,

$$df/dt = cW.$$

I estimated the value of c by measuring the rate at which a patch of duckweed expanded into a defined area when it was not subject to stranding. I estimated the area covered by mapping and the results are shown in Fig. 11. The slope of the line relating the natural logarithm of the area to time allows c to be estimated, and it can be shown by simple mathematical argument that c is equal to half the value of the slope in Fig. 11 because it concerns only one dimension, length. Therefore the rate of change of width of the population will be given by

$$dW/dt = cW - a \cot \theta$$

where $c = 6.5$ and $a = 0.5$ cm/day. After a period of time t , the relationship between the initial size (W_0) and its new size (W_t) will be

$$W_t = (W_0 - a \cot \theta) e^{ct} + a \cot \theta.$$

This equation relates the parameters that determine the survival of a duckweed patch.

To test the hypothesis I measured the relationship between the occurrence of dense patches and the slope of the adjacent shore line on several occasions (23 June, 18 August, and 19 September 1970). The distribution of all dense patches was recorded and the slope of sections of the shore was measured

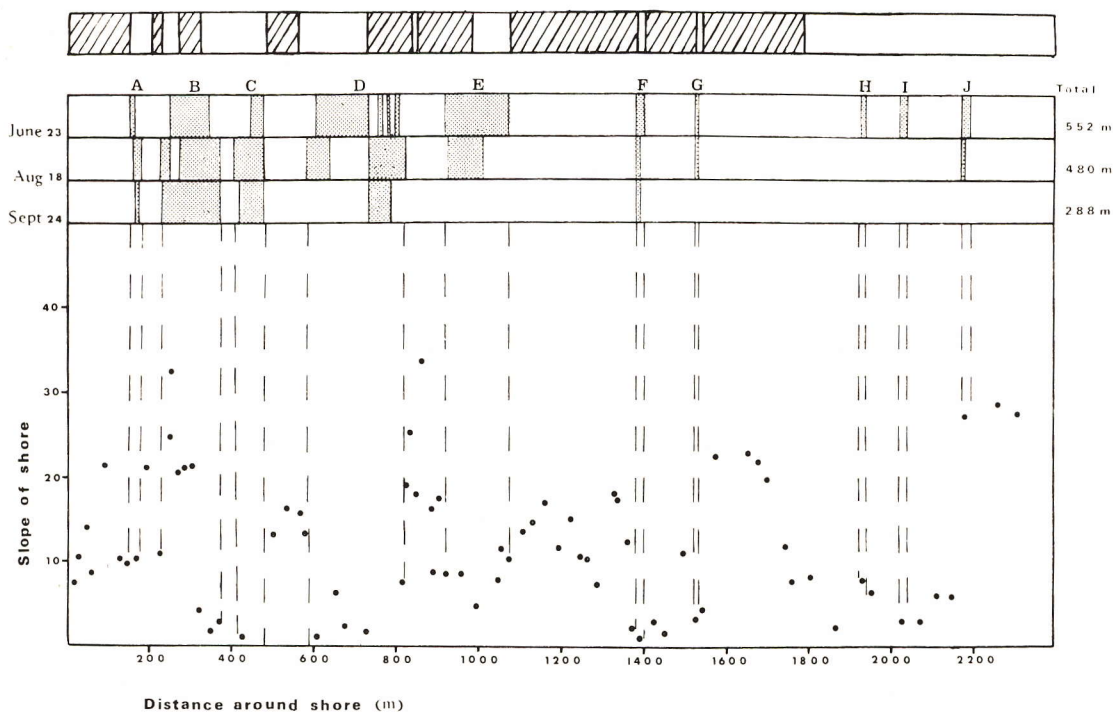


FIG. 12. The distribution of dense areas (A-J) of *L. perpusilla* in relation to the slope of the shore. (Map in Fig. 2 gives their location in the lake.) The length of the shoreline (measured from the eastern corner of the edge of the dam at the south end of the lake) occupied by dense duckweed is shown for 23 June, 18 August, and 24 September 1970. The sum of these lengths is indicated in the margin. The vertical, dashed lines mark the limits reached by each dense area of duckweed around the shore. Across the top is shown the extent of the *Scirpus* zone (cross-hatched) and shore zone (blank) around the lake edge.

wherever it changed noticeably (Fig. 12). Patches of dense duckweed from the *Scirpus* zone were included because during the summer the distribution changed with the decline in water level and expansion of the duckweed so that all dense patches eventually ended up at the edge of the water. Fig. 12 shows that some patches which were separate coalesced as they grew towards each other while others broke up as the water fell away more quickly in adjacent areas. As a result of stranding, the total length of shoreline occupied by dense duckweed declined from 552 to 288 m despite its rapid growth. There are nine independent dense areas, and if the slopes of the shore included within the maximum limits of each area are compared, it will be found that dense patches are not in fact exclusively associated with shores of large slope. They tend to be associated with slopes of 10° or less rather than with large slopes as expected.

An alternative idea concerns the zone of wet mud on which the duckweed can live after it has been stranded. The width of this zone is much larger on shores of small slope, where duckweed is stranded at a faster rate. Therefore since growth is stimulated on wet mud (Table 7) this might allow buildup on these gently sloping shores of duckweed patches that

would be floated off when the winter rains raise the lake level.

The mud absorbs water from the lake and transports it upwards to replace water lost at the surface by evaporation. The height (k) that moisture can be lifted above the water table depends largely upon the nature of the mud. If k is a constant, independent of the slope of the shore, then the relationship between the width of the wet zone (w) and the slope (θ) should be (Fig. 10):

$$w = k \operatorname{Cosec} \theta = k / \sin \theta.$$

When $\theta = 90^\circ$, $w = k$, and as θ becomes smaller w becomes very large. To test this relationship I measured the width of wet mud on selected shores of different slope on 23 September 1970. There is a clear relationship between the width and slope (Fig. 13) and, when measurements taken beneath *Scirpus* stems are distinguished, it can be seen that they differ. The equation relating w and θ was fitted using a least-squares method to solve for k ; the values obtained were 9.3 cm for exposed shores and 17.6 cm for *Scirpus*-covered shores. The form of the relationship is the same for both shores but under *Scirpus* stems the water rises higher. It seems likely that the mud has the same capacity to transport water but

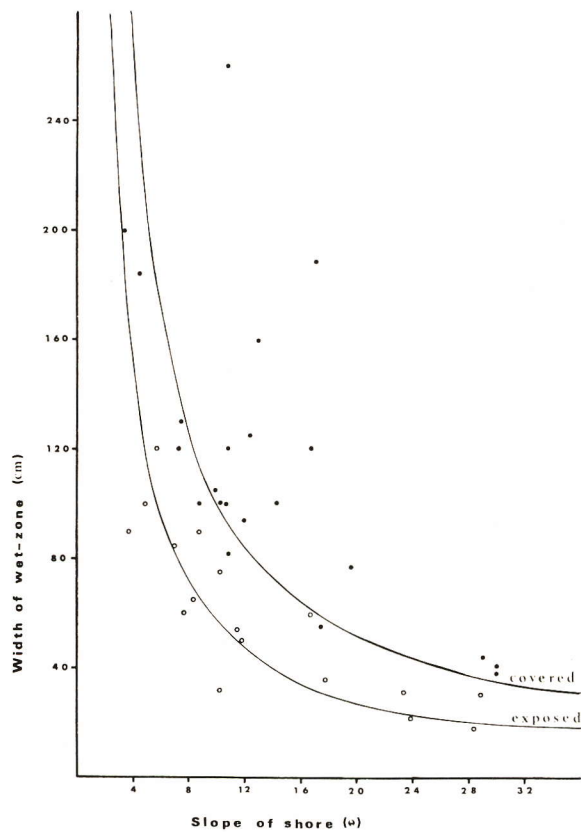


FIG. 13. The relationship between the width of the zone of wet mud beside the water and the slope of the shore. The lines shown were fitted by a least-squares method to each set of data: shores covered by *Scirpus* (closed circles), exposed shores (open circles).

it is being lost at a faster rate from the exposed shores, making the wet zone narrower.

For the proposed mechanism for maintenance of dense patches to work, the duckweed must be able to leave the mud on which it has been growing, after it has been submerged. Samples of mud supporting stranded duckweed were collected from the lake and submerged under 10 cm of water and the plants that floated were removed. The proportion of plants that floated was initially very large but the rate at which it increased gradually declined (Fig. 14). The duckweed that floated first was not attached to the mud in any way and the plants remaining began to photosynthesize and produce bubbles of oxygen which applied an extra buoyant force. All the submerged plants in the samples eventually reached the surface, some requiring almost 3 wk but these did not appear any the worse for their long period under water. The rate at which plants are released from soft mud is much faster than the rate they are released from mud that has been allowed to dry a little and harden (Fig. 14). In 25 hr 90% of plants had left the soft mud but this took 280 hr on firmer mud.

TABLE 10. The effects of various treatments on the emergence of duckweed from samples of mud from Lake Los Carneros

	Total fronds removed ^a
Control (kept at room temp.)	3
Treat. A (12 h at 4°C)	9
Treat. B (24 h at 4°C)	11
Treat. C (48 h at 4°C)	12
Treat. D (4 days at 4°C)	10
Treat. E (kept at 4°C)	0
Treat. F (add water, remove and dry for 1 day, add water again)	15
Treat. G (air-dried mud first, then add water)	13
Mean no. fronds/cm ² of mud surface ^b	0.17

^a Number of fronds removed from three replicates over a period of 7 mo, i.e., from 60 cm² of mud surface.

^b Not including Treatment E.

Growth on wet mud seemed to be a feasible explanation of the patches of duckweed in the shore zone until I found that most of the plants on the mud died off before the water level rose to cover them in November. Therefore the distribution of dense areas in the shore zone cannot result from this mechanism.

Of the two possible effects of shore slope on the duckweed population the quantity stranded that remains alive must be definitely rejected as a factor in the development of dense patches. As the summer proceeds water gradually moves out of most of the shore zone into the *Scirpus* zone with the result that most duckweed in these zones is stranded. A closer examination of the dense patches reaffirms the importance of stranding. The importance of slope seems to be reflected not only in the presence of the patches but more especially in their persistence. The patches of duckweed solely affected by stranding are (Figs. 2, 12) labeled C, D, E, G, H, and I. Only C and D survived; these dense patches persisted because the slope suddenly changed from very small to larger as the water receded. The other patches, unable to keep up with the receding water, did not survive beyond 18 August 1970. Patch F survived on a shore of very small slope because it grew alongside the inflow stream which kept the mud sufficiently damp. The only patches to survive largely intact were A, B, and J, all of which grew alongside shores of comparatively steep slope (>10°). Above a 10° slope the rate of loss changes little (Fig. 10). Although all other conditions are optimal it seems that duckweed in the shore zone is indeed prevented from becoming dense because it cannot grow fast enough to keep up with the receding water.

Maintenance of dense patches of duckweed

The annual pattern of growth observed in Lake Los Carneros was the appearance of duckweed in

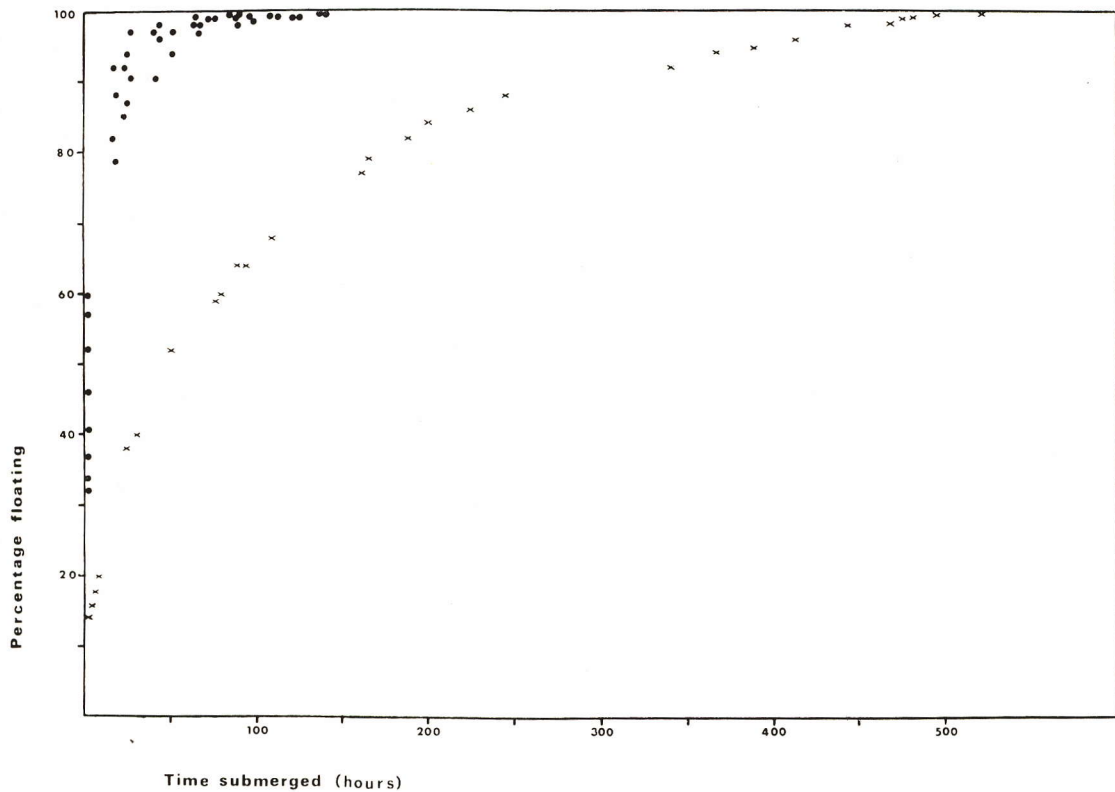


FIG. 14. Flotation of duckweed from submerged mud. The cumulative percentage floating for plants growing on moist mud (closed circles) and drier mud (crosses) are plotted against the time submerged.

the spring, its growth throughout the summer, and during the fall either dying off or being consumed by ducks. In the *Scirpus* zone dense areas of duckweed began from among the stems adjacent to open patches of water and expanded. Duckweed patches near the shore expanded both laterally along the shore and out into the water, the pattern of their movement in shallow water often being dictated by the roughness of the bottom, because the receding water level was continually eroding the population.

Most duckweeds can survive unfavorable periods as seeds or resting bodies (turions) (Guppy 1895, McCann 1942, Jacobs 1947, Henssen 1954), which are modified fronds lacking intercellular air spaces and having cells packed with starch grains. Turions are produced from reproductive pockets in the normal way, but as soon as they break free they sink to the bottom. *Lemna perpusilla* produces seeds (Hillman 1961) but it is not known whether it produces turions. Duckweed from the lake was not examined for turions, but samples of mud (20 cm² of mud surface or 90 cm³ in total) were taken from dried-out shore, covered with lake water, and subjected to periods of low temperature, which should stimulate turions to germinate (Jacobs 1947). Three replicate cores were subjected to each of the treatments listed in Table 10

and duckweed was recovered from all samples except those kept at 4°C. No one treatment seemed more effective than the others in stimulating germination. Clearly *L. perpusilla* is able to survive desiccation either as seeds or turions but the number which survive is very small in relation to the population that produced them. Since the average density of fronds on the shore was 48.23 cm² the reduction in the population as a result of desiccation was 100 (1-17/48.23), or 99.7%. Adequate time (7 mo) was allowed for the new fronds to appear and so either the plants produce very few resting bodies or else there is very poor survival. It may be that a longer period of desiccation is required for them to emerge when water returns; if so, resting bodies produced in deeper water may never germinate. Turions seem able to survive long periods of drought: those of *Spirodela polyrhizza* were kept dry for 2 yr by McCann (1942) and commenced growth as soon as water was added.

A problem remaining is that duckweed in the *Scirpus* zone began at high density from beneath the *Scirpus* stems in conditions entirely unsuitable for its growth. Apparently, because of the poor survival, the duckweed that germinates over a wide area must become concentrated. The association of patches

with breaks in the distribution of *Scirpus* stems may be not only because there is more light but also because there are no stems to impede the initial aggregation of the plants as they germinate. The tendency of duckweed to aggregate can be verified by a simple experiment conducted with an artificial "stem" in a shallow dish of water. Therefore the *Scirpus* stems appear to have a dual role: it keeps duckweed from becoming dense not only because of low light intensity but also because the stems inhibit dispersal and concentration.

DISCUSSION

The several approaches to the study of plant or animal distribution differ in their explanation of the nature of the pattern. One is the "tolerance limit" approach, which is essentially physiological and involves determining the tolerance limits of the organism to certain factors and then examining the distribution of the intensity of the factors and the organism to see if the two coincide. This approach has been especially favored by ecologists working in the intertidal region of the seashore where there are rapidly changing physical gradients. A problem is that this approach assumes the influence of these factors to be in fact the major components of the mortality suffered by the organism in its natural environment, when the most important factor may well be one that has no physiological basis, e.g., predation. Another approach makes use of multiple regression methods to obtain correlations between abundance and certain environmental factors (e.g., Clark et al. 1967, Morris 1963). These methods have been proposed by Yarranton (1969) for use in the study of vegetation. Despite their descriptive usefulness they seem to be a sophisticated method for defining the species "preference" without indicating the reasons. There are no means of testing the explanation and no reason to believe that the correct factors have been measured. The observations cannot be used as both the source of the explanation and also the means of testing it, a conflict with classic scientific method that has been noted by Mead (1971). Some manipulation of the environment is essential to verify correlations.

The study of causal factors determining the distribution of vegetation is considered a prime objective of ecology (Greig-Smith 1964); yet little attempt has been made to pursue this widespread idea by experimentation. Extensive amounts of information have been accumulated about the composition and structure of plant communities but very little about the interaction of species. A fortunate aspect of the present study has been that only four organisms (*Lemna*, *Scirpus*, *Potamogeton*, *Rhizoclonium*) have had to be dealt with, thus making possible some experimentation with all of them. These experiments

have shown that *Lemna* is influenced strongly by *Scirpus* and that there may be some deleterious effects of both *Lemna* and *Potamogeton* on one another. These and the apparent exclusion of *Potamogeton* by *Scirpus* emphasize the importance of plant-plant interactions in determining the structure of the plant community.

It is apparent from the results presented in this paper that the character of the aquatic plant community along the shore of Lake Los Carneros is chiefly derived from the presence of *Scirpus californicus*. The shade produced and the stabilization of waves structure the environment and affect the presence of other plant species. Clearance of stems along the shore of moderate slope should result in resident sparse duckweed becoming dense within one or two summers. Similarly spread of *Scirpus* into currently dense areas of duckweed should result in a decline in the density. An important unsolved question is why there should be any breaks in the *Scirpus* cover that give *Lemna* the chance to multiply. The upper limit of *Scirpus* on the shore is probably set by the length of time that the mud remains dry during the summer since this plant is unable to live in dry soil.

A traditional approach to the study of aggregation is through examination of the occurrence of a species in sampling units (Bliss 1969). The natural distribution of the duckweed is easily seen to be patchy and large numbers of samples are not required. Random samples drawn from a gridded map of the lake would clearly show the patchiness; however they would not reveal that in different parts of the lake patchiness had different origins. This points to a difficulty, often overlooked, in the measurement of patchiness. It is often assumed that the area from which the samples were drawn was homogeneous and that the scale of the patches is a measure of the lack of dispersal of progeny from parents. However, environmental heterogeneity is also likely and may provide an alternative explanation. The distribution of *Lemna* is produced by both lack of dispersal and unequal habitability of the area, which stems from more than one cause. The analysis of vegetation pattern that is commonly performed (e.g., Grieg-Smith 1964) should be followed up by experiments.

The aquatic vegetation types in Lake Los Carneros are far from arbitrary in their distinction because they are composed of almost pure stands, as is common in other lakes (Sculthorpe 1967). This widespread occurrence of pure stands is attributed to the closed structure and vigorous vegetative reproduction of these plants. The distribution of duckweed spans several zones and it does not fit into the kind of framework called "direct gradient analysis" (Whittaker 1967), in which species are arranged along gradients that change smoothly as some function of a spatial dimension. Profiles drawn at right angles

to the shore in different parts of the lake would show quite different relationships between abundance and distance. Within the same environment no two duckweed distribution profiles would be the same. The patchlike distribution of factors mold the development of the duckweed population by suppressing its growth in some areas and yet creating conditions for explosive rates of increase in others.

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