POPULATIONS AND PRODUCTION OF BENTHIC ANIMALS IN TWO CONTRASTING SHALLOW LAKES IN NORFOLK

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INTRODUCTION

The Norfolk Broads from a series of shallow lakes, fringed with reedswamp and alder carr, which were created during medieval times when peat diggings became flooded (Lambert *et al.* 1960). Clear water and a rich flora of floating and submerged macrophytes have been characteristic of the broads (Ellis 1965). Recently, there has been a marked and rapid loss of aquatic vegetation from most of the broads, with an increase in turbidity, caused primarily by excessive eutrophication (Mason & Bryant 1975c; Mason 1976a). A corresponding loss in the diversity of the fauna of the open broads has occurred. The littoral zones, in contrast, remain very diverse in animals and emergent aquatic plants and are highly productive (Mason & Bryant 1974, 1975b, c; Mason 1976a, b).

With this change from a primary production system dominated by angiosperms (which are highly seasonal) to one dominated by algae (with an extended growing season in the broads), a change in the pattern of production in the zoobenthos is to be expected. Algae, whether living or dead, are probably more readily utilizable as food by benthic animals, while the decrease in faunal diversity may lead to reduced competition for those species able to tolerate the new conditions. The present study compares the populations (from November 1971 to June 1975 inclusive) and production (from June 1973 to May 1975 inclusive) of the macroinvertebrates of a broad which has been subject to recent cultural eutrophication (Alderfen Broad) with those inhabiting a broad which still retains clear water and a good growth of macrophytes (Upton Broad).

SITES

Basic physical and chemical data for the two sites (illustrated in Fig. 1) are given in Table 1. General observations were made from March 1971 to September 1975 inclusive.

Alderfen Broad was fed by a small inlet stream, draining agricultural land, and water left the broad over a sluice to the south. The broad was surrounded by alder carr and reedswamp (total area 25·6 ha, mainly carr). Alderfen Broad was formerly rich in aquatic macrophytes and became dominated in the mid-1960s by *Ceratophyllum demersum* L. This had disappeared completely by 1970 and has since not returned, apart from a small amount of growth in 1973 and 1974 when it had probably been accidentally introduced from experimental pens. There were a few small beds of *Nymphaea alba* L. in Alderfen Broad.

Spirogyra developed extensively over the bottom of Alderfen Broad from late April
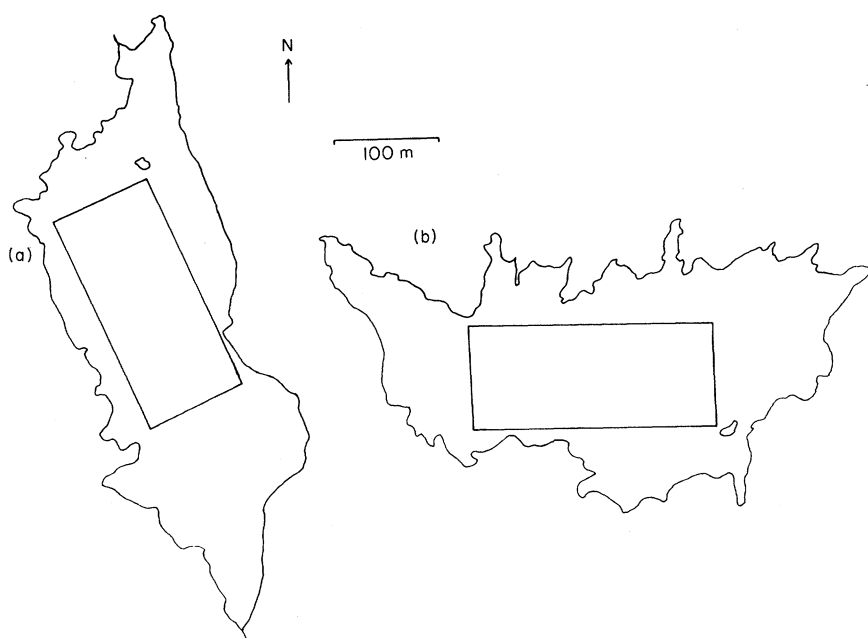
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FIG. 1. (a) Alderfen Broad and (b) Upton Broad, delimiting the areas in which sampling
took place.

each year, persisting until August. *Enteromorpha* sp. was also recorded in dense patches
in 1975. An almost permanent plankton bloom was present from summer 1971 to March
1974, when the water cleared, though it was again turbid by early April. Periods of
algal blooms then alternated with clear water until November 1974, when clear water
remained until the cessation of observations in August 1975.

Upton Broad had no inlet stream, being fed by run-off from the extensive fen carr
(113 ha) which surrounded it. There was a single outflow over a sluice at the eastern end.
The aquatic macrophyte flora was dominated by *Najas marina* L., which reached an
average density of sixteen plants m^{-2} and a peak biomass of approximately 252 g m^{-2},
dry weight (G. L. Phillips, personal communication). Growth began in early June (it
began some three weeks later in the cold spring of 1975) and the plants died back rapidly
during October, the species being annual. *Zanichellia palustris* L. formed localized dense
patches at the western end of Upton Broad and patches of *Nymphaea alba* were more
extensive than in Alderfen Broad. *Nuphar lutea* (L.) Smith, *Potamogeton pectinatus* L.
and *Chara* sp. were also recorded during the study period.

In Upton Broad *Spirogyra* was local in 1971 and 1972, but was fairly extensive in 1973
and had increased further in 1974, with a reduction in the area occupied by *Najas
marina*. During most of the period the water remained completely clear. Short periods
of turbidity occurred in July and August of several years during still, warm weather and
appeared to be due to the lifting of the bottom sediment.

The bottom sediment of Alderfen Broad was a typical, brown gyttja mud. The sediment
of Upton Broad was coarser and bright green in colour, due to the presence of a blue-
green alga, *Aphanotheca stagnina* (Spreng.) A. Braun embedded in the faecal pellets of
chironomids. This faecal pellet ooze was similar to that described from Mud Lake,
Florida, by Bradley & Beard (1969).

Table 1. *Some physical and chemical data for Alderfen and Upton Broads*

	Alderfen Broad	Upton Broad
Nat. Grid ref.	TG 354 196	TG 388 133
Area of open water (ha)	4·7	5·2
Average depth of water (m)	0·8	1·4
Water		
Range of pH	7·8–8·4	7·3–9·7
Range of total phosphorus (ppm)	0·07–0·42	0·01–0·08
Range of soluble phosphate (ppm)	0–0·42	0–0·008
Range of nitrate (ppm)	0–0·78	0–0·38
Range of chlorophyll *a* (mg m^{-3})	2·0–146·0	0·6–14·3
Sediment		
Range of pH	6·9–7·3	7·2–7·5
Particle size distribution, wet sieving, % by weight		
>2 mm	3·0	2·6
1·0–2·0 mm	2·0	2·2
0·5–1·0 mm	4·3	6·4
0·25–0·5 mm	11·8	34·7
0·125–0·5 mm	37·5	34·0
0·063–0·125 mm	41·1	20·1
% organic by weight (muffle furnace, 600° C)	62·0	54·0
Total phosphorus (mg g^{-1})	1·18	1·87
Total nitrogen (mg g^{-1})	42·24	37·76

Throughout the study period the weather remained mild. The surface of the two broads froze only rarely, the most extensive period being for ten days in December 1973. There was no development of a thermocline at either site.

METHODS

Sampling and sorting

Before a full sampling programme was developed, the influence of the littoral zone on the diversity of the benthic fauna was examined at Alderfen Broad. A series of samples was taken at intervals of 1 m away from the reed-bed in October and December 1971 and in May 1972. At distances greater than 1 m from the reed-bed the fauna was identical to that in the centre of the broad, the influence of the littoral vegetation on the fauna thus being very localized.

Sampling was conducted from a rowing-boat within the areas marked in Fig. 1. The boat was allowed to drift with the wind across the area and samples were taken at regular intervals. The areas were traversed several times with different starting points on each sampling occasion. Samples were taken at the beginning of each month at Alderfen Broad from November 1971 to June 1975 inclusive. At Upton Broad samples were initially taken once every two months from November 1971, but the frequency was increased to monthly from March 1973 to June 1975 inclusive. All samples were taken between 08.00 hours and 11.00 hours.

Thirty samples were taken each month at Alderfen Broad and twenty samples at Upton Broad, using a circular FBA pond-net (8 meshes cm^{-1}). The net was swept along the mud, with the bottom edge at a depth of 12 cm. This could be gauged accurately in Upton Broad and in Alderfen Broad when the water was clear, but the depth was only approximate on days when turbid water prevailed at Alderfen. The net, full of mud, was brought

carefully to the surface of the water. The mud was stirred and a 500-ml sub-sample was removed and placed in a polythene bag. During the growing season of *Najas* at Upton, those samples which contained large amounts of plant material were discarded before subsampling.

Sorting of samples began immediately on return to the laboratory. Samples kept overnight were stored in the dark at 5° C. Samples were passed through two sieves (500 μm and 250 μm aperture) using a gentle jet of water and the two retained fractions were washed into a white tray and sorted by hand, under strong illumination from bench lamps. All visible animals except copepods and cladocerans were removed. Worms and leeches were retained alive in dishes of filtered lake water, other animals were killed in 70% alcohol.

To obtain an estimate of sampling efficiency and to calibrate the net samples in terms of area of lake bottom, ten Birge-Ekman grab samples (2·51) and ten net samples were taken at Alderfen and Upton in May 1972. The contents of the grab were placed in a large polythene bag, stirred and a 500-ml subsample was removed. The net was sub-sampled as above. The subsamples and the remainders of the grab samples were sorted as described above for worms and chironomids. There was no significant difference between numbers of animals taken in the subsamples from the net and the grab. Neither was there any significant difference between the density of worms and chironomids in the subsamples with the remainder of the grab samples. It was therefore possible to convert the 500-ml net subsamples to an area basis knowing the surface area and volume of the grab. For animals other than worms and chironomids the conversion factor was assumed to be the same as that for chironomids.

A net was preferred to a grab for routine sampling because a grab was difficult to use from a small boat in the windy conditions prevalent in the area. The very fluid mud was also difficult to retain in a grab in a quantitative way. Grab sampling took some five times longer than net sampling.

Small worms and chironomids may not be retained efficiently in sieves (e.g. Jónasson 1955; Kajak 1963). To test the sorting efficiency for chironomids, ten samples were taken from Upton Broad in June 1974 at a time when it was known that a large number of small chironomids were present. Each sample was passed through sieves of 500 μm, 250 μm and 125 μm and the collected fractions were sorted separately. Of a total of 274 chironomids collected, 87% were retained in the 500-μm sieve, 11% in the 250-μm sieve and only 2% in the 125-μm sieve. The procedure was repeated for worms in August 1974 with ten samples collected from Alderfen Broad at a time when it was known that large numbers of small tubificid worms were present. Of a total of 192 worms collected, 82% were retained by the 500-μm sieve, 17% by the 250-μm sieve and only 1% by the 125-μm sieve. It was concluded that the method of sorting adopted in the routine sampling programme was adequate.

Mean monthly water temperatures were determined using Hartley integrating thermometers (Hartley & MacLaughlan 1969) permanently on site.

Biomass and respiration

For production estimates the lengths of all animals collected in samples were recorded from June 1973 to May 1975 inclusive. Worms and leeches were anaesthetized in menthol and the maximum length determined. The other animals, stored in alcohol, were measured within 48 h of sorting. For most species, the maximum length, excluding respiratory appendages, was measured. Caddis flies were removed from their cases. The maximum

shell diameter was measured in *Pisidium*, *Valvata* and planorbids and the maximum shell height for *Bithynia* and *Potamopyrgus*.

To determine length:weight relationships, animals were collected from the field and kept in filtered lake water at 10° C for two days to allow them to empty their guts. They were then measured and dried to constant weight in a vacuum oven at 80° C. Weighings were made on a Cahn G-2 electrobalance.

Respiration/length relationships were determined at 20° C and 8° C. Animals were collected from the field and acclimatized at the experimental temperature for five days prior to an experiment. The experimental medium was water from Alderfen Broad. The water was filtered, autoclaved and refiltered on the day preceding an experiment and was re-aerated overnight. For experiments at 20° C animals were placed in 7·5-ml vials filled with water at 100% saturation and tightly stoppered. After a period of 6–24 h (depending on the size of the animal) the partial pressure of oxygen in the water of each vial was determined using a thermostatted oxygen-electrode system (Radiometer, Copenhagen) at 20° C, the sample being injected through a hypodermic syringe. At 8° C the oxygen electrode was found to be unresponsive. Respiration rates at 8° C were therefore determined using standard Warburg manometry. For small species the respiration rate of up to ten animals of similar size placed together in one vessel had to be determined. At the end of the experiments animals were measured as above.

RESULTS

It proved impossible to routinely identify a number of groups to species and these are recorded as groups, at different levels of identification, in the following tables. From November 1971 to June 1975 inclusive, twenty-two species or groups were recorded from Alderfen Broad, of which seven could be described as of regular occurrence. From Upton Broad, over the same period, forty species or groups were recorded, seventeen occurring regularly.

The authorities of those species recorded in the last two years of the study are given in Tables 6 and 7.

Populations

Turbellaria and Hirudinea. Mesostoma ehrenbergi, Polycelis tenuis and *Planaria torva* (Müll) were recorded occasionally in the benthos of Upton Broad, though all were common in the littoral zone at both sites.

Helobdella stagnalis in Upton Broad occurred in low numbers through most of the year, with an increase in population (max. 141 m^{-2}) during the late spring and early summer. The species was sporadic in Alderfen Broad. Three other species of leeches (*Piscicola geometra, Erpobdella octaculata* and *Glossiphonia complanata*) were recorded in the benthos as vagrants. They were abundant in the littoral zone.

Oligochaeta. Very small numbers of *Tubifex tubifex* (Müll) and *Rhyacodrilus coccineus* (Vejdovsky) were recorded in the benthos of Alderfen Broad in the winter of 1971–72, but they subsequently disappeared, though they were still present in the littoral zone. The dominant oligochaete in Alderfen was *Potamothrix hammoniensis*. The population (Fig. 2) varied over the forty-four month period from 559±664 m^{-2} (mean±95% confidence limits, September 1973) to 22 531±5636 (November 1974). The mean coefficient of variation over the period was 21% with a range of 8·9% to 59·4%, the larger values occurring when the density was less than 1000 m^{-2}. The population was aggreg-
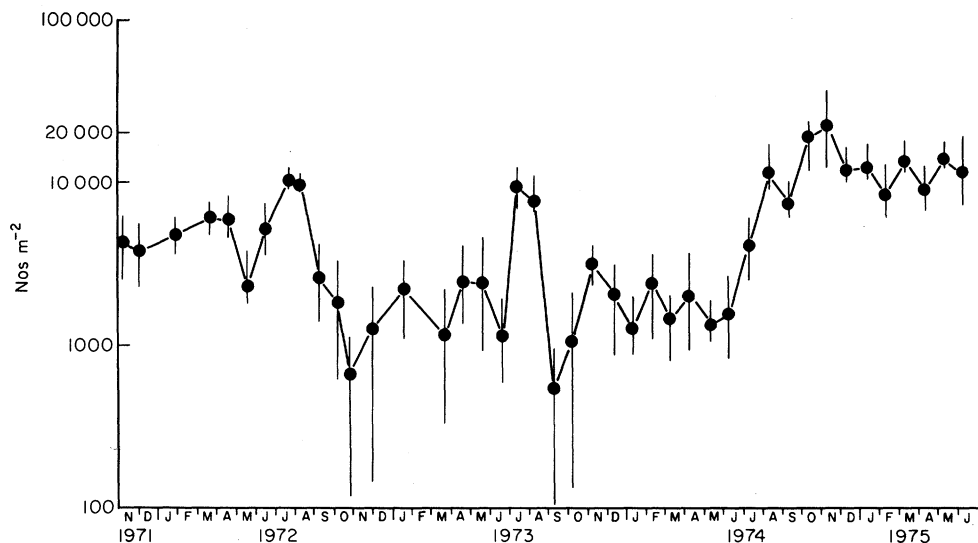
FIG. 2. The population density (nos m^{-2}) of *Potamothrix hammoniensis* in Alderfen Broad, November 1971–June 1975.

ated at all times. In all three seasons the population showed an increase in summer, and in 1972 and 1973 declined sharply in late summer, probably due to deoxygenated conditions or hydrogen sulphide production in the mud (the mud was noted as unusually foetid in September 1973 when samples were taken). There was some recovery of the population in the winters of both years. In 1974 the peak in population in the summer was higher than in previous years and continued increasing into the autumn. The population decline was delayed and smaller resulting in a higher over wintering population.

An examination of the size–frequency distribution of *P. hammoniensis* indicated that
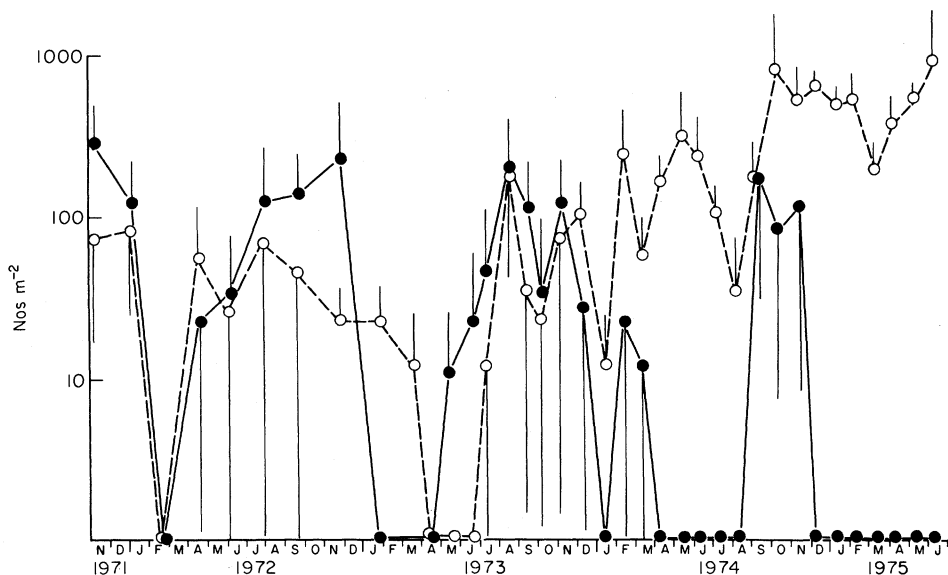

FIG. 3. The population densities (nos m^{-2}) of *Potamothrix hammoniensis* (○) and *Stylaria lacustris* (●) in Upton Broad. November 1971–June 1975.

some recruitment to the population took place over much of the year, but not in the coldest part of the winter. Little recruitment occurred in early spring and most was in the early summer, and also in the autumn of 1974. Growth occurred through the autumn and winter. Large worms disappeared in July and August, suggesting a post breeding mortality. The modal size of the population was smaller when the density was higher in 1974–75.

The naidid *Dero digitata* was first reported in Alderfen Broad in February 1974 and may have been introduced with *Ceratophyllum demersum* (see page 147). The population built up to a peak of 350 ± 246 m^{-2} in July 1974 and was last recorded in November 1974 by which time the macrophyte had also disappeared. A small population (peak 47 m^{-2}) *of Stylaria lacustris* was present in Alderfen Broad from May to July 1974, though the species was abundant in the littoral.

In Upton Broad, *Potamothrix hammoniensis* was the only tubificid recorded (Fig. 3) and the population was generally low (peak 903 ± 804 m^{-2}). There was a general trend of increase over 1974 and 1975, including the 1974–75 winter and in this respect the population resembled that of Alderfen Broad.

Stylaria lacustris in Upton Broad disappeared for a period in all four winters (Fig. 3). The population increased in the springs of 1972 and 1973 reaching a peak in the summer (1973) or early autumn (1972). In 1974 the species did not appear until August and in 1975 it had not appeared by June, when sampling ended. *Stylaria* was abundant in the littoral, from which it may recolonize the benthos each year; its presence may be related to growth of macrophytes, though the increase in the first two years of the study occurred before the germination of *Najas*.

Enchytraids occurred in small numbers in both broads, mainly in the autumn and winter in Alderfen (maximum density 58 m^{-2}) and in the summer in Upton (maximum density 44 m^{-2}).

Mollusca. No molluscs were recorded in the benthos of Alderfen Broad though they were abundant in the littoral (Mason & Bryant, 1974). At Upton Broad (see Fig. 4)
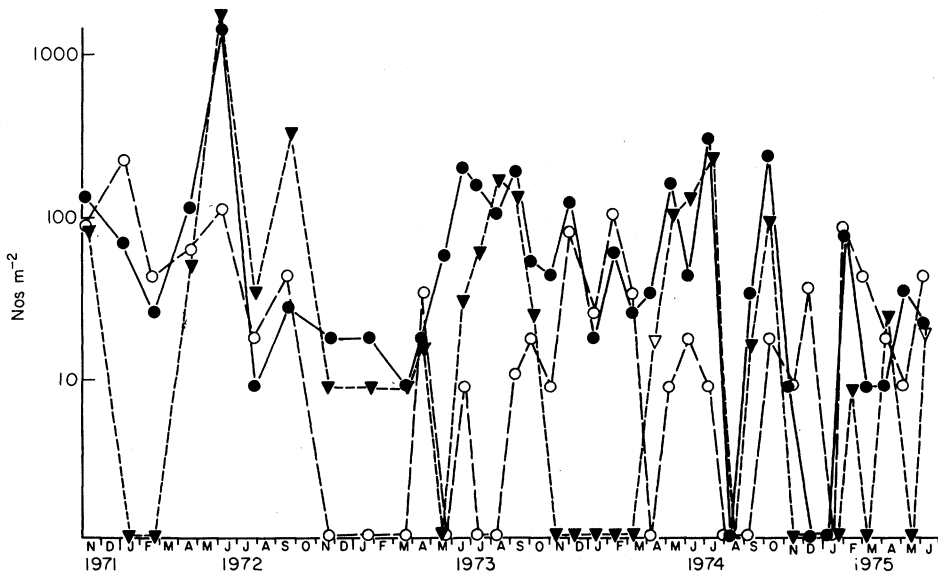

Fig. 4. The population densities (nos m^{-2}) of *Valvata piscinalis* (●), *Bithynia tentaculata* (○) and *Pisidium casertanum* (▼) in Upton Broad, November 1971–June 1975.

Valvata piscinalis was usually the most abundant species, being recorded on most samp-
ling dates. The population reached a peak in the spring and early summer of each year.
Bithynia tentaculata was more irregular in occurrence and no particular pattern emerged.
Planorbis albus also showed peaks in spring and early summer (maximum 259 ± 154 m^{-2}
in June 1972) and, except for 1971–72, was absent for a period during the winter. The
bivalve *Pisidium casertanum* (Fig. 4) showed a similar pattern, being most abundant in
spring and early summer and absent for a period during the winter.

   Potamopyrgus jenkinsi was first recorded in Upton Broad in August 1973 and the
highly aggregated, local population reached a peak density of 590 ± 1142 m^{-2} in October
1974. *Lymnaea peregra* (Müll), *Segmentina nitida* and *Planorbis leucostoma* occurred
occasionally.

   Crustacea. Ostracods, which were not further identified, were the only crustaceans to
be recorded regularly in the benthos of both broads (copepods and cladocerans were not
collected). The populations were relatively small, only once exceeding 100 m^{-2} (at
Alderfen Broad in January 1973). They fluctuated irregularly. *Asellus aquaticus*, *A.
meridianus* and *Gammarus pulex* were recorded occasionally.

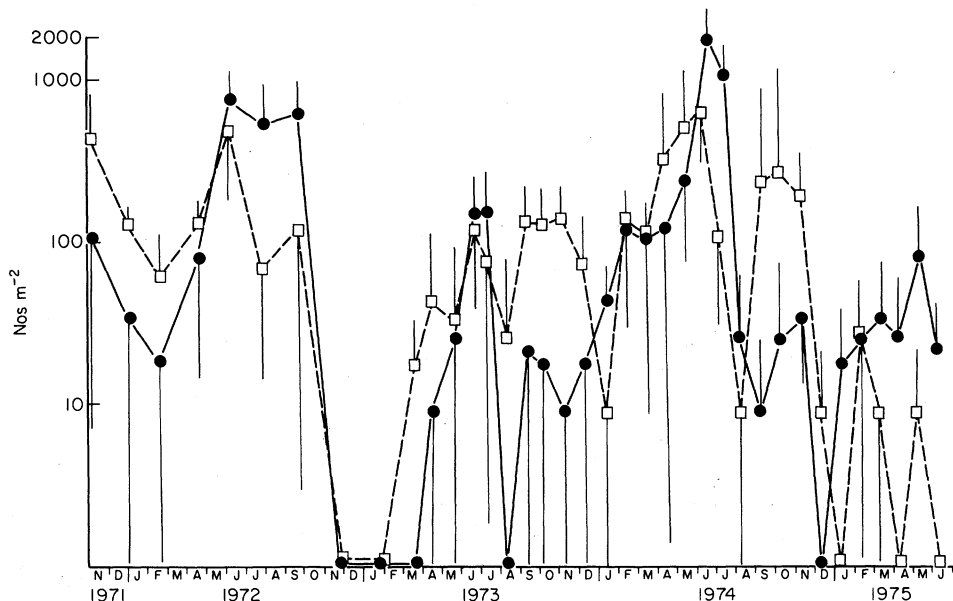   *Ephemeroptera. Caenis horaria* in Upton Broad (Fig. 5) was scarce or absent during the

FIG. 5. The population densities (nos m^{-2}) of *Caenis horaria* (●) and *Mistacides longicornis*
(□) in Upton Broad, November 1971–June 1975.

winter months. The population reached a peak during early summer, for instance of
1857 ± 942 m^{-2} in June 1974. The animals present in spring may have emigrated from
the littoral zone. The few individuals present in the benthos in winter grew very little,
but growth was rapid during the spring.

   Cloëon dipterum occurred in small numbers in the benthos of Upton Broad and
Caenis horaria in Alderfen Broad (where it was abundant in the reedbed).

   Trichoptera. Mistacides longicornis in Upton Broad (Fig. 5) reached a peak during the
late spring and summer (peak density 651 ± 306 m^{-2} in June 1974), though an increase
was not apparent in the late spring of 1975. The few animals which remained in the

benthos in winter were small (<6 mm long) and growth began during April. As there
was no increase in the small numbers of small instars in the benthos in the spring, it
can be assumed that the population increase was due to emigration from the littoral
zone.

Phryganea grandis L., *Cyrnus flavidus* and *Limnephilus* sp. were recorded very in-
frequently in the benthos of Upton and/or Alderfen Broads.

Diptera. The population densities of chironomids are illustrated for Alderfen Broad
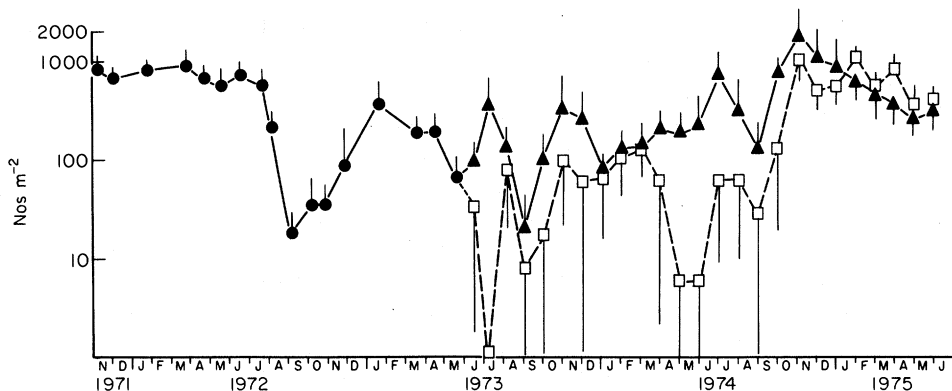in Fig. 6 and for Upton Broad in Fig. 7. No quantitative identifications were made until

FIG. 6. The population densities (nos m^{-2}) of chironomids at Alderfen Broad, November
1971–June 1975. (● total, ▲ *Chironomus plumosus*, □ Tanypodinae).
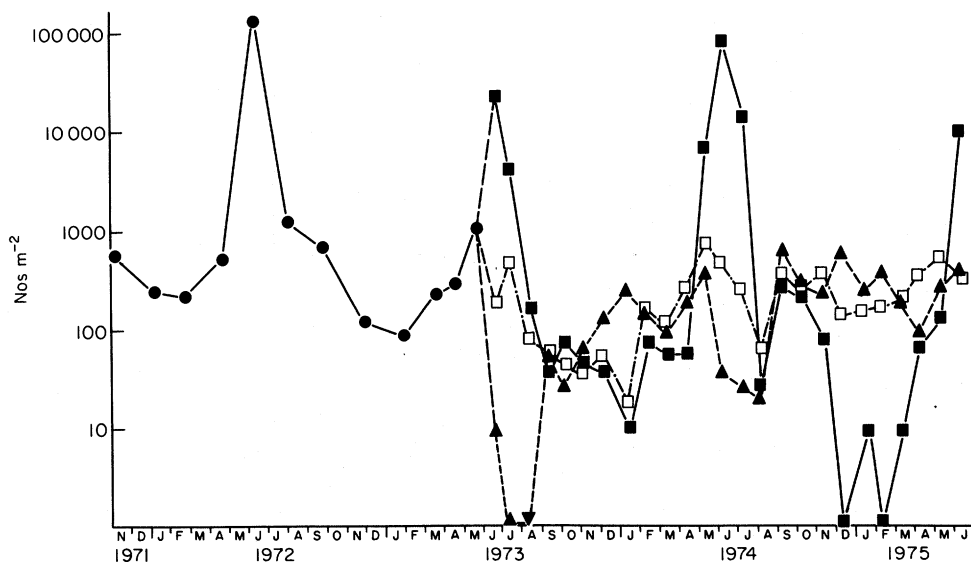
FIG. 7. The population densities (nos m^{-2}) of chironomids at Upton Broad, November
1971–June 1975. (● total, ■ *Tanytarsus holochlorus*, ▲ *Chironomus tentans*, □ Tanypodinae.

the production study began in 1973. The Tanypodinae were not identified to species
quantitatively, though *Anatopynia* sp. was abundant at both sites.

Chironomus plumosus was the dominant chironomid in Alderfen Broad. In 1973
and 1974 the population reached peaks (of 387±112 m^{-2} and 704±332 m^{-2} respec-

tively) in early summer, thereafter falling sharply (to 20 ± 24 m^{-2} and 129 ± 86 m^{-2} respectively) on eclosion. In 1974 there was a further peak in autumn (1807 ± 260 m^{-2}) and the population declined steadily through the winter and following spring. An examination of size–frequency distributions indicated that there were two generations per year. The emergence of adults extended through the spring and summer.

Chironomus tentans replaced *C. plumosus* in Upton Broad, *C. tentans* being restricted in Alderfen Broad to the littoral zone where it was abundant. The *C. tentans* population built up to a peak during the winter and early spring, (e.g. 369 ± 158 m^{-2} in May 1974 and 590 ± 350 in December 1974) and fell sharply during June to August, when the main hatch occurred. Some hatching however occurred over most of the spring and summer. An examination of size–class distributions suggested that two generations of *C. tentans* were present.

Through most of the year the population of *Tanytarsus holochlorus* in Upton Broad was very low (<100 m^{-2}) but it began to increase rapidly in May to reach an enormous peak in June (e.g. $130\,000\pm76\,000$ m^{-2} in 1973, $84\,270\pm31\,440$ m^{-2} in 1974) when the whole of the bottom of the broad was a mass of green tubes formed by the midge. The population declined in July, on emergence, and by August was back to its low level. During July, especially after heavy rain, the edges of the broad were covered with a thick scum composed of the corpses of adult *Tanytarsus*. As there were so few larvae in the mud during the winter and there was no large reservoir of the species in the littoral, the majority must have developed very rapidly from eggs hatched in May and June. It is conceivable that the few larvae present during the winter were of a different species of *Tanytarsus*, though adults were not successfully reared from winter larvae to confirm this.

Polypedilum sp., *Micropsectra* sp. and *Paratanytarsus* sp. occurred in Alderfen Broad in small numbers (<30 m^{-2} total) from November 1973 to November 1974 inclusive, and were probably introduced on *Ceratophyllum demersum* (page 147). *Dicrotendipes* sp. was first recorded in Upton Broad in November 1974 and built up to a peak population of 572 ± 534 m^{-2} in February 1965.

The larval population of predatory Tanypodinae in Alderfen Broad showed two declines, in spring and in summer. The summer hatch was dominated by *Anatopynia* sp. The tanypod peak in Upton Broad occurred in Spring, followed by a decline during the summer, which carried on into the winter in 1973. There was no evidence of two peaks of hatching.

Orthocladinae were first recorded in the benthos of Upton Broad in September 1974 and were then regular in small numbers (up to 62 m^{-2}). They occurred only once in Alderfen Broad.

Chaoborus flavicans was present in both broads in relatively small numbers (maxima 299 ± 134 m^{-2}, November 1971 in Alderfen and 199 ± 102 m^{-2}, December 1973 Upton). The larvae occurred chiefly during the winter and were absent for a period during the summer. However, they were very scarce in Alderfen Broad during the winters 1972–73 and 1974–75. In Upton *C. flavicans* was also scarce in 1972–73 but not in the latter winter.

Ceratopogonids were not routinely identified to species, though the large *Bezzia nobilis* occurred in both broads. There were two larval peaks in Upton Broad, one in the autumn/winter and one in the spring. Numbers were fairly small, with a peak of 211 ± 144 m^{-2} in May 1974. At Alderfen Broad the pattern of peaks was less distinct and the population was much smaller.

Ptychoptera albimana occurred infrequently in the benthos of Alderfen Broad and

Culex pipiens infrequently in Upton Broad, though both species were abundant in the reedbeds.

Other insects. The damselfly larvae *Ischnura elegans* and *Erythromma najas* were recorded in small numbers in the benthos of Upton Broad (maximum populations 26 m^{-2} and 22 m^{-2} respectively). *Ischnura elegans* occurred sporadically in Alderfen Broad (maximum 6 m^{-2}). The larvae of the beetle *Gyrinus* sp. were occasional in Upton Broad. The heteropteran *Sigara falleni* was recorded in small numbers (maximum 44 m^{-2}) each summer in Upton Broad and occasionally in Alderfen Broad, while *Corixa punctata* was also recorded from Upton. All these species were abundant in the littoral zone of both broads.

Hydracarina. Several unidentified species occurred in both broads and winter and summer peaks were noted in the populations. Peak populations were 188 ± 88 m^{-2} in January 1973 at Alderfen Broad, and 264 ± 140 m^{-2} in June 1974 at Upton Broad.

Temperature

The mean monthly water temperatures from May 1973 to June 1975 inclusive for Alderfen and Upton Broads are shown in Table 2.

Biomass, respiration and production

For a number of uncommon species and for a few more common species which disappeared before measurements were made, the relationships between biomass, respiration and length were not determined. In these cases biomass and respiration was estimated from the relationships of the following species most similar in size and taxonomy

Table 2. *Integrated mean monthly temperatures (° C), May 1973–June 1975 inclusive at Alderfen and Upton Broads*

	Alderfen	Upton		Alderfen	Upton
May 1973	13·5	15·0	June 1974	16·0	17·0
June 1973	18·0	18·0	July 1974	16·0	14·5
July 1973	17·5	17·0	August 1974	15·5	15·5
August 1973	18·0	18·5	September 1974	12·0	13·1
September 1973	12·0	12·0	October 1974	7·0	8·0
October 1973	11·5	11·0	November 1974	4·0	7·0
November 1973	7·0	4·0	December 1974	2·5	4·5
December 1973	1·0	2·5	January 1975	3·0	5·0
January 1974	1·5	3·5	February 1975	3·5	5·1
February 1974	4·5	5·0	March 1975	4·5	4·0
March 1974	6·5	7·0	April 1975	8·0	9·1
April 1974	11·5	12·0	May 1975	11·0	11·5
May 1974	13·0	13·5	June 1975	16·0	17·0

(uncommon species given in parentheses): *D. lacteum* (other flatworms); *H. stagnalis* (other leeches); *P. albus* (other planorbids); *A. aquaticus* (*A. meridianus*); *C. flavidus* (*Limnephilus* sp.; *Gyrinus* sp.); *C. plumosus* (*Ptychoptera albimana*); *Dicrotendipes* sp. (*Polypedilum* sp.); *T. holochlorus* (*Micropsectra* sp.; *Paratanytarsus* sp.); *C. flavicans* (*Culex pipiens*); *E. najas* (*Ischnura elegans*); *S. falleni* (*Corixa punctata*).

In addition the biomass of *Dero digitata* was determined from *Stylaria lacustris* and the respiration of *Dero digitata* and *Stylaria lacustris* at 8° C from *Potamothrix hammoniensis* at 8° C.

The relationships between dry weight and length were determined for twenty-six taxa (Table 3). No relationships were found for ostracods and mites, so the following means

Table 3. *Relationships between dry wt* (y *mg*) *and length* (x *mm*) (*log base* 10)

	Regression			r	n
Dendrocoelum lacteum	log (y × 10)	= 0·0869 x	+0·4924	0·81	17
Potamothrix hammoniensis	log (y × 100)	= 1·9359 log x	−1·0579	0·89	49
Stylaria lacustris	log (y × 100)	= 1·2059 log x	−0·1751	0·88	22
Enchytraeidae	log (y × 10)	= 0·0404 x	−0·4015	0·86	10
Helobdella stagnalis	log (y × 10)	= 0·1972 x	−0·6046	0·85	10
Bithynia tentaculata	log (y × 10)	= 2·6800 log x	+0·1700	0·71	23
Potamopyrgus jenkinsi	log (y × 10)	= 0·2176 x	+0·6885	0·94	16
Valvata piscinalis	log y	= 2·9487 log x	−0·9228	0·89	27
Planorbis albus	log (y × 10)	= 0·5199 x	−0·1893	0·69	13
Pisidium casertanum	log (y × 10)	= 0·4846 x	−0·1236	0·86	24
Asellus aquaticus	log (y × 10)	= 0·1934 x	−0·0302	0·90	29
Gammarus pulex	log (y × 10)	= 0·1300 x	+0·3300	0·95	18
Cloëon dipterum	log (y × 1000)	= 0·3001 x	+0·9323	0·93	19
Caenis horaria	log (y × 100)	= 0·3087 x	+0·1241	0·94	21
Erythromma najas	log (y × 10)	= 0·0915 x	+0·3967	0·80	35
Sigara falleni	log (y × 10)	= 0·1725 x	+0·2400	0·82	29
Mystacides longicornis	log (y × 100)	= 0·2165 x	+0·2972	0·94	32
Cyrnus flavidus	log (y × 10)	= 0·1102 x	+0·3443	0·84	18
Ceratopogonidae	log (y × 100)	= 0·1537 x	+0·3376	0·82	34
Chaoborus flavicans	log (y × 100)	= 0·1321 x	+0·1464	0·87	18
Chironomus plumosus	log (y × 10)	= 0·0769 x	−0·1377	0·94	36
Chironomus tentans	log (y × 10)	= 0·0687 x	−0·0113	0·98	33
Dicrotendipes sp	log (y × 100)	= 0·2042 x	−0·2104	0·95	22
Tanytarsus holochlorus	log (y × 100)	= 0·2384 x	−0·3942	0·95	56
Tanypodinae	log (y × 100)	= 0·2011 x	+0·1677	0·94	23
Orthocladinae	log (y × 10)	= 0·0497 x	+0·3277	0·42	26

(±95% confidence limits) were calculated; Ostracoda 0·44±0·04 mg dry weight (n = 29); Hydracarina 0·28±0·14 mg dry weight (n = 30).

The relationships between respiration rates and length were determined for twenty-one taxa at 8° C and 20° C (Table 4). As the regressions were not significant for six taxa as either of these temperatures, means and 95% confidence limits were calculated (Table 5).

These relationships were used to calculate the biomass and the respiration (in conjunction with population estimates and field temperatures) for each species in each month from June 1973 to May 1975 inclusive at Alderfen and Upton Broads. The periods June 1973–May 1974 inclusive and June 1974–May 1975 inclusive, are designated year 1 and year 2 respectively, and estimates were made of the monthly biomass of each taxon (Tables 6 and 7) and the total monthly biomass (Table 8). Estimates were also made of the mean annual respiration of each taxon (Tables 9 and 10) and the total monthly respiration for the two sites (Fig. 8).

Annual production (Tables 9 and 10) was calculated from annual respiration using eqn (6) of McNeil & Lawton (1970).

Potamothrix hammoniensis, *Chironomus plumosus* and Tanypodinae accounted for most of the monthly biomass and respiration at Alderfen Broad. The biomass and respiration of these was markedly higher in the second year of the study. At Upton Broad chironomids were responsible for much of the monthly biomass and respiration. *Tanytarsus holochlorus* and *Chironomus tentans* showed an increase in biomass and respiration in year 2, but there was no increase in tanypods. Molluscs also formed a high proportion of the total biomass in Upton Broad, but they were less important in terms of respiration; biomass and respiration of molluscs was lower in year 2.

At Alderfen Broad (Table 8) there was a small peak in biomass in the summer and a

Table 4. *Relationships between oxygen consumption* ($\mu l\ h^{-1}$) *and length* (x *mm*) (*log base* 10)

	Regression	r	n
8° C			
Dendrocoelum lacteum	$\log(y \times 10) = 0.0502\ x + 0.5485$	0·59	15
Potamothrix hammoniensis	$\log(y \times 100) = 0.0083\ x + 1.4584$	0·35	54
Enchytraeidae	$\log(y \times 10) = 0.0032\ x + 0.3305$	0·31	10
Helobdella stagnalis	$\log(y \times 100) = 0.2215\ x - 0.3137$	0·83	10
Bithynia tentaculata	$\log(y \times 10) = 0.0215\ x + 0.3188$	0·23	26
Valvata piscinalis	$\log(y \times 100) = 0.3323\ x + 0.0475$	0·56	18
Planorbis albus	$\log(y \times 10) = 0.1108\ x + 0.2632$	0·88	10
Pisidium casertanum	$\log(y \times 100) = 0.0602\ x + 1.2200$	0·43	19
Asellus aquaticus	$\log(y \times 100) = 0.1407\ x + 0.7926$	0·88	23
Gammarus pulex	$\log(y \times 10) = 0.1164\ x + 0.0657$	0·94	27
Cloëon dipterum	$\log(y \times 10) = 0.1368\ x + 0.0165$	0·43	27
Caenis horaria	$\log(y \times 100) = 0.1992\ x + 0.9437$	0·29	24
Erythromma najas	$\log(y \times 10) = 0.0455\ x + 0.3553$	0·63	22
Mystacides longicornis	$\log(y \times 100) = 0.1924\ x + 0.6318$	0·59	36
Cyrnus flavidus	$\log(y \times 10) = 0.0715\ x + 0.1799$	0·63	28
Chironomus plumosus	$\log(y \times 100) = 0.0515\ x + 1.0855$	0·70	49
Chironomus tentans	$\log(y \times 10) = 0.0359\ x + 0.1387$	0·59	25
Tanytarsus holochlorus	$\log(y \times 100) = 0.0709\ x + 0.8816$	0·32	46
Orthocladinae	$\log(y \times 100) = 0.0099\ x + 1.3960$	0·01	27
20° C			
Dendrocoelum lacteum	$\log(y \times 10) = 0.0942\ x + 0.5973$	0·45	14
Potamothrix hammoniensis	$\log(y \times 10) = 0.0101\ x + 0.4685$	0·59	60
Dero digitata	$\log(y \times 10) = 0.0923\ x - 0.1510$	0·83	18
Stylaria lacustris	$\log(y \times 10) = 0.0365\ x + 0.3468$	0·68	22
Enchytraeidae	$\log(y \times 10) = 0.0102\ x + 0.6467$	0·40	10
Helobdella stagnalis	$\log(y \times 10) = 0.0334\ x + 0.6395$	0·47	31
Bithynia tentaculata	$\log(y \times 10) = 0.0767\ x + 0.6365$	0·50	27
Valvata piscinalis	$\log(y \times 10) = 0.4271\ x - 0.4575$	0·87	21
Planorbis albus	$\log(y \times 10) = 0.2041\ x + 0.1305$	0·72	20
Pisidium casertanum	$\log(y \times 100) = 0.0924\ x + 1.0070$	0·22	21
Asellus aquaticus	$\log(y \times 10) = 0.0980\ x + 0.6551$	0·84	25
Gammarus pulex	$\log(y \times 10) = 0.1219\ x + 0.3025$	0·88	12
Cloëon dipterum	$\log(y \times 10) = 0.0584\ x + 0.4767$	0·35	16
Caenis horaria	$\log(y \times 10) = 0.0369\ x + 0.6280$	0·79	44
Erythromma najas	$\log(y \times 10) = 0.0837\ x + 0.4291$	0·95	21
Mystacides longicornis	$\log(y \times 10) = 0.2516\ x - 0.4524$	0·95	18
Cyrnus flavidus	$\log(y \times 10) = 0.0699\ x + 0.5356$	0·84	11
Chironomus plumosus	$\log(y \times 10) = 0.0493\ x + 0.5131$	0·93	38
Chironomus tentans	$\log(y \times 10) = 0.0369\ x + 0.6280$	0·79	34
Tanytarsus holochlorus	$\log(y \times 10) = 0.0724\ x + 0.2835$	0·53	41
Orthocladinae	$\log(y \times 10) = 0.1077\ x + 0.1033$	0·44	25

Table 5. *The oxygen consumption* ($\mu l\ h^{-1}$) *of animals whose respiration rate was independent of size* ($\pm 95\%$ *confidence limits*)

	8° C		20° C	
	$\mu l\ h^{-1}$	n	$\mu l\ h^{-1}$	n
Potamopyrgus jenkinsi	0·23 ± 0·02	23	0·62 ± 0·28	12
Ostracoda	0·20 ± 0·06	10	0·33 ± 0·10	10
Sigara falleni	1·19 ± 0·26	18	4·81 ± 0·64	15
Ceratopogonidae	0·17 ± 0·08	20	0·45 ± 0·12	22
Chaoborus flavicans	0·21 ± 0·08	16	0·43 ± 0·42	46
Dicrotendipes sp	0·26 ± 0·04	23	0·86 ± 0·18	26

Table 6. *The mean monthly biomass (mg dry weight m^{-2}) of animals at Alderfen Broad*

	Year 1	Year 2
Potamothrix hammoniensis (Michaelson)	1536·7	4835·1
Dero digitata (Müll)	3·2	2·7
Stylaria lacustris (L)	0·1	0·5
Enchytraeidae	22·0	14·0
Helobdella stagnalis (L)	0	4·1
Erpobdella octoculata (L)	0	14·4
Glossiphonia complanata (L)	0	2·9
Ostracoda	3·1	2·8
Chironomus plumosus L	503·9	1361·6
Polypedilum sp	3·5	0
Micropsectra sp	3·7	1·5
Paratanytarsus sp	0·8	0
Orthocladinae	0	0·3
Tanypodinae	70·4	655·7
Ptychoptera albimana (Fabr)	0	0·2
Chaoborus flavicans (Meig)	7·9	1·3
Ceratopogonidae	2·4	3·2
Ischnura elegans (van der Linden)	12·8	0
Sigara falleni (Fieb)	0	4·2
Hydracarina	13·9	14·9

Table 7. *The mean monthly biomass (mg dry weight m^{-2}) of animals at Upton Broad*

	Year 1	Year 2
Mesostoma ehrenbergi	0·7	0
Polycelis tenuis (Ijima)	0·6	0
Potamothrix hammoniensis	15·0	67·8
Stylaria lacustris	4·4	3·1
Enchytraeidae	2·7	0·5
Helobdella stagnalis (L.)	29·8	23·1
Piscicola geometra (L.)	0	4·3
Valvata piscinalis (Müll.)	498·1	335·9
Bithynia tentaculata (L.)	830·7	545·3
Potamopyrgus jenkinsi (Smith)	13·7	199·4
Planorbis albus Müll.	52·7	8·1
Planorbis leucostoma Millet	0	1·8
Segmentina nitida (Müll.)	3·2	0
Pisidium casertanum (Poli)	77·6	128·5
Gammarus pulex (L.)	1·7	0·8
Asellus aquaticus (L.)	4·9	0
Asellus meridianus Rac.	1·9	0·3
Ostracoda	12·9	6·2
Chironomus tentans Fabr.	318·8	581·5
Dicrotendipes sp.	0	31·9
Tanytarsus holochlorus (Edmunds)	373·6	1850·7
Tanypodinae	103·1	108·0
Orthocladinae	0	8·9
Chaoborus flavicans	33·6	17·5
Ceratopogonidae	3·8	5·9
Culex pipiens	1·1	1·1
Ischnura elegans	5·1	0
Erythromma najas (Hansem)	197·2	2·4
Caenis horaria (L.)	14·1	132·5
Cloëon dipterum (L.)	16·9	1·1
Sigara falleni	28·5	19·4
Corixa punctata (Illig.)	9·7	0
Mistacides longicornis (L.)	63·3	51·3
Cyrnus flavidus (McLachlan)	0	0·4
Limnephilus sp.	0	0·1
Gyrinus sp.	0·2	0·2
Hydracarina	23·1	18·6

Table 8. *The monthly total biomass (mg dry weight m^{-2}) at Alderfen and Upton Broads*

	Alderfen Broad	Upton Broad
June 1973	475	5906
July 1973	2365	1784
August 1973	1747	1247
September 1973	284	3113
October 1973	720	1330
November 1973	3304	874
December 1973	2780	4040
January 1974	1364	1778
February 1974	4066	4967
March 1974	2974	1446
April 1974	4027	1854
May 1974	2087	3694
Mean, year 1	2183	2669
June 1974	1552	24,711
July 1974	4901	6583
August 1974	5397	55
September 1974	3014	1313
October 1974	8513	4062
November 1974	12 228	1634
December 1974	9733	4077
January 1975	10 967	653
February 1975	4815	2452
March 1975	8027	1647
April 1975	5591	1305
May 1975	8324	1371
Mean, year 2	6922	4155

Table 9. *The mean annual respiration (KJ m^{-2}) and production (KJ m^{-2}) of zoobenthos at Alderfen Broad*

|	Respiration		Production	
	Year 1	Year 2	Year 1	Year 2
Potamothrix hammoniensis	235·84	873·85	73·35	216·50
Dero digitata	1·20	3·01	0·06	2·02
Stylaria lacustris	0·08	0·44	0·04	0·27
Enchytraeidae	0·54	0·28	0·32	0·18
Helobdella stagnalis	0	0·71	0	0·41
Erpobdella octoculata	0	0·66	0	0·38
Glossiphonia complanata	0	0·49	0	0·20
Ostracoda	0·23	0·21	0·16	0·15
Chironomus plumosus	53·33	142·68	21·48	48·43
Polypedilum sp.	0·07	0	0·04	0
Micropsectra sp.	0·18	0·36	0·13	0·23
Paratanytarsus sp.	0·01	0	0·01	0
Orthocladinae	0	0·01	0	0·01
Tanypodinae	1·91	12·36	1·37	6·41
Ptychoptera albimana	0	0·02	0	0·01
Chaoborus flavicans	0·61	0·09	0·35	0·05
Ceratopogonidae	0·11	0·06	0·04	0·02
Ischnura elegans	0·10	0	0·04	0
Sigara falleni	0	0·10	0	0·04
Hydracarina	1·94	1·47	1·39	1·11
Total	296·15	1036·78	98·78	276·42
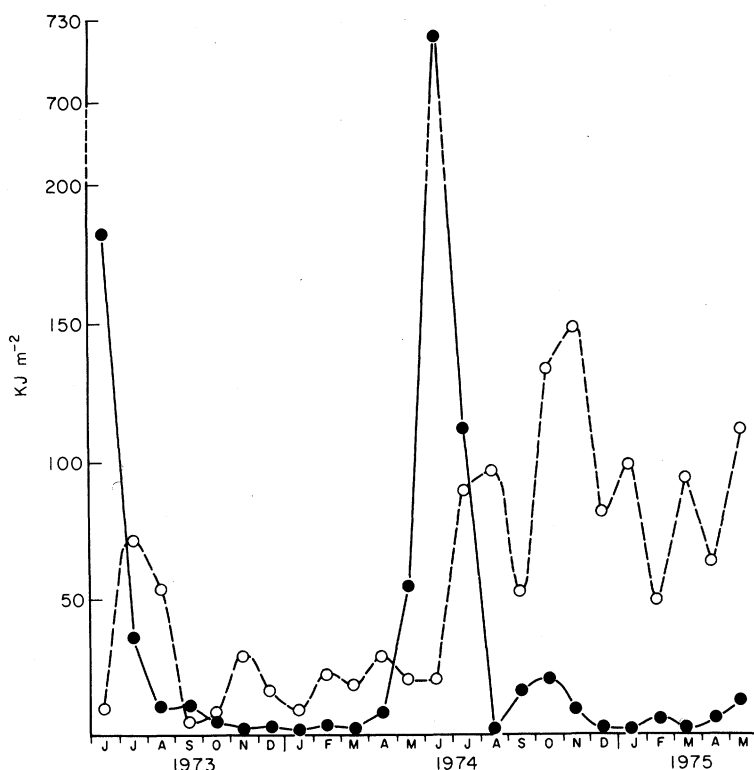
FIG. 8. The monthly community respiration (KJ m^{-2}) at Alderfen Broad (○) and Upton Broad (●), June 1973–May 1975.

larger peak during the autumn. At Upton Broad (Table 8) the peak in biomass occurred in June and was largely due to *Tanytarsus holochlorus*. The monthly respiration (Fig. 8) showed similar patterns. At Alderfen Broad there was a peak in respiration in the summer, and another peak in the late autumn, the summer peak being larger in year 1 and much smaller in year 2. At Upton Broad the respiration was very low for most of the year but increased markedly during May to reach a very large peak in June, followed by a large decline in July to a low August level. The annual respiration was 3·5 times higher in year 2 than in year 1 at Alderfen Broad. In Upton Broad the respiration in year 2 was 2·8 times higher than in year 1.

The annual production at Alderfen Broad amounted to 99 KJ m^{-2} in year 1 and 276 KJ m^{-2} in year 2 (an increase of 2·8 times). At Upton Broad the annual production was 130 KJ m^{-2} in year 1 and 273 KJ m^{-2} in year 2 (an increase of 2·1 times). The annual production was thus similar at the two sites.

In Alderfen Broad *Potamothrix hammoniensis* accounted for 74% and 78% of the total production in year 1 and year 2 respectively, and 22% and 18% was accounted for by *Chironomus plumosus*. In Upton Broad 54% and 70% of the total production was due to *Tanytarsus holochlorus* in the two years respectively. The proportion of the annual production of the zoobenthos due to predators was 3·2% and 3·1% in the two years at Alderfen Broad and 12·2% and 3·8% at Upton Broad.

Estimates of the overall P:B ratios were made by assuming an average energy value of

Table 10. *The mean annual respiration (KJ m^{-2}) and production (KJ m^{-2}) of zoobenthos at Upton Broad*

	Respiration		Production	
	Year 1	Year 2	Year 1	Year 2
Mesostoma ehrenbergi	0·15	0	0·11	0
Polycelis tenuis	0·14	0	0·11	0
Potamothrix hammoniensis	6·76	20·60	3·90	9·79
Stylaria lacustris	3·15	1·37	2·07	1·04
Enchytraeidae	0·85	0·21	0·47	0·14
Helobdella stagnalis	2·45	2·14	1·69	1·51
Piscicola geometra	0	0·21	0	0·14
Valvata piscinalis	11·60	8·94	6·09	4·91
Bithynia tentaculata	1·56	1·39	1·16	1·06
Potamopyrgus jenkinsi	0·20	4·21	0·14	2·63
Planorbis albus	1·01	0·45	0·24	0·27
Planorbis leucostoma	0	0·06	0	0·03
Segmentina nitida	0·03	0	0·01	0
Pisidium casertanum	2·57	1·89	1·75	1·36
Gammarus pulex	0·16	0·05	0·08	0·02
Asellus aquaticus	0·50	0	0·30	0
Asellus meridianus	0·18	0·08	0·13	0·04
Ostracoda	1·33	0·61	1·02	0·36
Chironomus tentans	18·20	27·39	8·83	12·39
Dicrotendipes sp.	0	4·83	0	2·95
Tanytarsus holochlorus	224·51	750·15	70·42	190·80
Tanypodinae	10·12	9·76	5·44	5·28
Orthocladinae	0	0·94	0	0·51
Chaoborus flavicans	2·91	1·66	1·94	1·21
Ceratopogonidae	1·42	2·50	1·07	1·71
Culex pipiens	0·08	0·04	0·05	0·02
Ischnura elegans	0·55	0	0·33	0
Erythromma najas	6·62	0·24	3·83	0·17
Caenis horaria	6·57	45·34	3·81	18·78
Cloëon dipterum	0·50	0·21	0·30	0·15
Sigara falleni	3·88	4·47	2·46	2·77
Corixa punctata	0·59	0	0·35	0
Mistacides longicornis	19·84	22·05	9·50	10·35
Cyrnus flavidus	0·20	0·21	0·14	0·14
Limnephilus sp.	0	0·13	0	0·07
Gyrinus sp.	0·24	0·11	0·17	0·06
Hydracarina	3·55	3·06	2·29	2·02
Total	332·39	915·25	130·20	272·69

zoobenthic tissue of 22 KJ g^{-1}. The P:B ratios were 2·1 and 1·8 at Alderfen Broad and 2·2 and 3·0 at Upton Broad in the two years respectively.

DISCUSSION

The checks made on the sampling and sieving methods used in the present survey showed the methods to be very efficient, though it is likely that small animals were still being missed as small worms and first instar chironomid larvae appeared to be under-represented in the samples. These losses, however, probably had little effect on the production estimates. Indeed, Maitland *et al.* (1972) found that, using a 500-μm sieve alone, the production of chironomids was underestimated by only 2·7%. The depth of sampling (12 cm) was also likely to have collected the majority of invertebrates (Kajak & Dusoge 1971).

The net samples failed to collect *Anodonta cygnaea* (L.), though they were observed in small numbers (approx $0 \cdot 1$ m^{-2}) in both broads, especially in the sub-littoral. With its large size and long life the species may be important in the ecology of the broads even at low densities.

In the present study the respiration experiments all commenced with an oxygen saturation of 100%. The concentration of oxygen in the field could affect respiration rates. However, Berg, Jónasson & Ockelman (1962) examining a number of benthic species, found that oxygen tensions had little effect on respiration rates down to low levels, where a critical point was reached when oxygen consumption declined markedly. Platzer-Schultz (1970) made similar observations with *Chironomus strenkei* Fittkau. With shallow, turbulent, non-stratified waters, such low oxygen levels would only rarely occur in Alderfen Broad and probably never in Upton Broad.

Production was calculated from respiration using the regression equation derived by McNeil & Lawton (1970). McLusky & McFarlane (1974) showed that production of chironomids determined in this way was similar to production calculated from Allen curves, though the production of the larger populations was consistently lower. If this is generally true the production values in the present study may be under estimates.

Twenty-two taxa of invertebrates were recorded in the benthos of Alderfen Broad and forty taxa in Upton Broad during the study. Only seven taxa could be described as of regular occurrence in Alderfen Broad compared with seventeen taxa in Upton Broad. The low diversity in Alderfen Broad was due to the absence of aquatic macrophytes; the littoral zone had a rich fauna (Mason & Bryant 1974). The sediments of the broads, while being potentially rich in food, are very fluid and do not provide a stable substrate for oviposition. As described by Wortley (1974) macrophytes assume an exaggerated importance in the unstable, shifting mud of the broads. Wortley (1974) showed that gastropods in Upton Broad laid their eggs on *Najas marina* and their breeding season was delayed to coincide with the late emergence of this plant. Furthermore artificial substrates (polypropylene ropes) were quickly colonized by many invertebrates when positioned in Alderfen Broad (Wortley 1974). The epiphytes of *Najas* and artificial substrates were grazed by young snails. Clearly macrophytes are extremely important in maintaining the diversity of the benthic fauna. Should macrophytes become re-established, recolonization could take place rapidly from the littoral zone.

Najas marina would have contained, from June to October, a fauna intimately related to the benthic community described in the present study. This would have led to an underestimate of the production of the macro-invertebrate community in the body of Upton Broad as a whole. Wortley (1974) studying mainly gastropods, showed that a maximum of only 9% of the total biomass of *Valvata piscinalis* was present on *Najas*. Pulmonates, such as *Planorbis albus* occurred in greater numbers on the macrophyte. However, considering the short growing season of *Najas*, and the observation that the dominant producer (*Tanytarsus holochlorus*) was almost entirely benthic, the under-estimate of production in Upton Broad was unlikely to be large.

Populations and production of individual groups

The peak in the population of *Helobdella stagnalis* in the summer at Upton Broad was similar to that described by Learner & Potter (1974a) for Eglwys Nunydd Reservoir, Wales, though their population was higher. Assuming an energy conversion factor of 22 KJ g^{-1} the production of *H. stagnalis* in Eglwys Nunydd was $6 \cdot 8$ KJ m^{-2} and $26 \cdot 1$

$KJ\ m^{-2}$ in two consecutive years, higher than the values of $1\cdot7\ KJ\ m^{-2}$ and $1\cdot5\ KJ\ m^{-2}$ recorded for Upton Broad. The P:B ratios, however, were similar, being $3\cdot2$ and $3\cdot0$ in Eglwys Nunydd and $2\cdot7$ and $3\cdot1$ in Upton Broad.

In the benthos of Alderfen Broad the population of *Potamothrix hammoniensis* showed a peak in summer, followed by a sharp decline, with usually a smaller peak in winter. In the final year of the study, however, the late summer decline was small and the population increased into the winter. A similar pattern with two peaks was recorded by Šapkarev (1975) from Lake Dojran, Macedonia. The summer peak of small worms was most likely derived from cocoons produced in the spring, though Jónasson & Thorhauge (1972) suggested that worms in their first two years were lost through a $280\ \mu m$ sieve. Recruitment to the population of *P. hammoniensis* in Alderfen Broad occurred through most of the year, but not in the coldest part of the winter. Thorhauge (1975) recorded cocoon production at temperatures of $4\cdot5°$ C and above, which would accord with the prolonged breeding season at Alderfen. Cocoon production and embryo development is temperature dependent (Thorhauge 1975), explaining the large input of small worms into the Alderfen population in summer.

The summer decline in the *P. hammoniensis* population in Alderfen Broad resulted in the loss of many of the adults. Jónasson & Thorhauge (1972) similarly found a loss of bred adults in the summer in Lake Esrom, Denmark. However, Thorhauge (1975) has recently observed that few worms died after breeding in the laboratory. The adult mortality may not be related directly to senescence but suggests a reduced ability to survive adverse environmental conditions after breeding, for example low oxygen tensions or hydrogen sulphide formation in the sediments. *P. hammoniensis* is well adapted to survive the brief periods of deoxygenation encountered in Alderfen Broad. Hydrogen sulphide may have been responsible for the observed mortality and the sediment in Alderfen Broad smelt very strongly of the gas in September 1973 at a time when the population crashed. Thorhauge (1975) reported that embryos of *P. hammoniensis* did not develop in the presence of hydrogen sulphide and Fisher & Beeton (1975) suggested the gas may have important effects on the burrowing behaviour of *Limnodrilus hoffmeisteri* Claparède. The reactions of zoobenthic populations to hydrogen sulphide deserves further study.

The production of *Potamothrix hammoniensis* in Alderfen Broad amounted to $73\cdot4$ $KJ\ m^{-2}$ and $216\cdot5\ KJ\ m^{-2}$ in year 1 and year 2 respectively. The corresponding values for the small population of *P. hammoniensis* in Upton Broad were $3\cdot9\ KJ\ m^{-2}$ and $9\cdot8\ KJ\ m^{-2}$. Studies in the U.S.S.R. have recorded production figures of $155\cdot8\ KJ\ m^{-2}$ (Pidgaiko *et al.* 1972) and a mean over six year of $117\cdot6\ KJ\ m^{-2}$ (range $7\cdot3\ KJ\ m^{-2}$ $-237\cdot5\ KJ\ m^{-2}$) (Grigelis 1974). Jónasson (1975) observed an average production of *P. hammoniensis* over four years of $33\ KJ\ m^{-2}$ in Lake Esrom. Using the same energy conversion factor for tubificid biomass as Jónasson (1975, from Johnson & Brinkhurst 1971), viz. $22\cdot11\ KJ\ g^{-1}$, P:B ratios for *P. hammoniensis* at Alderfen Broad were $2\cdot2$ and $2\cdot0$ for year 1 and year 2 respectively, and at Upton Broad were $11\cdot8$ and $6\cdot5$. Jónasson (1975) recorded a range of P:B ratios of $0\cdot69$ to $1\cdot02$ in Lake Esrom over four years and Pidgaiko *et al.* (1972) a P:B ratio of $5\cdot5$. For a population of *Limnodrilus* spp. Potter & Learner (1974) recorded P:B ratios of $6\cdot8$ and $10\cdot8$ in two years in Eglwys Nunydd Reservoir.

The mollusc populations recorded in Upton Broad in the present study were similar to those described by Wortley (1974), though *Planorbis albus* was generally scarcer, probably because it occurs in greater abundance in the *Najas* beds. Both *Valvata piscinalis*

and *Bithynia tentaculata* were recorded as eating *Aphanotheca stagnina* readily in the field (Wortley 1974), suggesting an almost unlimited food supply.

An examination of the population curves and size-class distributions of *Chironomus plumosus* and *C. tentans* indicated that there were two generations present in a year, with peak emergence of adults in spring and summer. Most populations of *Chironomus* appear to be bivoltine (e.g. Mundie 1957; Hilsenhoff 1967; Jankovic 1971; Learner & Potter 1974b); though univoltine populations (Hilsenhoff & Narf 1968) and trivoltine populations (Yamagishi & Fukuhara 1971) have also been recorded. *Chironomus* species feed largely on algae and detritus (Oliver 1971) and Hall, Cooper & Werner (1970) have described *C. tentans* feeding by filtering plankton during the day and searching the sediment surface at night. The production of *C. anthracinus* closely followed the algal production in Lake Esrom (Jónasson & Kristianson 1967) and both generation time and adult size in *C. tentans* was influenced by food quality (Hall *et al.* 1970).

The Tanytarsini are described generally as bivoltine (Reiss & Fittkau 1971) and bivoltine populations of *Tanytarsus holochlorus* were recorded by Humphries (1938), Mundie (1957), Sandberg (1969), Learner & Potter (1974b) and Potter & Learner (1974). In Upton Broad there was an immense emergence of adults in June and a later emergence, if it occurred at all, would have been very small. The larval development was also different to that described by Potter & Learner (1974) in Eglwys Nunydd Reservoir. They found the majority of larvae overwintering as instar 3, with some first and second instars. In Upton Broad the overwintering population of *T. holochlorus* was very low (less than 100 m^{-2}) and the population increased rapidly in May. Potter & Learner (1974) point out that small instars would not be retained in sieves with a mesh size of 150 μm diameter. However, large numbers of larvae as small as 0·5 mm length were recorded in samples in May and June and it seems inconceivable that they would be missed, if present, over the rest of the year, even if sampling methods were inefficient. Armitage's (1970) observations that Tanytarsini spend the cold part of the winter in cocoons and are hence inefficiently sampled also seems an unlikely explanation in view of the relatively warm waters in Upton Broad compared with Finnish lakes. It would therefore appear that the majority of *T. holochlorus* larvae hatched in May from eggs laid in the previous summer. The Tanytarsini, like the Chironomini, are largely algal and detrital feeders (Oliver 1971).

As the Tanypodini were not identified to species little can be said of their life history in the broads. Most species appear to be bivoltine (Mundie 1957; Learner & Potter 1974b). They are chiefly carnivores, though algal food is sometimes taken in quantity (Kajak & Dusoge 1970) and first instar larvae probably feed entirely on algae (Smith & Young 1973). Tanypods were frequently seen eating *Potamothrix hammoniensis* in samples collected from Alderfen Broad and they are known to eat oligochaetes voraciously (Loden 1974). Small *Tanytarsus holochlorus* may have formed the chief diet of tanypods in Upton Broad, where oligochaetes were present in small numbers only.

The annual production of *Chironomus plumosus* in Alderfen Broad amounted to 21·5 KJ m^{-2} and 48·4 KJ m^{-2} in year 1 and year 2 respectively. The comparable values for *C. tentans* in Upton Broad were 8·8 KJ m^{-2} and 12·4 KJ m^{-2} respectively. Using an average conversion factor for chironomids of 22·67 KJ g^{-1} (Cummins & Wuycheck 1971) it is possible to compare these estimates of production with other studies. Potter & Learner (1974) recorded an annual production for *C. plumosus* of 79·8 KJ m^{-2}. Production figures of *C. plumosus* from lakes in U.S.S.R. (eight studies varied from 10·4

KJ m^{-2} y^{-1} to 469·7 KJ m^{-2} y^{-1} (Borutsky, Sokolova & Yablonskaya 1971). Andronikova et al (1972) in Red Lake, U.S.S.R., estimated an annual production of C. plumosus of 30·1 KJ m^{-2} compared with 36·8 KJ m^{-2} for C. anthracinus. Over three years, the annual production of C. anthracinus in Lake Esrom ranged from 314·9 KJ m^{-2} to 923·3 KJ m^{-2} (Jónasson 1975). Production by Chironomus spp. in the broads is thus low compared with other studies.

The P:B ratios of C. plumosus in Alderfen Broad were 1·9 and 1·6 in the two years respectively, compared with 1·2 and 1·1 for C. tentans in Upton Broad. These values are rather lower than previously recorded P:B ratios for C. plumosus, which range from 4·2 to 8·8 (Borutsky et al. 1971; Andronikova et al. 1972; Winberg et al. 1972; Potter & Learner 1974).

The annual production of Tanytarsus holochlorus in Upton Broad was 70·4 KJ m^{-2} and 190·8 KJ m^{-2} in year 1 and year 2 respectively, with P:B ratios of 8·3 and 4·5. Potter & Learner (1974) recorded an annual production for this species in Eglwys Nunydd Reservoir of 35·1 KJ m^{-2} with a P:B ratio of 6·6. Winberg et al. (1972) recorded P:B ratios of 8·4 to 9·8 for the Tanytarsini in general.

Total chironomid production in the benthos of Alderfen Broad was 23·0 KJ m^{-2} and 55·1 KJ m^{-2} in year 1 and year 2 respectively, with predatory tanypods accounting for 5·9% and 11·6% respectively. Overall chironomid P:B ratios were 1·7 and 1·2. The total chironomid production in Upton Broad amounted to 84·7 KJ m^{-2} and 211·9 KJ m^{-2} in the two years, with tanypods accounting for 6·4% and 2·5% of the total. Overall P:B ratios were 4·7 and 3·6. The total chironomid production in five Soviet lakes varied from 2·2 KJ m^{-2}yr^{-1} to 87·3 KJ m^{-2}yr^{-1}, with a mean of 35·7 KJ m^{-2}yr^{-1} (Alimov et al. 1972; Winberg et al. 1972). Borutski et al. (1971) recorded an annual chironomid production of 54·4 KJ m^{-2} in Uchinskaye Reservoir, U.S.S.R. The production of chironomids in the arctic Lake Char in two years was 9·6 KJ m^{-2} and 11·7 KJ m^{-2} (Welch 1976). Loch Leven had an annual chironomid production of 682 KJ m^{-2} in the muddy areas (Charles et al. 1974) and 952 KJ m^{-2} and 363 KJ m^{-2} over two years in the sandy areas (Maitland & Hudspith 1974). Potter & Learner (1974) recorded an annual production of 476 KJ m^{-2} in Eglwys Nunydd Reservoir while Jónasson (1972) observed 363 KJ m^{-2} for annual chironomid production in Lake Esrom. In a sewage lagoon in Oregon, U.S.A., Kimerle & Anderson (1971) reported an annual chironomid production of 2040 KJ m^{-2}. The chironomid production in the two broads was thus similar to those recorded by Soviet workers, but is lower than from many temperate lakes.

The populations of the dominant caddis, Mistacides longicornis, and mayfly, Caenis horaria, in Upton Broad appeared closely related to the growth of Najas. Neither occurred regularly in the benthos of Alderfen Broad, though they would readily colonize artificial substrates there (Wortley 1974). Hall et al. (1970) showed that Caenis simulans McDunn populations responded inversely to nutrient levels and this was despite the increasing dominance of macrophytes in high nutrient ponds. They suggested that inadequate food or antagonism with Chironomus tentans, acting on small instars, may have been responsible.

Community production and general conclusions

The total, annual zoobenthic production at Alderfen Broad was 98·8 KJ m^{-2} and 276·4 KJ m^{-2} in year 1 and year 2 respectively. Corresponding values for Upton Broad were 130·2 KJ m^{-2} and 272·7 KJ m^{-2}. Overall P:B ratios were 2·1 and 1·8 for Alderfen

Broad, and 2·3 and 3·0 for Upton Broad. The proportion of annual production due to predators was 3·2% and 3·1% in the two years at Alderfen Broad, and 12·2% and 3·8% at Upton Broad.

The overall production of the zoobenthos of nine Soviet lakes ranged from 7·7 KJ m^{-2} to 712·3 KJ m^{-2}, with a mean of 114·7 KJ m^{-2} (Winberg 1972). The proportion of production due to predators averaged 16% and the overall P:B ratios ranged from 0·64 to 4·8. In Red Lake, U.S.S.R., Andronikova *et al.* (1972) recorded a total zoo-benthic annual production of 85·3 KJ m^{-2}, predators accounting for 5% of this. The overall P:B ratio was 4·3. Kajak, Hillbricht-Ilkowskca & Piecznska (1972) observed annual zoobenthic production ranging from 2·1 KJ m^{-2} to 836·0 KJ m^{-2} (mean 426·8 KJ m^{-2}) for five Polish lakes. This value excluded carnivore production, which amounted to a further 10%. Lake Esrom had an annual production of zoobenthos of 418 KJ m^{-2} (Jónasson 1972) and Eglwys Nunydd a production of 635 KJ m^{-2} (Potter & Learner 1974). For Loch Leven, a speculative annual production of 2500 KJ m^{-2} was calculated (Morgan & McLusky 1974). The total zoobenthic production in the two broads thus appears to be on the lower end of the production range for lakes.

Alderfen and Upton Broads had similar values for annual zoobenthic production and both showed increased production in the second year of the study. The pattern of community metabolism (see Fig. 8), however, was strikingly different at the two sites and this could have had considerable implications for the higher trophic levels in the broads and especially for long-lived fish. The biomass of zoobenthos in Alderfen re-mained high and fairly constant through the year and its chief source of food was likely to have been the large production of phytoplankton. In Upton Broad the biomass of zoobenthos was very low for much of the year, but increased markedly in the period May–July. This coincided with the emergence of *Najas* seedlings, which were not them-selves eaten, but which developed a rich epiphytic flora. The waters of Upton were clear and little phytoplankton production appeared available as food to the zoobenthos, though it is possible that the intense filtering activity of a large population of *Tanytarsus holochlorus* in May and June may have substantially aided the maintenance of water clarity. Benthic primary production in the clear waters of Upton Broad was probably greater than at Alderfen Broad, providing an additional food source.

The constant biomass of zoobenthos at Alderfen Broad enabled a large population of fish (bream *Abramis brama* (L.), tench *Tinca tinca* (L.) and roach *Rutilus rutilus* (L.)) to be maintained. In Upton Broad, with its seasonal benthic production, the fish popu-lation was low.

Recruitment to the fish population in Alderfen Broad tended to be large and the young fish grazed heavily and selectively on large zooplankton, the resulting community being dominated by copepods (R. T. Leah, personal communication). Copepods grazed only nannoplankton and bacteria, resulting in a large algal biomass. This would have pro-vided additional food for the zoobenthos, whose greater biomass could support a larger adult fish population, with potentially greater recruitment. A positive feedback leading to greater algal blooms can thus be envisaged. In Upton Broad the primary production was dominated by a dense growth of *Najas*, which provided a highly structured environ-ment enabling a high survival of large zooplankton due to less successful predation by planktivorous fish (Hall *et al.* 1970). The zooplankton community in Upton Broad was dominated by large cladocerans (R. T. Leah, personal communication) which would limit the algal biomass and reduce the food supply to the zoobenthos. The lower zoobenthic biomass through much of the year would not support a large fish population, recruitment

to the fish population would be low and clear water conditions would be maintained.

These hypotheses are undoubtedly simplistic and ignore other influences on the community such as weather or the littoral zone (important in the biology of small lakes). However, they do suggest that the highly structured and diverse community of Upton Broad may be unstable in the face of external perturbations (for a theoretical examination of the stability of complex ecosystems see May (1973)). For example, a sudden large input of nutrients from agricultural land into Upton Broad in spring could stimulate phytoplankton growth, thus reducing the light available for late developing macrophytes. A response to the phytoplankton growth by zooplankton would be contained by increased predation by fish due to the reduced habitat heterogeneity. Thus a greater phytoplankton biomass would develop, with a greater food supply to the benthos and hence fish, as suggested for Alderfen Broad. Once started the eutrophication process could accelerate, resulting in a rapid loss of aquatic vegetation and reduced faunal diversity. There is much evidence to suggest that cultural eutrophication of the broads has proceeded very rapidly (Mason & Bryant 1975a; Mason 1976a).

Working with the experimental ponds of Hall et al. (1970), Moss (1976) concluded that blue-gill sunfish (Lepomis macrochirus Raffinesque) increased the biomass of macrophytes at high nutrient levels, possibly by eating amphipods which heavily graze the plants. This is a different conclusion to that given above for the broads, but here heavy grazing of macrophytes by invertebrates does not occur.

These small lake habitats are eminently suited to experimental manipulation and such experiments will be essential if a rational strategy to reverse the eutrophication of the Norfolk Broads is to be developed.

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SUMMARY

(1) The populations of benthic invertebrates were studied in Alderfen and Upton Broads from November 1971 to June 1975 inclusive. Production estimates were made for the last two years. Both lakes are small and shallow. Alderfen Broad was culturally enriched, with a phytoplankton bloom and absence of aquatic macrophytes. Upton Broad was naturally eutrophic, with clear water and a dense growth of Najas marina.

(2) Twenty-two species or groups occurred in Alderfen Broad, seven of them regularly. Forty species or groups were present in Upton Broad, seventeen of them regularly. The greater diversity at Upton Broad was related to the presence of Najas.

(3) Potamothrix hammoniensis was abundant in Alderfen Broad (maximum population 22 500 m^{-2}). Chironomus plumosus was also common. At Upton Broad C. tentans occurred and Tanytarsus holochlorus formed seasonally large populations (up to 130 000 m^{-2}). Molluscs, Caenis horaria and Mistacides longicornis were also common at Upton Broad.

(4) Annual respiration and production estimates are presented for individual species. The overall production amounted to 99 KJ m^{-2} and 176 KJ m^{-2} in the two years at Alderfen Broad. Corresponding values for Upton Broad were 130 KJ m^{-2} and 273 KJ m^{-2}. Overall P:B ratios were estimated as 2·1 and 1·8 at Alderfen Broad and 2·2 and 3·0 at Upton Broad.

(5) Production was higher at both sites in the second year. Biomass and community metabolism remained higher over the year at Alderfen Broad. At Upton Broad biomass and community metabolism was low for most of the year, but was very high from May to July.

(6) The significance of these patterns of production to the population of long-lived predators, especially fish, is discussed. It is suggested that a nutrient perturbation in the diverse but essentially fragile ecosystem of a shallow lake such as Upton Broad could result in accelerating eutrophication through positive feedback interactions in the community once environmental heterogeneity is reduced.

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