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14.—The Zoobenthos of Loch Leven, Kinross, and Estimates of its Production in the Sandy Littoral Area during 1970 and 1971. By

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Synopsis

The available information, both published and unpublished, on the zoobenthos of Loch Leven has been studied and tabulated. There have been a number of major changes in the community over the last 100 years—notably a reduction in diversity of the fauna with the disappearance of many species of invertebrates, particularly Ephemeroptera, Odonata and Coleoptera. The existing macro-invertebrate fauna is dominated by larval Chironomidae, but Nematoda, Mollusca, Annelida and Crustacea are also of importance. Dramatic changes have taken place in the chironomid population during the present study (1968–71), notable among which has been the disappearance of *Endochironomus*. Production studies of the two dominant larval Chironomidae (*Glyptotendipes* and *Stictochironomus*) in the sandy littoral area (42 per cent of the loch bed) gave annual estimates of 40·5 and 1·2 g (dry weight)/m^2 respectively for 1970 and 5·0 and 10·2 g/m^2 for 1971. Speculative estimates of the entire zoobenthos production in 1970 gave a value of 46·5 g/m^2. The significance of these results is briefly discussed.

Introduction

As part of a project sponsored by the International Biological Programme, the main aim of the present work was to study the production of zoobenthos in shallow water in Loch Leven in parallel to a similar study being carried out in deep water (Charles *et al.* 1974). Much of the early work in this study was concerned with evaluating the most appropriate methods to adopt at Loch Leven in view of the nature and distribution of invertebrates and sediments there. Some of this preliminary work has been described elsewhere (Maitland 1969, Maitland *et al.* 1972) or will appear in future publications. This paper describes the present status of the zoobenthos of Loch Leven in relation to previous records and presents data on the production of this community in the sandy littoral area of the loch during 1970 and 1971.

The main physical and chemical characteristics of Loch Leven have been described fully elsewhere (Holden 1974; Smith 1974; respectively). It is sufficient for the purposes of the present paper to note that Loch Leven, which lies on the plain of Kinross some 30 km north-west of Edinburgh, has a surface area of 13·31 km^2, a mean depth of 3·9 m and a maximum depth of 25·5 m. The loch lies on Old Red Sandstone overlain by glacial drift and its modal surface water level is some 107 m above sea level. The surface fluctuates through a maximum of about 1 m about this level. The loch is very exposed to prevailing winds and subject to severe wave action from time to time. Water temperatures range from 0°C in winter (with occasional ice cover) to 22°C in summer (with occasional periods of stratification during calm weather).

The Zoobenthos

Historical Record

Though Loch Leven has never previously been a major site for limnological investigation it has long been famous as a rich trout loch and an example of a shallow

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eutrophic lake. Thus there are sporadic accounts of its invertebrates in relation to the fishery and as a result of collections made by various specialists from time to time. The former (e.g. Burns-Begg 1874) are rarely of value since the accounts given are not sufficiently detailed to know precisely which invertebrates are being discussed. Specialist collections (some of them previously unpublished) are of great value, however, and are the main source of information about previous invertebrate communities at Loch Leven. The major species lists known to the author are included in table 1 along with records obtained during the present studies (see also Bryant and Laybourn 1974).

TABLE 1
Invertebrate species recorded from Loch Leven

	A. Scott (1891)	B. Scott (1898)	C. Scott (1906)	D. Balfour-Browne (1938–38)	E. Waterston (1934–35)	F. Macan (1938)	G. Balfour-Browne (1947–50)	H. Balmain and Shearer (1952)	I. Kevan (1958)	J. Waterston (1967)	K. Recent (1966–72): Sand	L. Recent (1966–72): Mud	M. Recent (1966–72): Plankton	N. Guthrie (1968)
PROTOZOA														
MASTIGOPHORA														
Anisonema acinus Dujardin														×
Nephroselmis olvacea S.														×
Peranema trichophorum (Ehrenberg)														×
Siderodendron margariferum (Pringsheim)														×
SARCODINA														
Acanthocystis aculeata (Hennig & Lessen)														×
Actinophrys sol (Ehrenberg)														×
Amoeba dubia (Schaeffer)														×
Arcella vulgaris (Ehrenberg)														×
Cyphoderia ampulla (Ehrenberg)														×
Difflugia oblonga (Ehrenberg)	×													×
Difflugia urceolata (Carter)														×
Difflugia corona Wallich	×													×
Pelomysea palustris (Greeff)														×
CILIATA														
Aspidisca lynceus (E)														×
Coleps elongatus (E)														×
Coleps hirtus (Muller)														×
Coleps octospinus (Noland)														×
Dileptus anser (Muller)														×
Halteria grandinella (Muller)														×
Hemiophrys procera (Penard)														×
Homalozoon verniculare (Stokes)														×
Lacrymaria olor (Muller)														×
Lacrymaria pupula (Muller)														×
Lembadion bullinum (Perty)														×
Loxodes striatus (Penard)														×
Loxodes magnus Stokes														×

TABLE 1 (*cont.*)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Loxophyllum helus (Stokes)														×
Loxophyllum setigerum Quennerstedt														×
Spirostomum minus Roux														×
Stentor coeruleus Ehrenberg														×
Stentor polymorphus (Ehrbg-Stein)														×
Urocentrum turbo (Muller)														×
Uroleptus piscis														×
Vorticella convallaria (L.)														×
COELENTERATA														
HYDROZOA														
Hydra oligactis Pallas												×	×	
PLATYHELMINTHES														
TURBELLARIA														
Rhabdocoela														
Otomesostoma auditivum (Du Plessis)												×	×	
Tricladida														
Polycelis nigra (Muller)											×	×		
Polycelis tenuis (Ijima)												×		
ROTIFERA														
Asplancha priodonta Gosse													×	
Keratella cochlearis (Gosse)													×	
Keratella quadrata (Muller)													×	
Polyarthra dolichoptera Id.													×	
Porpholyx sulcatam Huds.													×	
NEMATODA												×	×	
MOLLUSCA														
GASTROPODA														
Valvata cristata Muller	×				×									
Valvata piscinalis (Muller)	×				×			×	×	×	×	×		
Potamopyrgus jenkinsi (Smith)					×				×	×	×			
Lymnaea truncatula (Muller)	×				×	×								
Lymnaea palustris (Muller)	×				×	×			×					
Lymnaea auricularia (L.)					×					×				
Lymnaea peregra (Muller)	×				×	×		×	×	×	×			
Physa fontinalis (L.)	×				×	×			×		×			
Planorbis carinatus Muller									×					
Planorbis planorbis (L.)					×									
Planorbis albus Muller	×				×	×			×		×			
Planorbis crista (L.)	×				×	×								
Planorbis contortus (L.)	×				×	×			×					
Ancylus fluviatilis Muller					×					×	×			
BIVALVIA														
Anodonta anatina (L.)	×				×					×	×			
Sphaerium corneum (L.)	×				×					×	×			
Pisidium amnicum (Muller)											×			
Pisidium casertanum (Poli)					×						×			
Pisidium milium Held.					×						×	×		
Pisidium subtruncatum Malm.					×						×	×		
Pisidium lilljeborgi Clessin					×				×					
Pisidium hibernicum Westerlund											×			
Pisidium nitidum Jenyns	×				×						×	×		

TABLE 1 (*cont.*)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
ANNELIDA														
OLIGOCHAETA														
Naididae														
Stylaria lacustris (L.)					×						×			
Nais pardalis Piguet												×		
Nais variabilis Piguet												×		
Tubificidae														
Aulodrilus pluriseta (Piguet)												×		
Tubifex tubifex (Muller)	×													
Euilyodrilus hammoniensis (Michaelsen)												×		
Limnodrilus hoffmeisteri Claparede												×		
Enchytraeidae											×			
Lumbriculidae														
Lumbriculus variegatus (Muller)											×	×		
HIRUDINEA														
Theromyzon tessulatum (Muller)										×	×			
Glossiphonia heteroclita (L.)											×			
Glossiphonia complanata (L.)	×									×	×			
Helobdella stagnalis (L.)										×	×	×		
Erpobdella octoculata (L.)	×									×	×			
ARTHROPODA														
CRUSTACEA														
Cladocera														
Sida crystallina (Muller)		×												
Diaphanosoma brachyurum Lieven	×													
Daphnia pulex (De Goer)	×													
Daphnia longispina Muller	×													
Daphnia hyalina Leydig		×						×			×		×	
Simocephalus vetulus (Muller)		×												
Bosmina longirostris (Muller)	×	×												
Ilyocryptus sordidus (Lieven)	×	×												
Eurycercus lamellatus (Muller)	×	×								×	×			
Monospilus dispar Sars	×	×												
Acroperus harpae Baird	×	×												
Alonopsis elongata Sars	×	×												
Alona affinis Leydig		×									×			
Alona quadrangularis (Muller)	×	×									×			
Alona guttata Sars		×												
Alonella nana (Baird)	×	×												
Alonella exigua (Lilljeborg)	×	×												
Pleuroxus trigonellus (Muller)	×	×												
Pleuroxus uncinatus Baird	×	×												
Chyodorus piger Sars		×												
Chyodorus sphaericus (Muller)	×	×												
Polyphemus pediculus (L.)	×													
Bythotrephes longimanus Leydig	×	×						×					×	
Leptodora kindti (Focke)	×	×						×					×	
Ostracoda														
Cypria opthalmica (Jurine)	×	×												
Cypria exsculpta (Fischer)	×		×											
Cyclocypris laevis (Muller)		×												
Cyclocypris serena (Koch)	×	×												

TABLE 1 (*cont.*)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Cyclocypris globosa (Sars)			×											
Cypris fuscata (Jurine)		×	×											
Cypris virens (Jurine)		×	×											
Herpetocypris reptans (Baird)	×	×	×											
Herpetocypris tumefacta Brady & Robertson	×	×												
Herpetocypris strigata (Muller)	×	×	×											
Cypridopsis villosa (Jurine)	×	×	×											
Pionocypris vidua (Muller)	×	×	×											
Potamocypris fulva Brady	×	×	×											
Candona neglecta Sars	×	×	×											
Candona lactea Baird	×		×											
Candona compressa (Fischer)	×	×	×											
Candona kingsleii Brady & Robertson	×	×												
Ilyocypris biplicata (Koch)	×		×											
Lymnicythere inopinata (Baird)	×	×	×											
Lymnicythere sancti-patricii Brady & Robertson	×	×	×											
Cytheridea lacustris (Sars)	×	×	×											
Copepoda														
Diaptomus gracilis Sars	×	×									×		×	
Canthocamptus staphylinus (Jurine)		×												
Canthocamptus minutus Claus	×													
Canthocamptus pygmaeus (Sars)		×												
Canthocamptus zschokkei Schmeil		×												
Canthocamptus crassus Sars	×	×												
Moraria brevipes (Sars)		×												
Moraria duthiei Scott		×												
Moraria mrazeki Scott		×												
Cyclops agilis (Koch, Sars)	×	×						×						
Cyclops macrurus (Sars)		×												
Cyclops fimbriatus (Fischer)		×												
Cyclops strenuus abyssorum Sars	×	×									×		×	
Cyclops viridis (Jurine)														
Cyclops vernalis (Fischer)		×												
Cyclops bicuspidatus (Claus)		×												
Cyclops bisetosus (Rehberg)		×												
Cyclops crassicaudis (Sars)	×	×												
Malacostraca														
Gammarus pulex (L.)	×	×						×		×	×			
Asellus aquaticus L.								×		×	×	×		
INSECTA														
Plecoptera														
Chloroperla torrentium (Pictet)											×			
Ephemeroptera														
Caenis horaria (L.)											×	×		
Centroptilum luteolum (Muller)								×						
Cloeon simile Eaton								×						
Odonata			×											
Hempitera														
Gerris thoracicus Schummel											×			

TABLE 1 (*cont.*)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Callicorixa praeusta (Fieber)						×					×			
Callicorixa wollastoni Douglas & Scott						×			×	×	×			
Arctocorisa germari (Fieber)						×								
Sigara dorsalis (Leach)						×			×	×	×			
Sigara striata (L.)						×		×						
Sigara distincta (Fieber)						×								
Sigara falleni (Fieber)						×		×		×	×			
Sigara semistriata (Fieber)						×								
Sigara concinna (Fieber)						×								
Micronecta poweri Douglas & Scott										×				
Trichoptera														
Oecetis ochracea Curtis											×			
Tinodes waeneri L.											×			
Coleoptera														
Haliplus confinis Stephens				×			×							
Haliplus lineatocollis (Marsham)				×			×			×				
Haliplus ruficollis (Degeer)				×										
Haliplus lineolatus Mannerheim				×			×							
Haliplus immaculatus Gerhardt				×			×							
Haliplus wehnckei Gerhardt				×										
Haliplus fulvus (Fabricius)				×			×							
Hygrotus inaequalis (Fabricius)				×			×							
Coelambus novemlineatus (Stephens)				×			×							
Deronectes depressus (Fabricius)				×										
Deronectes elegans (Panzer)							×							
Oreodytes septentrionalis (Gyllenhal)				×										
Oreodytes rivalis (Gyllenhal)				×										
Hydroporus striola (Gyllenhal)				×										
Hydroporus palustris (L.)				×										
Hydroporus planus (Fabricius)				×										
Agabus sturmii (Gyllenhal)							×							
Agabus chalconatus (Panzer)							×							
Agabus bipustulatus (L.)							×							
Platambus maculatus (L.)							×							
Ilybius fuliginosus (Fabricius)				×			×				×			
Rantus exsoletus (Forster)							×							
Rantus frontalis (Marsham)							×							
Colymbetes fuscus (L.)				×										
Dytiscus marginalis L.							×							
Gyrinus natator (L.)							×							
Hydraena riparia Kugelann							×							
Helophorus aquaticus (L.)				×			×							
Helophorus brevipalpis Bedel				×										
Helophorus flavipes Fabricius				×			×							
Laccobius minutus (L.)				×			×							
Laccobius alutaceus Thompson							×							
Chaetarthria seminulum (Herbst)							×							
Limnius volckmari (Panzer)											×			
Oulimnius tuberculatus (Muller)											×			
Haemonia appendiculata (Panzer)				×										

TABLE 1 (*cont.*)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Diptera														
Pentaneura monilis L.											×			
Procladius choreus Meigen											×			
Chironomus anthracinus Zetterstedt											×			
Chironomus plumosus L.											×			
Limnochironomus pulsus Walker											×			
Cryptochironomus supplicans Meigen											×			
Glyptotendipes paripes Staeger											×			
Microtendipes nitidus Meigen											×			
Stictochironomus rosenscholdi Zetterstedt											×			
Stictochironomus histrio Fabricius											×			
ARACHNIDA														
Hydracarina											×	×	×	
BRYOZOA														
Cristatella mucedo Cuvier											×	×		

The principal interest in such species lists lies in comparing the status of various animals at different times. One major difficulty in doing this is the fact that none of the lists obtained has ever been comprehensive and several are restricted to one particular group. Nevertheless, where adequate data for the same groups are available for different periods it is possible to make interesting comparisons, and the overall picture obtained from the whole table is of great value.

More than 200 invertebrate species have been recorded from Loch Leven to date (table 1). A few groups have never been examined systematically (e.g. Hydracarina and Bryozoa); others have been examined in detail on only one occasion (e.g. Nematoda and Ostracoda). Of greatest value are those groups which have been collected and systematically listed on two or more occasions, and important in this respect are Mollusca and some orders of Crustacea (Cladocera, Copepoda and Malacostraca) and Insecta (Ephemeroptera, Hemiptera and Coleoptera). There have clearly been important changes in the invertebrate communities during the last 100 years as far as these groups are concerned: some of these have already been discussed by Morgan (1970). Among the more important of these are the disappearance and subsequent reappearances of *Daphnia hyalina* between 1950 and 1970, the virtual disappearance of several species of Ephemeroptera, Odonata, Trichoptera and Coleoptera over a similar period, and a number of minor changes in other groups. The significance of some of these long-term and short-term changes is discussed below.

The records for Mollusca shown in table 1 indicate that a rich and varied community has persisted at the loch over the period of historical record. The main feature of change is the apparent disappearance of several species of *Lymnaea* and *Planorbis* in recent years. This is probably related to the changes in macrophytes with which many of these species are commonly associated. The larvae of Ephemeroptera, Odonata and Trichoptera are described by Scott (1891) as being common at Loch Leven, but very few species of these groups occur there now and none are abundant.

The list of Coleoptera in table 1 depends mainly on collections made there by Professor Balfour-Browne between 1930 and 1950. A number of collections especially for members of this order has been made recently with almost complete lack of success: it is evident that many of the Coleoptera present 30 years ago no longer occur there.

Existing Fauna

The recent data for the species list included in table 1 have been obtained from a number of sources, the most important of which have been a series of shore collections taken in 1967, and an extensive survey of the zoobenthos of the whole loch carried out in 1968. In addition, a number of quantitative studies on various parts of the loch have been carried out since 1968: these have involved emergence traps and the laboratory rearing of adult Chironomidae which are normally difficult to identify accurately in the immature stages.

The most detailed single study of the entire zoobenthos was a combined sediment/benthos survey which took place in 1968 and which will be described in detail elsewhere (Maitland in preparation). During this study, which was carried out in 10 days in October, more than 100 points evenly distributed over the whole loch were sampled and cores taken for physico-chemical and faunal analysis. Graphical analyses and more complex correlation analyses by computer have indicated that the major distinction among the sediments lies between sand and mud, and that there are fundamental differences between the benthic communities associated with these two types. This distinction, combined with the fact that no single instrument was available for sampling both sand and mud efficiently, necessitated a division of the research on zoobenthos in Loch Leven into two facets, one concerned with sand, the other with mud.

The major substrate types found in Loch Leven are sand (42 per cent of the area of the loch bed), mud (57 per cent) and stones (less than 1 per cent). (The fauna of stones in the loch was examined during preliminary shore sampling in 1967 but was not included in further sampling.) The great reduction in macrophytes since the beginning of the century (Morgan 1970) meant that these too occupied less than 1 per cent of the loch bed in 1967. As reported elsewhere, however (Jupp *et al.* 1974), the macrophytes started growing intensively again in 1971 and covered many areas of the bottom in shallow water in 1971 and 1972. As with stones, though the fauna of macrophytes was examined during the preliminary sampling in 1967, it was not included in further studies.

Some quantitative aspects of the invertebrate fauna of sand and mud in October 1968 are shown in table 2. The dominant animals by number in the community were Coelenterata (*Hydra*), Nematoda, Oligochaeta (mainly Tubificidae but with some Naididae, Enchytraeidae and Lumbriculidae), Diptera (almost entirely Chironomidae but with some Ceratopogonidae) and Mollusca (mainly *Valvata* and *Pisidium*). Other animals found in lesser numbers were Hirudinea, Crustacea (*Asellus* and *Gammarus*) and Trichoptera. In terms of biomass, Oligochaeta and especially Diptera were the two outstanding groups. The average numbers of benthic invertebrates in October 1968 were 58 013/m^2 (0·5 mm mesh sieve) with a dry weight of 11·407 g/m^2.

There are several notable differences between the communities found in sand and mud; a number of these are indicated in table 2 and have been consistent over the whole period of recent study. Some animals occur commonly over both substrates (e.g. *Valvata, Pisidium,* Tubificidae, Lumbriculidae, *Helobdella, Limnochironomus,* and *Glyptotendipes*); others are much more common on or restricted to sand (e.g. Nematoda, Naididae, Enchytraeidae, Orthocladiinae, *Cryptochironomus, Stictochironomus,*

TABLE 2

Numbers and weights of invertebrate benthos in Loch Leven in October 1968

	Sand		Mud		Mean	
Fauna	nos/m²	mg/m²	nos/m²	mg/m²	nos/m²	mg/m²
COELENTERATA						
Hydra	413	26	2,590	117	1,575	75
PLATYHELMINTHES						
Rhabdocoela	240	32	140	16	188	23
NEMATODA	34,953	1,078	2,650	200	17,705	609
GASTROPODA						
Valvata	255	186	545	503	410	355
BIVALVIA						
Pisidium	995	529	1,145	259	1,075	385
OLIGOCHAETA						
Naididae	2,173	364	45	4	1,038	172
Tubificidae	11,520	1,202	12,223	1,533	11,895	1,379
Enchytraeidae	11,583	163	640	8	5,740	80
Lumbriculidae	658	1,192	723	940	693	1,057
HIRUDINEA						
Helobdella	158	176	163	183	160	180
CRUSTACEA						
Ostracoda	145	14	345	21	253	17
Asellus	33	31	113	52	75	42
INSECTA						
Pentaneura	163	3	388	10	280	7
Procladius	828	91	3,950	540	2,608	331
Orthocladiinae	470	17	50	3	220	10
Chironomus	25	74	318	956	183	642
Limnochironomus	600	234	588	222	593	228
Cryptochironomus	428	129	60	14	230	67
Glytotendipes	4,515	5,469	2,310	3,304	3,338	4,313
Endochironomus	208	254	195	147	203	197
Stictochironomus	2,543	889	0	0	1,185	414
Polypedilum	298	134	1,713	880	1,053	532
Tanytarsini	11,333	264	1,668	42	6,860	146
Ceratopogonidae	500	87	18	6	198	44
OTHERS	250	130	145	77	255	102
Totals	85,287	12,768	32,725	10,037	58,013	11,407

Tanytarsini and Ceratopogonidae) or to mud (e.g. *Hydra, Asellus, Pentaneura-Procladius, Chironomus* and *Polypedilum*). In spite of these differences the relative biomass occupying the two substrates was very similar: 12·768 g/m² in sand and 10·037 g/m² in mud (dry weight).

PRODUCTION STUDIES IN THE SANDY LITTORAL AREA

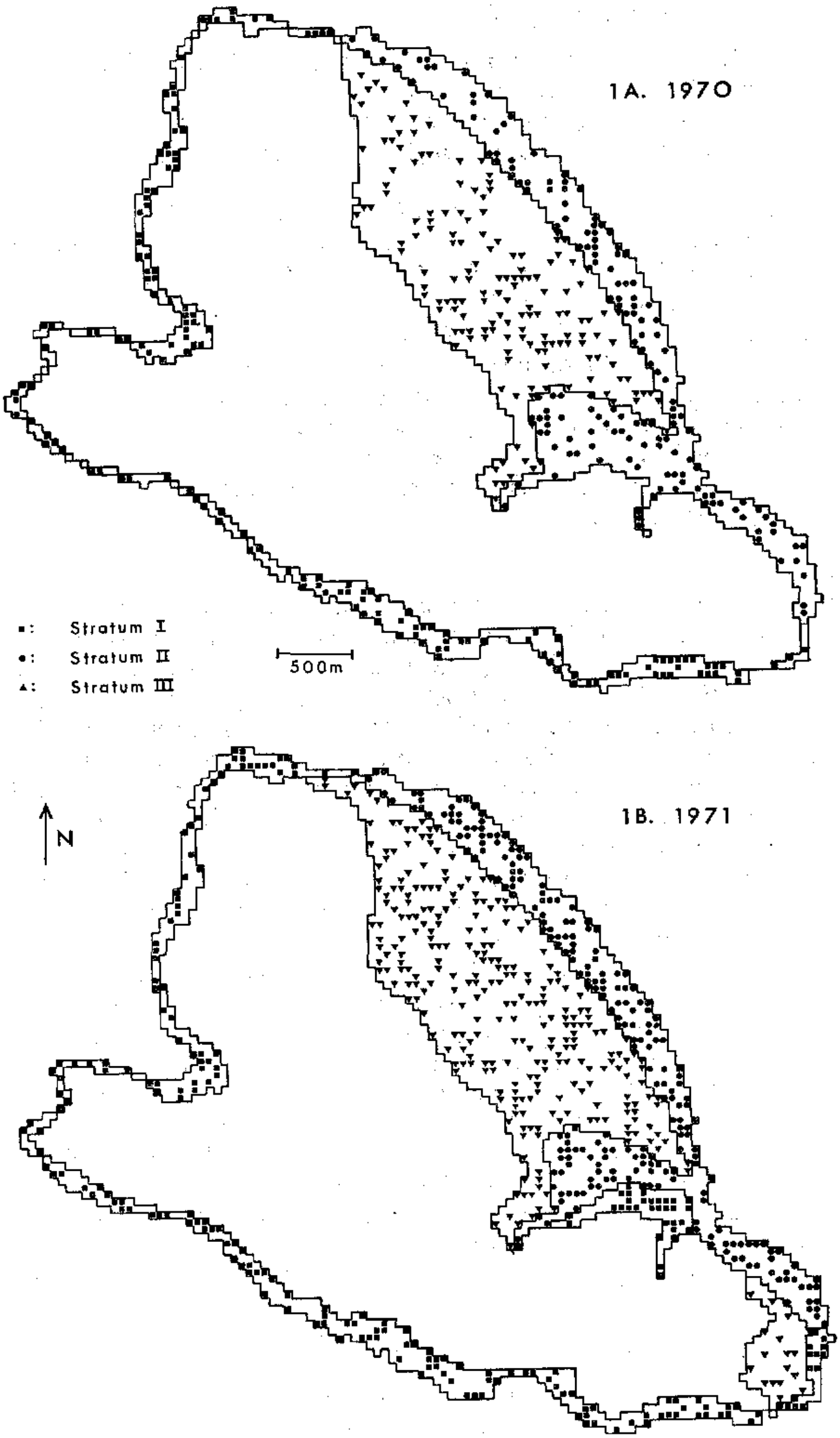
The major single group among the recent zoobenthos in most parts of the loch is clearly Chironomidae. The main vertebrate predators in the ecosystem are trout, *Salmo trutta* L.; perch, *Perca fluviatilis* L.; and tufted duck, *Aythya fuligula* (L.). Examination of the gut contents of samples of these between 1966 and 1970 revealed that Chironomidae appeared to be the major food item, though Mollusca and Crustacea were also of importance. Oligochaeta (the other major group in the benthos) were eaten only rarely. The main source of primary production in Loch Leven is algae: gut analyses have shown that these are eaten directly by many larval Chironomidae and some Bivalvia. Because of the importance of Chironomidae in the benthic community, as direct consumers of primary production and as food for tertiary consumers, the main effort throughout the present study has been concentrated on them—hence the emphasis on this group in the production studies outlined below.

Methods

As noted above, the major effort during the first stage of this study (1968 and 1969) was directed towards examining the distribution of the sand benthos in time and space, and developing efficient methods of collecting and handling samples. All later samples were taken with a corer developed at Loch Leven (Maitland 1969) which collects undisturbed samples of sand some 7 cm in diameter (there are exactly 250 of these cores per square metre) to a depth of 15 cm. This depth was shown by earlier trials to be adequate for the benthos in this substrate (Maitland *et al.* 1972). Cores taken from the loch bed were fixed in 4 per cent formaldehyde soon after collection and left for 48 hr to allow the animals to harden. They were then washed to separate the fauna from the remainder of the substrate. The washing method was a simple decantation one based on differences in specific gravity between invertebrates (even Mollusca and Trichoptera) and sand grains. The fluid in each sample was decanted into sieves. Water was then run into the sample vigorously so that all the sand was disturbed; as soon as it had settled the water was decanted again. This process was repeated four times: early trials showed that this was adequate for virtually 100 per cent separation of the animals and sediment concerned (Maitland *et al.* 1972).

The decanted material was collected in two sieves: first a coarse one (0·5 mm mesh opening), then a fine one (0·125 mm mesh opening). All the values presented in this paper are for fauna retained in the coarser sieve only (see below). Samples collected in the sieves were then sorted using stereomicroscopes ($\times 10$–$\times 40$) and invertebrates identified and counted. Species involved in production studies were measured for length and dried in a desiccator at room temperature for at least 48 hours. They were then weighed in batches on a Cl Electronics Mark MK2B Microbalance, to ± 2.5 μg in the case of small animals (*ca* 30 μg) or to $\pm 0{\cdot}1$ mg in the case of the largest larvae (3·5 mg). The dry weights produced in this way were subject to potential error since the larvae had been stored in 4 per cent formaldehyde for substantial periods.

During the second stage of the study (1970 and 1971) as full a sampling programme as possible in relation to the resources available was carried out over the whole of the sand area (*ca* 562 ha) in an attempt to measure the production of Chironomidae and other zoobenthos there. The area was divided for sampling purposes into three strata whose boundaries were based largely on the results of the sediment/benthos survey noted above (text-fig. 1). These boundaries were slightly readjusted between the 1970 and 1971 programmes. The three strata were (i) the west and south-west shore from 0 to 2 m, (ii) the north and east shore from 0 to 1 m and (iii) the north-east shore from 1 to 4 m. In 1970 at each sampling session pairs of cores were taken



TEXT-FIG. 1.—The extent of the sand area in stylised maps of Loch Leven and the squares (50 × 50 m) sampled randomly during 1970 (1A) and during 1971 (1B).

at 16 randomly selected points in each stratum: in 1971 this was increased to 24 points. However, in 1971, each stratum was subdivided into four parts and six pairs of cores were taken randomly in each of these: the preserved cores from within each stratum were then bulked to give six samples (each containing one core from each substratum).

Of each pair of cores, one was preserved in 4 per cent formaldehyde for the production work while the other was kept fresh for emergence and other studies in the laboratory. Starting in January 1970 the sand area was sampled regularly every few weeks (more frequently in summer than winter) until December 1971. There were 10 sampling sessions in 1970 and 12 in 1971, and during these 22 sessions about 2700 cores were taken from the sand area. The mean dates of all these sessions are given in tables 3 and 4. Though there were constant and interesting differences among the three strata, limitations of space prevent their full presentation and discussion here. Almost all results are presented in relation to the sandy littoral area as a whole and in combining the data, weighting to allow for the different sizes of the three strata has been carried out.

Production Data

General data on the invertebrate community in sand during 1970 and 1971 are presented in table 3. It can be seen that, apart from a notable decrease in the total numbers of invertebrates (particularly Nematoda) from the 1968 survey (table 2) the general composition of the fauna was much the same throughout the period of study, with Oligochaeta and larval Chironomidae dominating both numbers and biomass. In both 1970 and 1971 larval Chironomidae represented more than 70 per cent by number of the invertebrates retained by a 0·5 mm sieve. It is known that large numbers of small animals pass through this mesh size and that these can be important numerically. However, their contribution to the total weight and to production is likely to be small. Maitland *et al.* (1972) have shown that values obtained for *Stictochironomus* at Loch Leven in 1968 using a 0·5-mm sieve alone underestimated the annual production by only 2·7 per cent.

Comparable data of a more detailed nature for the larval Chironomidae are given in table 4. Of the larger genera, *Limnochironomus*, *Cryptochironomus*, *Glyptotendipes* and *Stictochironomus* were the most important. The Tanytarsini, though always abundant numerically, were much less important in biomass and this group also presented several difficulties in terms of production estimation (see below).

The preliminary sampling in 1967 of the invertebrate benthos and the food of trout, perch and tufted duck indicated that among the larval Chironomidae which dominated the benthos and formed the bulk of the vertebrate food, *Glyptotendipes*, *Stictochironomus* and *Endochironomus* were the most important (in that order). They formed, for example, 29, 16 and 5 per cent by bulk respectively of the benthos and 23, 16 and 5 per cent by bulk of the food of trout. By 1970 *Endochironomus* had disappeared completely from Loch Leven and the effort during production studies was concentrated on *Glyptotendipes* and *Stictochironomus*, and to a lesser extent on *Limnochironomus* and *Cryptochironomus*.

Studies carried out in 1968 and 1969 indicated that, for the most part, the populations of *Glyptotendipes* and *Stictochironomus* were univoltine. This meant that it was possible to follow the growth and survivorship of each generation. The main aim

TABLE 3A

Numbers per square metre of invertebrate benthos in the sand area of Loch Leven during 1970. Mean dry weights are also included

Fauna	A Jan 23	B Mar 5	C Apr 8	D May 15	E Jun 11	F Jul 9	G Aug 20	H Sep 30	I Oct 28	J Dec 16	Mean	Mean dry wt(mg/m²)
COELENTERATA												
Hydra	8	8	0	0	62	0	3	0	0	0	7	1
PLATYHELMINTHES												
Rhabdocoela	8	0	0	0	3	5	10	5	0	13	5	1
NEMATODA	0	57	187	227	263	441	940	402	243	95	285	9
GASTROPODA												
Valvata	102	119	93	174	80	133	54	74	162	13	99	124
Potamopyrgus	8	3	0	0	9	9	6	8	11	23	8	7
Lymnaea	0	8	0	3	62	0	10	22	33	20	15	29
BIVALVIA												
Pisidium	170	254	187	199	367	155	363	474	840	831	340	99
OLIGOCHAETA	1,452	3,612	2,500	3,330	4,177	6,348	4,179	3,706	3,729	3,435	3,597	1,213
HIRUDINEA												
Helobdella	62	62	18	8	25	11	106	71	63	27	47	48
Erpobdella	46	41	3	21	26	21	27	24	46	45	31	104
CRUSTACEA												
Ostracoda	16	23	3	0	0	8	125	58	198	0	46	6
Asellus	136	114	8	24	3	49	45	54	220	15	71	54
INSECTA												
Trichoptera	245	156	71	153	160	102	15	77	155	81	122	113
Chironomidae	24,873	25,137	19,810	16,784	12,033	54,221	24,892	21,858	23,039	19,249	24,400	9,555
Ceratopogonidae	35	94	24	23	15	42	95	88	153	28	62	18
OTHERS	3	15	0	0	40	0	5	0	8	0	6	14
Totals	27,164	29,703	22,904	20,946	17,325	61,545	30,875	26,921	28,900	23,875	29,241	11,395

TABLE 3B

Numbers per square metre of invertebrate benthos in the sand area of Loch Leven during 1971

Fauna	K Jan 26	L Mar 10	M Apr 7	N Apr 27	O May 19	P Jun 8	Q Jun 29	R Jul 20	S Aug 17	T Sep 14	U Oct 28	V Dec 17	Mean
COELENTERATA													
Hydra	0	0	0	0	0	0	0	0	0	3	0	0	0
PLATYHELMINTHES													
Rhabdocoela	29	26	0	0	0	0	0	0	0	0	146	52	31
NEMATODA	1,400	936	478	646	1,139	592	660	631	803	931	899	1092	907
GASTROPODA													
Valvata	103	86	47	19	21	16	5	0	19	60	45	168	59
Potamopyrgus	32	68	8	14	8	26	42	10	131	505	391	316	162
Lymnaea	16	5	3	0	3	3	0	3	5	26	16	10	9
BIVALVIA													
Pisidium	683	579	699	481	552	415	357	175	900	1,600	1,345	1,150	829
OLIGOCHAETA	3,968	1,810	2,501	1,733	3,618	2,322	3,087	2,304	2,699	3,415	4,217	1,753	2,904
HIRUDINEA													
Helobdella	43	22	37	15	6	21	6	13	29	43	29	37	28
Erpobdella	31	42	19	22	21	39	3	0	6	13	8	19	19
CRUSTACEA													
Ostracoda	121	63	47	11	14	10	0	3	26	94	19	62	47
Asellus	172	42	230	32	29	45	50	29	26	170	18	71	81
INSECTA													
Trichoptera	47	19	52	26	26	27	34	3	0	29	19	26	122
Chironomidae	11,143	10,240	10,724	8,669	6,465	3,561	7,567	13,119	13,816	24,278	24,940	16,294	13,973
Ceratopogonidae	92	89	35	87	115	16	5	32	34	87	97	138	77
OTHERS	5	3	0	0	0	0	0	0	3	3	0	8	2
Totals	17,885	14,030	14,880	11,755	12,017	093	11,816	16,322	18,497	31,257	32,189	21,196	19,250

TABLE 4A

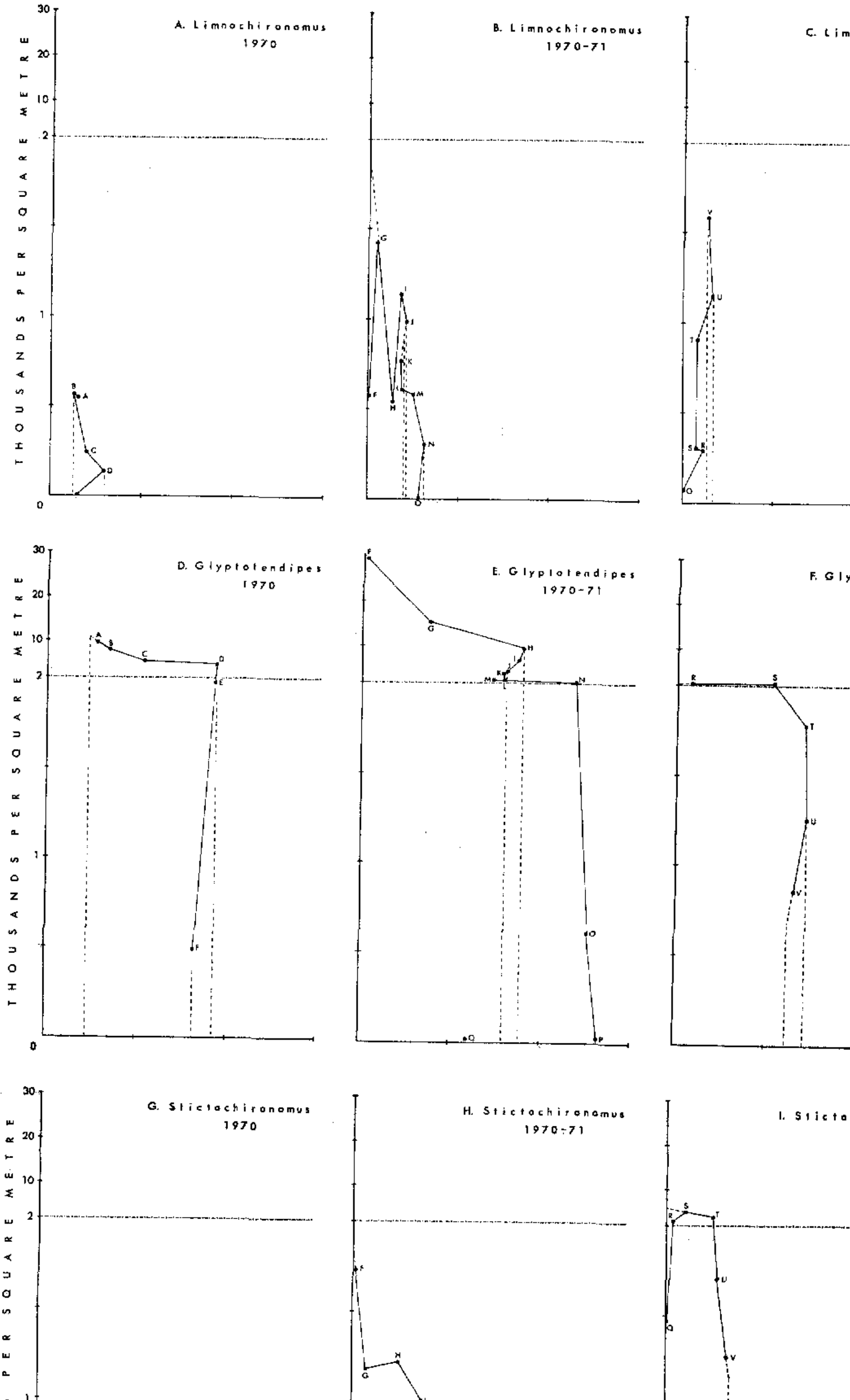
Numbers per square metre of larval Chironomidae in the sand area of Loch Leven during 1970. Mean dry weights are also included.

Chironomidae	A Jan 23	B Mar 5	C Apr 8	D May 15	E Jun 11	F Jul 9	G Aug 20	H Sep 30	I Oct 28	J Dec 16	Mean	Mean dry wt(mg/m²)
Pentaneura	57	26	18	90	0	476	93	52	20	49	88	10
Procladius	24	55	12	18	31	187	120	40	73	35	60	12
Diamesa	24	30	18	6	36	18	6	8	46	27	22	7
Orthocladiinae	853	644	326	262	1,042	568	371	176	328	106	461	45
Chironomus	0	0	0	0	0	18	65	8	31	23	16	15
Limnochironomus	546	566	241	138	3	569	1,424	536	1,139	984	653	166
Cryptochironomus	948	764	789	514	416	287	986	865	1,249	1,087	815	317
Glyptotendipes	9,944	8,010	5,754	5,134	1,974	30,074	15,265	9,896	6,940	4,476	9,926	8,139
Microtendipes	47	30	12	0	0	31	9	12	157	78	40	31
Stictochironomus	382	408	412	352	5	1,730	1,180	1,223	909	1,008	779	394
Polypedilum	0	0	0	0	0	0	62	0	54	38	17	7
Tanytarsini	12,028	14,601	11,598	10,267	8,495	20,252	5,136	9,019	12,067	11,326	11,491	394
Others	21	3	0	3	31	11	175	23	26	12	32	18
Totals	24,873	25,137	19,810	16,784	12,033	54,221	24,892	21,858	23,039	19,249	24,400	9,555

TABLE 4B

Numbers per square metre of larval Chironomidae in the sand area of Loch Leven during 1971

Chironomidae	K Jan 26	L Mar 10	M Apr 7	N Apr 27	O May 19	P Jun 8	Q Jun 29	R Jul 20	S Aug 17	T Sep 14	U Oct 28	V Dec 17	Mean
Pentaneura	32	44	151	35	52	0	188	29	183	99	14	16	64
Procladius	79	65	98	55	173	213	467	285	540	371	527	564	301
Diamesa	32	19	25	6	14	8	0	0	11	26	5	0	13
Orthocladiinae	81	58	36	21	3	81	42	478	788	558	1,126	381	360
Chironomus	21	5	5	5	0	0	162	560	402	71	162	128	123
Limnochironomus	769	613	586	297	8	0	68	290	300	907	1,144	1,576	668
Cryptochironomus	891	1,012	1,160	889	629	468	521	170	420	311	453	305	601
Glyptotendipes	4,075	2,605	2,647	2,316	607	24	21	2,027	2,392	1,780	1,251	852	1,877
Microtendipes	40	17	5	0	0	0	3	0	42	5	58	105	30
Stictochironomus	743	758	543	675	109	0	1,470	2,991	5,093	3,947	1,701	1,264	1,668
Polypedilum	16	0	5	11	0	0	11	42	0	21	125	32	28
Tanytarsini	4,361	5,044	5,445	4,356	4,870	2,767	4,614	6,242	3,645	16,182	18,369	11,071	8,228
Others	3	0	18	3	0	0	0	5	0	0	5	0	3
Totals	11,143	10,240	10,724	8,669	6,465	3,561	7,567	13,119	13,816	24,278	24,940	16,294	13,946



A. Limnochironomus
1970
B. Limnochironomus
1970-71
D. Glyptotendipes
1970
E. Glyptotendipes
1970-71
G. Stictochironomus
1970
H. Stictochironomus
1970-71
THOUSANDS PER SQUARE METRE
30
20
10
2
1
0

during the detailed studies in 1970 and 1971 was to obtain accurate data on numbers and weights of the larvae of these genera in order that production could be computed. As pointed out in Ricker (1968), production may be estimated either numerically

TABLE 5A

Production data for 1970 for Limnochironomus, Glyptotendipes *and* Stictochironomus

Date (1970)	Nos/m² Estimate		Nos/m² 95% C.I's	$\bar{w}$ dry (mg) (mean individual weight) Estimate		$\bar{w}$ dry (mg) 95% C.I's	B dry (g/m²/t) (mean biomass)	P dry (g/m²/t)	P dry (mg/m²/day)	P/B coefficient
Limnochironomus										
23·1	546	±	379	0·295	±	0·220	0·161			
5·3	566	±	360	0·250	±	0·346	0·142	−0·025	−0·610	−0·0040
8·4	241	±	180	0·395	±	0·200	0·095	0·059	1·735	0·0146
15·5	138	±	105	0·595	±	0·195	0·082	0·038	1·027	0·0116
11·6	3	±	6	0·300			0·001	−0·021	−0·778	−0·0187
9·7	569	±	308	0·013	±	0·007	0·007			
20·8	1,424	±	1,035	0·093	±	0·051	0·132	0·080	1·905	0·0274
30·9	536	±	451	0·287	±	0·184	0·154	0·190	4·634	0·0324
28·10	1,139	±	1,568	0·347	±	0·174	0·395	0·050	1·786	0·0065
16·12	984	±	1,302	0·412	±	0·144	0·405	0·069	1·408	0·0035
Glyptotendipes										
23·1	9,944	±	4,052	0·540	±	0·329	5·370			
5·3	8,010	±	2,754	0·678	±	0·254	5·431	1·239	30·220	0·0056
8·4	5,754	±	2,488	1·063	±	0·417	6·117	2·650	77·941	0·0135
15·5	5,134	±	2,010	1·858	±	0·441	9·539	4·328	116·973	0·0149
11·6	1,974	±	788	1·845	±	0·734	3·642	−0·046	−1·704	−0·0003
9·7	487	±	236	2·143	±	1·327	1·044	0·367	13·107	0·0056
9·7	29,587	±	17,094	0·052	±	0·043	1·539			
20·8	15,265	±	4,744	0·740	±	0·457	11·296	15·429	367·357	0·0572
30·9	9,896	±	3,123	1·778	±	0·594	17·595	13·059	318·512	0·0220
28·10	6,940	±	2,727	1·730	±	0·490	12·006	−0·404	−14·429	−0·0010
16·12	4,476	±	1,955	1·598	±	0·535	7·153	−0·754	−15·388	−0·0016
Stictochironomus										
23·1	382	±	377	0·788	±	0·535	0·301			
5·3	408	±	319	1·002	±	1·000	0·409	0·085	2·073	0·0058
8·4	412	±	366	1·063	±	0·421	0·438	0·025	0·735	0·0017
15·5	352	±	233	1·263	±	0·481	0·445	0·076	2·054	0·0047
11·6	5	±	11	1·350			0·007	0·016	0·593	0·0026
9·7	1,730	±	1,102	0·026	±	0·026	0·045			
20·8	1,180	±	820	0·155	±	0·153	0·183	0·188	4·476	0·0393
30·9	1,223	±	900	0·510	±	0·391	0·624	0·427	10·415	0·0258
28·10	909	±	505	0·688	±	0·277	0·625	0·190	6·786	0·0109
16·12	1,008	±	541	0·770	±	0·310	0·776	0·079	1·612	0·0023

or graphically; both methods (as recommended by Ricker) were used during the present study with substantially the same results. The data for each stratum were computed separately and then weighted means produced for the whole of the sand area (see table 5A).

In developing the Allen curves, the point estimates for weight survivorship were connected by straight lines. To compute values for each calendar year lines back to 1 January and forward to 31 December were extrapolated from production during the subsequent or previous period respectively. Negative production (either apparent or real) was not uncommon. The estimates given below are based on the maximum values attained each year and negative production has not been subtracted. The areas beneath the curves were measured by counting squares on graph paper.

Text-figs. 2A–2I are Allen curves drawn for the three generations of *Limnochironomus*, *Glyptotendipes* and *Stictochironomus* which were studied during 1970 and 1971. Only

TABLE 5B

Production estimates for 1970 and 1971 based on Allen curve data for Limnochironomus, Glyptotendipes *and* Stictochironomus *(A = 1st generation, B = 2nd generation in each year)*

	Limnochironomus		*Glyptotendipes*		*Stictochironomus*	
	mg/m²	J/m²	mg/m²	J/m²	mg/m²	J/m²
1970 A	137	3,067	9,643	212,917	313	6,326
1970 B	457	10,232	30,876	681,742	893	18,048
Total	594	13,299	40,519	894,659	1,206	24,374
P/B Value	3·58		4·98		3·06	
1971 A	163	3,650	2,557	56,459	483	9,761
1971 B	221	4,948	2,463	54,383	9,737	196,785
Total	384	8,598	5,020	110,842	10,220	206,546
P/B Value	1·90		1·85		9·80	

one of these generations (1970–71) was studied throughout its entire life cycle (text-figs. 2B, E and H). In general, these curves exhibit the decrease in numbers with increase in weight which is characteristic of populations showing growth but no recruitment. Negative production tended to occur in winter when the loss in mean weight was probably a real one, or during the emergence period when there may have been no actual loss. There is evidence that the larger larvae tend to pupate earliest, thus leaving behind a population with a lower mean weight. In a number of cases the density increased with time—often at the beginning of a new generation (e.g. text-fig. 2C). Apart from sampling error this was probably due to further recruitment to the population as eggs hatched or to small larvae (which passed through a 0·5 mm sieve in the early stages) growing large enough to be trapped.

Production estimates for *Limnochironomus*, *Glyptotendipes* and *Stictochironomus* for 1970 and 1971, based on Allen curve data, are given in table 5B. It can be seen that there were large differences in the production during each year. In 1970 the total production by these three genera was over 42 g/m^2 while in 1971 it amounted to less than 16 g/m^2. In 1970 the production was completely dominated by *Glyptotendipes* but in 1971 this fell dramatically and the major producer was *Stictochironomus*.

Fresh live material for these two genera was collected at sampling sessions during 1970 and dried in a desiccator immediately on returning to the laboratory. Samples were subsequently bulked to give sufficient weights for accurate energy determinations which were then carried out on nine samples of *Glyptotendipes* and three samples of *Stictochironomus*. The mean values of these calorific determinations, and similar data for *Limnochironomus* obtained by Charles *et al.* (1974), were then used to give the energy values shown in table 5B, taking into account the values for percentages of ash obtained at the same time (table 6).

TABLE 6

Ash and energy values for three genera of Chironomidae in 1970

Genus	Time period	% Ash	kJ/g (ash free)
Cryptochironomus	Jan–Apr	5·5	22·2
	May–Jul	6·4	24·9
	Aug–Dec	7·6	23·3
Glyptotendipes	Jan–Apr	8·1	23·1
	May–Jul	6·5	23·2
	Aug–Dec	8·0	26·0
Stictochironomus	Jan–Apr	13·8	24·2
	May–Jul	11·0	21·8
	Aug–Dec	13·1	23·4

It can be seen from tables 3 and 4 that Chironomidae represented the bulk of the biomass in the sandy littoral area during 1970 and that *Limnochironomus*, *Glyptotendipes* and *Stictochironomus* made up most of the biomass of Chironomidae. If one makes the assumption that annual production in all groups of zoobenthos bears the same relationship to mean standing crop as in these three genera of Chironomidae, then it is possible to produce an estimate of the total zoobenthos production in 1970. The figure calculated is 46·482 g/m^2. Assuming the same ash contents and calorific values as estimated for the three Chironomidae, this figure converts to 1002·152 kJ/m^2. Though most of the invertebrate species involved are univoltine, several of the smaller species of Chironomidae are likely to be multivoltine and a number of Oligochaeta reproduce asexually. These groups are likely to have higher P/B ratios than *Limnochironomus*, etc., and so the estimates given above are likely to be minimal ones.

DISCUSSION

Long-term changes in the zoobenthos and other components of the Loch Leven ecosystem have been discussed by Morgan (1970) and are mentioned above. At the start of the present study it was assumed that, though changes had occurred in the zoobenthos, it was likely to remain reasonably stable over a period of a few years, viz. the intended period of IBP study 1968–71. The most dramatic change in the Chironomidae has been the complete disappearance of *Endochironomus* from the system during 1969. There is no evidence as to the cause of its extinction. Almost as dramatic was the change in the status of *Glyptotendipes* and *Stictochironomus* which took place during 1971. With the development of the new generations that year it was clear that *Glyptotendipes* was being very much less successful than it had been the previous year; the opposite was the case with *Stictochironomus*. This change took place just at a time when the populations of algae and *Daphnia* were also changing dramatically (Bailey-Watts 1974) and there is likely to be some relationship between these events—possibly through food limitation. *Glyptotendipes* and *Stictochironomus* are known to have widely differing feeding habits, the former eating mainly planktonic the latter benthic algae.

In spite of careful consideration during 1968 and 1969 of the sampling problems involved, the limitations imposed by available manpower, the great extent of the area to be sampled and the discontinuous and varying distribution of the various species of benthos, have meant that the accuracy of the present data is not high (see table 5A). Although it has been possible to calculate the errors involved in some measurements (particularly major aspects of the important ones of density and growth) this has not been so with others (loss of small larvae due to mesh size, effect of formalin upon weights, variation in calorific values, etc.). For this reason no attempt has been made to give values for the accuracy of final production figures. The figures given above for production of the whole zoobenthos during 1970 are, of course, speculative. Such difficulties are usually the main reason for the inadequate or sometimes non-existent data in what are otherwise relatively sophisticated ecosystem studies (e.g. Krogius *et al.* 1972; Moskalenko and Votinsev 1972).

The figures given for the annual benthos production (46·5 g/m^2) are considerably higher than those calculated for many Russian lakes (e.g. Alimov *et al.* 1972; Andronikova *et al.* 1972; Winberg 1972), but of the same order of magnitude as recorded by Kajak *et al.* (1972) for the richer Polish lakes (e.g. Lake Taltowisko: *ca* 40 g/m^2). In 1970 the major single producer was undoubtedly *Glyptotendipes* whose production in the sandy littoral is estimated at over 40 g/m^2. This figure is still considerably less than the annual production of over 90 g/m^2 estimated by Kimerle and Anderson (1971) for the same genus in sewage lagoons in North America. The values estimated for Loch Leven therefore are by no means exceptional.

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