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The potential of artificial refugia for maintaining a community of large-bodied cladocera against fish predation in a shallow eutrophic lake

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Abstract

The Norfolk Broads are a series of shallow lakes which are highly eutrophic and typified by dense populations of phytoplankton and an absence of submerged aquatic plants. The zooplankton community is subject to intense predation pressure by young fish and is dominated by small-bodied organisms which have a low potential for reducing phytoplankton populations through grazing. Various designs and densities of artificial refugia for zooplankton against fish predation were established in Hoveton Great Broad in order to enhance populations of large-bodied Cladocera. Initially some of the refuges contained higher densities and larger individuals of *Daphnia* and *Ceriodaphnia* than the surrounding open water. However, towards the end of the first season and throughout the subsequent two years, population densities and size-structure were similar both within and outside the refuges, although there was still evidence of enhanced body-size of *Daphnia* within the refuges compared with the open water. The provision of habitat structures designed as refugia from fish predation did not enhance large-bodied cladoceran populations enough to promote this restoration strategy as feasible for eutrophic and shallow lakes.

Introduction

Biomanipulation of eutrophic lakes has, in the main, focussed on the removal or restructuring of zooplanktivorous fish populations to effect changes in the zooplankton from a community dominated by small-bodied cladocerans, copepods and rotifers to one dominated by large-bodied Cladocera, particularly of the genus *Daphnia* (Andersson *et al.*, 1978; Shapiro & Wright, 1984). Intense grazing by the induced large-bodied zooplankters can then lead to large-scale reductions in phytoplankton crop and consequent increases in water clarity (Lampert, 1985). One of the main problems associated with this approach is the rapid re-establishment of zooplanktivorous fish stocks and, through their size-selective feeding (Brooks & Dodson, 1965), a zooplankton community dominated once again by small individuals (Pace, 1984).

One alternative strategy to enhance populations of large-bodied cladocerans, other than fish removal, is to reduce predation by fish on the Cladocera by the provision of refugia for large and vulnerable Cladocera. In deep lakes this can be provided naturally by low oxygen concentrations or low light intensities in the deeper waters, tolerated by zooplankton but not by their fish predators. Vertical migrations by zooplankton at night (Meyers, 1980; Zaret & Suffern, 1976) enable them to utilise food present in the upper layers while avoiding visual predators. In shallow waters, an analogous strategy may involve reduced predation rates amongst aquatic plants (Crowder & Cooper, 1982) and horizontal feeding migrations. Timms & Moss (1984) demonstrated that large-bodied Cladocera harboured within a bed of water-lilies and filamentous algal mats were able to reduce phytoplankton populations sufficiently to maintain clear water despite the presence of high concentrations of nutrients. This study describes the effectiveness of different designs of artificial Cladocera-refugia installed within a small (31 ha), shallow (*ca.* 1 m deep) eutrophic lake, Hoveton Great Broad (National Grid reference: TG318164), situated in the heart of the Norfolk Broadland in the East of England. Like the majority of the Broads, Hoveton Great Broad has undergone severe changes associated with eutrophication and is largely devoid of submerged aquatic plant growth and its associated community of animals which, through their grazing activities, may reduce nutrient-induced increases of both epiphytic and planktonic algal populations (Kairesalo & Koskimies, 1987; Irvine, *et al.*, 1989).

Materials and methods

Four different designs of refuge were created, two of which were employed at differing densities.

1. Brushwood bundles

An individual brushwood bundle refuge consisted of a bunch of alder (*Alnus glutinosa* L. (Gaertn.)) twigs firmly secured at one end about 1 m along an alder pole, and more loosely attached half way along the bunch so that the twigs fanned out from their base. The brushwood bundle was positioned in the lake by driving the remainder of the alder pole, typically about 1 m, into the sediment. The bundle would then be firmly in place with the alder twigs approximately filling the water column. Three replicate treatments of each of three densities of brushwood bundles (50, 100 or 200 bundles) were positioned as 100-m^2 plots.

2. Polypropylene rope refuge

Strands of polypropylene rope, 1 m in length and 10 mm in diameter were attached to a 2.25 m^2 wooden and metal frame and placed onto the bed of the Broad. Owing to the buoyancy of the rope the refuges were further weighted by bricks tied to the frame. The high cost of this refuge (£ sterling 62 m^{-2}) permitted the construction of only a single one (rope density 400 strands m^{-2}) with four replicates.

3. Parallel strips of netting

Parallel strips of netting were placed within a 100 m^2 plot in one of two densities. The lower density consisted of eight 2 m × 10 m strips of netting with a mesh size of 12 mm × 12 mm and the higher density eighteen strips of netting, positioned about 1 m or 0.5 m apart respectively. Each density, replicated three times, was enclosed by a 2 m wide outer wall of thicker 'Cintoflex' netting with a mesh size of 17 mm × 25 mm. This thicker netting was used to prevent diving birds and fish from the dangers of entanglement by the fine inner netting.

4. Netting-box

To determine whether or not netting strips could serve as a fish exclusion zone and enhance populations of large-bodied cladocerans without an increase in habitat structure a simple box design was constructed and replicated three times. This consisted of an outer square wall of 2 m deep 'Cintoflex' with 10 m long sides enclosing an inner square of the thinner netting, 2 m deep with sides 7 m long. The corners of the inner square intersected the midpoints of the outer square's edges.

The positioning of the refuges within the lake was determined by dividing the western basin of the Broad into a grid of squares, each 2500 m^2. Refuges were then randomly assigned to the squares with two modifications. The first was that only one refuge would occupy any particular grid square. The second was that one of the three replicates for each brushwood and netting treatment and two of the polypropylene rope designs were sited in squares adjacent to the shore, in order to incorporate possible effects arising from the proximity of the shore. The large distances between plots guaranteed their statistical independence. Three replicate open-water stations were similarly designated to serve as controls.

The refuges were sampled from a boat four times in 1986 at roughly six-weeks intervals from 22 April to 28 August and three times during 1987 between 14 May and 4 August. The polypropylene rope and netting-box designs were excluded from the 1987 samples because it was clear at the end of the 1986 season that they offered little potential as a management tool for the enhancement of populations of large-bodied Cladocera. In addition, in 1988 the brushwood bundle refuges were sampled at weekly intervals from 4 June until 25 July, as it was apparent from the previous years' work that a summer decline of *Daphnia* occurred in the Broad during this period.

Zooplankton was sampled with a 4.5 cm diameter perspex tube *ca.* 1 m long. The tube was inserted into the water, either vertically or at a slight angle in order to obtain a representative sample of the whole water column, stoppered and withdrawn. Collected water was used to fill a 5 l bucket and animals removed by passing the sample through a 65 μm mesh-size nylon plankton net. On each sampling date in 1986 and 1987, five replicate 10 l samples were taken from each of the refuge treatments and control stations. In 1988 two replicate 20 l samples were collected from each of the brushwood bundle treatments and from each of three open water stations. Zooplankters were narcotized with chloroform water (Gannon & Gannon, 1975) and preserved in at least 70% industrial ethanol. Samples were normally sub-sampled in the laboratory using a 5 ml-capacity wide-bore pipette (Bottrell *et al.*, 1976) and counted under a Wild stereomicroscope. At least 50, but usually many more, individuals of the commonest species were counted from each sample. The lengths, excluding head-shields and abdominal spines, of at least 50, but usually more than 100, *Daphnia hyalina* Leydig were measured from each sampling station.

Results

Population density

Mean populations densities of Cladocera found amongst the refuges in 1986 and 1987 are shown in Figs. 1 and 2 respectively. Cladoceran densities on the first sampling date, 22 April 1986, were less than 5 ind. l^{-1} and are not shown. In 1986 there were clear indications that populations of the larger-bodied cladocerans could be enhanced by the refuge structures, but there were substantial variations between sampling dates. On 3 June the cladoceran community in the Broad was dominated by *Daphnia hyalina* with relatively low populations of *Ceriodaphnia quadrangula* (O. F. Muller) and *Bosmina longirostris* (O. F. Muller). Differences in population densities of *D. hyalina* between refuge treatments (Kruskal-Wallis, $P < 0.001$) could not clearly be related to the apparent complexity of each habitat.

In July 1986 densities of *D. hyalina* within the Broad had fallen and those of *C. quadrangula* and *B. longirostris* had increased relative to the June sampling. Whilst *Bosmina* numbers showed no obvious relationship with habitat structure other than relatively few being found amongst the polypropylene rope, there were increases in densities of both *Daphnia* and *Ceriodaphnia* populations with increasing habitat complexity. Significant differences in the abundance of both *D. hyalina* (Kruskal-Wallis, $P < 0.001$) and *Ceriodaphnia* (Kruskal-Wallis, $P < 0.001$) population sizes were detected between treatments. Densities of

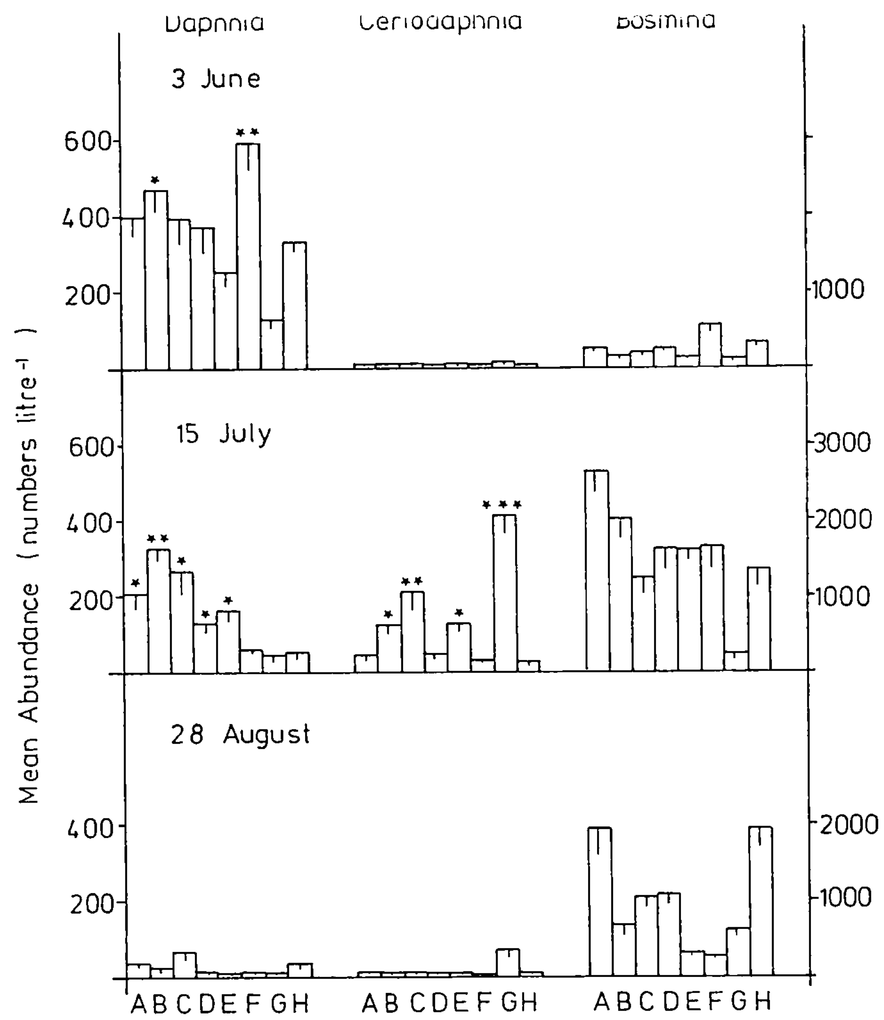


Fig. 1. Mean densities (ind. l^{-1}) of *Daphnia*, *Ceriodaphnia* and *Bosmina* populations found in the refuges during 1986. Low, medium and high density brushwood bundles are denoted by letters A, B and C respectively; D and E are the low and high density netting-strips, F refers to the netting-box and G to the polypropylene rope. Open water controls are denoted by H. Bars are standard errors (n = 15 for refuges A, B, C, D, E, F and H; n = 20 for refuge G). Significant increases compared with the open water (Mann-Whitney U test) denoted by $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

Ceriodaphnia were particularly high amongst the polypropylene rope, attributable to increases in populations of *C. reticulata* (Jurine) as opposed to *C. quadrangula* dominant in the open-water and other refuges.

Compared with the July samples, populations of *D. hyalina* and *C. quadrangula* had fallen markedly by late August. Densities of *D. hyalina* were significantly greater (Mann-Whitney U test, $P < 0.05$) in the open-water compared with all but two (low and high density brushwood bundles) of the refuge treatments. Sizeable populations of *Ceriodaphnia*, dominated by *C. reticulata* were found only amongst the polypropylene rope refuge.

During 1987 population densities of *D. hyalina* significantly differed between the treatments on May (Kruskal-Wallis, $P < 0.01$) and August 4 (Kruskal-Wallis, $P < 0.05$) but not in the July 7 samples. On May 14 significant differences were only detected between *D. hyalina* population densities amongst the low and high density netting-

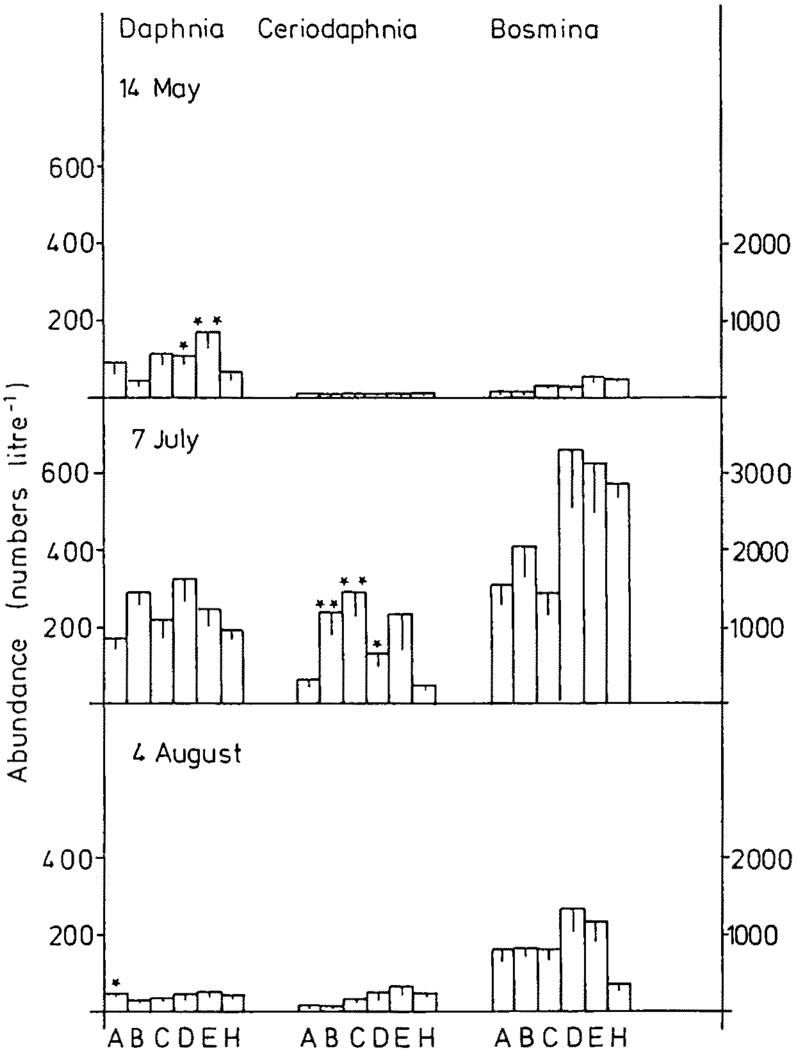


Fig. 2. Mean densities (ind. l^{-1}) of *Daphnia, Ceriodaphnia* and *Bosmina* populations found in the refuges during 1987. See Fig. 1 for explanation of lettering and significant symbols. Bars are standard errors (n = 15).

strips compared with the open-water. On August 4, only the low density brushwood bundles contained significantly more *D. hyalina* than the open-water. However densities of *D. hyalina* had, as in the previous year, generally declined in August compared with the earlier samples.

Ceriodaphnia populations were low during May and August and no significant differences between treatments were found. In July when populations were higher, significant differences in abundance were detected between treatments (Kruskal-Wallis, $P < 0.01$) and significantly more animals were found amongst the medium and high density brushwood bundles and amongst the low density netting-strips compared with the open-water. Differences between the low density brushwood bundles and high density netting strips were not significant.

In 1988 there were no significant increases of *D. hyalina* (Fig. 3) or *Ceriodaphnia* (Fig. 4) abundance amongst the refuges relative to the open-water on any of the dates sampled. *D. hyalina* abundance declined both in the open-water and amongst the refuges at the same time, towards the end of June.

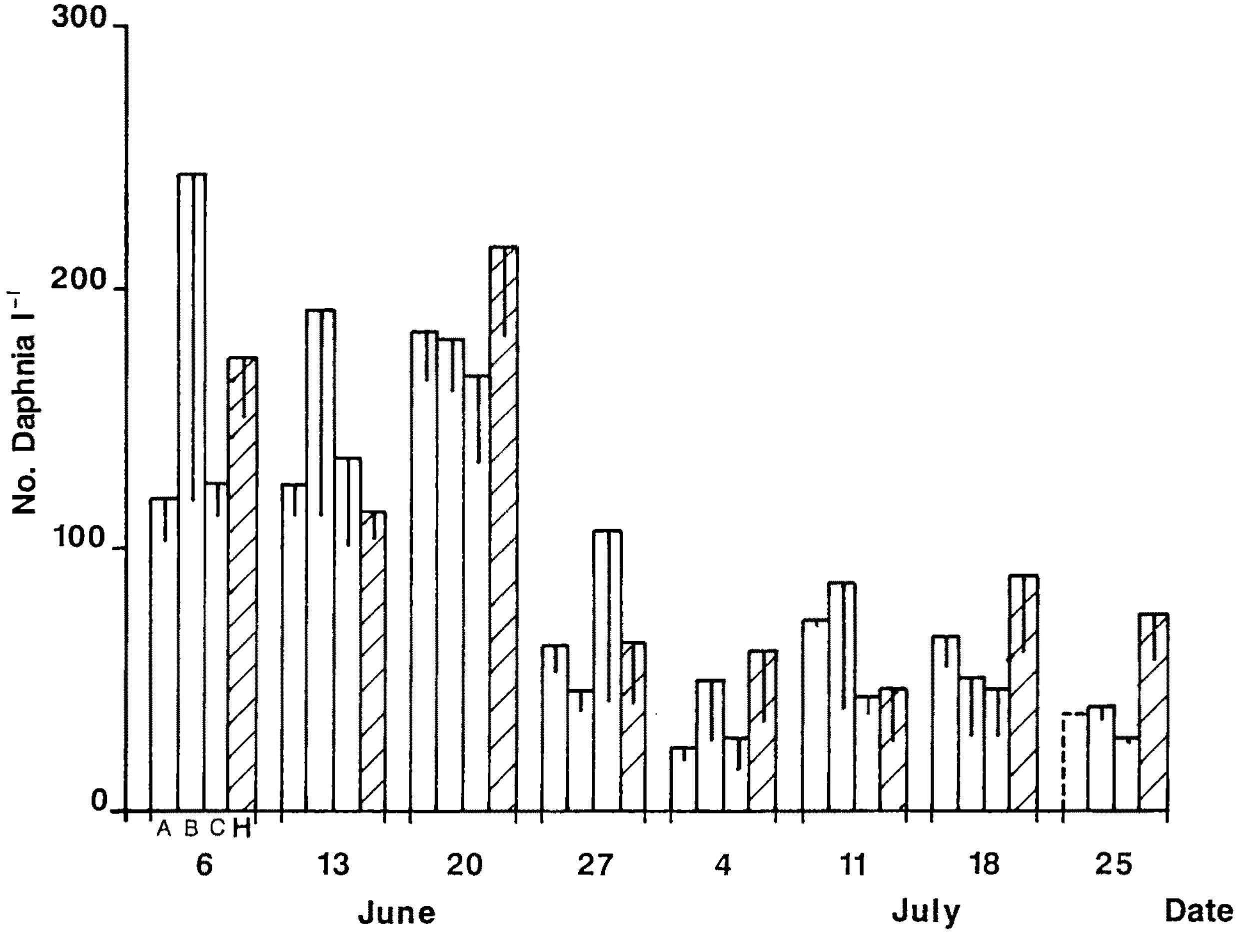


Fig. 3. Mean density of *Daphnia* populations found in the brushwood bundle refuges and open water controls during 1988. See Fig. 1 for explanation of lettering. Bars are standard errors (n = 15). Dashed line: only one refuge sampled (n = 5).

Daphnia hyalina *body-lengths*

The potential of artificial refuges for the enhancement of *D. hyalina* body-lengths was demonstrated well in 1986 and 1987 but less so in 1988. On all three dates in 1986 (Fig. 5) the median size of *D. hyalina* was greater (Table 1, $P < 0.01$) amongst the medium and high density brushwood bundles than in the open-water, but greater among the low density brushwood bundles refuge only from the August samples. Median size of *D. hyalina* from the netting-strip refuge was significantly ($P < 0.05$) larger than that in the open water during the June and July sampling and from the netting-box refuge in June. *D. hyalina* size was greater ($P < 0.05$) amongst the polypropylene rope compared with the open water on 15 July, but smaller than the control on the June and August sampling dates.

In 1987 (Table 1) there were fewer significant differences in *D. hyalina* body-lengths between the refuges and open-water control than in the previous year. Nonetheless significant differences were found between the refuges and open water in both May and July. On August 4, 1987 there were no significant increases in *D. hyalina* body-length in samples from refuge treatments compared with the open-water.

Median lengths of *D. hyalina* found amongst the refuges in the 1988 samples are shown in

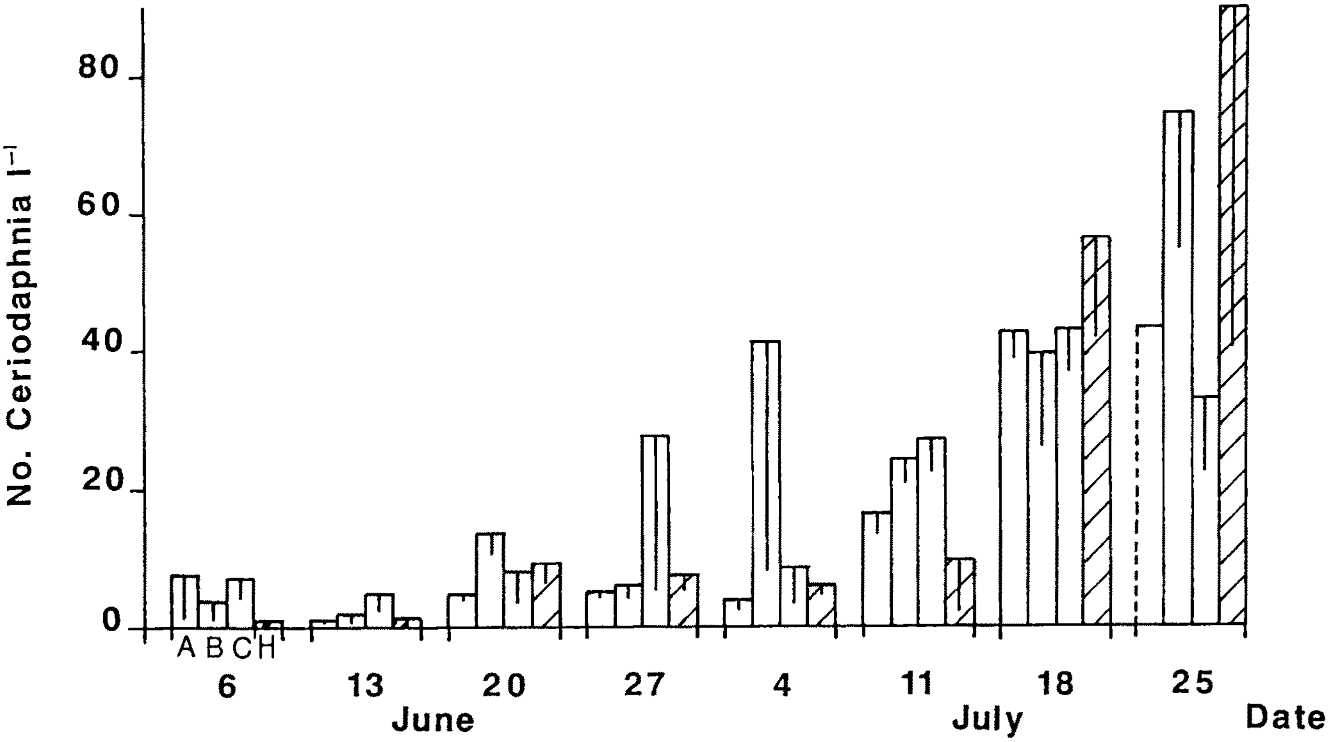
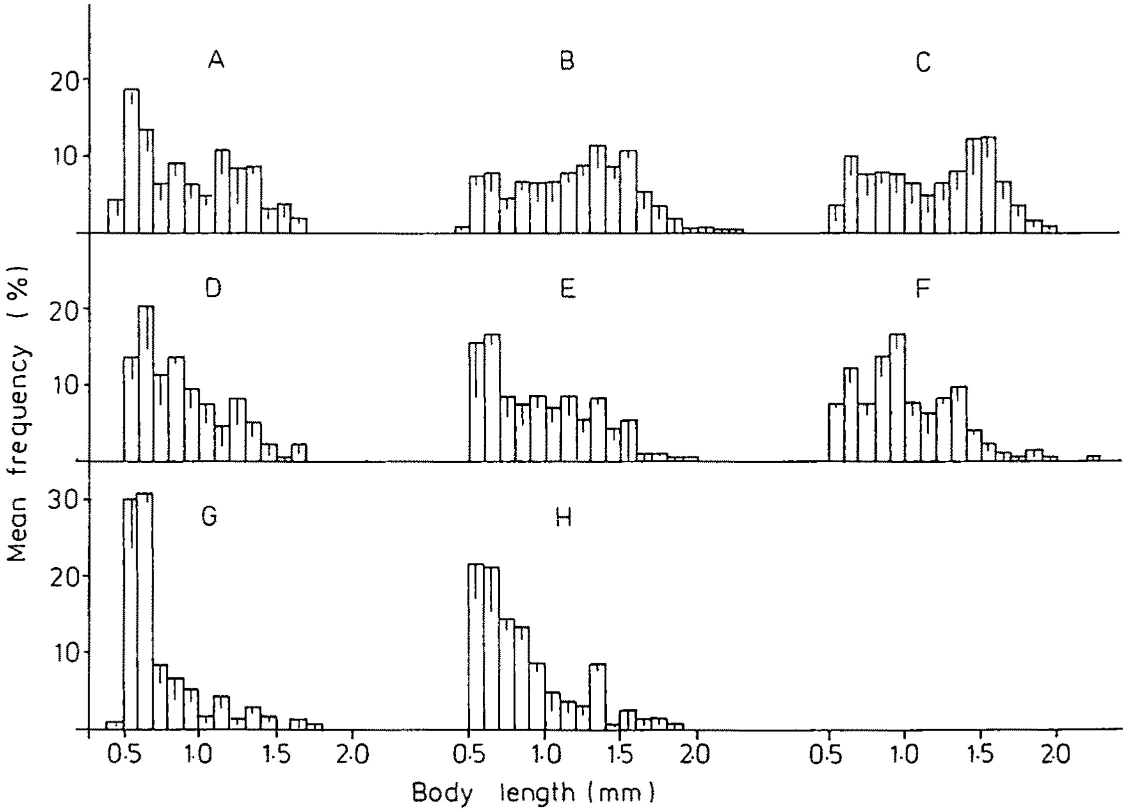


Fig. 4. Mean population density of *Ceriodaphnia* populations found in the refuges during 1988. See Fig. 1 for explanation of lettering and dashed line. Bars are standard errors (n = 15).



For caption see p. 386.

Fig. 5a.

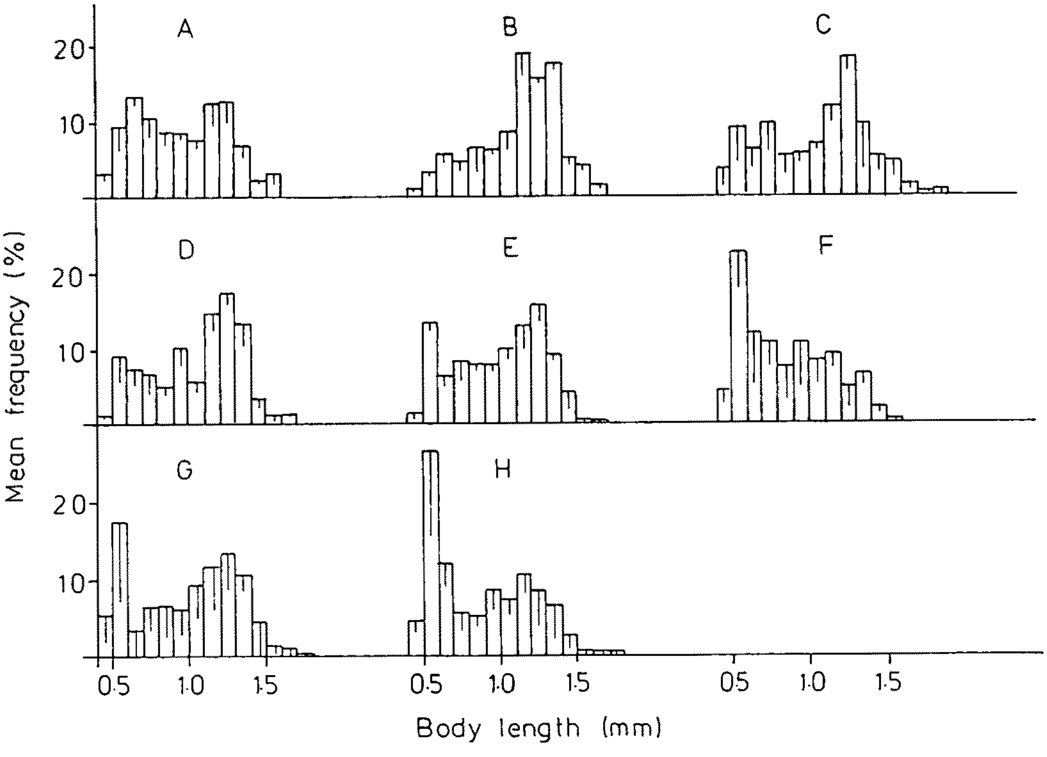


Fig. 5b.

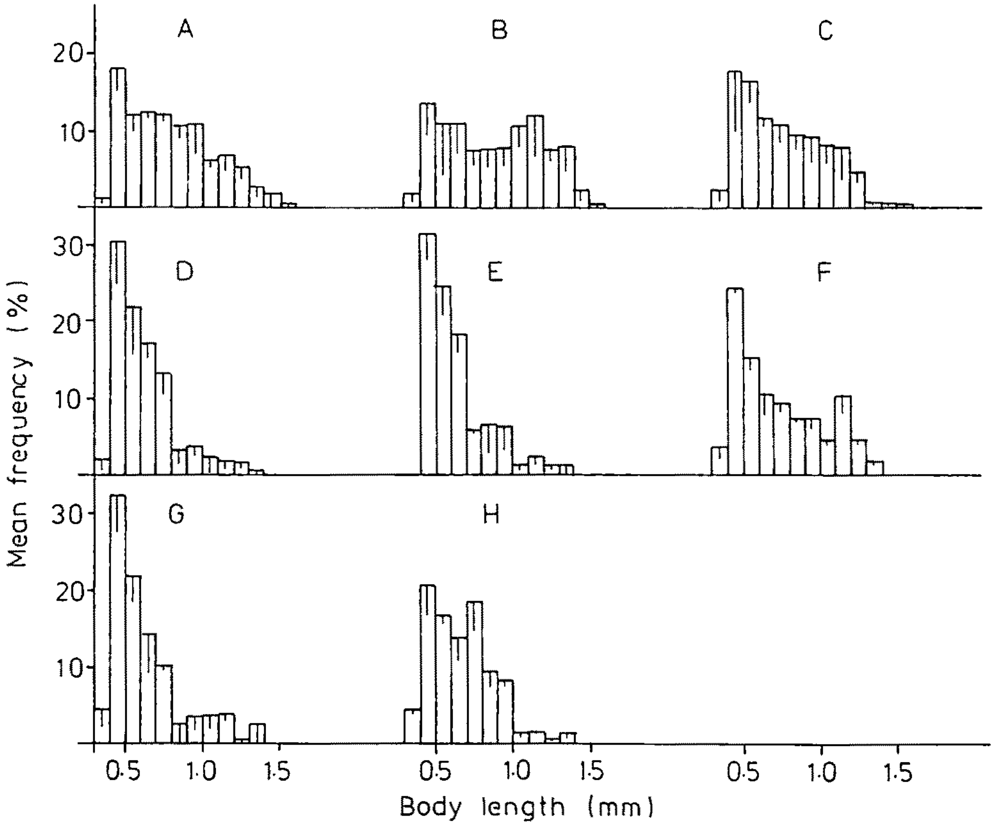


Fig. 5c.

Fig. 5. Mean frequency (%) of *Daphnia* size-classes found in the refuges on 3 June (a), 15 July (b) and 28 August (c) in 1986. See Fig. 1 for explanation of lettering. Bars are standard errors (*n* = 3, A, B, C, D, E, F and H; *n* = 4, G).

Table 1. Median lengths (mm) of *Daphnia* from populations found in the refuges and in the open water for sampling dates in 1986 and 1987. Significance of Mann-Whitney U test between refuges and open water. * 5%, ** 1%, *** 0.1%. Each size distribution based on > 50 individuals.

Refuge	1986			1987		
	3 June	15 July	28 Aug	14 May	7 July	4 Aug
A	0.85	0.95	0.75***	0.85*	0.75	0.75
B	1.25***	1.15***	0.85***	0.75	0.95**	0.65
C	1.25***	1.15***	0.75**	0.65	1.15***	0.75
D	0.85	1.15***	0.55	0.75	0.75	0.65
E	0.95	1.05*	0.55	0.85*	0.95*	0.75
F	0.95***	0.85	0.65	–	–	–
G	0.65	1.05*	0.55	–	–	–
H	0.75	0.85	0.65	0.75	0.75	0.65

Table 2. Even though body-length amongst the refuges compared with the open water significantly differed, these differences consistently represent an increase and not a decrease in size lengths amongst the refuges only between 13 June and 27 June.

Table 2. Median body-lengths (mm; $n > 200$ except A, 25 July, $n = 90$) of *Daphnia hyalina* found in the brushwood bundle refuges (A: low density, B: medium density; C: high density) and open-water (H) for sampling dates in 1988. Significant differences between refuges and open-water are designated by * 5%, ** 1%, *** 0.1%. For differences detected between medians of same value size in refuge: > open-water denoted by 1, < open-water denoted by 2.

	6 June	13 June	20 June	27 June
A	0.75***	0.75	0.75	0.90
B	0.95	0.85***	1.15***	1.05***
C	1.05	0.95***	1.15***	0.95
H	1.05	0.75	0.70	0.85
	4 July	**11 July**	**18 July**	**25 July**
A	0.65***	0.75	0.65*	0.65^{*1}
B	0.65***	0.85**	0.75	0.65^{**1}
C	0.95	0.75^{*2}	0.75	0.65
H	0.95	0.75	0.75	0.65

Discussion

Following the installation of refuges, the initial results indicated that artificial habitat structure may provide an alternative approach to biomanipulation other than the restructuring of fish populations. However, in the subsequent two years there was a marked decline in the effectiveness of the brushwood bundles and netting-strip refuges. Indeed, in the third year of the study populations of the larger-bodied Cladocera species were frequently less numerous and of smaller body-size amongst the refuges, than in the open water.

The reasons for the reduced effectiveness of the refuges following the first year are unclear, but may centre on behavioural differences between zooplanktivorous fish species present in the Broads. Fish communities in the Broads are currently dominated by small roach (*Rutilus rutilus* (L.)) which feed most effectively in the open water, with reduced feeding efficiencies amongst complicated habitat structure. Other species present in the Broads, although in smaller numbers, such as perch (*Perca fluviatilus* L.) and rudd (*Scardinius erythrophthalmus* L.) feed effectively amongst submerged habitat structure. The widespread loss of submerged aquatic plants in the Broads is likely to be a major factor in the present day composition of the fish community. It is likely, therefore, that the introduction of habitat structure into an otherwise structurally homogeneous environment would have an immediate effect of reducing overall predation rates on larger Cladocera by reducing feeding of roach within those structures. However, with time the refuges would be discovered by perch and rudd present in the system and provide these species with a suitable feeding environment. A build-up of numbers of these species within the vicinity of the refuges would consequently result in their reduced effectiveness as zooplankton refugia.

Hudsons Bay, in which Timms & Moss (1984) documented the clear water phases attributable to cladoceran grazing, is connected to Hoveton Great Broad and continues to support dense populations of lilies and submerged filamentous algal mats in association with increased water clarity. Large-bodied Cladocera have not been eliminated owing to perch predation. Reasons for the difference in refuge effectiveness between the submerged plants in Hudsons Bay and the artificial refuges in Hoveton Gt. Broad are unclear but may concern structural differences between the lilies and the artificial refuges. Illumination beneath water-lilies is probably considerably reduced and the submerged lily leaves offer a large surface area to which large Cladocera such as *Sida crystallina* (O. F. Muller) and *Simocephalus* spp. may physically adhere. These were not features of the refuges, and may be reflected in the fact that, in contrast to Hudsons Bay, large-bodied cladocerans capable of physical attachment were relatively uncommon amongst the artificial refuges. In addition, it is possible that horizontal water movements coupled with the active avoidance of substrates by some zooplankters (Siebeck, 1980) may have contributed to the reduced effectiveness of the artificial refuges. However overall physical conditions in the Broad were not noticeably different between the years of the study. It is also probably significant that the apparent effect of the refuges declined with each successive year. The artificial refuges were also permanent structures in contrast to the annual transience of aquatic plants. They may have acquired a different quality of periphyton from that on plants through a longer successional time and this may have been less favourable to littoral Cladocera.

The use of such artificial refuges therefore does not seem to be a feasible technique for the permanent enhancement of large-bodied cladoceran populations in shallow eutrophic waters. Habitat complexity alone appears insufficient in reducing size selective predation from a zooplanktivorous freshwater fish community, although it may affect the feeding efficiencies of particular species or size-classes. The scale of the experiment (100-m^2 refuges in a Broad over 300000 m^2 in area) may have been too small. Similar refuges but several hectares in area, may have obviated the edge effects of perch and rudd predation that we postulate led to progressive failure of small refuges. To test this, however, would require a very expensive restoration-scale experiment with an uncertain prognosis for success. Nonetheless the use of strategies other than whole-lake fish manipulations deserves further attention.

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