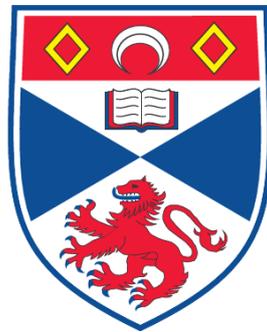


**THE FOOD AND FEEDING OF POWAN COREGONUS LAVARETUS
(L.) (SALMONIDAE: COREGONINAE) IN TWO SCOTTISH
LOCHS**

Patrick P. Pomeroy

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



1987

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The food and feeding of powan *Coregonus lavaretus* (L.)
(Salmonidae:Coregoninae) in two Scottish lochs.

by

Patrick P. Pomeroy

Department of Zoology
and Marine Biology,

University of St. Andrews.

A thesis submitted for the degree of Doctor of Philosophy

1987.



This work is dedicated to my parents.

Certificate.

I certify that Patrick Pomeroy has spent nine terms engaged in research work under my supervision and that he has fulfilled the conditions of General Ordinance No. 12 (Resolution of the University Court No. 1, 1967), and that he is qualified to submit the accompanying thesis for the degree of Doctor of Philosophy.



Dr. D.B.C. Scott,
Dept. Zoology and
Marine Biology.

DECLARATION

I Patrick Pomeroy hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

Signed  Date *19th March 1987*

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Acknowledgments.

I would like to thank everyone who helped me while this work was in progress, especially Mrs. Flora Slack and her late husband Harry for their support and accomodation at the Yett of Ptamigan.

North of Scotland Hydro-Electric Board and Mrs. K. Moffatt also provided fieldwork accomodation.

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ABSTRACT.

The present study is mainly a descriptive account of the food and feeding of the two Scottish powan populations from Loch Lomond and Loch Eck. Quantitative and qualitative comparisons of powan diet are made. Seasonal variations of diet are determined for the two populations and some aspects of the planktivorous feeding of adult powan in Loch Lomond are examined. The partitioning of the ingested energy into somatic and non-somatic growth is considered. Factors affecting the feeding of the two populations are discussed.

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CHAPTER 1. Sampling the powan populations of Loch Lomond and Loch Eck.

INTRODUCTION

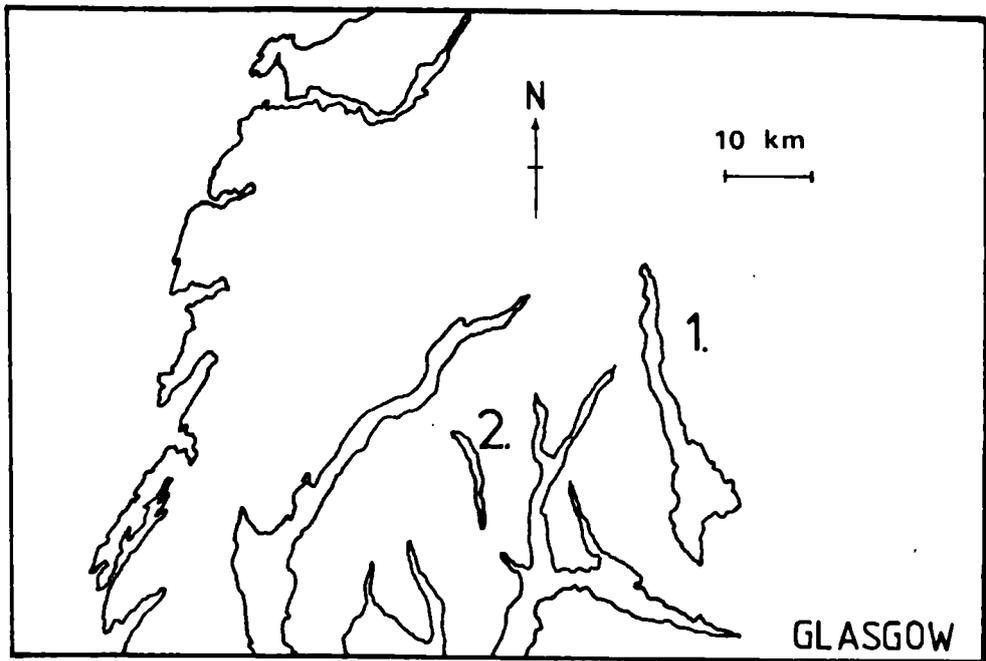
Powan are members of the Coregoninae, a sub-family of the Salmonidae. There are extensive fisheries for coregonines in North America, U.S.S.R., northern Europe and Scandinavia .

The coregonines are notoriously difficult to classify and show a wide geographic and ecological distribution (Svardson, 1979). The range of food types eaten by coregonines is extensive, with piscivorous, planktivorous and omnivorous habits displayed within the group and sometimes within species (Jacobson, 1981). Most of the northerly species are migratory, feeding for a period in the sea and returning to freshwater to spawn. In British waters only the rare houting Coregonus oxyrinchus (L.) maintains this habit. The remaining British coregonines exist as isolated populations which are probably relicts from the last Ice Age. The Welsh gwyniad C. lavaretus (L.) is found in Llyn Tegid. Haweswater, Ullswater and Red Tarn in the English Lake District contain schelly C. lavaretus (L.), while vendace C. albula were present until recently in Lochmaben and are still to be found in Derwentwater and Bassenthwaite in Cumberland. Ireland has pollan, C. autumnalis pollan Thompson, in Lough Neagh, the Fermanagh lakes and the Shannon system. Powan are endemic to Loch Lomond and Loch Eck in Scotland.

Loch Lomond lies approximately 30 km north-west of Glasgow with its long axis running north to south (National Grid reference 263598, Figs. 1.1,1.2). Its maximum length is 36.4 km and with a surface area of 71.1 km² it is the largest expanse of freshwater in mainland Britain. The northern part of the loch has a narrow steep sided basin which reaches a depth of 189.9m, but south of Ross Point opens out to form a wider basin to 66m depth. South of this middle basin the loch reaches a maximum breadth of 8.8 km and the depth rarely exceeds 20m. There are numerous islands in the southern loch. The physical differences between the basins of Loch Lomond and their catchments are geological in origin; the upper highland loch being formed by glacial action on a river valley composed of Dalradian rocks, while the lower loch was formed by accumulative glacial processes, ponding and marine incursions on the Carboniferous and Devonian rocks of the region. These differences are indicated by the water chemistry of the loch. The highland loch shows typical oligotrophic base-poor characteristics while the lower loch's water reflects a mainly lowland base-rich agricultural catchment. Geological and hydrological information are given by Slack (1957) and in Maitland (1981). Table 1.1 summarises Loch Lomond's hydrology.

Seasonal variations in the temperature regimes in the three basins of Loch Lomond have been described by Slack (1957) and are shown in Fig. 1.3. Stratification in the upper loch typically persists from May to December or January and in the middle basin from May to November, reaching a depth of 30m in September. In the shallow southern basin temporary stratification in the summer months requires suitably calm weather. Few British water bodies have such a diverse fish fauna as Loch Lomond. Salmon Salmo salar L., sea trout Salmo trutta trutta L., brown trout Salmo trutta fario L., powan Coregonus

Fig. 1.1 West Scotland, showing Loch Lomond
and Loch Eck.



1. L. Lomond

2. L. Eck

Fig. 1.1

Fig. 1.2

Loch Lomond showing netting sites :

R = Rowchoish P = Ptarmigan

C = Camus an Iosgainn.

Netting also took place in Sallochy Bay
and near the MacDougall Bank.

Soundings in metres.

(Modified after Fuller, Scott and
Fraser, 1976.)

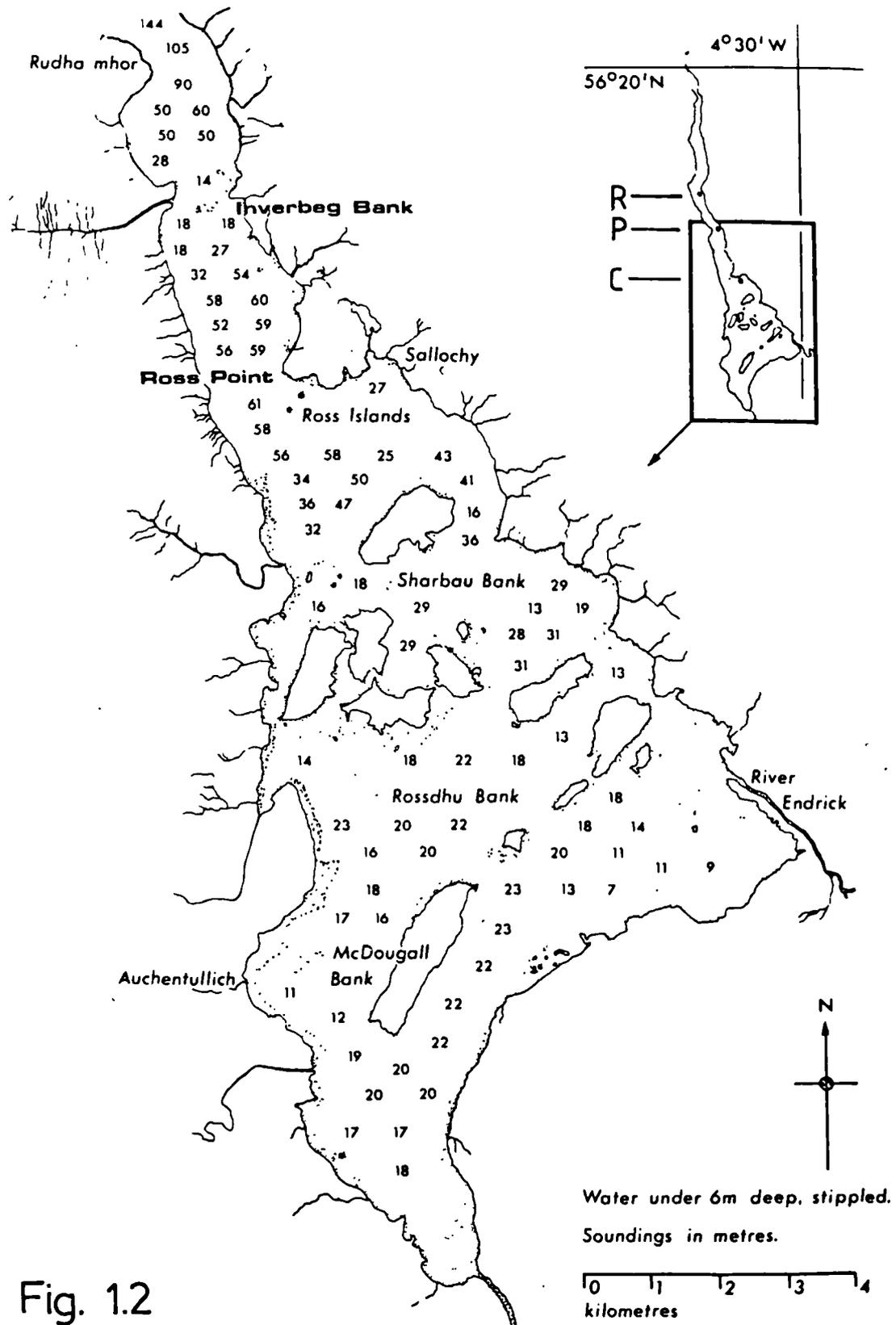


Fig. 1.2

Table 1.1

Summary of hydrological data for L. Lomond
 (from Maitland, 1981). Water chemistry data
 refer to annual means for the whole loch.
 Loch Eck data from Murray & Pullar, (1910).

Area	71.1 km ²	
Maximum depth	189.9 m	
Volume	2628 x 10 ⁶ m ³	
Conductivity	34 μS cm ⁻¹ at 20 °C	
Alkalinity	6.37 mg l ⁻¹ (measured as CaCO ₃)	
pH	6.78	
Secchi disc transparency	4.2 - 6.75 m	
Chlorophyll a	2.8 μg l ⁻¹ (south basin)	
Light attenuation: (south basin):		
filter type	optical mid point	1% attn depth m
Schott BG12	460 nm	2.2
VG9	540 nm	6.25

Loch Eck

Area	4.48 km ²	
Maximum depth	42.4 m	
Volume	67.8 x 10 ⁶ m ³	

Fig. 1.3 Temperature profiles of Loch Lomond in;
 (i) northern (highland) basin,
 (ii) mid (Luss) basin,
 (iii) south (Fault) basin.
 Temperatures in degrees C.
 (After Slack, 1957).

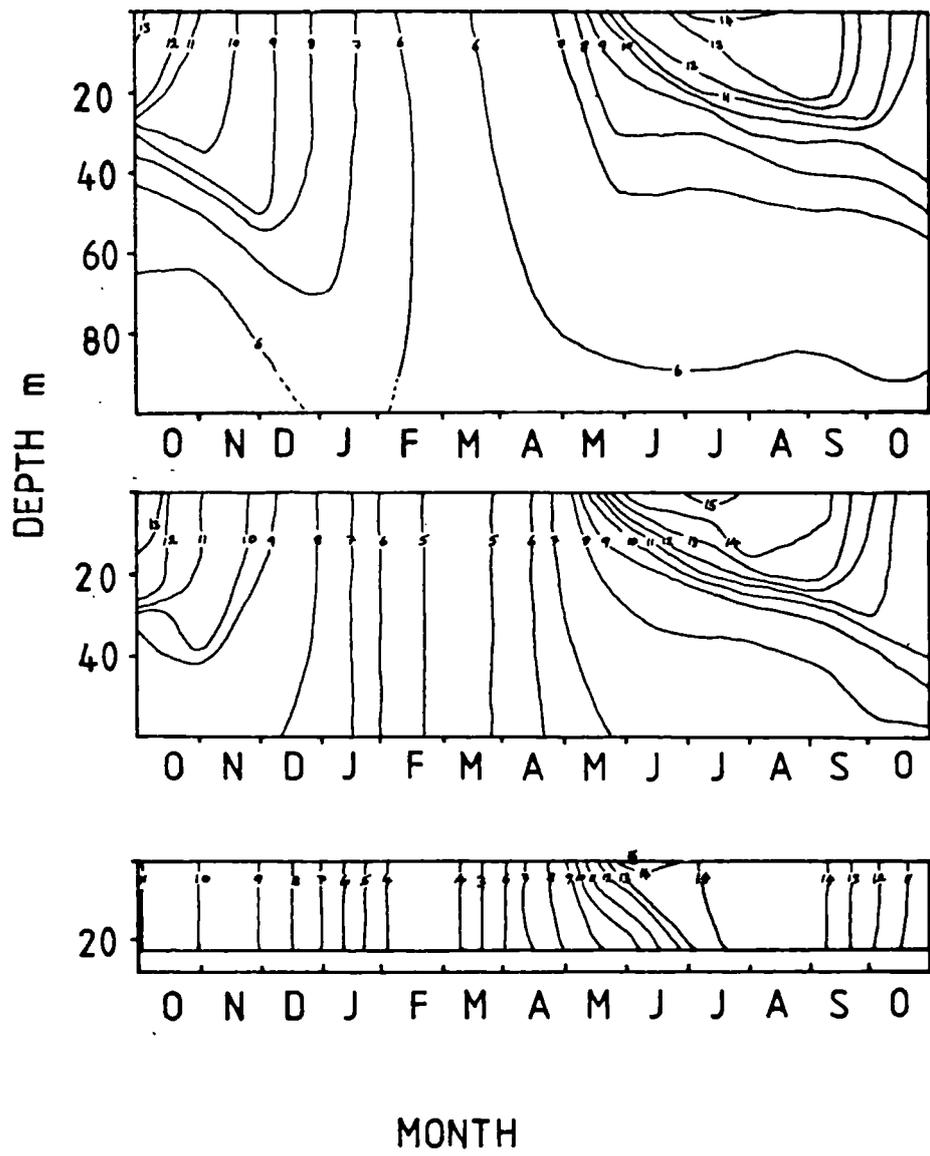


Fig. 1.3

lavaretus (L.), pike Esox lucius L., perch Perca fluviatilis L. three-spined stickleback Gasterosteus aculeatus L., ten-spined stickleback Pungitius pungitius (L.), sea, river and brook lamprey Petromyzon marinus L., Lampetra fluviatilis (L.), L. planeri (Bloch), roach Rutilus rutilus (L.), minnow Phoxinus phoxinus (L.), stone loach Noemacheilus barbatulus (L.), flounder Platichthys flesus (L.) and eel Anguilla anguilla (L.) are endemic. Gudgeon Gobio gobio (L.) are known to have become numerous in at least one of the loch's afferent rivers. Within the last few years ruffe Gymnocephalus cernua (L.) have become established in Loch Lomond, probably originating as escapees from anglers' live bait.

Loch Eck in Argyll is about 40 km to the west of Loch Lomond, running north to south between Loch Fyne at Strachur and the Holy Loch on the Clyde estuary (Figs. 1.1,1.4). Existing limnological information is restricted to that given in Murray & Pullar (1910). It is a narrow steep sided loch 9.6 km in length and has a maximum breadth of 0.6 km. The maximum depth of 42.4m is in a median basin 3 km from the entrance of the River Cur at the north end of the loch. Temperature profiles are given by Murray & Pullar (1910). The fish fauna of Loch Eck comprises salmon Salmo salar L., sea trout Salmo trutta trutta L., brown trout Salmo trutta fario L., powan Coregonus lavaretus (L.), charr Salvelinus alpinus (L.), three-spined stickleback Gasterosteus aculeatus L. and eel Anguilla anguilla (L.).

The Loch Lomond powan population was commercially fished until the 1930's when a combination of economic factors and a possible decline in fish numbers brought a halt to the operation (Lomond, 1930). Apart from a brief resurgence of the fishing during the last war, the population has been free from fishing artefact from this time (Scott, pers. comm.). Loch Lomond powan are rarely taken by anglers

Fig. 1.4

Loch Eck, Argyll.

RS = Rudha na Seamrig.

Soundings in metres

(After Murray and Pullar, 1910).

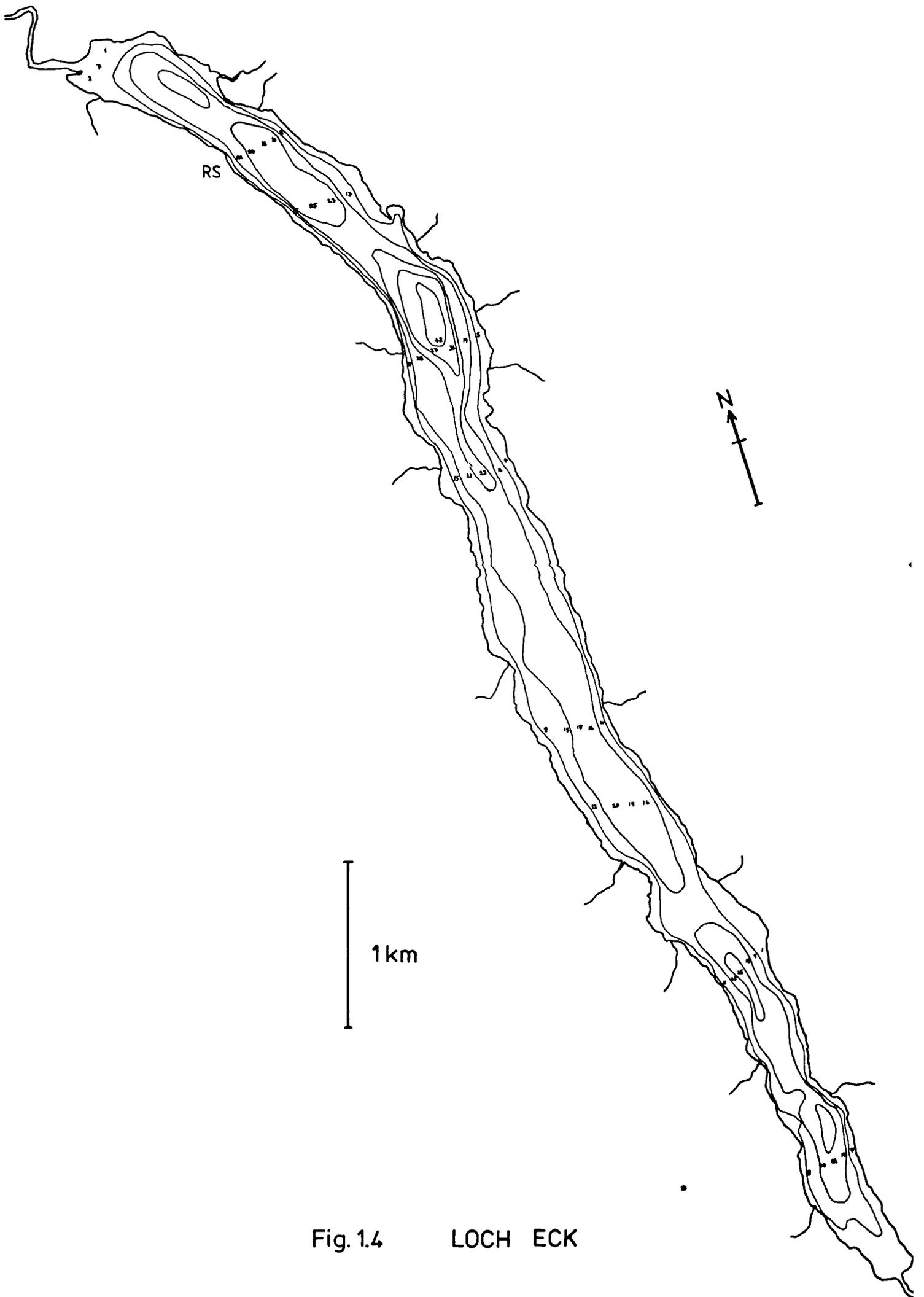


Fig. 1.4 LOCH ECK

and are netted only for research purposes. The reproductive cycle of Loch Lomond powan has been the subject of a long term phenological study investigating the control and integration of reproduction and other cyclical processes in teleost fish (Scott, 1979). A summary of the studies carried out on powan is to be found in an unpublished review (Scott, 1987). Loch Eck powan have received little attention. Slack et al. (1957) obtained a sample of 17 fish which were apparently seine and gill netted from the loch in May 1956. Maitland (1969) echo-sounded in Loch Eck and observed a diel vertical migration of fish which he assumed to be powan. A preliminary study of lipid stores in powan from Loch Eck (Kissack, 1986) is the only previous work to have investigated seasonal aspects of the biology of powan in Loch Eck.

MATERIALS & METHODS.

1.1 Sampling methods.

The investigation of powan diet was based on field samples which were assumed to be representative of the populations under consideration.

1.1.1 Netting.

Previous studies on Loch Lomond powan (Slack et al., 1957; Fuller et al., 1976; Scott, 1979; Hogg, 1980, McCulloch, 1981; Pomeroy, 1982; Rashid, 1984; O'Connell, 1984) have indicated that their activity patterns in the loch are complex, involving both seasonal and diel migrations. In order to sample the population optimally with regard to number and size range of fish, likelihood of feeding, with minimum stress to the fish, but accepting the limitations of available methods and manpower, the following approach was adopted.

Routine fish samples were obtained at approximately monthly intervals from a 400m gang of gill nets made up of 25m by 2m panels of 19mm, 26mm, 31mm and 39mm mesh size (knot-to-knot) of nylon thread no. 0 (Norsenet, Bergen) fished from nightfall to mid morning (approximately 2100-2300 until 1000-1400). Details of individual nettings are given in Table 1.2. Gill-netting has been shown to have effects on some aspects of the powan's physiology (Fuller et al., 1976) but is a consistently reliable method for obtaining large samples (>50) of fish from Loch Lomond (Scott, 1979; Rashid, 1983; O'Connell, 1984) and has proved equally reliable on Loch Eck. These routine nettings were supplemented by a number of additional studies designed to give information on the movement and feeding activity of fish. Nets were set over an extended period and inspected at

intervals, removing fish for immediate analysis. Inspection of nets was carried out as rapidly as possible to reduce disturbance time. Echo-soundings of rowed transects were taken on a number of occasions to check on the siting of nets. Seine net hauls of the Camus an Iosgainn bay and Sallochy beach were carried out in May of 1983 and 1984 (Fig 1.2). Although most nettings were taken from the mid basin of Loch Lomond in Sallochy bay, samples were obtained from the south basin near the McDougall Bank in May 1984 and January 1985 (Fig. 1.2). Nettings of the north basin were attempted in November 1982 at Ptarmigan Lodge and in March 1984 by Rowchoish (Fig. 1.2). Permission to net on Loch Eck was obtained in January 1984 and samples from that loch have been from routine settings in a standard position across the width of the loch from a shingle beach towards Rudha na Seamraig (Fig. 1.4), approximately 1 km from the north end of the loch. Nets were set approximately mid-afternoon and lifted at the same time next day. Most field samples taken after September 1984 were collected by D.B.C. Scott and E.A.R. Brown.

Catches were expressed as catch per unit of fishing effort. For the purposes of this study, catch per unit effort (cpue) was defined as:

cpue = number of powan caught per net gang (4 x 25m) per hour.

Two sets of cpue data are given. The first cpue (a) ignores the fact that on several occasions additional small (7mm and 14mm) mesh nets were fished in conjunction with the normal gangs. The second set of cpue figures (b) includes these small meshes in the calculations, but the contribution to the total catch attributable to these small mesh nets is so small that the first set of cpue data is more likely to give a representative estimate of the catch data.

The sex composition of the catch was investigated.

Treatment of catch.

Fish were covered in ice before being transported to the laboratory in large polythene bags within 30 minutes of catching. A number of contemporaneous research projects used the fish from each sample and not all fish caught were necessarily examined in any one analysis. Numbers of fish used in each investigation are detailed in the appropriate section. Each fish in a catch was individually identified by a numbered tag for cross-referencing. The following routine measures were recorded and stored on one of St Andrews University's Vax/vms 11/785 computers under the username [ZOSDS] :

1. Total length - measured to the nearest 1mm on a measuring board and defined as the greatest length of the fish from the anteriormost extremity to the posterior tip of the fully extended caudal fin.
2. Fork length - measured to the nearest 1mm on a measuring board and defined as the length of the fish from the anteriormost extremity to the posterior tip of the shortest median ray of the caudal fin.
3. Total weight - fish were wiped free of excess water and weighed to the nearest 2g on a Piper Chemicals (max. 1000g) electronic balance.
1. Gonad weight - gonads were dissected out and weighed to the nearest 0.01g on a Mettler P120 balance.
- . Sex of fish - testes were paired smooth whitish organs, ovaries were paired elongate orange organs (see Chapter 4).
- . Gut weight - the alimentary canal extending from the anterior end of the oesophagus to the posterior limit of the intestine was removed from the fish and the contents removed as detailed in Chapter 2. The weight of the gut including the

visceral fat body was recorded to the nearest 0.01g on a Mettler P120 balance.

7. Liver weight - the liver was dissected out and weighed to the nearest nearest 0.01g on a Mettler P120 balance.
8. Notes were recorded on any unusual features such as parasites or morphological abnormalities.

Analysis of data.

Wherever possible, data were analysed using statistical packages available locally on Vax/vms (SPSSX vers.2.2, Minitab vers. 5.1). Data which were unsuitable for these analyses were either reformatted or recoded using procedures within available packages and the main editor (EDT). Statistics in common use are not explained in the text, but where a method or analysis was judged to be less widely known, an account is given alongside its use in the relevant section. The main statistical references used were Sokal & Rohlf (1981) and Elliott (1977).

RESULTS

1.1.1 Catch per unit fishing effort.

The numbers of powan caught on each of the main sample dates are shown in Table 1.2, with the variation in catch with fishing effort. Weather conditions (summarised in Table 1.3) are averaged for three days (day before net set, day of net set, day of net lift) around sample dates for Loch Lomond 1982-1983. No single meteorological factor as noted here was strongly correlated to catch per unit effort data, although air temperature and catch per unit effort had a weak negative correlation (Table 1.3). The highest vulnerability of powan in Loch Lomond to the netting programme of 1983 was in February-March. It is not clear why this should be. Otherwise a relatively constant catch was obtained.

1.1.2 Sex composition of catches.

The proportions of the sexes found in the catches is shown in Table 1.4.

Loch Lomond

The observed ratios of mature males to females (M:F) in the catches were consistent with the null hypothesis of equal numbers of each sex for most samples. Exceptions to this occurred in the February 1983 ($0.05 > p > 0.01$, M:F 1.6:1), late March ($0.05 > p > 0.01$, M:F 1.6:1), April ($0.05 > p > 0.01$, M:F 2:1) and May ($0.01 > p$, M:F 2:1) samples. All catches were obtained from the same region of the loch (Salloch Bay area) except for that dated 15th May 1984 which was obtained from the south basin of Loch Lomond.

Table 1.2

Catch data per unit fishing effort.
Total catch refers to powan only.

date yrmody	net soak hours	nets a	nets b	total catch	cpue a	cpue b
Loch Lomond						
820901	17	16	16	112	1.647	1.647
820926	19	16	16	185	2.434	2.434
821019	17	16	16	95	1.397	1.397
821110	16	8	8	58	1.813	1.813
821111 Pt	20	2	5	1	0.010	0.002
821125	12	8	8	27	1.125	1.125
821201	15	16	16	111	1.850	1.850
830107	25	16	16	154	1.540	1.540
830121	17	8	8	54	1.588	1.588
830208	16	16	17	302	4.719	4.441
830302	19	16	17	274	3.605	3.393
830327	15	16	17	215	3.583	3.373
830416	15	16	17	65	1.083	1.020
830503 sn	0.5	1	1	0	0	0
830503	5	16	17	11	0.550	0.518
830503 sn	0.5	1	1	0	0	0
830504	19	16	17	74	0.974	0.916
830526	15	16	17	13	0.217	0.204
830527	23	16	17	135	1.467	1.381
830705	14.5	16	17	137	2.362	2.223
830726	14	16	17	86	1.536	1.445
830817	16	16	19	65	1.016	0.855
830905	18.5	12	12	69	1.243	1.243
831012	16	16	19	144	2.250	1.895
831116	15	16	19	134	2.233	1.881
831213	16	12	16	83	1.729	1.297
840110	17	12	16	55	1.078	0.809
840322 Ro	8	8	8	0	0	0
840514 sn	1	1	1	40	160.000	160.000
840514	24	4	4	9	0.375	0.375
840515 Mc	18	12	12	71	1.315	1.315
850110 Mc	20	8	8	21	0.525	0.525
850111 RI	25	8	8	54	1.040	1.040
850506	16	8	8	41	1.281	1.281

All catches were from gill nets set in Salloch Bay mid basin unless otherwise indicated :
Pt = Ptarmigan Lodge, Ro = Rowchoish, both north basin;
Mc = McDougall Bank, south basin;
RI = Ross Islands, mid basin; sn = seine net haul.
See Table 2.2 for details of diel nettings.

Table 1.2 (cont.)

Catch data per unit fishing effort.
 Total catch refers to powan only.

date yrmody	net soak hours	nets a	nets b	total catch	cpue a	cpue b
Loch Eck						
840112	6	12	12	131	7.278	7.278
840214	15.5	8	12	96	3.097	2.065
840927	16	12	12	157	3.271	3.271
841103	24	12	8	156	2.167	3.250
841217	24	12	8	188	2.611	3.917
850110	24	8	8	112	2.333	2.333
850130	24	8	8	95	1.979	1.979
850226	24	8	8	148	3.083	3.083
850226	24	8	8	77	1.604	1.604
850327	24	8	8	148	3.083	3.083
850517	24	8	8	182	3.792	3.792
850804	24	8	8	129	2.688	2.688

nets a = number of 25m lengths fished (19-39mm meshes)

nets b = nets a + 7 and 14 mm meshes

1 unit of fishing effort = 4 x 25m nets hour

Table 1.3

Weather information for sample dates,
Loch Lomond 1982-3.

Mo.	mean sun hrs	mean wind knots	mean temp °C	cpue
Sep	1.05	5.25	10.25	2.434
Oct	0.00	4.50	10.60	1.397
Nov	0.00	9.65	9.25	1.813
Nov	0.60	2.10	2.70	1.125
Jan	0.20	7.30	3.50	1.540
Feb	4.10	4.60	2.35	4.719
Mar	0.10	1.35	3.30	3.605
Mar	4.90	4.65	3.65	3.583
Apr	0.55	2.35	7.15	1.083
May	1.40	4.15	8.40	0.217
May	7.50	2.50	12.45	1.467
Jul	4.60	2.60	9.95	2.362
Jul	0.00	1.25	15.40	1.536
Aug	1.20	1.75	18.25	1.016
Sep	0.55	0.85	16.20	1.243
Oct	2.40	5.70	12.35	2.250
Nov	2.85	6.80	10.10	2.233
Dec	3.45	0.60	5.25	1.729
Jan	0.00	6.75	4.55	1.078
May	12.50	2.70	9.10	0.375

partial regression of weather factors and
catch data :

	sun	wind	temp	cpue
sun	-	-.1762	-.0074	-.0052
wind		-	-.2302	.1206
temp			-	-.3954 *

all correlations $p > 0.1$, except *, $p = 0.04$

Data obtained from Meteorological Office, Edinburgh
for Arrochymore weather station, N.G.R. NS(26) 415918
altitude 30m.

Table 1.4

Catch data : seasonal variation of sex ratios in samples.

Date of sample	No. males M	No. females F	1:1 chi-squared	Prob. p	observed ratio when not 1:1
L. Lomond					
19.10.82	45	47	0.011	ns	-
10.11.82	24	34	1.397	ns	-
25.11.82	13	14	0.037	ns	-
1.12.82	48	69	3.418	ns	-
7. 1.83	78	76	0.01	ns	-
8. 2.83	73	47	4.76	.05>p>.01	1.55:1
2. 3.83	52	48	0.09	ns	-
23. 3.83	61	39	4.41	.05>p>.01	1.56:1
16. 4.83	43	22	6.15	.05>p>.01	1.95:1
26/7.5.83	67	33	10.89	.001>p	2.03:1
5. 7.83	57	43	1.69	ns	-
17. 8.83	34	30	0.14	ns	-
5. 9.83	31	36	0.24	ns	-
12.10.83	53	37	2.5	ns	-
16.11.83	56	44	1.21	ns	-
13.12.83	41	39	0.01	ns	-
10. 1.84	20	34	3.13	ns	-
14. 5.84	14	11	0.16	ns	-
15. 5.84	40	31	0.9	ns	-
L. Eck					
12. 1.84	25	93	38.0	.001>p	1:3.72
14. 2.84	17	71	31.9	.001>p	1:4.18
27. 9.84	64	34	8.58	.01>p>.001	1.88:1
3.11.84	97	47	16.7	.001>p	2.06:1
17.12.84	62	50	0.44	ns	-
10. 1.85	32	59	7.43	.01>p>.001	1.84:1
30. 1.85	6	80	62	.001>p	1:13.3
26. 2.85a	28	60	10.9	.001>p	1:2.14
26. 2.85p	59	6	41.6	.001>p	9.83:1
27. 3.85	64	39	6.56	.05>p>.01	1.64:1
17. 5.85	74	35	13.25	.001>p	2.11:1
4. 8.85	92	31	29.3	.001>p	2.97:1

a, p refer to nets set across the width (a) and parallel to the shore (p) of Loch Eck on 26th February 1985.

Loch Eck

In contrast to the L. Lomond data, a single sample, that of 17th December 1984 was consistent with the null hypothesis of an even sex ratio. Samples obtained around the spawning period in February 1985 were particularly informative. In the shallow margins of the loch around spawning time the observed ratio of males to females in the nets was 9.8:1 (M:F). In the deeper central basin of the loch at the same time, the sex ratio was 1:2.1 (M:F). The female portion of this catch numbered 68 mature fish, of which 64 (94%) were spent. In 1984, nets set within yards of the same netting site in 1985 (but in deeper water) produced catches with sex ratios of (M:F) 1:3.7 and 1:4.2 (January 1984 and February 1984). Siting of nets at this time is obviously of crucial importance to the resulting catch. It would appear that there is considerable segregation of the sexes at spawning time with mature males staying on the spawning grounds for a lengthy period while individual females come onto the spawning grounds to ovulate. A similar situation has been observed on the spawning grounds in Loch Lomond, (Scott, 1979; O'Connell, 1984). For the remainder of the year, a male:female sex ratio of approximately 2:1 (M:F) was observed for samples taken from nets set across the deep central basin of the loch.

DISCUSSION

In comparing the catch data from Lochs Lomond and Eck it may appear at first sight that the Loch Eck population is more abundant than the Loch Lomond one. However, it is more likely that the morphology of Loch Eck, together with the method of fishing the nets makes that population more vulnerable to gill netting. The Loch Lomond population has a much greater 'refuge' area, i.e. the unfished loch, by comparison.

In the situation where a constant fishing effort is expended, changes in fish behaviour will produce variation in catch per fishing effort. On the 26th May 1983 a catch of 13 fish from 17 lengths of net set near Camus an Iosgainn was recorded, while the following day's (27th) catch was 135 fish from the same number of lengths of net. An error in the positioning of the net while setting it in darkness meant that the first day's (26th) net was sited in deep water whilst that of the 27th was placed as intended on an inshore ridge. There was no certain method of reducing catch variability.

Saturation of gear.

Presence of species other than powan in the nets may have affected the catch of powan to an unknown degree. In 1982 and 1983 many young perch and a small number of trout were found in the nets. Towards the latter part of the study ruffe (Gymnocephalus cernua L.) were extremely numerous in any inshore netting.

Variation in catch per unit effort is likely to result from a combination of factors. Weather conditions at the time of sampling may have considerable influence in affecting the detection of the net by fish. No single meteorological factor was significantly correlated with the observed catch per unit effort in this study. Craig et al.,

(1986) have discussed the variability of gill net catches.

Catch per unit effort data may be used as an index of fish abundance if a single homogeneous population is being fished and effort is proportional to rate of fishing (Ricker, 1975) but usually such considerations apply only to large scale (commercial) studies. The fact that no detailed records of commercial catches survive is to be regretted.

Net selectivity.

The selectivity of gill-netting as a sampling technique has been investigated for a wide variety of species (Hamley, 1975). McCombie & Fry (1960) studied the role of selectivity on catches of lake whitefish, using girth measurements as a basis for their study.

The observed selectivity of a given net is a function of several components: the probability of the fish encountering the net, being initially captured on contacting the net, and escaping after the initial encounter. Factors determining the above are: mesh size, elastic and inelastic stretching of the net, hanging coefficient of the net, strength and flexibility of the twine, visibility of the twine, shape of fish (including compressibility of the body), degree to which fish are caught up by parts of the body other than the pectoral area, behavioural patterns of fish, and method of fishing the net. The most important measure determining the retention of fish by a given mesh is its girth. Not all fish of the same length will have the same girth; girth will depend on variables such as time of year, sex, fullness of gut and depth. For fish such as powan, which lack spinous projections (including teeth), entrapment is largely a function of a girth measurement, but not necessarily maximum girth. The largest fish caught by one mesh size should be those 'gilled' by

the mesh, while the smallest should be those whose maximum girth is sufficiently greater than the mesh perimeter to ensure capture. A bimodal catch curve for a single mesh size is therefore possible. When fish become tangled in the net, perhaps as a result of it hanging in loose folds in the water, the catch curve tends to become broader and more skewed to the right. Early workers on the subject believed the net capture process to depend solely on the relative geometrical relationships between fish and mesh. It follows from this that plots of selectivity against fish girth/mesh perimeter should have abscissas of the same scale, as similar selectivity ranges (and efficiencies) should be exhibited for all mesh sizes. However, when a range of mesh sizes are fished, the smallest and most numerous size classes are under represented in the catch. Furthermore, it has been found by Hamley & Regier, (1973) that larger mesh sizes are more effective for walleye (Stizostedion vitreum), ie: the selectivity curves show increasing height with increasing mesh size. The net selectivity for powan from Lochs Lomond and Eck has been examined by McCulloch during 1982-1984 and a fuller treatment of the catch data is to be found in McCulloch (in prep.).

CHAPTER 2. Diet analysis and seasonal variation of powan diet.

INTRODUCTION.

Seasonal fluctuations of environmental conditions largely determine the food available to fish in the two lochs studied. Some food items are available for a limited part of the year while others are more abundant or individually larger at certain times. Slack et al., (1957) described changes in the diet composition of powan in Loch Lomond, from a plankton-based diet in summer to a benthos-based diet in winter. Their account was limited by occasional small sample sizes. The diet of a single May sample of powan from Loch Eck (17 fish) was described by Slack et al., (1957) as consisting of planktonic organisms.

A comparative study of the diets of powan from Loch Lomond and Loch Eck was carried out by analysing the stomach contents of gill and seine netted fish.

A. Review of the use of stomach contents analysis in fish biology.

Investigation of fish diet by analysis of stomach contents is a commonly used method in fishery research, yet there are numerous potential sources of error in the practice.

Collection of fish for the analysis of stomach contents must not only provide a representative sample of the population under study but in addition aim to sample fish in a way that will provide maximum information on the subjects' diet. The ideal sampling method should consistently produce a large number of fish (representing the size-frequency distribution of the population) which can be examined

immediately after capture to reduce problems with post-capture digestion, without risk of food regurgitation or feeding under abnormal conditions.

Available methods.

The various methods of quantifying fish diets can be classified according to three main types: numerical, volumetric and gravimetric. The selection of appropriate methods is determined largely by the type and purpose of study. Windell & Bowen (1978) categorise two study types; (i) those which compare diets of different groups of fish, or relate the fish's diet to available food: and (ii) those which attempt to assess the energetic/nutritional value of the diet.

Numerical analysis has been recommended for data from the first type of study, since relative abundances of food items are required. If large size differences exist between food items, supplementary methods such as volumetric analysis should clarify the relative contributions of each food item to the diet. In many studies, frequency of occurrence (ie: the proportion of fish stomachs in a sample which contain a particular food item) has been used as an indication of food importance, or even preference. Frost (1977) found % frequency of occurrence particularly appropriate when few food categories were present. However, since there is no indication of the amount of an item in the population's diet, such information may be difficult to interpret. In addition, similar frequencies of occurrence can result from very different sample sizes. The preference of fish for a food type, as defined by Chesson (1978), cannot be ascertained from frequency of occurrence information alone since high frequency of occurrence values could result from a high abundance of an item in the available food or strong selection of an

item by fish. Perhaps the most useful application of the measure is when food categories which cannot be quantified readily are present, and a presence/absence treatment gives a rapid indication of diet composition.

Volumetric analysis of stomach contents can be either direct or indirect. The direct method requires separation of the stomach contents into different food categories and the volume of each determined by displacement or settlement. A major source of error in this method is the presence of associated water or other extraneous material which must be removed by blotting, centrifugation or other means. The method is labour-intensive. Hellowell & Abel (1971) described a method of determining small volumes by a series of squash preparations using specially constructed cells of known depth. The area covered by a squash of food material was projected onto a measuring screen. The overall error estimated in the method was 3.5%. For some applications Hellowell & Abel's (1971) method may be enhanced by the use of microcomputer area analysis, especially where non-particulate food is taken. Hynes (1950) turned to more indirect methods for his subjective "points" method, where the bulk of each food type was allotted an arbitrary value. Larimore (1957) compared small species with geometric blocks to estimate volumes of different prey types from body shape. This was found particularly useful for microorganisms. If prey items are found to be in different stages of digestion, number/volume regressions using selected whole animals may be attempted to "reconstruct" volumes of prey.

Gravimetric analysis of stomach contents determines the weights of the various dietary components and may be carried out on "wet" or "dry" material. For wet weights, superficial water must be removed as for volumetric analysis. In dealing with food consisting of many

microcrustacea, problems may be encountered from appreciable air drying of the food during the weighing process. Hyslop (1980) suggests that bulky diets are probably best treated by wet weights while Berg (1979) suggests that dry weights are more accurate when dealing with the food of planktivorous fishes since most extraneous material associated with a plankton diet is water. Food weights may be expressed as a proportion of the total weight of material ingested, or as a proportion of total fish weight. Alternatively they may be analysed using standard statistical methods such as analysis of variance and analysis of covariance. Whereas numerical methods tend to overestimate the contribution of small items in the diet, gravimetric methods tend to over-emphasise the contribution of single heavy items. In energetic studies, weight to calorific value regressions can be used. An additional factor to be considered in this context is the proportion of the total weight of food material which is available to the fish. Parker (1963) describes the increase in weight of material stored in formalin, indicating possible errors if fresh weights are compared to preserved weights.

Attempts to combine the results from the different types of analysis in some form of compound index such as those proposed by Hynes (1950), Hureau (1969, in Berg 1979) and Pinkas *et al.*, (1971) add little information and are of questionable value. Macdonald & Green (1983) subjected their number, weight and percentage frequency of occurrence data on the food of five demersal fish from the Bay of Fundy area to principal components analysis. They concluded that a large degree of shared information was present in the measures examined.

Food consumption and digestion.

Dietary investigations must take into account the possibilities of differential digestion. Berg (1979) found concentrations of calanoid and harpacticoid copepods greater and lower respectively in the stomach compared to the gut as a whole. As this situation was observed for a number of fish from different samples, he concluded that calanoids passed through the gut quicker than harpacticoids. The rate of digestion of food in the gut has been found to depend on a number of factors; food deprivation (Elliott, 1972), presence of indigestible body fragments in the prey (Miller, 1974), fat content of the prey (Windell, 1966; Elliott, 1972) and water temperature (Elliott, 1972; Doble & Eggers, 1974; Elliott & Persson, 1978) have been cited by Hyslop (1980). Windell (1978) includes fish size and meal size as additional factors to be considered. Differences in the degree of digestion of prey items have been used as an indicator of peak feeding (Swenson & Smith, 1973; Eggers, 1977).

B. Diet studies of coregonines.

As a result of their commercial importance in the Northern Hemisphere, coregonines have been the subject of considerable fishery investigation. The feeding relationships between important coregonines and sympatric species have formed the basis for studies in northern America (Engel, 1976; Johnson, 1976; Janssen, 1978), Scandinavia (Nilsson, 1960, 1965; Nilsson & Pejler, 1973; Svardson, 1976; Enderlein, 1981a), U.S.S.R. (Skryabin, 1966; Pivazyan, 1972) and Europe (Berg & Grimaldi, 1965; Berg 1970; Giussani & De Bernardi, 1977). Nilsson (1958), Mann & McCart (1981), and Bergstrand (1982) investigated feeding relationships of sympatric coregonine species and sub-species. Further studies examined the role of coregonine feeding

within their environment (Hart, 1931; Giussani, 1974; Jacobsen, 1974; Giussani & Bernardi, 1977; Schulz, 1979; Karatygin et al., 1980; Enderlein, 1981b; Viljanen, 1983; Mills, 1985). Most of the early studies carried out on British coregonines include a description of the diet, while more recent studies give a more detailed analysis (Haram & Jones, 1971; Wilson, 1984). This is particularly true of the Irish coregonines. Yarrell (1841), Thompson (1856), Regan (1911), Dakin and Latarche (1913) and Gaffikin (1938) have given brief accounts of the food of pollan, Coregonus autumnalis pollan Thompson. Southern & Gardiner (1926) examined pollan from the Shannon, while Twomey (1956) described the contents of stomachs taken from the estuary of Lough Erne. Wilson (1984) examined the stomachs of pollan in Lough Neagh to assess the seasonal variation in feeding.

The schelly of Ullswater and Haweswater was studied by Swynnerton & Worthington (1940) and Knox (1834), Service (1906) and Maitland (1966a, b) studied the Lochmaben vendace.

Parnell (1838), Brown (1891), Malloch (1910), Lamond (1922, 1931), Slack (1955), Slack et al., (1957) have described the stomach contents of Loch Lomond powan. The latter study also described the stomach contents of seventeen powan reputed to have been caught in Loch Eck.

MATERIALS AND METHODS.

2.1.1 Netting and treatment of catch.

Details of individual nettings including location, times of set and lift, numbers of fish caught are given in Chapter 1. Fish were weighed, measured and sexed as described in Chapter 1. The alimentary tract from the anterior end of the oesophagus to the anus was removed intact for examination and divided into two portions at the pyloric sphincter. The upper portion comprising the oesophagus and stomach was opened by a longitudinal cut and the damp weight of contents obtained by weighing to the nearest 0.01g on a Mettler P120 top pan balance before and after removal of the material present. This material (subsequently referred to as "stomach contents") was preserved in individually labelled bottles of 5% formaldehyde solution. In many instances material removed from the stomach was apparently dry. Where liquid was observed associated with the contents they were blotted before weighing. Much of the material found in stomachs was compacted and formed into boluses. In the sample of fish obtained on 5th July 1983, stomach contents were surrounded by considerable quantities of mucus which undoubtedly introduced an additional unquantified error into the weights recorded.

The intestine was examined for contents: occasional samples of intestinal contents were preserved for later analysis in the same way to the stomach contents.

Examination of preserved stomach contents.

Formaldehyde - preserved stomach contents were transferred to 30% alcohol prior to examination. In some cases where material was plentiful, several changes of alcohol were necessary to reduce the formaldehyde smell of the preserved contents. Stomach contents were examined using either a Beck-Greenough binocular microscope (mag. x10 - x240), or a Kiowa dissecting microscope (x20, x40). Material was immersed in 10% ethanol solution in a petri dish scribed to give a grid background to facilitate fast and accurate counting of prey items. Various sizes of grids were used depending on the predominating size of prey items present in a sample. Where microcrustacea formed a large part of the stomach contents, the addition of a drop of detergent solution facilitated dispersion and reduced surface tension problems. Material from stomachs which contained relatively large amounts of contents tended to be formed into boluses. These aggregations of material were separated either by a gradual removal of material from around the periphery of the bolus using mounted needles and fine forceps, or by using gentle agitation and stirring to separate individual items. Care was taken to minimise damage to the prey items.

2.1.2 Occurrence of material in the alimentary tract.

Fish were assigned to one of four categories on the basis of the presence or absence of contents in the upper and lower alimentary canal. The relative proportions of the catch falling into these categories indicated the population's feeding pattern at the time of sampling.

The feeding categories were :

Category	Contents	
	Stomach	Intestine
E	= absent	absent
IO	= absent	present
SO	= present	absent
SI	= present	present

The composition of the catch for each sample according to this classification was investigated.

2.2 Numerical analysis of stomach contents.

2.2.1 Identification and counting criteria.

The majority of prey items were identified by reference to standard identification guides, particularly the F.B.A. handbooks on the identification of British freshwater invertebrates. Where additional information was required, advice and identifications were obtained from the British Museum (P.S. Cranston, Chironomidae) and the F.B.A. at Windermere (J.M. Elliott, G. Fryer, Insecta, cyclopoid Copepoda, Ostracoda) and the River Laboratory in Dorset (L.C.V. Pinder, Chironomidae). Identification of prey items was facilitated by the powan's lack of dentition. Many prey items reached the stomach intact, and remained whole during examination of the stomach contents. It was possible to measure the size distribution of some prey items, as detailed in Chapter 3.

Prey items which were not whole presented a problem to the accurate enumeration of the stomach contents. By counting body parts which are readily identified as belonging to a particular prey species or group,

it is possible to obtain an estimate of the numerical abundance of that species in the stomach contents. However, if the part of the body chosen for counting is resistant to digestion, an overestimate of the numerical importance of that species can be obtained (Miller 1972). Conversely, if the chosen part is readily digested, the prey species may be under-estimated (Berg 1979). Many of the planktonic Crustacea and most of the benthic fauna encountered possessed some feature of the body which was readily identifiable and allowed counting of individuals amongst mixed debris. It was found that whole animals tended to fragment in a fairly standard fashion, leaving predictably discrete body portions in the resulting mixture. Bosmina tended to lose the swimming antennae from the rest of the body, and frequently the head shield plus antennae became separated from the rest of the body. Daphnia were found to fragment similarly. Bythotrephes individuals frequently parted company from their long tail spines. Inevitably, occasions arose when the presence of a particular prey species was indicated by the remains available, but the characteristic body part used to count it was missing from the sample. In cases such as this the presence of the species was noted but no count recorded. Counts of prey categories were expressed in a number of ways.

2.2.2 Percentage frequency of occurrence.

The frequencies of occurrence of prey categories were calculated for samples and expressed as percentage frequency of occurrence according to ;

$$\text{Percentage frequency of occurrence} = \frac{\text{number of fish containing species 1}}{\text{total number of feeding fish}} \times 100$$

2.2.3 Percentage composition by number.

Percentage composition by number was calculated as follows:

$$\text{Percentage composition by number} = \frac{\text{sum (counts of species 1)}}{\text{sum (counts of i species)}} \times 100$$

where i = total number of species

2.2.4 Counts of prey organisms.

In many samples the distribution of the counts of individual prey species or groups was found to be non-normal. Macdonald & Green (1983) found that numerical data obtained from examining stomach contents of five fish species from the Bay of Fundy area of Canada required a variety of transformations (including $\log (x + 1)$ and (square root (x)) before normal methods could be employed. In the present study, since some of the samples contained counts obtained from sub-sampling the total stomach contents, non-parametric methods were used to display medians and inter-quartile ranges of counts. Maximum counts were also recorded.

2.2.5 Concordance : Kendall's W.

The agreement existing between ranking of prey species (in terms of numerical abundance) for the fish within each sample was tested using Kendall's coefficient of concordance, W (Siegel, 1956). Kendall's W expresses the degree of association among ranked variables, and gives some idea of the consensus of ranking among k sets of rankings. Where perfect agreement exists among k sets of rankings, the total sum of ranks, R_j , is equal to:

$$R_j = k, 2k, 3k, \dots, nk$$

If there is no agreement at all, the various R_j 's would be approximately equal. The degree of agreement is reflected by the variance among the sums of ranks;

$$W = \frac{s}{1/12 k^2 (n^3 - n)}$$

where s = sum of squares of the observed deviation from the mean of R_j , or the maximum possible sum of squared deviations, ie:

$$\text{where: } s = \sum \left(R_j - \frac{\sum R_j}{n} \right)^2$$

n = number of variables ranked

k = number of sets of rankings

W ranges from 0 (complete disagreement) to 1 (complete agreement). When n is larger than 7, $k(n-1)W$ approximates to the chi-squared distribution, ie: the probability associated with the occurrence (under the null hypothesis of unrelated k ranks) of any value as large as an observed W may be found by comparing the calculated chi-squared with that tabulated for $n-1$ degrees of freedom. If the calculated value equals or exceeds that tabulated for the chosen significance level, H_0 may be rejected and it may be said that the agreement among k judges is higher than that occurring by chance. It should be noted that where some community of preference exists, little is known about the distribution of W . If one group ranks variables with $W = 0.5$ and another group ranks the same variables with $W = 0.7$, all that can be said is that the second group agree more amongst themselves than the first. It is also possible that combining the data into rankings obscures trends in the original data, ie: where two lots are in complete disagreement about the same variables, but in complete agreement within themselves, combining the data produces the inference that no preference existed, when in fact the different preferences obscured each other.

Kendall's W was calculated for each sample as a whole, and separated by sex, using the SPSSX statistical package on Vax/Vms.

2.2.6 Diversity of diet: the Shannon-Wiener function.

The numerical abundance data may be used in a slightly different way to that described above to obtain an estimate of the diversity of the diet. The Shannon - Wiener function derived from information theory combines two components of diversity - number of species and evenness of allotment of individuals among the species. Ideally, the function should be used on random samples drawn from a large community in which the total number of species is known (Pielou 1966). The function can be used to estimate the equitability, E, of the powan diet. This is a measure of how the total food consumed is apportioned between the different food categories, where:

$$E \text{ (equitability)} = \frac{H}{H_{\max}} = \frac{\text{observed food species diversity}}{\text{maximum food species diversity}}$$

E ranges from 0 (maximum unevenness)
to 1 (maximum evenness)

H is given by :

$$H = - \sum_{i=1}^s (p_i) (\log_2 p_i)$$

where s = number of species or food categories
p_i = proportion of total sample belonging to
the i-th species

and

$$H_{\max} = \log_2 s$$

Food categories which could not be enumerated (eg: vegetation) were excluded from the analysis.

As with all such indices, the computed values are simply a derived statistic which serves to indicate trends in the data. The equitability, E , of a given sample is limited to indicating numerical evenness of utilisation of prey categories and cannot indicate other important information such as which prey categories are utilised. It is also prone to criticism in view of the fact that S , the total number of species, may not be entirely correct if some prey species remain undetected. The fact that most Lomond spring and summer stomachs were sub-sampled would also suggest that the number of species recorded in the diet is probably slightly underestimated.

2.3 Gravimetric analysis of stomach contents.

Weights of material found in the stomachs of sampled fish were analysed in several ways. The numbers of stomachs used in each analysis was not necessarily the same for each sample. In some cases, random samples of the available preserved stomach contents were analysed to reduce processing time.

2.3.1 Damp weights of stomach contents per unit fish weight.

As a preliminary analysis, damp weights of stomach contents were expressed as grams stomach contents per kilogram corrected total fish weight, where ;

corrected fish weight = (total weight - weight of gut contents).

The seasonal variation in stomach contents weights was examined by plotting these averaged data against sample date. Analysis of variance and t-test of sample pairs (Minitab 82.1) were used as exploratory tests of the data. The t-test employed assumes unequal variances in the two samples and is more conservative than the test which assumes homoscedasticity (Sokal & Rohlf, 1981).

Initial measurements of the weight of stomach contents recorded at the time of examination are crude estimates of the amount of food material in the stomachs at the time of capture because of three main factors;

(i) Degradation of contents in the interval between death of fish and examination.

(ii) Use of damp weights to estimate contents weights.

(iii) Presence of non-food material in the stomach contents.

These are considered below.

(i) Previous workers (Shafi 1969) have injected 4% formaldehyde solution into the viscera of fish to reduce the effects of (i), but the importance of obtaining fresh weights of liver, gonad and gut for my own and others' work precluded this approach.

(ii), (iii) The water content of stomach contents and the presence of non-food material was investigated.

Random subsamples of stomachs from catches taken from each loch throughout the year were analysed. Stomach contents were sorted, identified and counted, separated to species wherever possible and to different instars where applicable. Excess fluid was removed by blotting, then the samples were air dried for 6-12 hours before drying in an oven for 24 hours at 65°C. During the drying process, samples were stacked to prevent dust contamination but allow circulation. Dried samples were stored in a desiccator prior to weighing. Dry weights of contents were measured to the nearest 0.1mg on an Oertling top pan balance.

2.3.2 Dry/damp weight relationship.

The relationship between dry and damp weights of material ingested was investigated to determine if a constant correction factor could be employed to estimate dry weights. Total dry weights of contents were expressed as proportions of the damp weights originally recorded. After angular transformation, means and 95% confidence limits were calculated for each sample. In addition, data were analysed following Ricker (1973) using geometric mean regression to obtain a functional relationship between the dry and damp weights of contents.

2.3.3 Dry weights of food and non-food material.

The dry weights of the various components of the total stomach contents were analysed by separating material into food and non-food categories and the contribution of each to total dry weight was assessed. Corrected dry weights of food material in stomachs were obtained by subtracting weights of non-food material from total dry weights. Analysis of covariance was used to adjust corrected dry weights of food to a common corrected total fish weight and common slope, using two models to describe the relationship;

$$(i) \quad Y = a + bW$$

$$(ii) \quad \log Y = a + b \log W$$

where Y is corrected dry weight of food, W is corrected total fish weight and a, b are constants.

The hypotheses under test were :

- (a) H_0 = homogeneity of sample means ;

- (b) H_0 = homogeneity of sample means after adjustment for common fish weight assuming parallel slopes for the (dry wt. food / corr. tot. wt.) relationship.

Analyses were performed for data using two estimates of dry food weight for Lomond stomachs, 0.13 (derived from GM regressions of dry weight/damp weight above) and 0.18 (used by George 1981). Where empty cells occurred in the analysis, dummy cells were inserted from adjacent cells. A preliminary analysis indicated that this had a negligible effect on the overall result. These analyses were further developed by including water temperature as an additional variable. Water temperatures were either recorded at sampling or estimated from the data of Murray & Pullar (1910), Slack (1957), Chapman (1969) and Maitland (1981). Multiple regression models used were of the form:

$$Y = a + b_1 W + b_2 T \quad (\text{model iii})$$

$$\log Y = a + b_1 \log W + b_2 \log T \quad (\text{model iv})$$

where Y,W are as above, a is a constant, b1 and b2 are partial regression coefficients and T is water temperature °C.

Analyses were performed on groups of data as determined by previous analyses.

2.3.4 Maximum weights of stomach contents.

The maximum damp weight of stomach contents (y) for fish of corrected total weight (W) from a particular sample was estimated as:

$$\log y = \log a + b \log W$$

The points representing the highest stomach contents weights across the range of size classes present in the sample were regressed to obtain estimates of a and b. Following Ricker (1973), geometric mean regression analysis was used to estimate a and b as \bar{a}_y and $\bar{V}_{y.x}$. The

relationship between $\log y$ and $\log W$ was investigated using samples in which diets were approximately similar. Samples from Loch Lomond and Loch Eck were treated separately. Overall regressions were obtained for Lomond and Eck fish, separated by sex. Note that this estimation was for damp uncorrected weights of stomach contents.

Separate estimations were performed for determining maximum dry weights of food material. Regression lines were fitted to points obtained from log/log scatter plots of dry weights of food material against corrected total fish weight representing the maximum weights of food found in stomachs. A minimum of six points were used for each regression line. The fullness of the fish stomachs in a sample was estimated by assuming that the regression line obtained by the procedure above described the peak feeding of the fish in that sample. If the slope of this maximum line does not change for sub-maximal stomach contents, an estimate of the relative fullness of the other stomachs in the sample may be obtained by drawing lines parallel to the maximum line representing 75%, 50% and 25% of the maximal level, and counting the data points lying in each region.

RESULTS.

2.1 Occurrence of material in alimentary tract : routine nettings.

Feeding fish were taken in nets throughout the year. Sample sizes were relatively large for most Loch Lomond catches (more than thirty fish) and only two Loch Eck samples contained fewer than thirty-five fish.

Powan from Loch Lomond were found to have material in both stomach and intestine most frequently in the period from May to September (Table 2.1 and Fig. 2.1). The number of fish with remains in the intestine only (IO) or empty (E) during this period may reflect the elevated water temperatures and stomach evacuation rates, or individuals which had been in the net longer than others. Fish without material in the stomach or intestine (E) were found in most samples, but the incidence of these was highest from October to March. At spawning time in early January the proportion of fish without material in the alimentary tract fell temporarily as powan cannibalised their spawned eggs. Individuals with material in the stomach alone were found most frequently in the late autumn samples, while fish with intestinal contents made up 10-20% of the total catch in early spring, summer and winter catches.

Loch Eck catches were characterised by a high (>80%) proportion of fish with material in both parts of the alimentary tract throughout the year (Table 2.1). The period about spawning time in February 1985 showed the greatest proportion of fish without contents in the alimentary tract. This was true of fish caught in the shallower inshore part of the loch (the presumed spawning areas), but not of fish caught in the open water of the mid basin (mostly comprising spent fish). Spawning catches are detailed below.

Table 2.1

Stomach contents : frequency of occurrence of material in
the alimentary tract : routine nettings.

sample date	number in category					% in category				
	E	IO	SO	SI	tot.	E	IO	SO	SI	
Loch Lomond										
23 Mar 83	67	12	14	7	100	67.0	12.0	14.0	7.0	
16 Apr 83	21	10	10	24	65	32.3	15.4	15.4	36.9	
27 May 83	1	1	3	83	88	1.1	1.1	3.4	94.3	
5 Jul 83	0	10	1	39	50	0.0	20.0	2.0	78.0	
26 Jul 83	3	7	2	54	66	4.5	10.6	3.0	81.8	
17 Aug 83	6	10	7	32	55	10.9	18.2	12.7	58.2	
5 Sep 83	1	1	1	43	46	2.2	2.2	2.2	93.5	
12 Oct 83	43	5	26	16	90	47.8	5.6	28.9	17.8	
16 Nov 83	31	28	13	28	100	31.0	28.0	13.0	28.0	
13 Dec 83	46	10	13	11	80	57.5	12.5	16.3	13.8	
10 Jan 84	17	10	6	21	54	31.5	18.5	11.1	38.9	
14 May 84	0	0	0	25	25	0.0	0.0	0.0	100.0	
15 May 84	0	0	0	71	71	0.0	0.0	0.0	100.0	
Loch Eck										
12 Jan 84	0	0	0	35	35	0.0	0.0	0.0	100.0	
14 Feb 84	0	0	1	87	88	0.0	0.0	1.1	98.9	
27 Sep 84	0	-	-	-	17	0.0	-	-	-	
3 Nov 84	0	-	-	-	17	0.0	-	-	-	
17 Dec 84	2	-	-	-	50	4.0	-	-	-	
10 Jan 85	17	-	-	-	95	17.9	-	-	-	
30 Jan 85	17	-	-	-	94	18.1	-	-	-	
26 Feb 85	2	-	-	-	52	3.8	-	-	-	
26 Feb 85	31	-	-	-	46	67.4	-	-	-	
27 Mar 85	5	-	-	-	99	5.1	-	-	-	
14 May 85	5	-	-	-	100	5.0	-	-	-	
4 Aug 85	3	-	-	-	100	3.0	-	-	-	

E = no contents in stomach or intestine

IO = contents in intestine only

SO = contents in stomach only

SI = contents in stomach and intestine

Fig. 2.1 Occurrence of material in alimentary tract
of powan from :

Loch Lomond -

SI = material in stomach and intestine

SO = material in stomach only

IO = material in intestine only

E = without material in alimentary tract.

Loch Eck -

percentage frequency of occurrence of
powan in catch without material in
alimentary tract.

a = offshore catch, net across width of loch,

p = inshore catch, net parallel to shore.

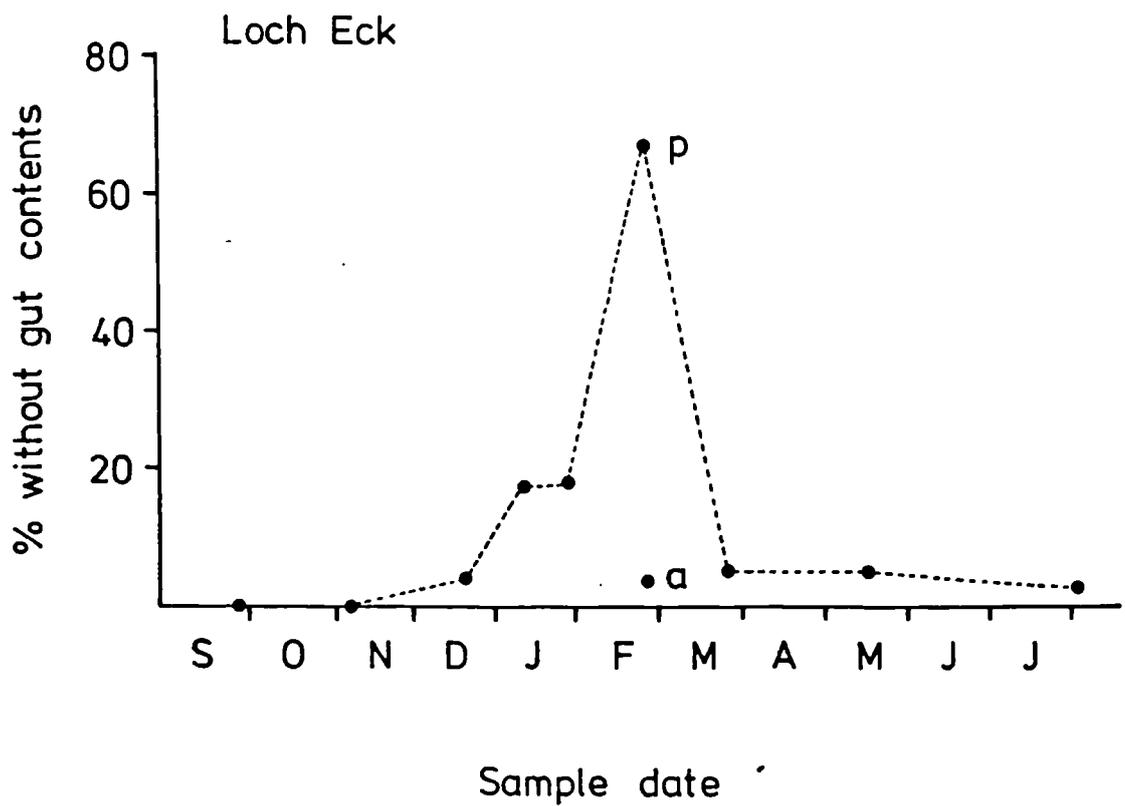
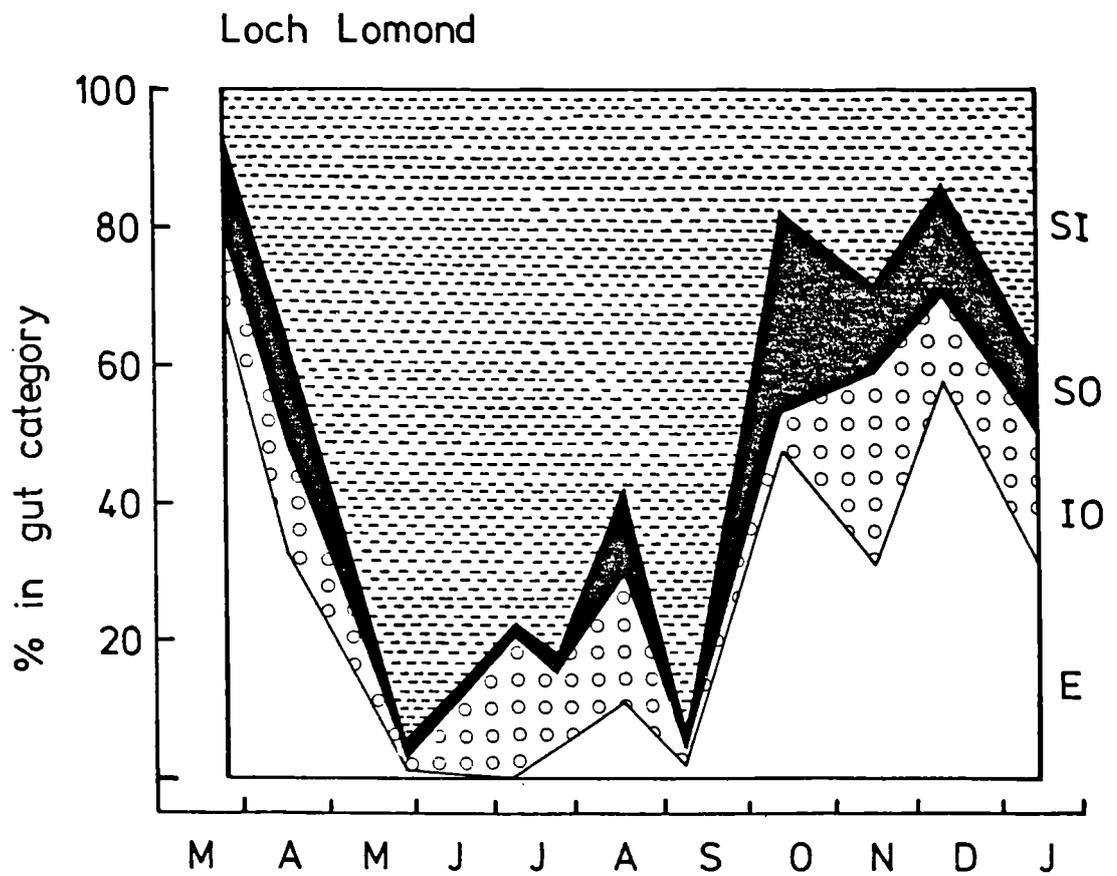


Fig. 2.1

Feeding of powan about spawning time Loch Eck, 1985.

	males		females					
	adult	imm.	spent	ovul.	pre-ov.	start.	imm.	total
30 Jan A								
total n	6	5	16	6	24	34	3	94
empty E	3	0	3	6	4	1	0	17
26 Feb A								
total n	12	2	26	0	1	11	2	54
empty E	0	0	2	0	0	0	0	2
26 Feb P								
total n	41	0	1	1	2	1	0	46
empty E	28	0	1	1	0	1	0	31

A,P = net set across or parallel to longitudinal axis of loch;

ovul. = ovulating; pre-ov. = immediately pre-ovulating;

start. = female with ovaries beginning to mature;

imm. = immature fish.

It is possible that changes in the timing of feeding bouts could influence the observed frequencies of occurrence of the four feeding categories SI, SO, IO, E.

The seasonal feeding activity of powan in Loch Lomond.

Diel feeding patterns indicated by catches obtained from a supplementary netting programme are shown in Table 2.2a,b. The total number of fish caught over the periods concerned was not high: this

Table 2.2a

Summary of long-term and sequential nettings to determine activity and feeding patterns, Loch Lomond 1982-5.

Date of sample	net lengths	Time of net set - lift	Total catch	sex		feeding category			
				mal	fem	E	IO	SO	SI
2 Dec 82	3	1300-1530	0						
	3	1600-1900	6	5	1	5	0	1	0
3 May 83	16+1	1300-1500	11	10	1	1	0	0	10
	seine	1400	0						
	seine	1800	0						
22 Aug 83	4 a	2130-0000	6	4	2	0	0	0	6
23 Aug 83		0030-0545	1	1	0	1	0	0	0
		0600-1030	7(10)	3	4	0	2	0	5
		1030-1230	2	1	1	0	0	0	2
" "	4+3 b	2130-0000	7	2	5	0	1	0	6
		0030-0545	0						
		0600-1030	0						
		1030-1230	0						
" "	1f	2130-0000	0						
		0030-0545	1	0	1	0	0	1	0
6 Dec 83	4	1230-1530	10	5	5	1	1	4	4
		1600-1930	2	0	2	0	1	0	1
		1800-0000	1	0	1	0	0	0	1
		0030-1130	6	1	5	3	0	1	1
14 May 84	seine	2200	25+	14	11	0	0	0	25
7 May 85	8+3	2030-1300	41	30	11	27	2	-	12-
8 May 85	8	1900-2300	14	10	4	1	0	5	8
		0000-0730	22	17	5	7	2	2	11
		0800-1315	12	6	6	1	1	2	8
		1345-1800	3	3	0	0	0	1	2

a = benthic gillnet set parallel to shore (10m water depth)

b = benthic gillnet set perpendicular to shore (2-18m water depth)

f = floating gillnet set across mouth of bay, Camus an losgainn.

net lengths : 16+1 indicates 16 lengths of 'standard' nets

(19-41mm) and 1 length of fine mesh net (7-14mm).

feeding category : E = no material, IO = material in intestine,

SO = material in stomach, SI = material in both.

Table 2.2b

Summary of long-term and sequential nettings to determine activity and feeding patterns, Loch Lomond 1982-5.

Date of sample	net lengths	Time of net set - lift	Total catch	predominant prey categories eaten	relative abundance
2 Dec 82	3	1600-1900	6	Daphnia, Cyclops	*
3 May 83	16+1	1300-1500	11	Bosmina, Bythotrephes, Insect pupae indet.	**
22 Aug 83	4 a	2130-0000	6	Daphnia, Bythotrephes, Leptodora, (Holopedium).	***
23 Aug 83		0030-0545	1	Daphnia, Bythotrephes.	*
		0600-1030	7(10)	Daphnia, Bythotrephes, Leptodora, (chironomids).	*
		1030-1230	2	Daphnia, Bosmina.	**
" " "	4+3 b	2130-0000	7	as for 22 Aug 2130-0000	***
" " "	1f	0030-0545	1	empty	
6 Dec 83	4	1230-1530	10	Daphnia, Cyclops.	*
		1600-1930	2	Daphnia.	*
		1800-0000	1	Daphnia.	*
		0030-1130	6	Diaptomus, Daphnia.	*
14 May 84	seine	2200	25+	Bosmina, Leptodora, Chironomus pupae. (Holopedium, Leptodora).	***
7 May 85	8+3	2030-1300	41	Chaoborus, Daphnia, Diaptomus.	*
8 May 85	8	1900-2300	14	Daphnia, Diaptomus.	*
		0000-0730	22	Chaoborus, Daphnia.	*
		0800-1315	12	Chaoborus, insect pupae, (Bosmina), (Pisces).	*
		1345-1800	3	(insect pupae), (Trichoptera), (Pisces).	*

legend as in Table 2.2a.

Prey categories are given in numerical order of abundance and refer to the majority of feeding fish at the specified time. Bracketed prey were the most important items in the stomach contents of a small number of fish at the specified time.

Table 2.3

The following prey types have been detected in powan stomachs in Loch Lomond (L) and Loch Eck (E).

	L	E
Rotifera		
colonial spp.	*	
Cladocera		
Cladocera indet.	*	*
Daphnia hyalina var. galeata Sars (helmet 'round')	*	
" " " (helmet 'peak')	*	
" " " (helmet 'intermediate')	*	
" " indet.	*	
Sida crystallina (O.F. Muller)	*	
Bosmina coregoni obtusirostris (Sars)	*	
Chydorus spp.	*	*
Bythotrephes longimanus (Leydig)	*	
Leptodora kindti (Focke)	*	*
Holopedium gibberum Zaddach	*	
Polyphemus pediculus (L.)	*	
Eurycercus lamellatus (O.F. Muller)	*	
Diaphanosoma brachyurum Lieven	*	
Simocephalus sp.	*	
Alona sp.		*
Ostracoda		
Ostracoda spp.	*	*
Cypria ophthalmica		*
Isopoda		
Asellus aquaticus (L.)	*	*
Copepoda		
Eudiaptomus gracilis Sars	*	
Acanthocyclops viridis (Jurine)	*	*
Cyclops strenuus abyssorum Sars	*	
Mesocyclops leuckarti (Claus)	*	
Diptera		
indet. insect larva (mainly chironomids)	*	*
" " pupa	*	*
" " adult	*	*
Chironomidae:		
Chironomus anthracinus (Zetterstedt)	*	*
Protanypus morio (Zetterstedt)	*	
Monodiamesa bathyphila (Kieffer)	*	
Procladius spp.	*	*
Polypedilum sp.		*
Macropelopia spp.		*
Apsectrotanypus trifascipennis (Zetterstedt)		*
Chaoborus flavicans (Meigen) larva	*	*
Ceratopogonidae spp.	*	*
Ephemeroptera larva (mainly Caenis horaria (L.))	*	*
" adult	*	
Trichoptera larva (Hydroptilidae & Phryganeidae)	*	*
Plecoptera larva (Leuctra & Neomura spp.)	*	*

Table 2.3 cont.

Prey species in powan stomachs; Loch Lomond , (L) Loch Eck (E).

	L	E
Hydracarina		
Hydrachnellae spp.	*	*
Mollusca		
Pisidium spp.	*	*
Limnaea pereger (Mull.)	*	
Hydrobia sp.	*	
Sphaerium sp.	*	
Pisces		
Salmonidae indet. (juveniles approx. 30mm T.L.)	*	
fish egg (Coregonus)	*	*
Miscellaneous		
gravel	*	*
debris	*	*
amorphous material	*	*
vegetation	*	*
Cestoda	*	*
Nematoda		*
fish scale	*	

may be due to the relatively small fishing effort, disturbance of nets or other factors.

Composition of the diet as observed in the catches from the supplementary netting programme broadly reflected the diet observed in routine monthly samples. Exceptions were noted - many of the catch from 6 December 83 had been feeding on *Daphnia*, but in a routine sample taken a week later povan had been feeding mainly on benthic food. In some samples there was evidence to suggest that composition of the diet changed diurnally (seine sample, May 84). Individual variation in the relative proportions of prey species in the diet was considerable, particularly in spring and summer samples. Some fish had stomach contents comprised of prey items not utilised by other fish in the sample. Feeding intensity could be judged by the variation in amount of food present. Most feeding activity in winter was confined to daylight hours, with little or no feeding at night. In spring, the fish had least food in their stomachs about dawn, presumably after a non-feeding period during the hours of darkness. Feeding occurred throughout the remainder of the day. Feeding activity in the summer months was concentrated during the daylight hours with a decline in stomach contents at night.

2.2 Numerical analysis.

2.2.1 Counting methods.

A description of the counts used and sub-sampling validation is given in Appendix 1.

2.2.2 Percentage frequency of occurrence.

The occurrence of prey groups in the diet of powan from Lochs Lomond and Eck is shown in Fig. 2.2.

Loch Lomond

Distinct seasonal trends were apparent in the Loch Lomond samples. Winter samples (December - March) were characterised by the presence of Pisidium, Acanthocyclops viridis, vegetation and debris, powan eggs (at spawning time) and an assortment of benthic invertebrates including Trichoptera, Chironomidae and Chaoborus larvae. Early spring samples showed an increased occurrence of Trichoptera and Chironomidae larvae, as well as insect pupae, which occurred most often in May. The occurrence of the planktonic crustaceans in the diet of Lomond fish changed quickly from very low levels in early spring to high occurrences (50-100% of fish) in May. The length of time which individual prey species occur in the Loch Lomond powan diet varies. Leptodora kindti and Holopedium gibberum occurred in the diet from March, but were most frequently found in the fishes' diet from May to September. Bythotrephes longimanus occurred over a similar period, but was also found in October samples. During the period of their occurrence in the diet, the above three species were found in a large proportion of all stomachs examined. The small cladoceran Bosmina coregoni was found in the diet of Loch Lomond powan through most of the year, but was most frequently encountered in spring samples. Daphnia hyalina occurred in the diet to some extent throughout the year, with its greatest occurrence in the spring and summer months. Two species which were frequently observed in winter samples, Acanthocyclops viridis and Chaoborus larvae were also found to some extent throughout the year in the Loch Lomond fish stomachs. The frequencies of occurrence observed for these species fluctuated

Fig. 2.2 Percentage frequency of occurrence data for food types found in powan stomachs.

Vgn = vegetation	Ost = Ostracoda
Egg = fish eggs	Cvr = Cyclops viridis
Clu = Cladocera indet.	Asl = Asellus aquaticus
Dah = Daphnia hyalina	Trl = Trichoptera larva
Bsm = Bosmina coregoni	Chl = chironomid larva
Byt = Bythotrephes	Inp = insect pupa
Lpt = Leptodora	Cbr = Chaoborus larva
Hol = Holopedium	Psd = Pisidium spp.
Hir = Hirudinea	

s1,s2 = seine and south catches of May '84.

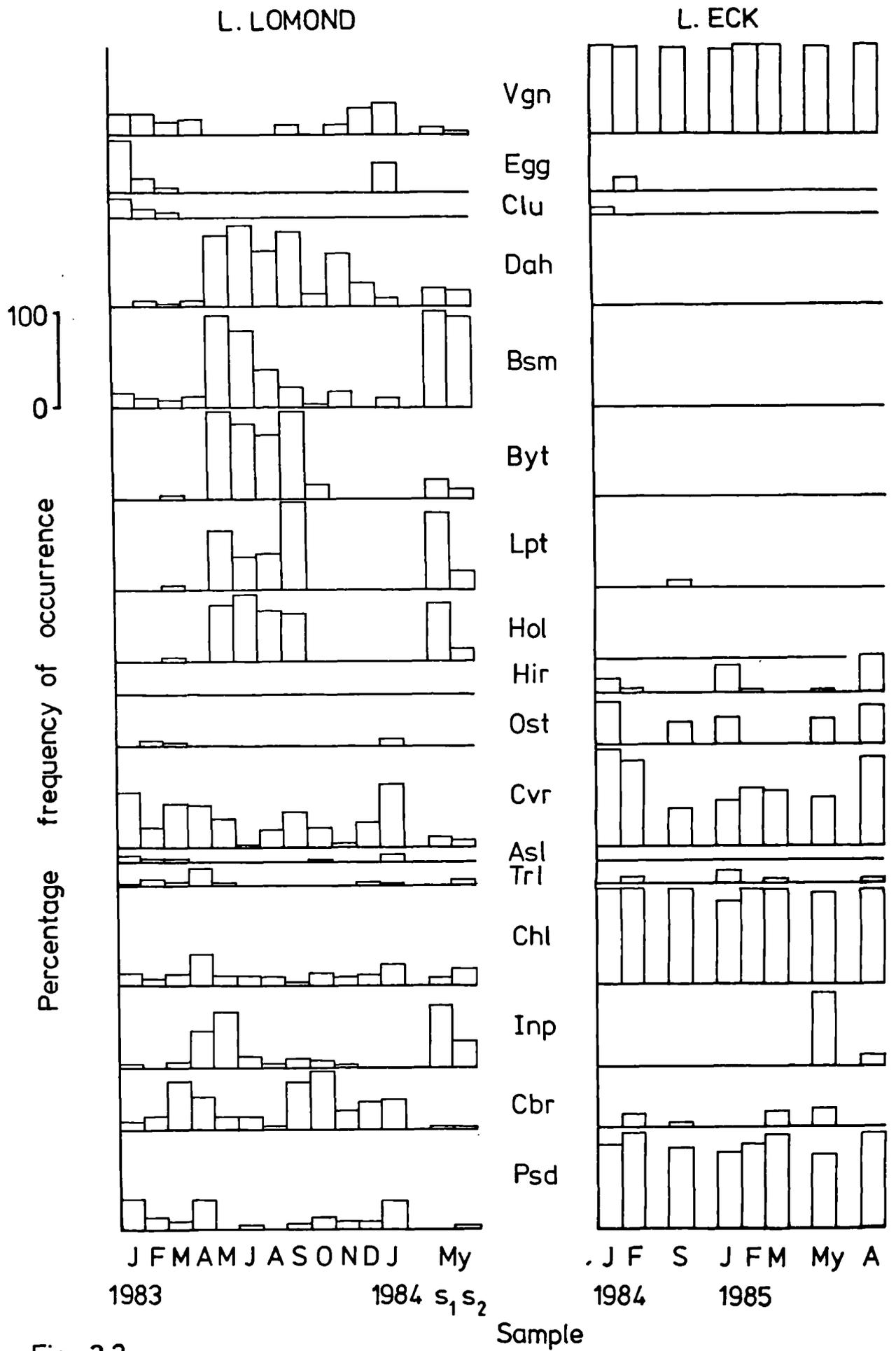


Fig. 2.2

over the summer months, with Acanthocyclops viridis declining in frequency of occurrence from 46% in March to 3.0% in July, rising to 37% in September only to fall to 5.0% in November before peaking at 67.0% in January (Fig. 2.2). Chaoborus larvae were less frequently observed in the diet over the summer months but became common (47-60%) in stomachs from the September and October samples. Chironomid larvae were found in the diet of a small proportion of fish throughout the year.

Loch Eck

The occurrence of prey items in the diet of Loch Eck powan bears little or no resemblance to that observed in Loch Lomond. Stomach contents taken throughout the year showed remarkable consistency of composition (Fig. 2.2). In all samples, the majority of stomachs (>90%) examined contained vegetation and debris. Chironomid larvae and Pisidium were present in high proportions (>70%) in the stomach contents of all Loch Eck samples. Acanthocyclops viridis was found in samples throughout the period of study, but its occurrence in stomachs fluctuated from 100% (January 1984) to 52.9% (September 1984). Other prey items were found less frequently in Loch Eck fish stomachs. Ostracoda occurred in most samples in up to half of the stomachs examined. Chaoborus larvae were found occasionally as were Trichoptera larvae, while the pupae of Chironomus anthracinus were found in 75% of stomachs examined from the May 1985 sample. Stomachs were found to contain Hirudinea on a number of occasions. The most outstanding difference between Loch Eck stomach contents and those of Loch Lomond was the virtual absence of the planktonic crustaceans which comprised most of the Loch Lomond powan diet over spring and summer. The only occasion on which any of the characteristic planktonic prey items found in Loch Lomond powan were found in Loch

Eck stomach contents was September 1984 (Leptodora in 5.9% of stomachs).

2.2.3 Percentage composition by number.

The numerical composition of the diets of Loch Lomond and Loch Eck powan is shown in Fig. 2.3.

Loch Lomond

The winter diet of Loch Lomond powan was characterised by food items which were mainly benthic in origin. Following spawning in early January, the greatest numerical proportion of the diet (67.1%) was powan eggs. The large cyclopoid copepod Acanthocyclops viridis and the bivalve Pisidium were taken in significant quantities. In the next few months, Acanthocyclops viridis and Chaoborus larvae were the main constituents of the diet, occasionally supplemented by Trichoptera and chironomid larvae. Some Pisidium, Asellus aquaticus and insect pupae were also found. During this time, the total number of items found in stomachs was not large; (2001 prey items January 1983, from 95 fish; 853 items February 1983, 43 fish, 1012 items March 1983, from 24 fish). In April, Acanthocyclops viridis and Chaoborus again formed the majority of prey items in the diet but Diaptomus, Bosmina, Daphnia and C. abyssorum also occurred in small amounts. After April, the planktonic Crustacea became the most numerous component of the powan's diet. In May Bosmina accounted for 77.3% of the total number of prey individuals recorded from stomach contents (corresponding to an estimated 43 thousand prey individuals from 30 fish). Also included in the diet at this time were the larger Cladocera Bythotrephes, Leptodora and Holopedium. Together these three species accounted for 15.6% of total prey numbers (8400 items). In the following year (1984) May samples were examined from a

Fig. 2.3 Percentage composition by number data for food types found in powan stomachs.

Egg = fish eggs	Ost = Ostracoda
Clu = Cladocera indet.	Cvr = Cyclops viridis
Dah = Daphnia hyalina	Asl = Asellus aquaticus
Bsm = Bosmina coregoni	Trl = Trichoptera larva
Byt = Bythotrephes	Chl = chironomid larva
Lpt = Leptodora	Inp = insect pupa
Hol = Holopedium	Cbr = Chaoborus larva
Hir = Hirudinea	Psd = Pisidium spp.

s1,s2 = seine and south catches of May '84.
Circles "o" indicate prey which contributed less than 1% of total prey numbers.

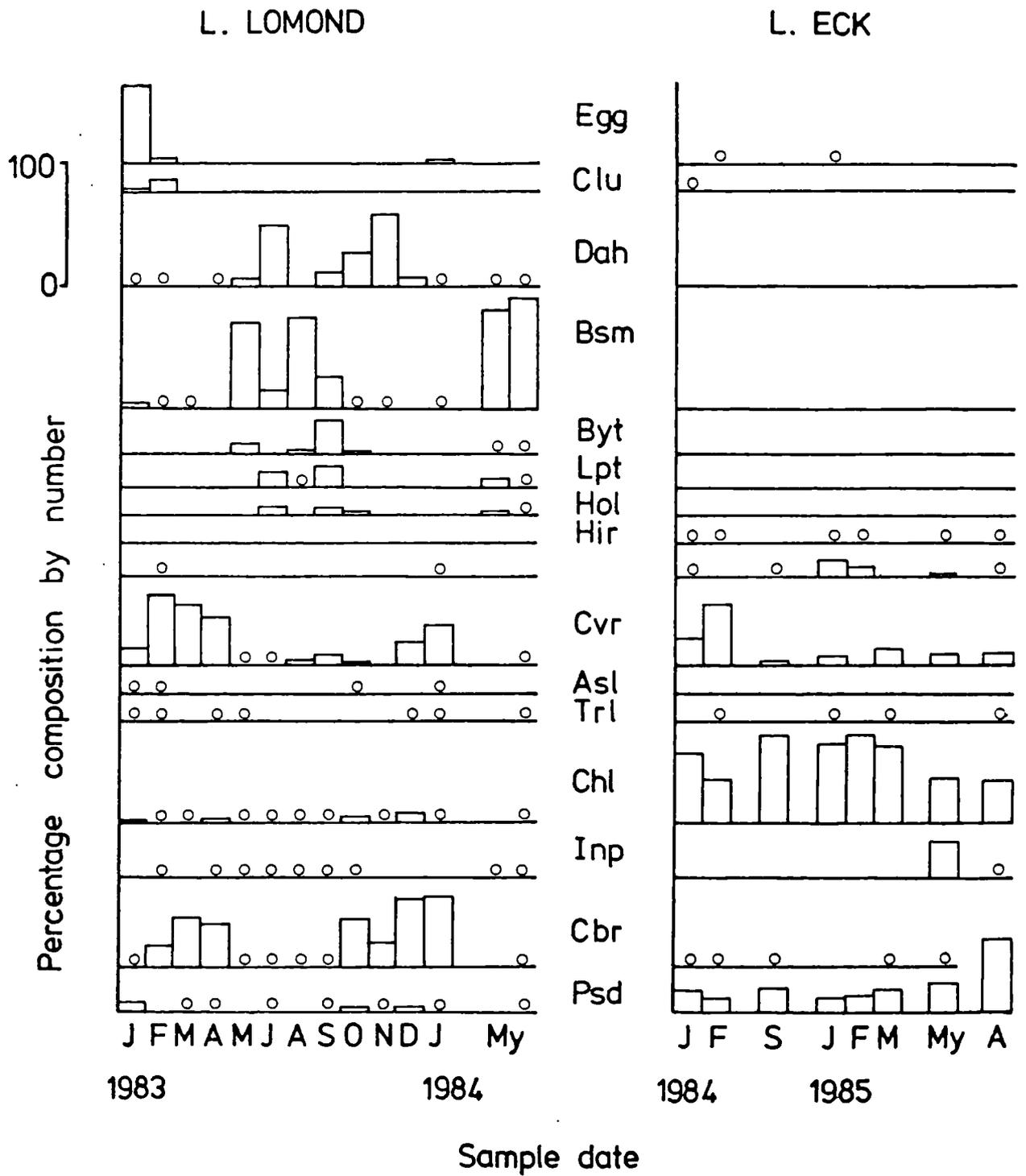


Fig. 2.3

seine-netted sample of fish and also from the southern basin of Loch Lomond. Bosmina comprised 88.4% and 99.4% of the total number of animals in stomachs from these samples (approximately 68 thousand individual Bosmina in 25 stomachs, seine sample; 252 thousand Bosmina from 32 stomachs in the sample from Loch Lomond's south basin. The representation of the larger Cladocera in these samples was small; 11% for the seine sample (7400 individuals, mainly Leptodora) and less than 1% for the south sample (150 individuals). In both the May 83 and south May 84 samples, small numbers of some prey species such as Acanthocyclops viridis, Chaoborus, chironomid and Trichoptera larvae were found. Insect pupae (mostly pharate adults of C. anthracinus) were taken at this time in small but significant numbers in all May samples.

By July, the preponderance of Bosmina in the diet had decreased to the stage where 17.1% of the total prey numbers (4530 individuals from 30 fish) were Bosmina. Daphnia hyalina was the most numerous component of the diet at this time, accounting for 51.7% (13 thousand individuals) of the total prey numbers. Leptodora and Polyphemus were found in roughly equal proportions (approximately 13% of the total or 3450 individuals each). The presence of Polyphemus suggests an inshore feeding bout at this time as it is thought to be more typically littoral than truly planktonic (Scourfield & Harding, 1966). Occasional representations of the familiar early season prey species such as Chaoborus and chironomid larvae continued to be found. In addition, late instars of the ephemeropteran Caenis horaria were recorded. The August diet was once more characterised by large numbers of Bosmina (81.7% of the total number or 86 thousand prey items from 31 fish). Holopedium accounted for 5.1% (or 5360 individuals) of the total numbers of prey, while Bythotrephes represented 3.0% (or 3180 individuals). Daphnia comprised 3.3% of the

total (3460 individuals). A greater contribution to the total August diet was made by Acanthocyclops viridis individuals, totalling 6.6% or 6930 individual prey items.

September's powan sample had several numerically important dietary prey species. Bosmina made up 29% of the total prey numbers (19250 individuals from 30 fish). Bythotrephes (28.8%), Leptodora (17.2%) and Holopedium (2.0%) were prominent dietary items, with Daphnia accounting for 12.4% of the total. At this time Acanthocyclops viridis made up 10.3% of the prey numbers, and a small number of early instars of Chaoborus larvae were found in this sample. The October sample saw a large reduction in the total number of prey items recorded from fish stomachs. The largest contribution to total prey numbers at this time was by Chaoborus larvae (41.7% or 756 individuals from 42 fish). Daphnia made up 30.1% (546 individuals) of the total, while Diaptomus accounted for 10.6% (192 animals). Pisidium and chironomid larvae were found, as well as Acanthocyclops viridis.

November's sample was dominated by Daphnia (71.8% of the total prey numbers or 3987 individuals from 42 fish). Chaoborus larvae accounted for most of the remainder (23.7% or 1312 animals). Although Copepoda were taken, they represented less than 4% of the total prey numbers. In December 1983 and January 1984 stomach samples were characterised by relatively high numbers of Chaoborus larvae (982 individuals from 24 fish or 60.5% of all prey in December and 2765 individuals from 30 fish or 61.3% of all prey in January). In both cases, the majority of the remaining food items consisted of Acanthocyclops viridis individuals (21.9% and 35.4% respectively). The December samples contained Daphnia as 7.8% and chironomids as 7.1% of total prey numbers. Both samples contained small numbers of Pisidium, while the

January sample also contained Asellus aquaticus.

Loch Eck

The numerical composition of the Loch Eck powan diet was recorded for eight samples taken over the period from January 1984 to August 1985 (Fig. 2.3). For all samples examined, the overall composition of the diet was remarkably constant. For all samples except February 1984 and August 1985 chironomid larvae formed the largest percentage of the total number of prey items. Over the samples examined chironomids made up from 36.9% (1642 larvae from 15 fish, February 1984) to 77% (1972 larvae from 17 fish, September 1984) of the total prey numbers. Pisidium and Acanthocyclops viridis were the two prey species accounting for most of the remaining prey items. In the February 1984 sample, Acanthocyclops viridis comprised 52.7% (2348 animals from 15 fish) of total prey number. In August 1985's sample, 52.7% of the total prey numbers were Pisidium. Occasional species forming a small proportion of the total number of prey items in the diet included Hirudinea (found in most samples), Trichoptera larvae, Chaoborus larvae (found in very small numbers unlike Loch Lomond), unidentified Cladocera, and powan eggs taken after spawning. The pupae (pharate adults) of Chironomus anthracinus formed 30.7% (618 animals from 20 fish) of the total prey numbers in the May 1985 sample. Ostracoda were present in the diet in most samples, but their accurate enumeration proved difficult because of the presence of debris, so that actual numbers recorded may well underestimate the numbers ingested.

2.2.4 Counts of individual prey - medians and inter-quartile ranges.

Counts of individual prey items are shown for the examined stomachs from samples in Table 2.4. Samples from Loch Lomond were examined according to the sub-sampling procedure so that samples from May 1983 up to and including October 1983 were sub-sampled, and the counts recorded are for one-sixth of the total stomach contents. Stomach samples from Loch Eck were examined in full and the counts represent the total number of individuals found in each stomach over the whole sampling period.

The information obtained by examining the medians and quartiles of the counts of individual prey items in the diet is essentially the same as that displayed by the percentage composition by number data. Perhaps the most important aspect of the raw counts as shown in Table 2.4 was the nature of their distributions. For most types of prey in the Loch Lomond winter and early spring samples the distributions of counts were plainly non-normal. Many of the spring and summer samples exhibited similar characteristics. The maximum observed counts for each prey group in each sample gives some indication of the range of predation intensity exhibited by powan, e.g. in the April 1983 sample of thirty-three fish, the median number of A.viridis in stomachs was 0, but the maximum number found in a single stomach was 473. Similarly in the August 1983 sample, the median number of Bosmina recorded from examining one-sixth of the total stomach contents was 0, while the maximum was 8260. The variation in number of prey of a particular type in stomachs was considerable in most samples. Counts of prey items from the Loch Eck samples were made up of a relatively limited number of prey categories (usually 5-7). Median counts of the main prey groups fluctuated to a lesser extent than those for Loch Lomond fish over the period of study. An almost total absence of

Table 2.4 Counts of prey categories in stomach contents.

For each sample date (shown as YRMO) the number of sampled fish is indicated by n. The figures shown indicate the maximum count, the upper quartile Q3, the median count and the lower quartile Q1. A star '*' indicates prey categories which were not found in the stomach contents of that sample.

N.B. In most Lomond samples between May and November, counts represent one-sixth of the total stomach contents because of sub-sampling.

The prey groups indicated are as follows :

egg = fish egg (Coregonus)
clu = unidentified Cladocera
dhr = Daphnia hyalina var. galeata Sars (helmet round)
dhp = '' '' '' (helmet peak)
dha = '' '' '' (helmet intermediate)
dhu = '' '' (indet.)
dht = Daphnia (all)
sid = Sida crystallina (O.F. Müller)
bsm = Bosmina coregoni obtusirostris Sars
cyd = Chydorus spp.
byt = Bythotrephes logimanus Leydig
lpt = Leptodora kindtii (Focke)
hol = Holopedium gibberum Zaddach
ply = Polyphemus pediculus (L.)
ery = Eurycerus lamellatus (O.F. Müller)
ost = Ostracoda spp. (mainly Cyprina ophthalmica)
asl = Asellus aquaticus (L.)
dia = Eudiaptomus gracilis
cvr = Acanthocyclops viridis (Jurine)
cab = Cyclops str. abyssorum Sars
iul = indet. insect larva (mainly Chironomidae)
iup = '' '' pupa
iua = '' '' adult
eml = Ephemeroptera larva (mainly Caenis horaria (L.))
trl = Trichoptera larva (Hydroptilidae & Phryganeidae)
pll = Plecoptera larva (Leuctra & Neomura spp.)
krl = chironomid larva
krp = '' pupa
cbr = Chaoborus flavicans (Meigen) larva
hdr = Hydrachnellae spp.
psd = Pisidium spp.
lim = Limnaea pereger (Mull.)

Total number of stomach contents analysed : Lomond 784, Eck 166.
Sub-samples Lomond : Nov. 82, May 83 - Oct. 83 incl., May 84.

Table 2.4 Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	N	EGGS	CLU	DHR	DHP	DHA	DHU	DHT	SID
8210	30	*	*	55.0	50.0	10.0	170.0	285.0	*
8210	30	*	*	21.0	6.3	0.0	71.0	98.3	*
8210	30	*	*	2.0	0.0	0.0	35.0	37.0	*
8210	30	*	*	0.0	0.0	0.0	6.0	6.0	*
8211	29	*	*	60.0	21.0	3.0	227.0	311.0	*
8211	29	*	*	5.5	0.0	0.0	95.0	100.5	*
8211	29	*	*	0.0	0.0	0.0	13.0	13.0	*
8211	29	*	*	0.0	0.0	0.0	0.0	0.0	*
8211	5	*	*	*	*	*	*	*	*
8211	5	*	*	*	*	*	*	*	*
8211	5	*	*	*	*	*	*	*	*
8211	5	*	*	*	*	*	*	*	*
8212	17	*	*	3.0	*	*	15.0	*	*
8212	17	*	*	0.0	*	*	0.5	*	*
8212	17	*	*	0.0	*	*	0.0	*	*
8212	17	*	*	0.0	*	*	0.0	*	*
8301	95	427.0	12.0	*	*	*	1.0	*	3.0
8301	95	4.0	0.0	*	*	*	0.0	*	0.0
8301	95	1.0	0.0	*	*	*	0.0	*	0.0
8301	95	0.0	0.0	*	*	*	0.0	*	0.0
8302	43	1.0	11.0	2.0	*	*	*	*	19.0
8302	43	0.0	0.0	0.0	*	*	*	*	0.0
8302	43	0.0	0.0	0.0	*	*	*	*	0.0
8302	43	0.0	0.0	0.0	*	*	*	*	0.0
8303	23	*	*	*	*	*	*	*	*
8303	23	*	*	*	*	*	*	*	*
8303	23	*	*	*	*	*	*	*	*
8303	23	*	*	*	*	*	*	*	*
8304	33	*	2.0	*	*	*	1.0	*	*
8304	33	*	0.0	*	*	*	0.0	*	*
8304	33	*	0.0	*	*	*	0.0	*	*
8304	33	*	0.0	*	*	*	0.0	*	*
8305	41	*	*	30.0	*	*	63.0	*	*
8305	41	*	*	8.5	*	*	16.5	*	*
8305	41	*	*	0.0	*	*	1.0	*	*
8305	41	*	*	0.0	*	*	0.0	*	*
8307	30	*	*	160.0	27.0	17.0	180.0	384.0	*
8307	30	*	*	60.0	9.0	3.3	42.5	114.8	*
8307	30	*	*	18.0	3.5	0.0	12.5	34.0	*
8307	30	*	*	2.0	0.0	0.0	4.5	6.5	*

Table 2.4 cont. Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	N	EGGS	CLU	DHR	DHP	DHA	DHU	DHT	SID
8308	31	*	*	27.0	46.0	2.0	100.0	175.0	*
8308	31	*	*	3.0	3.0	0.0	8.0	14.0	*
8308	31	*	*	1.0	0.0	0.0	2.0	3.0	*
8308	31	*	*	0.0	0.0	0.0	0.0	0.0	*
8309	30	*	*	42.0	63.0	6.0	94.0	205.0	*
8309	30	*	*	12.3	18.0	1.0	30.2	61.5	*
8309	30	*	*	5.0	12.0	0.0	16.5	33.5	*
8309	30	*	*	1.8	2.0	0.0	2.7	6.4	*
8310	42	*	*	2.0	6.0	*	35.0	*	*
8310	42	*	*	0.0	0.0	*	0.0	*	*
8310	42	*	*	0.0	0.0	*	0.0	*	*
8310	42	*	*	0.0	0.0	*	0.0	*	*
8311	42	*	*	217.0	75.0	*	570.0	*	*
8311	42	*	*	5.5	2.2	*	65.0	*	*
8311	42	*	*	0.0	0.0	*	3.0	*	*
8311	42	*	*	0.0	0.0	*	0.0	*	*
8312	12	*	*	544.0	26.0	*	900.0	*	*
8312	12	*	*	77.0	14.5	*	120.0	*	*
8312	12	*	*	6.0	0.0	*	13.0	*	*
8312	12	*	*	0.0	0.0	*	0.0	*	*
8312	24	*	*	3.0	*	*	72.0	*	*
8312	24	*	*	0.0	*	*	0.8	*	*
8312	24	*	*	0.0	*	*	0.0	*	*
8312	24	*	*	0.0	*	*	0.0	*	*
8401	30	53.0	*	*	*	*	3.0	*	*
8401	30	1.0	*	*	*	*	0.0	*	*
8401	30	0.0	*	*	*	*	0.0	*	*
8401	30	0.0	*	*	*	*	0.0	*	*
8405	25	*	*	11.0	1.0	*	5.0	*	*
8405	25	*	*	0.0	0.0	*	0.0	*	*
8405	25	*	*	0.0	0.0	*	0.0	*	*
8405	25	*	*	0.0	0.0	*	0.0	*	*
8405	9	*	1.0	*	*	*	2.0	*	*
8405	9	*	0.0	*	*	*	0.0	*	*
8405	9	*	0.0	*	*	*	0.0	*	*
8405	9	*	0.0	*	*	*	0.0	*	*
8405	32	*	*	*	*	*	1.0	*	*
8405	32	*	*	*	*	*	0.0	*	*
8405	32	*	*	*	*	*	0.0	*	*
8405	32	*	*	*	*	*	0.0	*	*

Table 2.4 cont. Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	BSM	CYD	BYT	LPT	HOL	PLY	ERY	OST
8210	60.0	1.0	60.0	10.0	23.0	2.0	1.0	*
8210	12.5	0.0	22.0	2.0	1.5	0.0	0.0	*
8210	4.5	0.0	7.5	0.0	0.0	0.0	0.0	*
8210	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*
8211	100.0	*	3.0	4.0	*	*	*	*
8211	36.5	*	0.0	0.0	*	*	*	*
8211	6.0	*	0.0	0.0	*	*	*	*
8211	0.0	*	0.0	0.0	*	*	*	*
8211	*	*	*	*	*	*	*	*
8211	*	*	*	*	*	*	*	*
8211	*	*	*	*	*	*	*	*
8211	*	*	*	*	*	*	*	*
8212	105.0	*	1.0	*	*	*	*	*
8212	0.5	*	0.0	*	*	*	*	*
8212	0.0	*	0.0	*	*	*	*	*
8212	0.0	*	0.0	*	*	*	*	*
8301	8.0	*	*	*	*	*	*	1.0
8301	0.0	*	*	*	*	*	*	0.0
8301	0.0	*	*	*	*	*	*	0.0
8301	0.0	*	*	*	*	*	*	0.0
8302	3.0	*	*	*	*	*	*	1.0
8302	0.0	*	*	*	*	*	*	0.0
8302	0.0	*	*	*	*	*	*	0.0
8302	0.0	*	*	*	*	*	*	0.0
8303	3.0	*	*	*	*	*	*	*
8303	0.0	*	*	*	*	*	*	*
8303	0.0	*	*	*	*	*	*	*
8303	0.0	*	*	*	*	*	*	*
8304	22.0	*	*	*	*	*	*	*
8304	0.0	*	*	*	*	*	*	*
8304	0.0	*	*	*	*	*	*	*
8304	0.0	*	*	*	*	*	*	*
8305	2160.0	*	143.0	17.0	208.0	*	2.0	*
8305	204.0	*	26.0	2.0	2.5	*	0.0	*
8305	40.0	*	5.0	0.0	0.0	*	0.0	*
8305	2.0	*	0.0	0.0	0.0	*	0.0	*
8307	310.0	*	340.0	26.0	122.0	30.0	*	*
8307	3.3	*	15.3	1.0	28.0	0.0	*	*
8307	1.0	*	8.0	0.0	4.5	0.0	*	*
8307	0.8	*	0.8	0.0	0.0	0.0	*	*

Table 2.4 cont. Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	BSM	CYD	BYT	LPT	HOL	FLY	ERY	OST
8308	8260.0	*	178.0	18.0	310.0	*	*	*
8308	2.0	*	17.0	1.0	24.0	*	*	*
8308	0.0	*	5.0	0.0	1.0	*	*	*
8308	0.0	*	0.0	0.0	0.0	*	*	*
8309	3200.0	*	500.0	735.0	46.0	*	1.0	*
8309	0.0	*	151.0	61.0	8.5	*	0.0	*
8309	0.0	*	72.0	42.0	0.5	*	0.0	*
8309	0.0	*	8.0	14.0	0.0	*	0.0	*
8310	1.0	*	4.0	*	*	*	4.0	*
8310	0.0	*	0.0	*	*	*	0.0	*
8310	0.0	*	0.0	*	*	*	0.0	*
8310	0.0	*	0.0	*	*	*	0.0	*
8311	3.0	*	*	*	*	*	*	*
8311	0.0	*	*	*	*	*	*	*
8311	0.0	*	*	*	*	*	*	*
8311	0.0	*	*	*	*	*	*	*
8312	1.0	*	*	*	*	*	*	*
8312	0.0	*	*	*	*	*	*	*
8312	0.0	*	*	*	*	*	*	*
8312	0.0	*	*	*	*	*	*	*
8312	*	*	*	*	*	*	1.0	*
8312	*	*	*	*	*	*	0.0	*
8312	*	*	*	*	*	*	0.0	*
8312	*	*	*	*	*	*	0.0	*
8401	4.0	*	*	*	*	*	3.0	1.0
8401	0.0	*	*	*	*	*	0.0	0.0
8401	0.0	*	*	*	*	*	0.0	0.0
8401	0.0	*	*	*	*	*	0.0	0.0
8405	1263.0	*	4.0	143.0	182.0	*	*	*
8405	709.0	*	0.0	64.0	11.0	*	*	*
8405	525.0	*	0.0	21.0	3.0	*	*	*
8405	38.0	*	0.0	2.5	0.0	*	*	*
8405	193.0	*	*	8.0	2.0	*	*	*
8405	156.5	*	*	0.0	0.0	*	*	*
8405	121.0	*	*	0.0	0.0	*	*	*
8405	11.0	*	*	0.0	0.0	*	*	*
8405	6660.0	*	3.0	7.0	1.0	*	1.0	*
8405	1740.0	*	0.0	0.0	0.0	*	0.0	*
8405	985.0	*	0.0	0.0	0.0	*	0.0	*
8405	444.0	*	0.0	0.0	0.0	*	0.0	*

Table 2.4 cont. Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	ASL	DIA	CVR	CAB	IUL	IUP	IUA	EML
8210	*	22.0	1.0	115.0	2.0	2.0	*	1.0
8210	*	0.0	0.0	0.0	0.0	0.0	*	0.0
8210	*	0.0	0.0	0.0	0.0	0.0	*	0.0
8210	*	0.0	0.0	0.0	0.0	0.0	*	0.0
8211	*	15.0	*	146.0	*	*	*	*
8211	*	0.0	*	45.0	*	*	*	*
8211	*	0.0	*	8.0	*	*	*	*
8211	*	0.0	*	0.0	*	*	*	*
8211	*	*	*	*	*	*	*	*
8211	*	*	*	*	*	*	*	*
8211	*	*	*	*	*	*	*	*
8211	*	*	*	*	*	*	*	*
8212	*	47.0	14.0	*	1.0	1.0	*	*
8212	*	0.0	3.5	*	0.0	0.0	*	*
8212	*	0.0	0.0	*	0.0	0.0	*	*
8212	*	0.0	0.0	*	0.0	0.0	*	*
8301	9.0	4.0	33.0	*	1.0	*	*	1.0
8301	0.0	0.0	5.0	*	0.0	*	*	0.0
8301	0.0	0.0	1.0	*	0.0	*	*	0.0
8301	0.0	0.0	0.0	*	0.0	*	*	0.0
8302	1.0	2.0	310.0	*	1.0	1.0	*	1.0
8302	0.0	0.0	0.0	*	0.0	0.0	*	0.0
8302	0.0	0.0	0.0	*	0.0	0.0	*	0.0
8302	0.0	0.0	0.0	*	0.0	0.0	*	0.0
8303	*	1.0	246.0	2.0	2.0	*	*	*
8303	*	0.0	13.3	0.0	0.0	*	*	*
8303	*	0.0	0.0	0.0	0.0	*	*	*
8303	*	0.0	0.0	0.0	0.0	*	*	*
8304	*	153.0	473.0	350.0	*	2.0	*	*
8304	*	0.0	4.0	0.0	*	1.0	*	*
8304	*	0.0	0.0	0.0	*	0.0	*	*
8304	*	0.0	0.0	0.0	*	0.0	*	*
8305	*	*	16.0	6.0	*	36.0	*	*
8305	*	*	1.0	0.0	*	1.0	*	*
8305	*	*	0.0	0.0	*	0.0	*	*
8305	*	*	0.0	0.0	*	0.0	*	*
8307	*	2.0	1.0	6.0	*	1.0	*	5.0
8307	*	0.0	0.0	1.0	*	0.0	*	0.0
8307	*	0.0	0.0	0.0	*	0.0	*	0.0
8307	*	0.0	0.0	0.0	*	0.0	*	0.0

Table 2.4 cont. Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	ASL	DIA	CVR	CAB	IUL	IUP	IUA	EML
8308	*	*	1000.0	1.0	*	4.0	*	*
8308	*	*	0.0	0.0	*	0.0	*	*
8308	*	*	0.0	0.0	*	0.0	*	*
8308	*	*	0.0	0.0	*	0.0	*	*
8309	*	*	1110.0	*	*	1.0	*	*
8309	*	*	1.0	*	*	0.0	*	*
8309	*	*	0.0	*	*	0.0	*	*
8309	*	*	0.0	*	*	0.0	*	*
8310	*	*	*	*	*	*	*	*
8310	*	*	*	*	*	*	*	*
8310	*	*	*	*	*	*	*	*
8310	*	*	*	*	*	*	*	*
8311	*	17.0	67.0	32.0	*	1.0	1.0	*
8311	*	1.3	0.0	2.0	*	0.0	0.0	*
8311	*	0.0	0.0	0.0	*	0.0	0.0	*
8311	*	0.0	0.0	0.0	*	0.0	0.0	*
8312	*	1.0	1.0	23.0	*	*	*	*
8312	*	0.0	0.0	7.5	*	*	*	*
8312	*	0.0	0.0	0.0	*	*	*	*
8312	*	0.0	0.0	0.0	*	*	*	*
8312	*	3.0	172.0	3.0	*	*	*	*
8312	*	0.0	0.8	0.0	*	*	*	*
8312	*	0.0	0.0	0.0	*	*	*	*
8312	*	0.0	0.0	0.0	*	*	*	*
8401	1.0	3.0	345.0	*	*	*	*	*
8401	0.0	0.0	22.0	*	*	*	*	*
8401	0.0	0.0	1.0	*	*	*	*	*
8401	0.0	0.0	0.0	*	*	*	*	*
8405	*	5.0	1.0	4.0	*	7.0	*	*
8405	*	0.0	0.0	0.0	*	3.0	*	*
8405	*	0.0	0.0	0.0	*	1.0	*	*
8405	*	0.0	0.0	0.0	*	0.0	*	*
8405	*	1.0	4.0	*	*	1.0	*	*
8405	*	0.0	1.0	*	*	1.0	*	*
8405	*	0.0	0.0	*	*	0.0	*	*
8405	*	0.0	0.0	*	*	0.0	*	*
8405	*	1.0	1.0	*	*	25.0	*	7.0
8405	*	0.0	0.0	*	*	0.8	*	0.0
8405	*	0.0	0.0	*	*	0.0	*	0.0
8405	*	0.0	0.0	*	*	0.0	*	0.0

Table 2.4 cont. Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	TRL	PLL	KRL	KRP	CBR	HDR	PSD	LIM
8210	1.0	*	5.0	2.0	80.0	*	3.0	*
8210	0.0	*	0.0	0.0	15.0	*	0.0	*
8210	0.0	*	0.0	0.0	5.0	*	0.0	*
8210	0.0	*	0.0	0.0	2.7	*	0.0	*
8211	11.0	1.0	1.0	*	2.0	*	*	*
8211	0.0	0.0	0.0	*	0.0	*	*	*
8211	0.0	0.0	0.0	*	0.0	*	*	*
8211	0.0	0.0	0.0	*	0.0	*	*	*
8211	*	*	1.0	*	1.0	*	3.0	*
8211	*	*	0.5	*	0.5	*	2.5	*
8211	*	*	0.0	*	0.0	*	1.0	*
8211	*	*	0.0	*	0.0	*	0.0	*
8212	2.0	*	*	1.0	2.0	*	1.0	8.0
8212	0.0	*	*	0.0	0.5	*	0.0	0.0
8212	0.0	*	*	0.0	0.0	*	0.0	0.0
8212	0.0	*	*	0.0	0.0	*	0.0	0.0
8301	1.0	*	4.0	1.0	3.0	*	34.0	*
8301	0.0	*	0.0	0.0	0.0	*	1.0	*
8301	0.0	*	0.0	0.0	0.0	*	0.0	*
8301	0.0	*	0.0	0.0	0.0	*	0.0	*
8302	1.0	*	5.0	*	146.0	*	36.0	*
8302	0.0	*	0.0	*	0.0	*	0.0	*
8302	0.0	*	0.0	*	0.0	*	0.0	*
8302	0.0	*	0.0	*	0.0	*	0.0	*
8303	*	1.0	1.0	*	159.0	*	2.0	*
8303	*	0.0	0.0	*	1.0	*	0.0	*
8303	*	0.0	0.0	*	0.0	*	0.0	*
8303	*	0.0	0.0	*	0.0	*	0.0	*
8304	6.0	*	117.0	*	308.0	*	13.0	*
8304	0.0	*	1.5	*	1.5	*	1.0	*
8304	0.0	*	0.0	*	0.0	*	0.0	*
8304	0.0	*	0.0	*	0.0	*	0.0	*
8305	1.0	1.0	5.0	*	10.0	5.0	6.0	*
8305	0.0	0.0	0.0	*	0.0	0.0	0.0	*
8305	0.0	0.0	0.0	*	0.0	0.0	0.0	*
8305	0.0	0.0	0.0	*	0.0	0.0	0.0	*
8307	*	*	5.0	*	30.0	*	28.0	*
8307	*	*	0.0	*	0.0	*	0.0	*
8307	*	*	0.0	*	0.0	*	0.0	*
8307	*	*	0.0	*	0.0	*	0.0	*

Table 2.4 cont. Counts of prey categories in stomach contents.
 Maxima, q3, medians and q1 are shown.
 Loch Lomond samples.

DATE	TRL	PLL	KRL	KRP	CBR	HDR	PSD	LIM
8308	*	*	1.0	*	1.0	2.0	*	*
8308	*	*	0.0	*	0.0	0.0	*	*
8308	*	*	0.0	*	0.0	0.0	*	*
8308	*	*	0.0	*	0.0	0.0	*	*
8309	*	*	1.0	*	7.0	1.0	*	*
8309	*	*	0.0	*	1.3	0.0	*	*
8309	*	*	0.0	*	0.0	0.0	*	*
8309	*	*	0.0	*	0.0	0.0	*	*
8310	*	*	*	*	*	*	2.0	*
8310	*	*	*	*	*	*	0.0	*
8310	*	*	*	*	*	*	0.0	*
8310	*	*	*	*	*	*	0.0	*
8311	*	*	6.0	*	600.0	*	1.0	*
8311	*	*	0.0	*	0.0	*	0.0	*
8311	*	*	0.0	*	0.0	*	0.0	*
8311	*	*	0.0	*	0.0	*	0.0	*
8312	*	*	1.0	*	1.0	*	*	*
8312	*	*	0.0	*	0.0	*	*	*
8312	*	*	0.0	*	0.0	*	*	*
8312	*	*	0.0	*	0.0	*	*	*
8312	2.0	*	110.0	*	665.0	1.0	17.0	*
8312	0.0	*	0.0	*	2.0	0.0	0.0	*
8312	0.0	*	0.0	*	0.0	0.0	0.0	*
8312	0.0	*	0.0	*	0.0	0.0	0.0	*
8401	1.0	*	4.0	*	880.0	*	14.0	*
8401	0.0	*	0.3	*	3.0	*	1.3	*
8401	0.0	*	0.0	*	0.0	*	0.0	*
8401	0.0	*	0.0	*	0.0	*	0.0	*
8405	*	*	1.0	*	1.0	*	*	*
8405	*	*	0.0	*	0.0	*	*	*
8405	*	*	0.0	*	0.0	*	*	*
8405	*	*	0.0	*	0.0	*	*	*
8405	*	*	1.0	*	32.0	*	*	*
8405	*	*	0.5	*	0.5	*	*	*
8405	*	*	0.0	*	0.0	*	*	*
8405	*	*	0.0	*	0.0	*	*	*
8405	2.0	*	41.0	*	2.0	61.0	18.0	*
8405	0.0	*	0.0	*	0.0	1.0	0.0	*
8405	0.0	*	0.0	*	0.0	0.0	0.0	*
8405	0.0	*	0.0	*	0.0	0.0	0.0	*

Table 2.4 cont. Counts of prey categories in stomach contents.
 (cont.) Loch Eck samples.
 Maxima, q3, medians and q1 are shown.

DATE	N	HIR	LPT	OST	CVR	IUL	IUA
8401	35	4.0	*	4.0	180.0	*	*
8401	35	0.0	*	1.0	26.0	*	*
8401	35	0.0	*	0.0	8.0	*	*
8401	35	0.0	*	0.0	5.0	*	*
8402	15	1.0	*	*	2200.0	*	*
8402	15	0.0	*	*	16.0	*	*
8402	15	0.0	*	*	7.0	*	*
8402	15	0.0	*	*	5.0	*	*
8409	17	*	1.0	2.0	36.0	*	1.0
8409	17	*	0.0	0.5	3.0	*	0.0
8409	17	*	0.0	0.0	1.0	*	0.0
8409	17	*	0.0	0.0	0.0	*	0.0
8501	24	7.0	*	290.0	50.0	*	*
8501	24	0.0	*	1.0	12.5	*	*
8501	24	0.0	*	0.0	1.0	*	*
8501	24	0.0	*	0.0	0.0	*	*
8502	16	1.0	*	*	49.0	40.0	*
8502	16	0.0	*	*	6.8	0.0	*
8502	16	0.0	*	*	3.5	0.0	*
8502	16	0.0	*	*	0.3	0.0	*
8503	19	*	*	*	80.0	*	*
8503	19	*	*	*	16.0	*	*
8503	19	*	*	*	4.0	*	*
8503	19	*	*	*	0.0	*	*
8505	20	1.0	*	11.0	63.0	*	*
8505	20	0.0	*	1.8	6.8	*	*
8505	20	0.0	*	0.0	3.0	*	*
8505	20	0.0	*	0.0	0.0	*	*
8508	20	8.0	*	10.0	72.0	1.0	*
8508	20	1.0	*	3.0	38.8	0.0	*
8508	20	0.0	*	0.0	16.0	0.0	*
8508	20	0.0	*	0.0	2.2	0.0	*

Table 2.4 cont. Counts of prey categories in stomach contents.
 (cont.) Loch Eck samples.
 Maxima, q3, medians and q1 are shown.

DATE	N	TRL	PLL	KRL	KRP	CBR	PSD
8401	35	*	1.0	118.0	*	1.0	49.0
8401	35	*	0.0	68.0	*	0.0	24.0
8401	35	*	0.0	57.0	*	0.0	12.0
8401	35	*	0.0	32.0	*	0.0	2.0
8402	15	1.0	1.0	181.0	*	2.0	102.0
8402	15	0.0	0.0	155.0	*	0.0	38.0
8402	15	0.0	0.0	111.0	*	0.0	22.0
8402	15	0.0	0.0	81.0	*	0.0	10.0
8409	17	*	*	391.0	*	1.0	124.0
8409	17	*	*	150.0	*	0.0	57.0
8409	17	*	*	92.0	*	0.0	13.0
8409	17	*	*	41.0	*	0.0	2.0
8501	24	1.0	1.0	229.0	*	*	111.0
8501	24	0.0	0.0	110.0	*	*	11.8
8501	24	0.0	0.0	69.0	*	*	2.5
8501	24	0.0	0.0	21.0	*	*	1.0
8502	16	*	*	178.0	*	*	85.0
8502	16	*	*	146.0	*	*	24.2
8502	16	*	*	88.0	*	*	7.5
8502	16	*	*	35.6	*	*	2.7
8503	19	1.0	*	364.0	*	1.0	142.0
8503	19	0.0	*	54.0	*	0.0	25.0
8503	19	0.0	*	36.0	*	0.0	7.0
8503	19	0.0	*	30.0	*	0.0	1.0
8505	20	*	*	88.0	130.0	1.0	60.0
8505	20	*	*	57.8	39.8	0.0	43.3
8505	20	*	*	32.5	8.5	0.0	16.5
8505	20	*	*	18.0	0.5	0.0	0.3
8508	20	1.0	*	255.0	*	*	396.0
8508	20	0.0	*	144.3	*	*	205.0
8508	20	0.0	*	85.0	*	*	99.0
8508	20	0.0	*	47.2	*	*	54.0

zooplankton from the diet of Loch Eck fish was recorded over the study period which included late spring and summer samples. The largest variation in counts of prey numbers from sampled stomachs occurred with the cyclopoid copepod *A. viridis* (February 1984 sample, median count 7, maximum count 2200).

It is apparent that the counts of prey items recorded from stomachs showed considerable variation, even within the same sample. This variation could be due to a number of factors either singly or collectively. Preferential feeding by fish, exploitation of different habitats, asynchronous feeding and differential digestion rates could contribute to the observed composition of stomach contents.

2.2.5 Within sample variation of food species : concordance = Kendall's W.

The values of Kendall's W calculated separately for males, females, immatures and all fish in each sample are shown in Table 2.5. Sample sizes at each date are indicated. The concordance estimate W ranges from zero (complete disagreement on rankings of variables) to unity (complete agreement on rankings of variables) and is influenced by the number of subjects (judges) ranking the variables. The seasonal pattern of concordance for the sexes was examined before the whole sample pattern.

Loch Lomond

Agreement between males within a particular sample on the ranking of prey categories on a numerical basis was maximal in the samples of October 1982, May, July, September and December 1983 and the seine sample from May 1984. ($W = 0.52-0.75$). For the other samples, agreement was lower, but in all samples except February 1983 the agreement between males in ranking prey categories was greater than

Table 2.5

Stomach contents , numerical analysis of abundance.
Kendall's coefficient of concordance, W.

sample date	all fish		males		females		immatures	
	n	W	n	W	n	W	n	W
Loch Lomond								
19 Oct 82	30	0.580	10	0.519	7	0.553	13	0.743
10 Nov 82	29	0.484	5	0.396	9	0.294	15	0.795
25 Nov 82	5	0.449	4	0.381 *	0	0.000	0	0.000
1 Dec 82	17	0.199	5	0.344	6	0.218 ~	6	0.347
7 Jan 83	95	0.367	37	0.279	44	0.463	14	0.440
8 Feb 83	43	0.075	23	0.055 ~	16	0.146	4	0.531
23 Mar 83	23	0.307	9	0.264	14	0.354	0	0.000
16 Apr 83	33	0.277	15	0.310	11	0.313	7	0.416
27 May 83	41	0.485	22	0.516	13	0.430	6	0.644
5 Jul 83	30	0.588	16	0.644	10	0.519	4	0.650
17 Aug 83	30	0.417	15	0.382	14	0.506	2	0.459 ~
5 Sep 83	31	0.686	13	0.752	12	0.583	5	0.865
12 Oct 83	30	0.258	17	0.456	15	0.316	10	0.212
16 Nov 83	42	0.308	19	0.293	16	0.238	7	0.640
6 Dec 83	12	0.431	3	0.658	9	0.379	0	0.000
13 Dec 83	24	0.166	13	0.169	8	0.238	3	0.449 ~
10 Jan 84	30	0.307	13	0.310	15	0.343	2	0.500 ~
14 May 84	25	0.626	14	0.689	10	0.607	0	0.000
14 May 84	9	0.434	3	0.416 ~	6	0.503	0	0.000
15 May 84	32	0.436	10	0.486	15	0.422	7	0.652
Loch Eck								
12 Jan 84	35	0.828	9	0.792	13	0.842	13	0.872
14 Feb 84	15	0.831	0	0.000	15	0.831	0	0.000
27 Sep 84	17	0.746	11	0.703	6	0.849	0	0.000
10 Jan 85	24	0.630	5	0.731	19	0.622	0	0.000
26 Feb 85	16	0.836	6	0.776	8	0.930	2	0.750 *
27 Mar 85	19	0.850	13	0.864	6	0.830	0	0.000
14 May 85	20	0.703	12	0.709	8	0.727	0	0.000
4 Aug 85	20	0.830	12	0.857	6	0.812	2	0.848

Unless indicated, the significance level of a calculated W for n cases and 31 d.o.f. was less than $p = 0.001$, ie there was more agreement in the ranking than could be expected by chance.

* indicates $p < 0.05$, ~ indicates $p > 0.05$ (ns).

might be expected by chance ($p < 0.05$). Agreement between males in the February 1983 sample was the lowest recorded value of W and was not significant ($W = 0.055$, $m = 23$, $d.o.f. = 31$, $p > 0.05$). Female fish were treated together, ie: no distinction was made between the various sub-stages of the reproductive cycle such as pre-spawning and spent individuals. Maximal concordance on food categories for females was observed in the samples of October 1982. January, July, August and September of 1983 and the two May samples of 1984 from the mid-basin of the loch ($W = 0.46-0.61$). Agreement was lowest in the sample of December 1982 ($W = 0.218$, $m = 6$, $d.o.f. = 31$, $p > 0.05$), but in all other samples, the concordance was significantly greater than might be expected by chance. Around spawning time in January 1983, females were observed to concur on the numerical importance of food categories to a greater extent than males at the same time. This was also particularly true of the February, March and August 1983 samples, while at other times of the year concordance values were similar to or less than those for male fish. Where immature fish were available for examination, the agreement between individual immature fish on prey rankings was in every case greater than either males or females from the same sample, ($W = 0.347-0.865$) the one exception to this occurring in October 1983 ($W = 0.212$). Taken together, the highest agreement between all fish in a sample was observed in the September 1983 and seine May 1984 samples. Lowest agreement on prey rankings occurred in February 1983 ($W = 0.075$) but in every sample the agreement between fish was significant at the 0.05 level.

Loch Eck

Concordance values for males ranged from 0.703 (September 1984) to 0.864 (March 1985), with all samples displaying significant concordance. Females displayed a wider range of W values from 0.622

(January 1985) to 0.93 (February 1985). Females taken from the January 1985 sample were in the pre-spawning period, while the February 1985 sample comprised mostly spent females. The concordance values for females were higher than those for males in the January and September 1984 samples and February 1985 samples. Immature fish from Loch Eck exhibited similarly high concordance values in the one sample where more than two fish were examined (January 1984, $W = 0.872$, $m = 13$, $d.o.f. = 31$, $p < 0.001$).

The concordance values for Loch Eck fish indicate that a much greater community of preference for certain prey categories exists within a given sample at most times of the year than is the case in Loch Lomond for much of the year. At their maximal concordance, the Loch Lomond fish approached the lowest level of concordance exhibited by the Loch Eck fish.

2.2.6 Diversity of diet - Shannon-Wiener function.

Table 2.6 shows the results of calculating Shannon-Wiener statistics for the numerical data obtained from analysis of stomach contents. For comparative purposes, the evenness estimate E was calculated for the sample of 26th May 1983 using all of stomach contents and then again for a sub-sample of one-sixth of the total stomach contents. In using a sub-sample of the contents, three fewer species were detected than in examining all the contents with the result that a higher evenness value was obtained. Most samples comprised 20-40 fish, but some had fewer than this. The number of prey groups encountered in a sample varied from a minimum of three from five fish in late November 1982 to a maximum of twenty-two from thirty fish in the October 1982 sample. In general, fewer prey categories were encountered in winter and early spring samples than at

Table 2.6

Shannon-Wiener information statistic calculated
for fish stomach content samples.

sample	n	H calc	S categories	E evenness
Loch Lomond				
821019	30	2.749	22	0.616
821110	29	1.945	13	0.526
821125	5	1.061	3	0.670
821201	17	2.412	13	0.652
830107	95	1.606	17	0.393
830208	43	1.834	17	0.449
830302	24	1.136	9	0.358
830416	33	1.925	11	0.556
830526	11	2.022	15	0.518
830526	11	1.987	12	0.554
830527	41	1.349	16	0.337
830705	30	2.821	17	0.690
830817	31	1.111	14	0.292
830823	20	2.677	13	0.724
830905	30	2.515	15	0.644
831012	42	2.502	13	0.676
831116	42	1.914	12	0.534
831206	12	1.208	9	0.381
831213	24	1.655	11	0.478
840110	30	1.197	12	0.334
840514	25	0.672	13	0.182
840514	9	0.467	10	0.140
840515	32	0.064	15	0.016
Loch Eck				
840112	35	1.479	8	0.493
840214	15	1.377	8	0.459
840927	17	0.936	7	0.333
850110	24	1.460	8	0.487
850226	16	1.097	5	0.473
850327	19	1.261	5	0.543
850517	20	1.942	7	0.692
850804	20	1.407	7	0.501

other times. The total number of species encountered was in some cases greater, but for practical reasons groups of prey species such as chironomid larvae were treated as a single category. Details of prey species encountered are given in Table 2.4. The evenness or equitability estimate E ($E = 1$ when all individuals divided evenly amongst prey categories = maximum diversity) of the way the total prey numbers were apportioned between prey categories shows considerable variation for the Loch Lomond samples. Evenness values of 0.6 and greater were observed for samples in which planktonic food was the norm although lower values of $E = 0.34$ and 0.29 were observed in the 27th May 1983 and 17th August 1983 samples respectively. Similarly low values of E were recorded for many of the winter samples (0.39 January 1983, 0.33 January 1984). The lowest evenness values were recorded from the May 1984 samples. This reflects the numerical dominance of the zooplankter Bosmina in these samples.

In the Loch Eck samples examined the total number of species categories did not fall below 5 and did not exceed 8. Observed values of E for the Loch Eck samples varied between 0.33 (September 1984) and 0.69 (May 1985). The evenness of these samples depended mainly on the division of the total prey numbers among the few prey categories which were present in the diet for most of the year. None of the Loch Eck samples examined showed the imbalance due to numerical dominance of a particular prey category seen in the Loch Lomond spring samples.

The assignation of prey to categories was in some cases the possible cause of some of the variation in the calculated values of E . Where the larvae and pupae of insects were placed in different categories, the total number of possible categories encountered was increased but with no increase in the total number of species encountered. However the detection of feeding patterns justifies the

increased categorisation of the diet.

2.3 Gravimetric analysis.

2.3.1 Damp weight of stomach contents per unit corrected total fish weight.

The mean damp weights of stomach contents (expressed as grams stomach contents per kilogram corrected total fish weight) and 95% of confidence limits were plotted for the sample dates from the two lochs, separated by sex. These are shown in Figs. 2.4 a,b.

Oneway analysis of variance indicated significant differences between mean damp weights of contents for both sexes and from each loch (see below).

Analysis	d.o.f.	F _{0.005}	F _{calc}	prob.
Lomond males	15,263	2.37	10.45	p<0.005
Lomond females	15,238	2.37	7.07	p<0.005
Eck males	10,252	2.71	16.84	p<0.005
Eck females	11,270	2.54	3.24	p<0.005

Differences in mean stomach contents weights per kilogram fish weight between the two lochs were large for most of the year. Lomond mean contents weights ranged from 0.34 gkg⁻¹ in March '83 to 3.78 gkg⁻¹ in May '84, while Eck mean contents weights ranged from 7.37 gkg⁻¹ to 9.09 gkg⁻¹ over a similar period. The smallest differences in stomach contents weights between Lomond and Eck fish were observed for spawning time catches. The exact timing of spawning differs from year to year and by loch and this should be noted in comparing samples from the two lochs. Sample pairs were compared by using a t-test (Minitab 82.1) of the null hypothesis that the two population means (estimated

Fig. 2.4a Loch Lomond powan samples : mean damp weight
of stomach contents expressed as grams per kg
corrected total fish weight.
Means and 95% confidence limits.

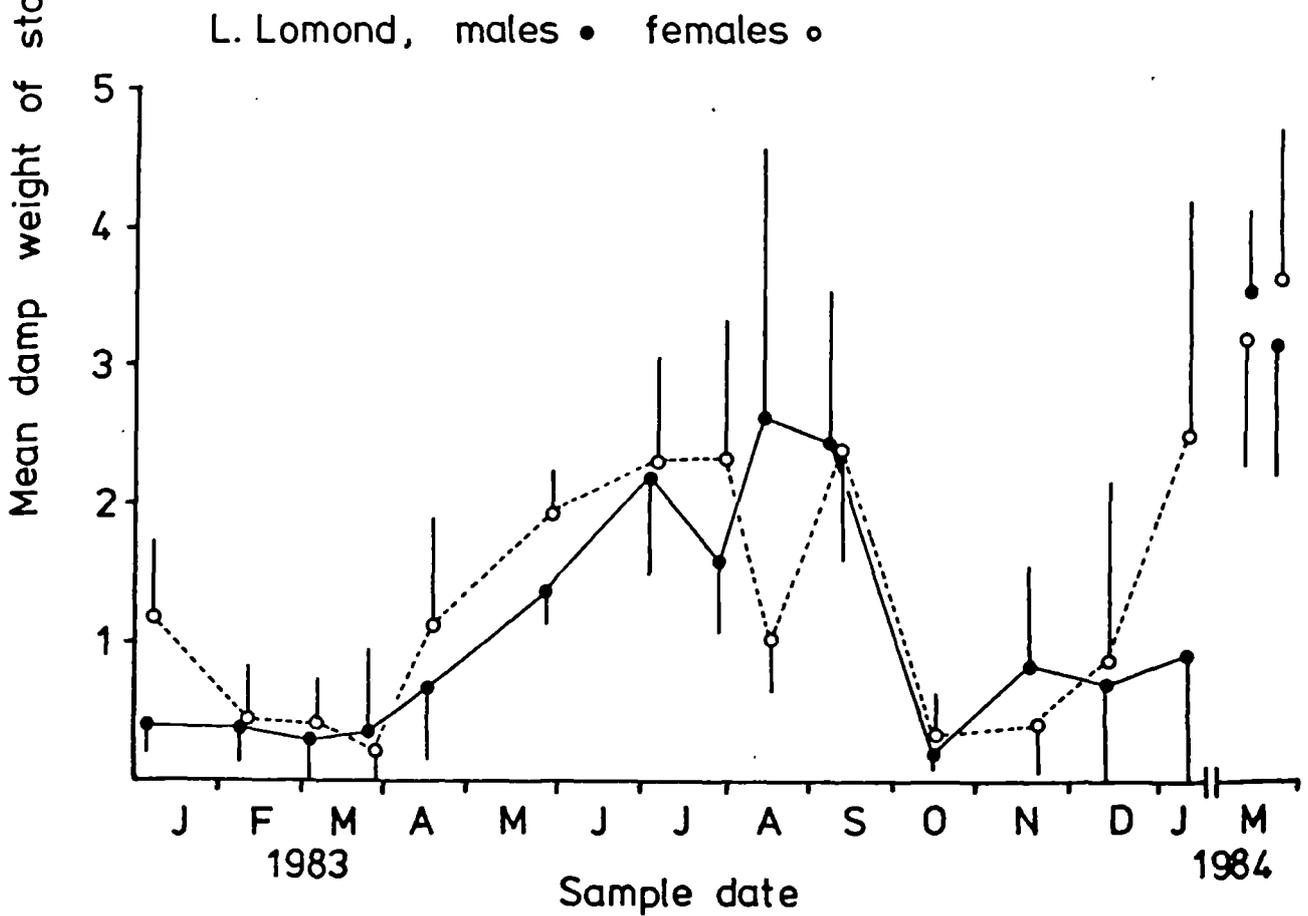
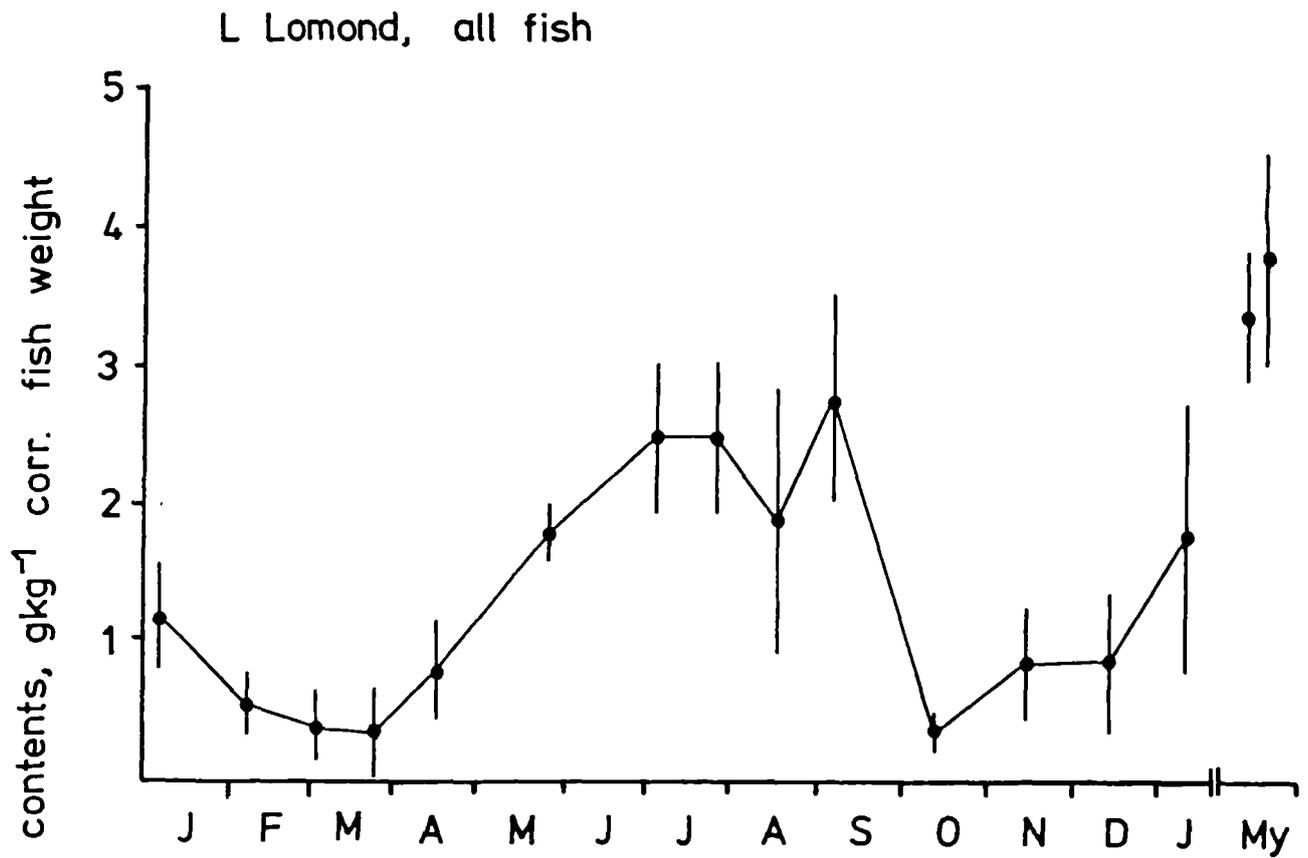


Fig. 2.4a

Fig. 2.4b Loch Eck powan samples : mean damp weight
of stomach contents expressed as grams per kg
corrected total fish weight.
Means and 95% confidence limits.

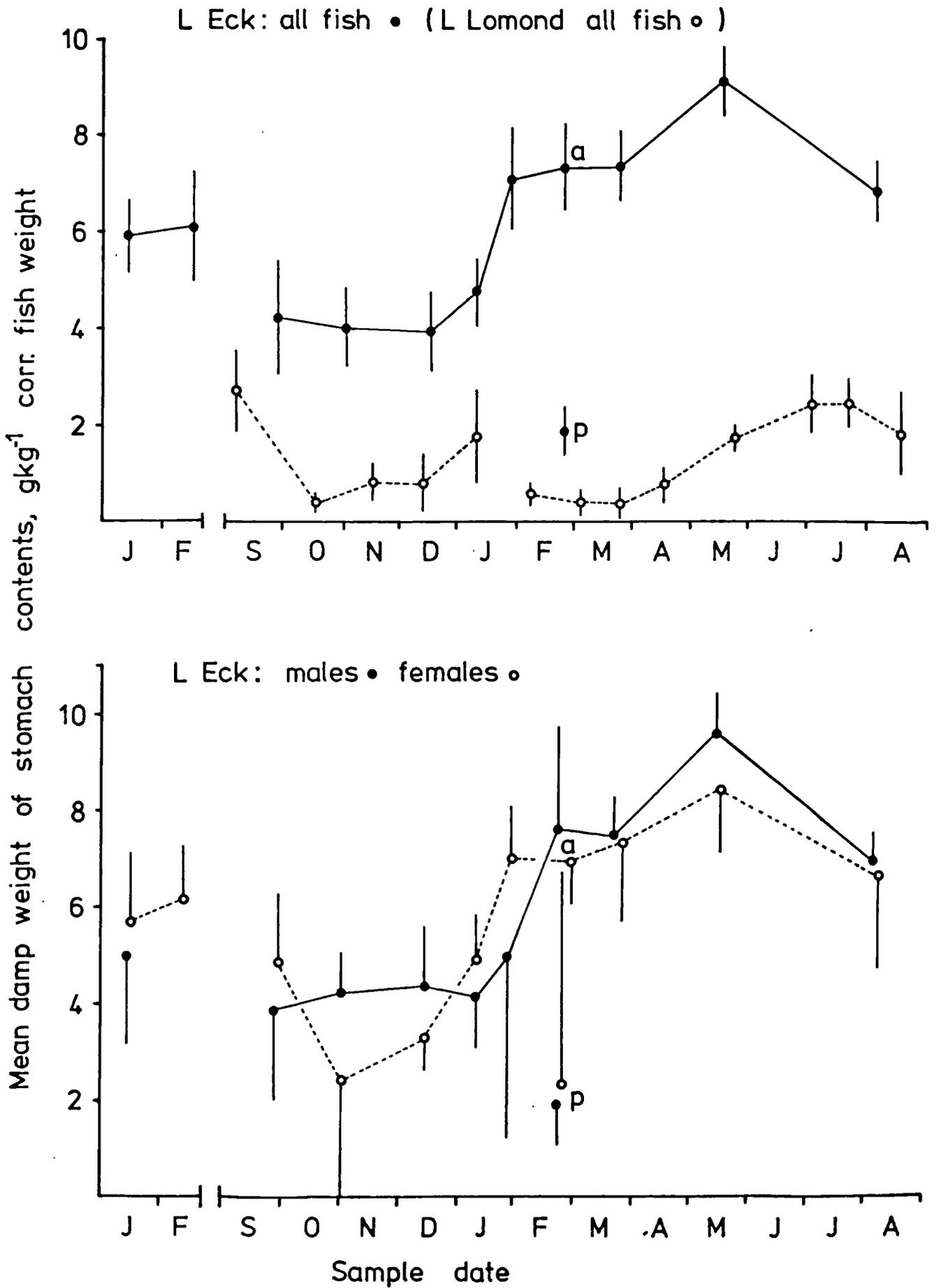


Fig. 2.4b

by the sample means) were the same. When the samples taken at spawning time in Loch Lomond 1984 (January 10th) and Loch Eck 1985 (February 26th, spawning ground) were compared, males (m) from the two lochs and females (f) from the two lochs could not be shown to have significantly different weights of stomach contents per kilogram body weight;

$$t(m,m) = 1.89 \text{ d.o.f.} = 13.6, p > 0.05;$$

$$t(f,f) = -0.25 \text{ d.o.f.} = 11.3, p > 0.05).$$

However, the mean values for Eck fish captured in the deeper mid-basin of the loch on the same date (mostly spent individuals) were much higher than those of the spawning ground fish (Fig. 2.4b). The Lomond samples showed two occasions where the weight of contents for the two sexes in the same sample differed significantly i.e.:

$$\text{January 1983 } t(m,f) = -3.02, \text{ d.o.f.} = 5.16 \quad 0.005 > p > 0.001$$

$$\text{and May 1983 } t(m,f) = -3.11, \text{ d.o.f.} = 40.1 \quad 0.005 > p > 0.001.$$

(m = males f = females)

The January sample was taken about the spawning time for Lomond fish in 1983, when spent females were found to have gorged themselves on eggs and benthic food, while males did not have much food in their stomachs. There is no apparent reason why females should have been observed to have significantly higher stomach content weights per kilogram body weight than males in May 1983. On other sample dates means for the two sexes differed considerably but the variances associated with the means together with small sample sizes meant that differences were not significant (e.g. July, August 1983). May samples from Lomond in two successive years (1983 and 1984) were compared. Males from both the seine (sn) and south (st) May 1984 samples differed significantly from males in the May 1983 (M3) sample:

$t(\text{sn}, \text{M3}) = -6.68, \text{d.o.f.} = 16.8, p < 0.001$

$t(\text{st}, \text{M3}) = -3.96, \text{d.o.f.} = 13.6, 0.005 > p > 0.001$

the same was true of the data for females in these samples:

$t(\text{sn}, \text{M3}) = -2.85, \text{d.o.f.} = 11.8, 0.05 > p > 0.01$

$t(\text{st}, \text{M3}) = -3.36, \text{d.o.f.} = 16.7, 0.005 > p > 0.001$

In all cases the 1984 weights were higher than those in 1983. Differences in mean weights of stomach contents per kilogram body weight were not significant for either males or females from the seine and south samples of May 1984, although the mean value for males was higher than that for females in the seine sample and lower than that for females in the south sample. The seine-netted sample was taken at dusk (2200) and suffered virtually no delay in processing compared to the late morning sample from the south basin of Loch Lomond which was gill-netted overnight and took two hours to transport to the laboratory.

The Loch Eck samples showed no significant differences between sample means for males and females on all sample dates. The main differences in mean stomach contents weights were observed at spawning time in February 1985 when two nets were fished simultaneously in different regions of the loch. When the data for males taken from nets fished on the probable spawning grounds (p) were compared to males taken from deeper water in the mid-loch (a), highly significant differences were observed;

$(t(\text{a}, \text{p}) = 5.75, \text{d.o.f.} = 14.2, p < 0.001).$

Data for females from these two nettings were significantly different;

$(t(\text{a}, \text{p}) = 8.36, \text{d.o.f.} = 4.9, 0.005 > p > 0.001),$

although only two females were netted in the inshore catch. The large differences in weights of stomach contents were further analysed in the following sections.

2.3.2 Dry weight/damp weight relationship.

In Loch Lomond samples dried stomach contents averaged 3.3% to 10.9% of damp weights for samples taken in May, September, November of 1983 and January 1984 (Table 2.7). Analysis of variance on the transformed percentage data showed highly significant differences between sample means ($F(\text{calc})_{3,101} = 7.50$, $F(0.01)_{3,100} = 3.51$). A Tukey-Kramer MSD test (Sokal & Rohlf 1981, p251) showed the November sample mean to be significantly lower than the other samples. The dry/damp weight relationship observed appears to be species sensitive. The low November dry/damp percentages were recorded from a sample in which fish were feeding almost exclusively on one of two prey species; Daphnia hyalina or Chaoborus flavicans larvae. Most fish fed on Daphnia, and the percentage dry weight/damp weight contents relationship derived for these fish varied from 1% - 7%. The dry/damp weight relationship for Chaoborus was 14.3%.

In the May samples, most stomachs contained Bosmina, either exclusively or in combination with other Cladocera and prey types. The mean dry weight/damp weight proportions of the prey species combinations in this sample varied between 6.6% (Bosmina -Daphnia) to 16.3% (Bosmina-Bythotrephes).

For stomachs collected in September, the variation of dry/damp proportions was similar for several prey species combinations. The large cladoceran Bythotrephes longimanus was the main dietary constituent in this sample, along with Leptodora kindti and Daphnia hyalina. Combinations of the above gave dry/damp weight percentages of around 10%.

January's stomach contents were shown to have dry/damp weight percentages quite similar to those of May and September. Many of the stomachs from this sample contained non-food material in addition to

Table 2.7

Stomach contents : dry weight/damp weight relationship,
(all material).

sample	n	mean %	95% C.I.	Vy.x	av	r ²
Loch Lomond						
27 May 83	29	7.9	5.5 - 10.6	0.1256	-0.0085	0.709
5 Sept 83	26	10.9	8.9 - 13.0	0.1147	-0.0049	0.821
16 Nov 83	27	3.3	2.0 - 5.1	0.1439	-0.0080	0.986
10 Jan 84	20	10.6	5.6 - 17.6	0.1355	0.0111	0.584
Loch Eck						
12 Jan 84	27	22.0	20.0 - 24.1	0.2536	-0.0186	0.920
14 Feb 84	15	23.5	20.5 - 26.8	0.2691	-0.0444	0.884
27 Sep 84	16	23.5	17.3 - 30.3	0.1776	-0.0269	0.852
10 Jan 85	24	19.7	14.6 - 25.3	0.3060	-0.0156	0.841
26 Feb 85	16	20.4	17.9 - 22.0	0.2687	-0.0600	0.972
27 Mar 85	19	21.4	19.3 - 23.5	0.2507	-0.0613	0.885
14 May 85	18	21.2	18.0 - 24.5	0.3333	-0.1876	0.812
4 Aug 85	20	23.2	21.4 - 24.9	0.2471	-0.0151	0.962

Vy.x and av are the Geometric Mean regression coefficient and intercept respectively, used to estimate the predictive relationship between dry and damp weights of material. r² is the coefficient of determination.

Analysis of variance -

Loch Lomond :

F(calc)3,101 = 7.50, F(0.01)3,100 = 3.51, p < 0.01

Loch Eck :

F(calc)7,154 = 0.66, F(0.05)7,150 = 2.07, p > 0.05

items such as powan eggs, Chaoborus larvae and cyclopoid copepods. Where stomachs were free of non-food material, dry/damp percentages were directly comparable to those of other samples.

Loch Eck mean dry/damp weight percentages for samples showed less variation than those of Lomond (Table 2.7). Analysis of variance on the transformed data showed no significant differences ($F(\text{calc})_{7,154} = 0.66$, $F(0.05)_{7,150} = 2.07$) between sample means. The consistently higher dry/damp proportions observed for Eck samples was mainly due to the presence of non-food material in the stomach contents.

The geometric mean regression statistics for the dry/damp weight relationship estimated for the samples from both lochs are included in Table 2.7.

2.3.3 Dry weight composition.

Loch Lomond : non-food material in powan stomachs.

Some stomach samples from Loch Lomond contained material other than food. Two classes of non-food material were distinguished for Lomond stomachs - gravel, (defined as particulate stones or pebbles greater than 0.5mm diameter) and debris (defined as fine sand less than 0.5mm diameter and mud). The quantification of debris in stomachs was not attempted since the amount of material involved was low but its occurrence was noted (Table 2.8). It is apparent that gravel in stomachs occurred mostly in mid-winter and especially around spawning time. During the remainder of the year, the ingestion of gravel was much less frequent. In the sample of 126 fish in January 1983, 95 were observed to have stomach contents, of which 40 fish had stomach contents including gravel; of these 4 contained gravel and debris alone. In 38 stomachs with gravel present, the total damp

Table 2.8

Occurrence of non-food material in stomach contents.
Loch Lomond : gravel and debris.

Date	n conts.	n gravel	n debris
821019	31	1	0
821110	29	0	0
821125	5	5	0
821201	17	2	0
830107	95	40	4
830208	43	3	1
830302	24	0	1
830416	33	1	0
830526	11	0	0
830705	30	0	1
830817	31	0	0
830823	20	0	0
830905	30	0	2
831012	42	0	6
831116	42	0	4
831213	24	0	3
840110	30	8	8
840514	25	3	0
840515	32	2	1
850110	9	2	3
850111	8	8	1

n conts = number of fish in sample with material present in stomach

n gravel , n debris = number of fish with gravel or debris respectively in ingested material.

weight of contents was reduced from 14.42g to 8.75g when the total weight of gravel present was removed. Of the stomachs containing gravel, fewer than half contained more than or equal to 50% of their total damp weight of contents as gravel, with an average of 12.1 pieces of gravel found in stomachs where gravel was present. In subsequent January samples, stomachs with gravel present contained an average of 4 to 25 pieces of gravel per stomach. The occurrence of debris in the stomachs follows the same seasonal trend as the occurrence of gravel, with more stomachs in the autumn samples containing debris than gravel.

Most stomach contents from Loch Lomond may be regarded as containing food material alone, but those which contained non-food material (mainly winter samples) were individually corrected to food damp weights. Dry weights of food were then obtained by using the 0.13 and 0.18 conversion factors derived from this study and that of George (1981).

Loch Eck : non-food material in powan stomachs.

Virtually all stomachs collected from Loch Eck fish contained a substantial amount of non-food material along with food items. This was as true of August and September samples as it was of those collected in February and March. The non-food material consisted of mud and fine silt, mixed with fragments of vegetation and debris. The composition by weight of the contents of Loch Eck stomachs in terms of food and non-food material is shown in Table 2.9 which includes the available Lomond data for comparison.

Composition of diet by dry weight of food types - Loch Eck stomachs.

Table 2.9

Stomach contents : gravimetric analysis.
 Percentage composition of stomach contents
 i.e. $\frac{\text{dry weight of food}}{\text{total dry weight of contents.}} \times 100$

sample	n	mean %	95% conf.int.
Loch Lomond			
27 May 83	29	100.0 *	-
5 Sept 83	26	100.0 *	-
16 Nov 83	27	100.0 *	-
10 Jan 84	20	36.3	34.1 - 38.5
Loch Eck			
12 Jan 84	27	27.6	20.9 - 34.9
14 Feb 84	15	29.2	17.5 - 42.5
27 Sep 84	16	22.3	17.2 - 27.8
10 Jan 85	24	34.9	20.3 - 51.2
26 Feb 85	16	24.3	18.4 - 30.8
27 Mar 85	19	14.5	9.4 - 20.6
14 May 85	18	21.6	13.5 - 31.0
4 Aug 85	20	38.4	32.1 - 45.1

Loch Lomond: samples with '*' were effectively 100% food, although some debris was present in a few stomachs from September and November samples.

Analysis of variance - mean % dry weight of food;

Loch Eck $F(\text{calc}) 7,154 = 2.99, 0.001 < p < 0.01$

A Tukey - Kramer test showed the samples (Jan '85, Mar '85) and (Mar '85, Aug '85) to be significantly different from each other.

Table 2.9b

Stomach contents: dry weights of food and non-food material.

sample	n	food (dry weight g)			non-food		
		mean	95% conf. int.		mean	95% conf. int.	
Loch Lomond							
27 May 83	29	0.0340	0.0239 - 0.0441		0.000	* - *	
5 Sept 83	26	0.0637	0.0450 - 0.0825		0.000	* - *	
16 Nov 83	27	0.0189	0.0000 - 0.0392		0.000	* - *	
10 Jan 84	20	0.0530	0.0080 - 0.0995		0.034	0.000 - 0.071	
Loch Eck							
12 Jan 84	27	0.0396	0.0270 - 0.0521		0.114	0.067 - 0.161	
14 Feb 84	15	0.1074	0.0820 - 0.1330		0.330	0.234 - 0.426	
27 Sep 84	16	0.0494	0.0291 - 0.0696		0.169	0.101 - 0.237	
10 Jan 85	24	0.0555	0.0300 - 0.0810		0.184	0.108 - 0.260	
26 Feb 85	16	0.0700	0.0430 - 0.0970		0.217	0.139 - 0.293	
27 Mar 85	19	0.0665	0.0280 - 0.1050		0.323	0.210 - 0.436	
14 May 85	18	0.1020	0.0550 - 0.1490		0.308	0.190 - 0.426	
4 Aug 85	20	0.1740	0.1160 - 0.2320		0.296	0.188 - 0.404	

Loch Lomond: samples with '*' were effectively 100% food material, although some debris was present in a few stomachs from the September and November '83 samples.

Analysis of variance:

Lomond $F(\text{calc}) 3,100 = 2.95$; $0.01 < p < 0.05$

Eck $F(\text{calc}) 7,147 = 7.58$; $p < 0.001$

Throughout the period of sampling Loch Eck powan stomach contents the greater part of the food material was composed of Pisidium and chironomid larvae (Table 2.10, Fig. 2.5). This was the case irrespective of the absolute dry weight of food material present in the stomachs or sample date. In most samples C. anthracinus accounted for over half of the total dry weight of chironomid larvae eaten, but in May '85 C. anthracinus pupae made up half of the mean total dry weight of all chironomids eaten. Pisidium formed a large part (>80%) of the mean total dry weight of food eaten in the August '85 sample, while in the September '84 sample Pisidium made up over half of the mean total dry weight of food. In the remaining Eck samples Pisidium accounted for one quarter to one half of the mean food weight. Cyclops viridis was found to comprise a small fraction of the mean total dry weight of food material in all samples, while the occasional prey species made up an almost negligible contribution to the mean dry weight of food in samples. The relative proportions of the various prey groups in the diet remained constant.

Dry weights of food.

Analysis of covariance was used to compare dry weight of food material in stomach contents by sample, adjusting for common corrected fish weight and common (dry weight food/corrected fish weight) relationship. Results are summarised in Table 2.11. The unadjusted mean dry weights of food in stomachs are shown in Fig. 2.6a and b. In the four data groups examined, preliminary one-way analysis of variance showed significant differences between mean dry weights of food found in the samples (Table 2.11, Analysis i). Mean weights of food from the two lochs differed significantly (Table 2.11, Analysis ii). Analysis of covariance indicated significant heterogeneity of slopes in the food/fish weight relationship between the different

Table 2.10

Analysis of diet : mean composition of L.Eck stomach contents by dry weight (mg).

Date	Jan4	Feb4	Sep4	Jan5	Feb5	Mar5	May5	Aug5
ntot.	27	15	16	24	16	19	18	20
mean dfwt.	39.6	107.4	49.5	55.5	70.0	66.5	102.0	173.9
st. dev.	31.7	46.4	37.9	59.5	51.3	79.4	95.0	124.0
Procladius spp.		19.2 14.7	6.6 5.0	7.4 8.2	8.4 6.1	4.2 3.4	3.2 1.7	19.0 18.5
Chironomus anthracinus		54.4 34.1	14.8 14.4	35.0 37.3	44.4 36.2	38.6 71.4	29.5 14.0	8.8 7.3
chironomid pupae							35.9 49.5	
chironomid (others)	22.2* 18.8	0.7 0.9	0 0	0 0	0.4 0.5	0.8 0.8	1.0 0.8	0.7 0.8
Pisidium spp.	15.9 17.9	26.7 29.6	27.6 27.4	12.3 25.4	16.3 28.2	21.7 33.9	31.6 33.0	143.9 108.0
Cyclops spp.	1.6 2.2	5.6 18.5	0.5 0.9	0.8 1.1	0.6 0.9	1.2 1.7	0.8 1.2	1.5 1.5
Miscell.	0 0	0.7 2.6	0 0	0.4 0.5	0.1 0.4	0.5 1.2	0.4 0.5	0.8 1.4

ntot = number of fish stomachs examined

mean dfwt = mean dry weight of food material (mg)

st. dev. = standard deviation of the mean

* = all chironomids

(Miscell. = Trichoptera, Plecoptera, Hirudinea, Ostracoda)

Fig. 2.5 Mean dry weights of prey groups in the diet of powan in Loch Eck.

Loch Eck: dry weight of prey groups in diet

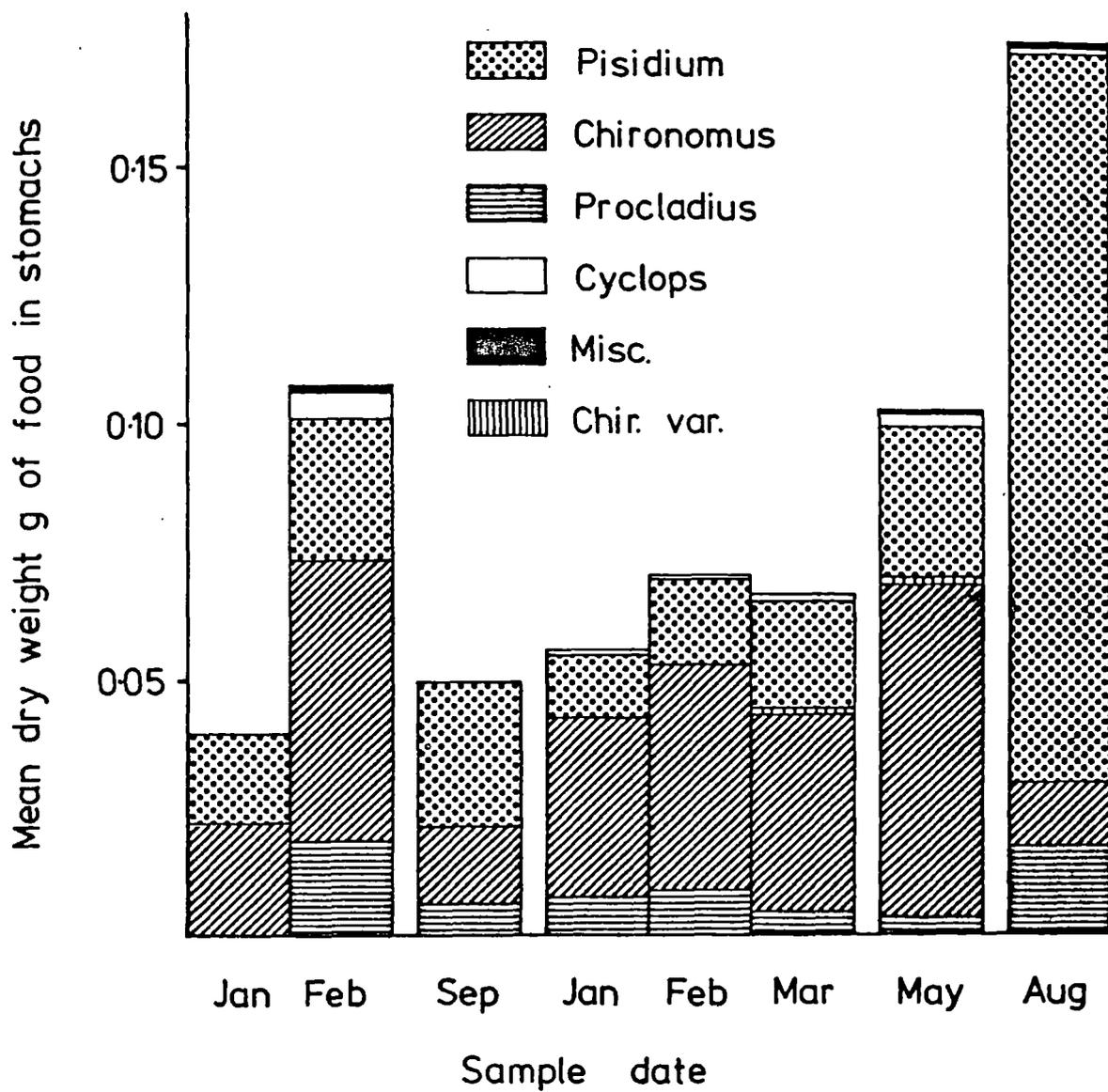


Fig. 2.5

Table 2.11

Analysis of variance and covariance on dry weights of food material for fish corrected total weight by loch, sex and sample date.

Model (1) : $Y = a + b W$

Data groups tested :

28 samples, Lomond & Eck, Lomond estimates of dry/damp weights = 0.13 ... (a)
 28 samples, Lomond & Eck, Lomond estimates of dry/damp weights = 0.18 ... (b)

Model (2) : $\log Y = a + b \log W$

Data groups tested :

28 samples, Lomond & Eck, Lomond estimates of dry/damp weights = 0.13 ... (c)
 28 samples, Lomond & Eck, Lomond estimates of dry/damp weights = 0.18 ... (d)

(i) Anova : one-way, dry weight of food by sample.

		Data group			
		a	b	c	d
Sample	F	22.69	18.85	38.45	42.15
term	p	0	0	0	0

(ii) Anova : one-way, dry weight of food by loch.

		Data group			
		a	b	c	d
Loch	F	123.2	68.9	272.7	228.2
term	p	0	0	0	0

Table 2.11 (cont.)

(iii) Ancova : one-way, dry weight of food by sample with corrected total fish weight.

Ancova		Data group			
		a	b	c	d
Interaction term, tests parallel b's	F p	6.36 0	4.91 0	2.14 0.001	2.15 0.001

(iv) Ancova : two-way, dry weight of food by sample and sex with corrected total fish weight.

Ancova		Data group			
		a	b	c	d
Interaction term, tests parallel b's	F p	0.82 0.82 ns	1.84 0 ***	1.13 0.24 ns	1.95 0 ***
Pooled regression coefficient + 1 S.E.	B	.000309 .00002	-	.8204 .0504	-
regression's sex by sample term	F p	1.61 .004	-	2.19 0	-
intercept a		.004128	-	-3.2424	-

Table 2.11 (cont.)

Groups (a) and (c) subdivided into sexes :

(a) = Model 1 : Y,W

(c) = Model 2 : log Y, log W

(v) Ancova: one-way ancova, dry weight of food by sample with corrected total fish weight for each sex.

		(a)			(c)		
		male	female	other	male	female	other
anova							
Sample	F	19.6	5.04	2.08	26.9	10.73	8.07
	p	0	0	0.003	0	0	0
ancova							
Inter.	F	3.75	2.17	1.09	2.26	1.16	1.24
term	p	0	.001	.37	0	.26	.22
	b' s	***	***	ns	***	ns	ns
regr.	F	(19.4)	(6.88)	2.40	(31.7)	15.1	12.6
sample	p	0	0	0	0	0	0
term		***	***	***	***	***	***
regr.	B	(.0003)	(.0003)	.00066	(.8368)	.7818	.9288
coeff.				.00006		.0794	.1654
+ 1 S.E.							
intercept	a	-	-	-.08726	-	-3.120	-3.409

Table 2.11 (cont.)

Model (1) : Y, W group (a)

(vi) Ancova : one-way ancova, dry weight of food by sample with corrected total fish weight for (loch,sex) sub-groups.

		Lomond			Eck		
		male	female	other	male	female	other
n		264	237	116	266	271	64
Anova	F	6.91	2.16	1.72	21.2	7.34	2.86
	p	0	.009	ns	0	0	.005
Ancova							
Inter.	F	1.99	1.76	2.05	4.89	2.55	0.10
term	p	.018	.044	.024	0	.005	1.0
b's		*	*	*	***	**	ns
regr.	F	(7.17)	(3.59)	(1.82)	(22.3)	(7.04)	2.11
sample	p						.036
term							*
regr.							
coeff.	B	.165	.375	.680	-	-	.570
+ 1 S.E.		.04	.06	.06			.15
(E-3)							
intercept							
a		.0066	.0349	-.0268	-	-	.0031

Model (2) : log Y , log W group (c)

(vii) Ancova : one-way ancova, dry weight of food by sample with corrected total fish weight for (loch,sex) sub-groups.

		Lomond			Eck		
		male	female	other	male	female	other
Anova	F	14.8	6.37	7.72	19.1	6.52	5.05
sample	p	0	0	0	0	0	0
Ancova							
Inter.	F	2.34	.631	1.59	1.17	1.64	.303
term	p	.004	.846	.099	.307	.087	.976
b's		**	ns	ns	ns	ns	ns
regr.	F	16.6	8.90	5.16	22.2	6.12	5.29
sample	p	0	0	0	0	0	0
term		***	***	***	***	***	***
regr.							
coeff.	B	.9943	1.1195	.8864	.7793	.6777	1.073
+ 1 S.E.		.1680	.1975	.2213	.0639	.0728	.1948
intercept							
a		-3.9680	-4.1506	-3.4492	-2.9490	-2.7046	-3.4736

Fig. 2.6a Mean dry weights of food in powan stomachs :

Loch Lomond -

s1,s2 = seine and south samples May '84.

solid line, circles = 0.13 conversion estimate
of wet weights ,

broken line, squares = 0.18 conversion estimate
of wet weights.

Loch Eck -

a = catch from net across width of loch (deep)

p = catch from net parallel to shore (shallow).

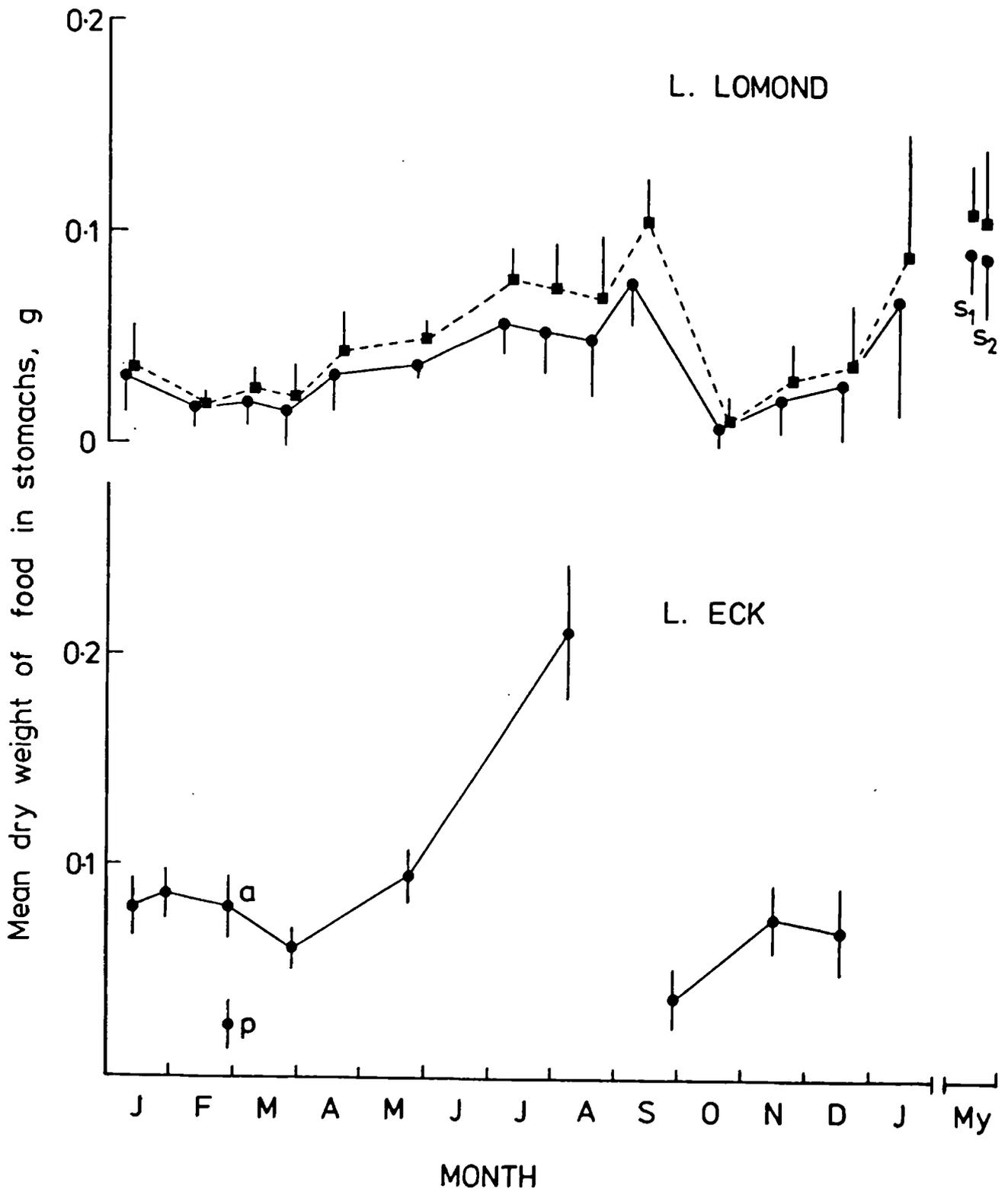


Fig. 2.6a

Fig. 2.6b Mean dry weights of material in powan stomachs
(including debris material) :

Loch Lomond -
sn, st = seine and south samples May '84.

Loch Eck -
a = catch from net across width of loch (deep)
p = catch from net parallel to shore (shallow).

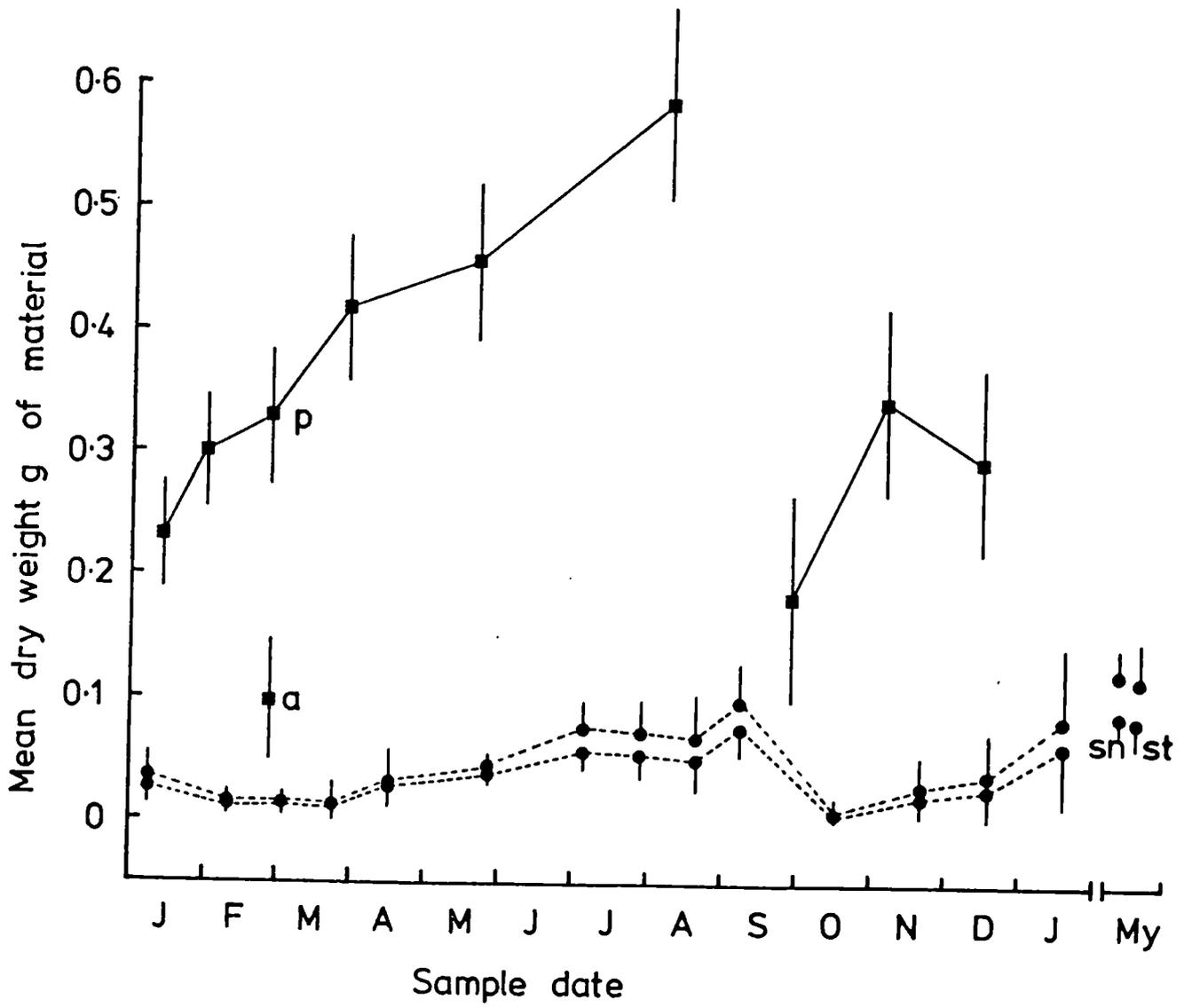


Fig. 2.6b

samples in each of the four data groups (Table 2.11, Analysis iii). However, two-way analysis of covariance between mean dry weights of food in groups of fish classified by sex and sample date and adjusted for common fish weight showed the assumption of parallel slopes to be unjustified in each of data groups (b) and (d) containing the 0.18 estimates of Lomond weights (Table 2.11, Analysis iv).

The two data groups (a) and (c) were then analysed separately for the three sex categories. (Table 2.11, Analysis v)

All sexes showed significant differences in food weights across samples. Analysis of covariance for males and females indicated significantly different separate slopes from the pooled regression coefficient in the raw data group (a), but parallel slopes were indicated for the third sex (immatures and others). Males in group (c), the log₁₀ transformed data, also had significantly different separate slopes from the pooled regression. Significant heterogeneity of mean dry weights of food over sample dates was indicated for each of the different sexes when adjusted for common fish weight.

Groups (a) and (c) were classified by loch and sex, (Table 2.11, Analyses vi, vii) Preliminary oneway analysis of variance showed that sample date had a significant effect on the mean dry weights of food observed for each sex in the two lochs, with the exception of the Loch Lomond "others" in group (a). Analysis of covariance suggested that parallel slopes could not be assumed for any of the sex categories in group (a) except the third sex from Loch Eck. When the logged data (group c) were similarly analysed, all sexes except Loch Lomond males were found to have parallel slopes. Significant differences in mean dry weights of food were indicated over sample dates for Loch Lomond females and others and for each of the Loch Eck sexes.

The above analyses indicated sample date as a major influence on the

dry weight of food found in powan stomachs but in the analyses performed no attempt was made to include water temperature variation. The effect of temperature was included in the next analysis of food weight. Data fitted to the two models are summarised in Table 2.12a,b. The 'goodness of fit' of models was assessed by two criteria, the value of the coefficient of multiple determination, R-squared, and by examining residuals in the models. On the basis of the first criterion, the simple linear model (3) is a better fit to the whole data set, and to most of the sub-groupings except for Lomond males and Eck others, where the log model (4) provided a better fit. The largest proportion of the variance in the data explained by the regressions was for Lomond others (Model (3) ; $R^2 = 0.589$) and Eck males (Model (4) ; $R^2 = 0.526$). Inclusion of the temperature term in the regression equation did not always increase the proportion of the variance explained by the regression. Table 2.12 indicates instances where the temperature factor made a non-significant contribution to the regression. The 'other' groups contained the dummy cells referred to earlier and therefore cannot be compared directly to the other groups. In general, the proportion of the variance in the data explained by the regression increased as the data is differentiated by sex and loch. The log model showed least systematic deviation in its residual plots compared to the residuals for Model 3. In fact since the error associated with the two variables is likely to be different the multiple regression may not necessarily indicate the true relationship between the variables under consideration.

2.3.4 Maximum weights of stomach contents.

Maximum weights from predictive equations :

Table 2.12a

Least-squares analysis of fit of two models of the relationship between dry weight of food in stomachs (Y), body weight (W) and temperature (T). Y in mg, W in g, T in °C.

Model 3 : $Y = a + b_1 W + b_2 T$

Data group	Intercept a ± 1 S.E.	Partial regression coefficient b1 ± 1 S.E.	Partial regression coefficient b2 ± 1 S.E.	Coefficient of multiple determination R ²
all	-0.0108	0.000320	0.00159	0.263
fish	0.0054	0.000016	0.00052	
mal	-0.0519 0.0091	0.000371 0.000027	0.00464 0.00083	0.340
fem	0.0244 0.0091	0.000263 0.000029	-0.00131 0.00088	0.144
oth	-0.0185 0.0071	0.000631 0.000053	0.00015 0.00058	0.457 *
Lm	-0.0258 0.0126	0.000154 0.000041	0.00374 0.00099	0.126
Lf	-0.0245 0.0198	0.000277 0.000058	0.00143 0.00142	0.106 *
Lo	-0.0471 0.0101	0.000672 0.000056	0.00221 0.00080	0.589
Em	-0.0541 0.0102	0.000347 0.000030	0.00949 0.00106	0.526
Ef	0.0083 0.0103	0.000286 0.000031	0.00336 0.00137	0.268
Eo	-0.0030 0.0124	0.000628 0.000126	-0.00067 0.00099	0.295 *

mal = all males fem = all females oth = all others

Lm, Lf, Lo = Lomond (males, females, others)

Em, Ef, Eo = Eck (males, females, others)

* indicates a non-significant contribution to the regression by the temperature variable.

Table 2.12b

Least-squares analysis of fit of two models of the relationship between dry weight of food in stomachs (Y), body weight (W) and temperature (T). Y in mg, W in g, T in °C.

Model 4 : $\log Y = a + b_1 \log W + b_2 \log T$

Data group	Intercept a ± 1 S.E.	Partial regression coefficient b1 ± 1 S.E.	Partial regression coefficient b2 ± 1 S.E.	Coefficient of multiple determination R ²
all	-2.9868	0.7603	-0.1402	0.156
fish	0.1291	0.0523	0.0712	
mal	-3.6886 0.2576	0.9488 0.1903	0.1143 0.1190	0.105 *
fem	-2.1496 0.2196	0.5083 0.0397	-0.4155 0.1054	0.076
oth	-4.1619 0.3605	1.3207 0.1696	0.0221 0.1597	0.263 *
Lm	-4.8623 0.5322	0.9147 0.2200	1.1436 0.2275	0.174
Lf	-3.3089 0.5630	0.5625 0.2226	0.5024 0.2118	0.055
Lo	-5.6548 0.4753	1.5499 0.1984	1.0105 0.2525	0.391
Em	-3.3287 0.1847	0.8033 0.0798	0.3931 0.0949	0.363
Ef	-2.7767 0.1809	0.7071 0.0730	0.0080 0.1148	0.245 *
Eo	-3.4349 0.3658	1.0606 0.1851	-0.0200 0.1379	0.474 *

mal = all males fem = all females oth = all others

Lm, Lf, Lo = Lomond (males, females, others)

Em, Ef, Eo = Eck (males, females, others)

* indicates a non-significant contribution to the regression by the temperature variable.

Fig. 2.7 Multiple regression of untransformed mean dry weights of food, corrected total fish weights and temperature : residuals from the model plotted against predicted values ;

- (i) all males
- (ii) all females
- (iii) log transformed data, all males
- (iv) log transformed data, all females.

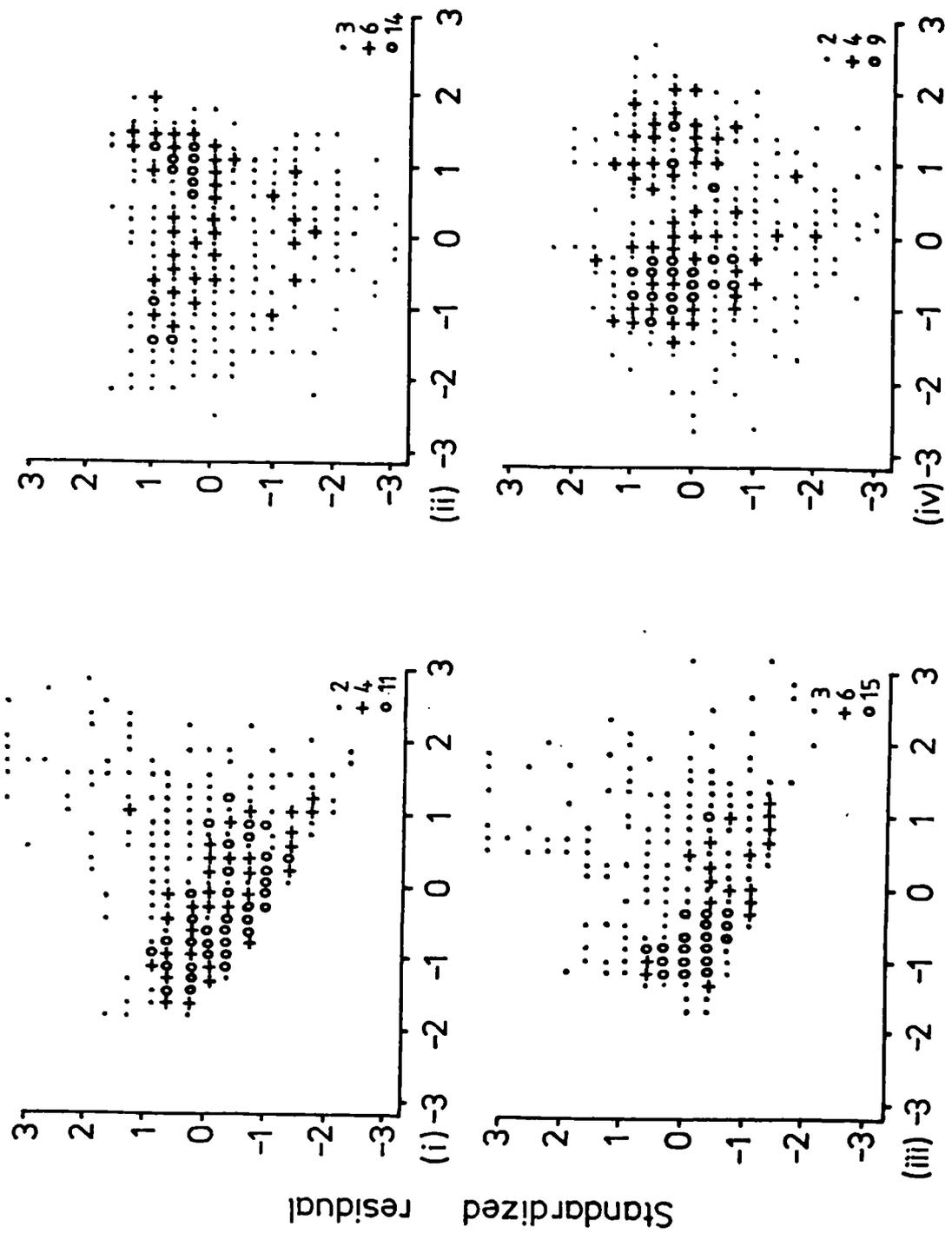


Fig. 2.7

Fig. 2.8 Multiple regression of log transformed maximum dry weights of food, corrected total fish weights and temperature : residuals from the model plotted against predicted values ;
(i) Loch Lomond maxima
(ii) Loch Eck maxima
(iii) combined maxima.

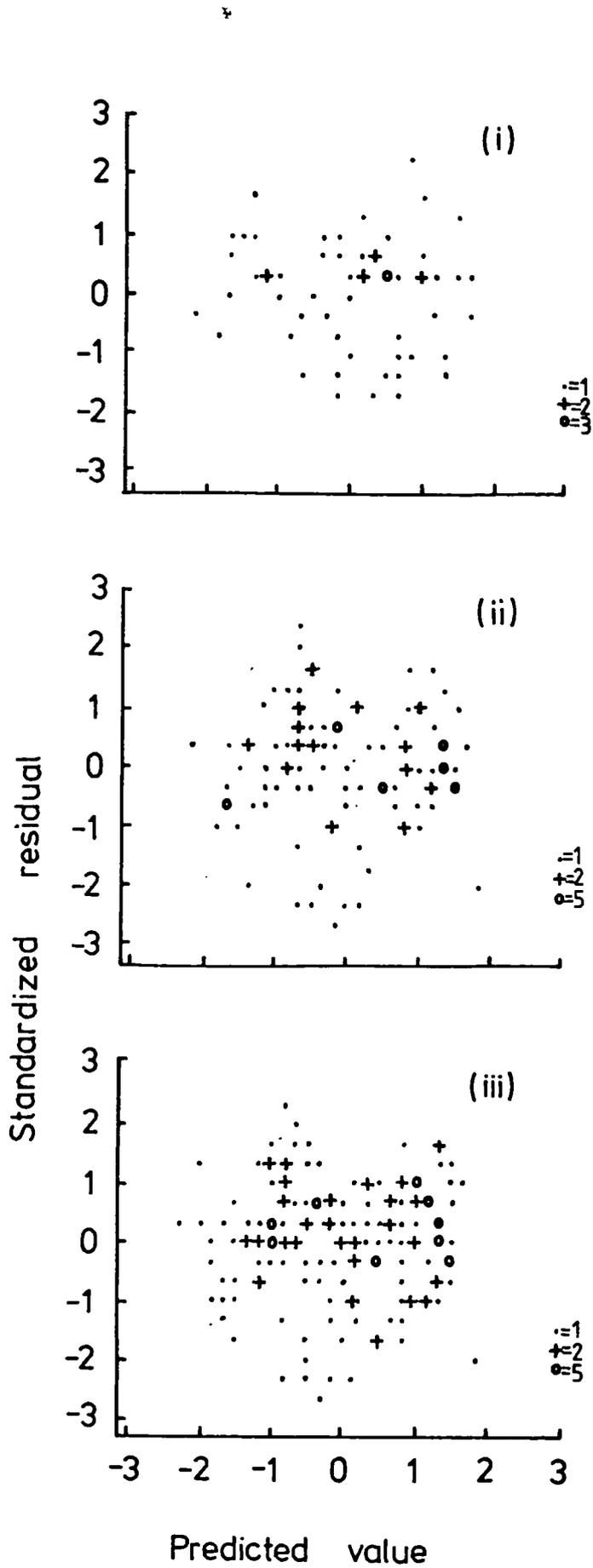


Fig. 2.8

The geometric mean (GM) regression coefficients for the (log damp weight stomach contents/log corrected total fish weight) relation lie in the range 0.67 - 2.01, excluding confidence limits. The regression coefficients were tested against the null hypothesis (H_0) that they should equal unity : ($H_0: V_{y.x} = 1$), ie the weight of stomach contents would be the same fraction of body weight in different sized fish. No significant differences were found between the estimated GM regression coefficients and unity in 10 of the 14 cases analysed (Table 2.13a). Significant differences were found for the following cases:

Sample	$V_{y.x}$	t(calc)	t(d.o.f.)	prob.
Lomond May 83	0.6745	4.21	2.36	0.01 > p > 0.001
Lomond females	2.0110	8.17	2.31	p < 0.001
Eck March 85	1.2104	2.49	1.98	0.05 > p > 0.01
Eck August 85	1.4646	4.51	2.20	0.01 > p > 0.001

In addition, particular pairs of regression coefficients were compared to each other using an F-test. The summary of the treatment on the regression statistics from several samples is shown below.

Samples compared	F_s	$F_{0.05}$	p	$ V_{y.x} $
	(1, n_1+n_2-4)			
Seine, south1 May 84	1.124	4.49	ns	$s_1 < s_2$
Seine, south2 May 84	0.003	4.49	ns	$s_1 \sim s_2$
Males, females Lom.	22.86	4.67	**	$m << f$
Males, females Eck.	2.70	4.67	ns	$m < f$
Males L., males E.	0.11	4.75	ns	$m_L < m_E$
Females L., females E.	11.64	4.60	**	$f_L > f_E$

(s_1, s_2 = highest and lowest values respectively for south May 84)

Regression coefficients for all pairs of compared samples except for

Table 2.13a

Geometric mean regression statistics calculated for the highest observed damp unadjusted weights of stomach contents against corrected total fish weight, using;

$$\log Y (\text{wt. conts.}) = \log av + V_{y.x} \log W (\text{corrected tot. fish wt.})$$

sample	n	$V_{y.x}$	95% C. I.	log av	r^2	p-value
L. Lomond						
May 83	9	0.674	0.492 - 0.857	-1.768	0.901	0.01 > p > 0.001
Jul 83	8	1.278	0.829 - 1.728	-2.975	0.856	p > 0.05 n. s.
Sep 83	7	0.961	0.665 - 1.257	-2.090	0.914	p > 0.05 n. s.
May 84 sn	10	0.940	0.657 - 1.223	-2.208	0.852	p > 0.05 n. s.
May 84 s1	10	1.230	0.937 - 1.522	-2.763	0.904	p > 0.05 n. s.
May 84 s2	10	0.942	0.741 - 1.144	-2.632	0.922	p > 0.05 n. s.
all (M)	7	0.920	0.475 - 1.366	-1.907	0.837	p > 0.05 n. s.
all (F)	10	2.011	1.726 - 2.296	-4.653	0.966	0.001 > p
L. Eck						
Jan 84	8	0.887	0.768 - 1.006	-1.853	0.978	p > 0.05 n. s.
Mar 85	93	1.210	1.043 - 1.377	-2.663	0.553	0.05 > p > 0.01
May 85	10	0.925	0.652 - 1.198	-1.694	0.852	p > 0.05 n. s.
Aug 85	13	1.465	1.235 - 1.694	-3.176	0.941	0.01 > p > 0.001
all (M)	9	1.062	0.861 - 1.262	-1.980	0.949	p > 0.05 n. s.
all (F)	8	1.361	0.990 - 1.731	-2.655	0.914	p > 0.05 n. s.

sn = seine net sample, 2200 14 May 84 Salloch L. Lomond.

s1 = highest values south sample, 1030 15 May L. Lomond.

s2 = lowest values south sample, 1030 15 May L. Lomond.

(Geometric mean regression confidence limits calculated using sb of the linear regression of Y on X as an estimate of sv. P-value estimated by t-test of null hypothesis that $V_{y.x} = 1$ according to :

$$t(\text{calc}) = (V_{y.x} - 1 / sv)$$

with (n-2) degrees of freedom.

r^2 is the coefficient of determination.)

Table 2.13b

Comparison of regression coefficients : geometric mean and linear regressions of maximum stomach contents damp weights against corrected fish weight. $V_{y.x}$ and b = respective regression coefficients, s_v estimated by s_b = the standard error of b , r^2 = coefficient of determination.

Fish sample	n	GM regr.		Linear regr.	r^2
		$V_{y.x}$	s_v/s_b	b	
L. Lomond					
May 83	9	0.6745	0.0773	0.6410	0.901
Jul 83	8	1.2783	0.1836	1.1967	0.856
Sep 83	7	0.9613	0.1152	0.9261	0.914
May 84 sn	10	0.9401	0.1228	0.8935	0.852
May 84 s1	10	1.2300	0.1268	1.1767	0.904
May 84 s2	10	0.9424	0.0876	0.9093	0.922
all (M)	7	0.9202	0.1732	0.9798	0.837
all (F)	10	2.0110	0.1238	1.9790	0.966
L. Eck					
Jan 84	8	0.8870	0.0488	0.8788	0.978
Mar 85	93	1.2104	0.0670	0.9038	0.554
May 85	10	0.9249	0.1184	0.8622	0.852
Aug 85	13	1.4646	0.0508	1.4236	0.941
all (M)	9	1.0616	0.0847	1.0376	0.949
all (F)	8	1.3606	0.1514	1.3091	0.914

sn = seine net sample, at 2200 14 May.

s1 = highest values south sample, 1030 15 May.

s2 = lowest values south sample, 1030 15 May.

the pairs (Lomond males : females), and (Lomond females: Eck females) were not significantly different at the 0.05 level. Virtually no post-catch digestion of food can have occurred in the seine-netted sample, while the southern sample was from an overnight setting of gill nets. However, it can be seen from the above that the seine net sample food weight maxima produced regression statistics which were almost identical to those of the lowest values for the south sample. It should be noted that all these stomachs contained considerable amounts of food. The regression coefficients obtained for the two sexes for Lomond fish are very significantly different, as are the coefficients for females from the two lochs. Predicted maximum stomach contents weights derived from these equations without taking into account error measures are shown below (Table 2.14). Although the exponent in the Lomond females equation is 2.01 (compared to 0.92 for males) the magnitude of the GM regressions' intercepts a_v , are such that over all but the largest size range of fish, females appear to have smaller maximum damp weights of stomach contents per unit body weight than males.

If the GM regression statistics are used to draw up a table of maximum stomach contents weights over the range of fish sizes sampled, it can be seen that the southern basin fish in May '84 have consistently higher contents weights than the seine sample, despite the seine netted fish being slightly heavier on average than the south basin fish.

The regression equations for powan from Loch Eck suggest a similar increase in damp food weight with increasing body weight to that observed for Lomond fish, but maximum weights of stomach contents are much greater over all fish weights for fish in Loch Eck (Table 2.14). Males in Loch Lomond have greater maxima than females up to

Table 2.14

Maximum (damp) weight of stomach contents calculated from GM regression equations of Table 2.13.

Sample	Corrected total fish weight					
	100g	150g	200g	250g	300g	350g
May seine '84	0.47	0.68	0.90	1.11	1.32	1.53
May south '84	0.50	0.82	1.17	1.54	1.92	2.32
Lomond males	0.83	1.21	1.57	1.93	2.28	2.63
Lomond females	0.23	0.52	0.93	1.45	2.10	2.86
Eck males	1.33	2.05	2.78	3.52	4.27	5.03
Eck females	1.16	2.01	2.98	4.04	5.17	6.38

the 350g size range while in Loch Eck females have a greater maximum than males from the size range 150-200g.

Maximum dry weights of food in stomachs.

The regression statistics obtained by estimation of maximum dry weights of food for fish weights are shown below (Table 2.15). For many of the samples from Loch Lomond exponents of the dry weight of food/corrected fish weight relationship are the same as those for damp weight relations. The Eck samples' exponents were generally within the 95% confidence limits of the damp weight exponents.

For the Loch Lomond samples, there were no significant differences in the mean maximum dry weights of food in stomachs over the sample dates. The slopes of the separate regressions were not parallel.

There were significant differences between the mean maximum dry weights of food calculated for Loch Eck samples, but since the slopes of the separate regressions were not parallel, it was not possible to tell if the differences were associated with fish total weight differences.

The relationship between maximum dry weight of food and fish weight was approximately linear over the range of fish examined.

The proportion of fish in Lomond samples with full or nearly full stomachs was minimal in winter. Spring and summer samples showed maximal fullness (Table 2.16). The samples of May '84 showed the largest proportions of the catch with stomach contents close to the estimated maximum contents weights (80% of fish in the seine sample with more than half the estimated maximum weight of food). This still represents considerable asynchrony of feeding. Loch Eck fish were estimated to have the greatest proportion of the catch with full or

Table 2.15

Estimation of maximum dry weights of food from observed sample maxima calculated as least-squares regressions of:

$$\log \text{ dry weight of food } y' = a + b \log W$$

Loch Lomond				
	a	b	r ²	n
Jan	-3.4435	0.9093	0.931	10
May	-2.5838	0.6410	0.903	9
Jul	-3.6853	1.1967	0.876	8
Sep	-2.9026	0.9261	0.928	7
May sn	-2.9885	0.8944	0.905	9
May so	-3.5328	1.1767	0.915	10
Loch Eck				
	a	b	r ²	n
Jan 84	-2.9518	0.8618	0.981	8
Feb 84	-2.3408	0.6717	0.871	8
Sep 84	-2.9300	0.7342	0.871	9
Nov 84	-3.1877	0.9040	0.950	9
Dec 84	-3.2504	0.9321	0.882	9
Jan 85a	-3.3276	1.0973	0.849	8
Jan 85b	-1.5223	0.3580	0.526	10
Feb 85a	-2.3093	0.5939	0.671	11
Feb 85b	-4.0239	1.1107	0.883	8
Mar 85	-3.8108	1.2081	0.843	10
May 85	-3.6812	1.2188	0.896	10
Aug 85	-3.4655	1.1469	0.961	9

Table 2.16

Stomach fullness estimates, based on maximum dry weights of food observed in samples.

	stomach fullness level				ntot.
	100-75%	75-50%	50-25%	25-0%	
	n (%)	n (%)	n (%)	n (%)	
L. Lomond					
Jan 83	5 (5.7)	1 (1.1)	10 (11.4)	72 (81.8)	88
Mar	3 (11.1)	1 (3.7)	6 (22.2)	17 (73.0)	27
May	17 (19.8)	10 (11.6)	40 (46.5)	19 (22.1)	83
Jul	17 (29.8)	5 (8.8)	24 (42.1)	11 (19.3)	57
Sep	4 (10.5)	2 (5.3)	16 (42.1)	16 (42.1)	38
Nov	7 (24.1)	0 (0)	2 (6.9)	20 (69.0)	29
May 84 sn	13 (52.0)	7 (28.0)	5 (20.0)	0 (0)	25
May 84 st	12 (33.3)	10 (27.8)	12 (33.3)	2 (5.6)	36
L. Eck					
Jan 85	9 (14.3)	7 (11.1)	25 (39.7)	22 (34.9)	63
Feb	10 (18.5)	12 (23.8)	27 (48.4)	5 (9.3)	54
Mar	13 (13.8)	18 (19.2)	50 (53.2)	13 (13.8)	94
May	31 (32.6)	27 (28.5)	30 (31.5)	7 (7.4)	95
Aug	27 (40.9)	23 (34.9)	15 (22.7)	1 (1.5)	66
Sep	11 (50.0)	4 (18.2)	3 (13.6)	4 (18.2)	22
Nov	13 (59.1)	5 (22.9)	3 (13.7)	1 (4.5)	21

nearly full stomachs in the late summer-early autumn, with least in winter. The maximum dry weight regressions obtained above were fitted to a multiple regression incorporating a term for the effects of water temperature ;

$$\log y = a + b_1 \log W + b_2 \log T$$

The regression statistics obtained from this model are shown in Table 2.17, along with estimates of the maximum dry weights of food predicted for fish in the size range 100-350g.

A comparison of dry weights of food found in the stomachs of the different sexes in each sample was made relative to fish weight. While this method is not ideal because of allometric considerations the comparisons are possible (see Figs. 2.4a,b for approximate relative differences).

In Loch Lomond samples, feeding females in January and February had a proportionately higher amount of food in their stomachs than males. This was also true of April, October and December samples. Males had proportionately more food than females in August. In Loch Eck samples, females had proportionately less food than males in the March, May, August and November samples, with the other samples showing little difference. For both lochs the third sex category (mostly composed of immature fish) contained proportionately more food than the adults, except in early spring. The seasonal trend for all sex categories was for minimal contents in late winter/early spring and maximal contents in summer, although the immature group also displayed high levels of stomach contents in December and January samples from both lochs. Powan in Loch Eck consistently had more food in their stomachs than powan in Loch Lomond. The only occasion on which powan from Loch Lomond had proportionately more food in their stomachs was the September samples (Table 2.9b).

Table 2.17

Multiple regression equations derived for maximum dry weights of food in powan stomachs, based on :

$$\log y = a + b_1 \log W + b_2 \log T$$

and maximum food weight equations.

	logten	partial		coefficient of multiple determination R-squared
	intercept a	regression coefficients b1	b2	
Lomond samples	-4.2625 0.3807	1.0907 0.1127	0.7959 0.2604	0.626
Eck samples	-2.9170 0.1942	0.9185 0.0792	-0.2210 0.1184	0.563
Lomond & Eck samples	-3.0848 0.1687	0.9468 0.0662	-0.0976 0.1007	0.553

Maximum dry weights of food for fish weights and samples, estimated as above.

	Corrected total fish weight					
	50g	100g	150g	200g	250g	300g
L. Lomond						
Mar 5 °C	0.014	0.030	0.046	0.064	0.081	0.099
May 8 °C	0.020	0.043	0.067	0.092	0.118	0.144
Jul 14 °C	0.029	0.063	0.097	0.133	0.170	0.208
L. Eck						
Mar 4 °C	0.032	0.061	0.089	0.116	0.142	0.168
May 8 °C	0.028	0.053	0.076	0.099	0.122	0.144
Aug 14 °C	0.024	0.046	0.067	0.088	0.108	0.127

SUMMARY

The seasonal variation in powan diet in Lochs Lomond and Eck can be summarised as follows.

In winter samples in Loch Lomond, a small proportion of powan fed at any one time although around spawning time in early January most fish were feeding. The winter diet of powan in Loch Lomond consisted of some planktonic organisms (Diaptomus, Daphnia and Bosmina) but mainly benthic prey such as Pisidium, Cyclops and a variety of insect larvae of which Chaoborus was most numerous. Some non-food material was found in the stomachs at this time. At spawning time the eggs of their own species were taken, sometimes in large numbers. The proportion of feeding fish in the catch rose substantially after April and remained high till early autumn.

The diet of powan in Loch Lomond during late spring - autumn relied heavily on the zooplankton populations of the loch. Over this time, the diet consisted almost entirely of Cladocera, although some insect larva and pupae were also taken. In terms of number, the two common cladocerans, Bosmina and Daphnia were the most important prey organisms for powan over these months. The extent to which Bosmina was found in the diet appeared to be inversely related to the abundance of Daphnia in the diet, and vice versa. Although of small individual size, (rarely exceeding 1.0mm in body length) the vast numbers of Bosmina consumed from May to August provided a substantial part of powan intake during the period. The majority of fish had Bosmina as the most numerous item in the diet, but a characteristic of all powan catches during the plankton feeding phase was the presence of some individual fish with atypical prey species in the stomach contents or with the same prey species but in opposite proportions to

those observed in the other fish. The larger cladocerans, Daphnia and Bythotrephes, along with Leptodora and Holopedium began to appear in the diet in spring, but formed the greater part of the diet in the summer and autumn months. Fewer fish were observed with food in stomachs from October onwards, with the diet at this time increasingly consisting of Chaoborus and Cyclops, with Daphnia making up a significant portion of the food.

Individual variation in prey categories found in stomachs within samples was found to differ seasonally, and to a certain extent by sex. The diets of individual immature fish differed less amongst themselves than those of either adult sex.

The weight of food found in powan stomachs in Loch Lomond was minimal in winter samples and reached maximal values in May and September and was thus generally correlated with water temperature.

In Loch Eck the majority of fish were feeding throughout the year, with most empty stomachs recorded around spawning time. In addition to recognisable food, powan in Loch Eck ingested mud and vegetation from the loch floor in a dry weight ratio to food of 3:1. The food items in the stomachs were almost exclusively chironomid larvae, Pisidium and cyclopoid copepods. The seasonal composition of the food differed mainly in the absolute amounts each prey group and in instars of larvae present. Zooplankton was recorded in the diet of Loch Eck powan on one occasion and involved a single prey. The dry weight of food in Loch Eck stomachs was significantly higher than that observed for Loch Lomond fish, particularly after spawning in late winter and also in early spring.

DISCUSSION.

The results of this study of the food of powan in Loch Lomond agree broadly with previous accounts of powan diet. Parnell's (1838) description of the contents of two Loch Lomond powan stomachs "several species of entomostraca, larva of insects, a few coleoptera, a number of small tough red worms little more than half an inch in length and about the thickness of a coarse thread besides a quantity of gravel ..." and "filled with ... entomostracous animals, presenting in the mass a granular appearance and a reddish colour" is wholly within the bounds of the present description of powan diet in factual content and far surpasses it in elegance of expression. Brown (1891) added "weeds" to the diet of bottom feeding fish. Malloch (1910) and Lamond (1931) included notes on the diet of powan in Loch Lomond, but the most extensive to date was that of Slack *et al.*, (1957). Over 700 fish were examined in the early 1950s, mainly from the southern basin of the loch. Estimations of relative stomach content volumes indicated Daphnia and Bosmina as the most important summer foods, with Cyclops, Bythotrephes and other littoral prey organisms also taken, as well as some adult insects from the water surface. Crustacea were estimated to account for 77% and Cladocera 59% of the total volume of food eaten by powan in summer. The winter diet included more benthos than plankton, with Eurycerus, Asellus and chironomids eaten. Spawn was an important constituent of the winter diet with up to 500 eggs found in a single stomach. These results indicate little qualitative difference to those of the present study. The absence of plankton from the food of Loch Eck powan at any time of year has been substantiated by subsequent samples (E.A.R. Brown, pers. comm.). This makes the account of the diet of a sample of Loch Eck powan in Slack *et al.*, (1957) difficult to explain. In addition, a sample of

several powan netted in Loch Eck in September 1978 by D.A.F.S. personnel had included zooplankton amongst their food (R. Greer, pers. comm.). Four possibilities suggest themselves; (i) the diet of Loch Eck powan has changed considerably in the past 30 years (ii) the sample obtained by Slack *et al.* was not representative of the population as a whole (17 fish in total were examined) (iii) the sample did not come from Loch Eck (iv) some coregonines in Loch Eck feed on plankton as available, becoming spatially segregated from the benthos-feeding population and escape sampling by gill nets. Since the examined fish were of a similar size to adult Loch Lomond fish, it is not possible that these were very young fish. It must be emphasised that of the hundreds of Loch Eck powan examined in this study, only one fish was found with zooplankton in its stomach, amongst the usual debris/chironomid/Pisidium association. Determination of the occurrence of planktonic feeding amongst Loch Eck powan would necessitate extensive sampling in summer.

The powan's closest taxonomic relatives in Britain are schelly and gywniad, both of which like powan live in relatively deep glacial lakes of characteristically low nutrient status. In Haweswater, schelly fed on entomostracous animals of the weed beds as well as some bottom fauna (Swynnerton & Worthington, 1940). Gwyniad in Llyn Tegid were described by Haram & Jones (1971) as opportunistic feeders, taking a mixture of zooplankton (mostly Cladocera) and benthos in summer. Dunn (1954) had described different diets for size-classes of gwyniad, but this account was based on a total of eight fish taken by two different gears and cannot be considered as representative.

Svardson (1979) has suggested that the diet preferences of populations of whitefish species have a considerable hereditary component. In different environments the feeding habits of the same species may vary depending on the habitat and prey species composition. Sympatric whitefish species often display morphological and behavioural feeding specialisations (Nilsson & Pejler, 1973; Bergstrand, 1983). A complication arises immediately in that coregonines are notorious for their facility for introgression and hybridization (Ferguson *et al.*, 1978; Svardson, 1957, 1979). The difficulty of distinguishing species, semi-species and hybrids is then added to the need for accurate description of habitat and conspecific relationships. Perhaps the most valuable diet descriptions are those from studies carried out before and after fish introductions (Berg & Grimaldi, 1966; Giussani & de Bernardi, 1977; Nilsson & Pejler, 1973). In Lago Maggiore the diets of introduced coregonines were compared to that of an endemic planktivore Alosa fallax. The coregonines showed virtually no differences in diets, but one coregonine was found to replace the other in the lake as a result of differing life history characteristics. This interaction did not affect the resident planktivore (Berg & Grimaldi, 1966; Giussani & de Bernardi, 1977). Where agreement exists over the identity of the coregonine species in a number of lakes, valuable dietary comparisons may be obtained (Kamler *et al.*, 1980). Populations of C. albula in Poland, Finland and Sweden show a very similar diet pattern. Pokrovskii (1960) described Karelian populations of C. albula as feeding mainly on zooplankton. This was confirmed by Viljanen (1983) for Finnish C. albula, whose most important foods were Daphnia, Bosmina and copepods. Hamrin (1983) recorded Bosmina, Holopedium and Daphnia as the most important food of C. albula during summer in forest lakes. Nilsson & Pejler (1973) noted the importance of Bosmina to C. albula, as did

Kamler et al., (1982). In the Baltic Sea, C. albula's summer diet consisted mainly of Bosmina and calanoid copepods (Enderlein, 1981b). Of the British and Irish coregonines, the pollan and vendace are most closely related to the northern European C. albula. The older references to pollan food refer to Mysis relicta as an important prey (e.g. Regan, 1911) but later accounts include chironomid pupae, Asellus, molluscs and crustaceans (Dakin & Latarche, 1913), Daphnia (Southern & Gardiner, 1926); while chironomids, Gammarus and Mysis were given by Gaffikin (1939). Crangon were said to be taken by estuarine pollan (Twomey, 1956). The more recent work of Wilson (1984) found Daphnia to be the most important summer food of adult pollan in Lough Neagh while from October to March chironomid larvae (and later pupae) were the principal food. Immature fish included other zooplankton species amongst their food. Only the fry of pollan fed on Cyclops.

Vendace (C. albula) of Lochmaben were found to eat mainly Cladocera Copepoda and Chaoborus larvae during the summer, feeding at the water surface at dusk (Maitland, 1966a, 1967b).

In North America, the ciscoes C. hoyi and C. artedii have been described as mid-water or surface feeders, taking a variety of planktonic crustaceans (Hoagman, 1973; Engel, 1976; Janssen, 1978) although Janssen (1978) described their ability to feed on benthic food. Cladocera were the most abundant prey in the diet of ciscoes over much of the year.

Russian studies have noted a variety of diet types for coregonines. Pizhyan (C. lavaretus pidschian) fed intensively on small perch from autumn to early spring contrasting to their summer diet of chironomid larvae and pupae (Kirillov, 1982). The ludoga whitefish (C. lavaretus ludoga) fed in the littoral zone in spring and summer on

amphipods and Diaptomus with some Pisidium, Hirudinea and chironomids also taken (Pivazyan, 1972). The seasonal importance of these prey changed as Diaptomus was heavily preyed upon in June, followed by Daphnia in the prespawning period as its abundance in the lake increased. Some benthic food was taken. At spawning time ludoga ate their own eggs.

In a eutrophic Norwegian lake C. lavaretus fed on Daphnia and other large Cladocera as they were available. No copepods were eaten. Fish continued to feed on the same prey species well after their maximum abundances (Jacobson, 1974).

Further aspects of the selectivity of powan for zooplankton prey are considered in Chapter 3.

A study of fish feeding which employs gill netting as its main capture method is prone to several weaknesses; (i) uncertainty of capture time and thus feeding chronology, (ii) possible post-catch digestion whilst in the net, (iii) fixed sampling station, (iv) selectivity of the gear.

Problems associated with (i) and (ii) are considered further in Chapter 4, but the main justification of the capture method may be summarised by its predictable success and the lack of a viable alternative technique. Although this results in lack of information on the younger part of the population (iv), practical considerations made extension of the investigation impossible.

CHAPTER 3. Selective predation of zooplankton by poman in Loch Lomond.

INTRODUCTION

Polyphagous animals are rarely indiscriminate predators. Selective predation occurs when a choice is exercised, given a number of equally available items. Therefore, if the relative frequencies of prey types in a predator's diet differ from the relative frequencies in the environment, preferential feeding can be said to have occurred. Some microcarnivorous fish display preferences for large invertebrate prey (Brooks, 1968; Werner & Hall, 1974; Giussani & De Bernardi, 1977) although the proposed mechanisms to explain this phenomenon have considered different aspects of the predator - prey interaction. Particular attention was directed to examining the "profitability" to the predator of prey size selection, which assumes a rapid increase in profit (= energy gain per unit time) for larger prey (Werner & Hall, 1974; Gardner, 1981). However, detectability of prey also increases with prey body size (Werner & Hall, 1974; Confer *et al.*, 1978; O'Brien, 1979; Hairston *et al.*, 1982). Active selection of the most profitable prey may be confused with the results of simply eating the most frequently detected prey. Fish were classified by Zaret (1980) as "gape-limited predators" because of the brief period at the beginning of their life-history when the largest prey items in the environment may be too large for the youngest fish to eat. Werner & Hall (1974) found that by the time bluegills reached a size of 50mm they could easily cope with the entire range of benthic insect food available.

Many previous laboratory studies on the selectivity of fish feeding have used Lepomis species as predators. Zaret (1980) questions the validity of extrapolating from experiments on a facultative zooplankton predator to broad generalisations on specialist planktivores such as clupeids and coregonines.

Coregonus species show a range of diet types with C. lavaretus typically displaying a facultative planktivorous diet over much of its distribution (Jacobson, 1981).

Powan in Loch Lomond consume zooplankton as the main part of their diet between May and October to such an extent that growth and gonadal recrudescence also occur at this time (Rashid, 1984; this work, Chapter 4). The powan's predation on zooplankton will be investigated in this chapter with the main emphasis of the work on the analysis of observed predation from field samples collected from Loch Lomond. The role of prey characteristics in determining predator catch in the present study was investigated using aspects of prey density, size and visibility. Field observations were supplemented by experiments on laboratory reared juvenile fish.

MATERIALS AND METHODS.

The powan's predation on planktonic organisms in the mid basin of Loch Lomond was monitored by comparing the contents of powan stomachs to the prey available in the loch plankton. Plankton sampling was carried out on the same date as fish sampling (or the following day) to provide relative abundance data for the main planktonic prey species in the loch.

3.1 Plankton sampling.

Qualitative plankton samples (vertical hauls) were taken from a small boat between 1100 and 1500 hours. A standard plankton net of 1m length and 28cm mouth diameter with a 250 μ m mesh was used for all hauls. A detachable phosphor-bronze filter (mesh size 100 μ m) was fixed at the weighted end of the net cone. Samples were obtained from the mid basin of Loch Lomond between Ross Point and Inchlonaig opposite Luss, in approximately 60m depth. On occasions, samples were taken closer inshore towards Sallochay Bay, but never from less than 20m depth. The net was lowered to the bottom (or 50m depth) and recovered by hand at a constant rate of approximately 1m per second. The filter was removed after washing down the sides of the net and placed in a labelled container of 5% formaldehyde solution. Five vertical hauls were taken on each sample date.

Additional samples were taken by horizontal tows of a standard plankton net between two fixed points. Tows were taken at various depths by using a diving plane with nets attached at intervals on the towing line. To provide some comparability between hauls, the duration, (5 mins.), distance and location of hauls was standardised. Quantitative samples were obtained using a 5 litre Freidinger-type

water sampler lowered to the required depth. Plankton samples were taken from Loch Eck as described above from the middle of the loch in approximately 25m water depth. The sampling site was 1-2km from the north end of the loch. Sub-samples were taken, identified and counted as described in Appendix 1. In spring and summer plankton samples, it was necessary to remove animals from accumulations of phytoplankton before sub-sampling. These were extracted and replaced before sub-sampling. Rotifera were found in many of the samples but were not counted and no further account of this group is given.

The body length distribution of the species Diaptomus gracilis, Bosmina coregoni, Cyclops strenuus abyssorum and Daphnia hyalina were recorded by measuring individuals using a Kiowa binocular microscope (x40) fitted with an ocular micrometer. Animals were measured to 50µm size - classes. All measurements were of the maximum body length, including Daphnia helmets but excluding caudal spines (Plates 7-13). Copepod body lengths were measured between the anterior extremity of the cephalothorax to the end of the furcal rami. Sexes were differentiated where appropriate and counts were recorded of eggs present. Counts were taken of helmeted and non - helmeted Daphnia morphs.

3.2 Measuring preference.

Of the measures which have been used to estimate preference, that advocated by Chesson (1978, 1983) is most useful. Based on the assumption that predator foraging behaviour is unaffected by encounters with prey which are not eaten, Chesson's preference value is obtained from a normalized version of Ivlev's (1961) electivity index, and in the simplest case where no food depletion occurs is given by:

$$\hat{\alpha}_i = \frac{r_i/n_i}{\sum_{j=1}^m r_j/n_j}, \quad i = 1, \dots, m.$$

where : $\hat{\alpha}_i$ is the maximum likelihood estimator of α_i
 r_i , n_i are the relative proportions of prey i in
the predator's diet and environment respectively,
 m is the number of prey types.

α_i for food type i can be interpreted as the proportion of the diet which would consist of type i if all food types were present in equal numbers in the environment. Therefore the α_i 's are relative measures which indicate the preference of a predator for a food type i relative to the other food types present (Chesson, 1983), and the α_i 's sum to unity. Using $\underline{\alpha}$, the vector with i th component α_i , the predator's deviations from random sampling of food types can be measured and further investigated. Where there is no appreciable prey depletion;

$$\underline{\alpha} = \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \vdots \\ \alpha_i \end{pmatrix}$$

Other commonly used measures of preference such as Ivlev's (1961) electivity index, E , and the forage ration, FR , have the undesirable properties of depending not only on predator behaviour but also on the absolute numbers of each food type present. Dependences of this sort preclude comparisons between observations obtained at different prey densities. This point is demonstrated by Chesson (1978).

It is possible to predict predator preferences in situations other than those originally obtaining, eg; for a subset of the original prey species assemblage, assuming there is no change in

predator behaviour. Preference values may be predicted for the relative preferences of a predator for two food types, given the predator's preference for each of them relative to a third food type.

If a number of estimations of α_i are available (eg. from a number (k) of individual fish) a sample of k values of α_i are obtained. If the individuals display different preferences and a single value of α_i estimated by combining the data for all k individuals, the resulting α_i will be different to that estimated by averaging the k individual α_i values (Chesson, 1983).

Electivity, ϵ .

The preference value α_i which would be obtained if the predator were selecting food at random ($\alpha_i = 1/m$) varies with the number of food types available (m) and accordingly, strength of preference can be difficult to ascertain for a particular prey type when selection is non - random but different numbers of alternative food types are present in different situations. Under such circumstances, an electivity index such as that suggested by Chesson (1983) can be used to display preferences. The preference α_i for a food type i relative to the average preference for all other food types can be used to calculate electivity :

$$\epsilon_i = \frac{m \alpha_i - 1}{(m-2)\alpha_i + 1}, \quad i = 1, \dots, m.$$

where $\alpha_i = 0$, $\epsilon_i = -1$ and where $\alpha_i = 1$, $\epsilon_i = +1$.

ϵ_i can take any value between -1 and +1.

Preferences α_i and electivities ϵ_i were calculated for Loch Lomond samples between October 1982 and May 1984, using percentage composition by number data from Chapter 2 to estimate r_i , the relative proportion of prey i in the diet, and relative plankton species abundance n_i , determined from the plankton samples described above.

Prey species considered : Only 8 prey species were considered here: Diaptomus gracilis, Bosmina coregoni var. obtusirostris, Daphnia hyalina, Cyclops strenuus abyssorum, Holopedium gibberum, Bythotrephes longimanus, Leptodora kindti and the larvae of Chaoborus flavicans. Although the latter is not wholly planktonic, it was taken in plankton samples over much of the year and was included in this analysis.

Occasionally, prey species were detected in the powan's diet when no individuals of that species had been recorded from corresponding plankton samples. In such instances the relative abundance of the prey type was set at an arbitrarily low value (0.01%) to enable complete calculation of preferences.

Calculations of preferences and electivities were restricted to the eight species above since no estimates of abundance were available for other prey species. As some of the prey species disappeared from the plankton over the winter months giving different ranges of prey species numbers at different times, comparison of preference between samples is better estimated by ϵ_i than α_i (Chesson, 1983).

3.2.1 Effects on α_i and ϵ_i of diel changes in zooplankton composition.

The overall percentage composition by number stomach data for the samples of October 1982 and April 1983 were compared to plankton samples taken on the same day but at different times.

3.2.2 Effects of different calculation methods on α_i and ϵ_i .

Preference values were calculated for samples between October 1982 and May 1984. Where the pooled percentage composition by number data for all fish in a sample was compared to the relative abundances of the corresponding plankton samples, the preference values did not have associated statistical error estimates. Within sample error estimates of preference were available when the sample mean preference was obtained from individual preference values.

Relative frequencies of plankton species in diel plankton samples were compared using a Kolmogorov - Smirnov 2 sample test with the null hypothesis of identity for the two sample distributions (p.441 Sokal & Rohlf, 1981; SPSSX). This is a nonparametric test for difference between two sample distributions. The test statistic D is defined as the largest absolute difference between the two relative cumulative frequency distributions with sample size n_1 and n_2 . Values of D multiplied by n_1, n_2 are compared to tables of critical values for a given probability level and appropriate n_1, n_2 . For the sample statistic Dn_1n_2 to be significant, it has to equal or exceed the tabled value. An approximation to a one-sided test may be obtained by doubling the nominal probability levels for critical values. The test has the advantage that no clumping of frequency classes is required as in the G-test (Sokal and Rohlf, 1981 section 13.11).

Statistical comparisons of the preference values obtained for the two calculation methods were performed using a t - test for paired comparisons (Sokal & Rohlf, 1981 p.359). The mean differences in sample preference pairs were tested against the null hypothesis of no difference between sample pairs.

Since direct comparison of preference values α_i , can be misleading if different numbers of prey species were available, electivity values ϵ_i , were calculated from mean preference values after Chesson (1983).

3.2.3 Individual variation in preference.

The standard deviations of the mean preference values calculated give an estimate of the different preferences exhibited by fish. Additionally, preferences greater than $(1/m)$ were recorded in each sample to determine the variation of preferred species in the diet. The 'effective plankton diet width' can be defined as the number of species for which powan show preferences greater than $1/m$. The magnitude of the highest preference exhibited (α_{max}) and the total number of prey species available will determine the effective plankton diet width for individual fish:

where $\alpha_i > 1/m$, preference is indicated for species i ,

and if $(1 - \alpha_{max}) < (1/m)$, 1 prey is preferred (α_{max}).

3.3 Factors influencing prey choice.

Possible factors influencing the powan choice of prey were examined.

3.3.1 Size selectivity in powan predation.

Preference and electivity values calculated in 3.2 above were compared to absolute prey body size. Of the prey species taken, Bosmina and Daphnia were not the largest but were consumed in large numbers by powan. Measurements of total body length of these two species were recorded from powan stomach contents whenever possible and from each plankton sample.

Length frequency distributions were compared using the Kolmogorov - Smirnov 2 sample test, with the null hypothesis of identity for the two sample distributions (Sokal & Rohlf, 1981, p.441) SPSSX.

In most stomach samples containing Daphnia as prey, it was possible to count morph frequencies and measure whole animals. Egg counts were also taken, although some of these were unrepresentative as the eggs could be lost from the shell valves. A comparison of the predation pattern on Daphnia morphs was carried out. Body length frequency distributions of peaked - helmeted morphs (including helmets) were compared to the body length frequency distributions of round - helmeted forms, in the plankton samples and in the stomach contents. The size frequency distributions of the two morphs were also compared between the plankton and powan diet. It was assumed that no bias was introduced into the measurements by differential damage to either morph or size range of prey in the course of ingestion, passage to the stomach or subsequent analysis.

Predator size classes were not differentiated as virtually all powan stomachs examined came from fish which were very much larger than their biggest prey.

Bosmina were examined for the presence of eggs within the shell valves. The relative frequencies of gravid and non - gravid individuals was recorded.

3.4 Observations on feeding of Coregonus larvae and fry in captivity.

The starvation time of early hatching larvae was compared to that of late hatching larvae. Animals were kept in tanks which may have acquired some protozoa, but no external food was supplied.

Feeding trials were carried out using Coregonus larvae and fry reared in the laboratory. Eggs and sperm collected from spawning fish in Loch Lomond from '82 - '85 were reared in hatchery trays kept in the open with a constant flow of water (hatchery tray volume = 0.15 m^3). Light environment and water temperature in the hatchery trays were uncontrolled.

Feeding trials were carried out in circular light gray polythene tanks (21). Trials were carried out on larvae from the time of hatching. Actively swimming larvae were placed in the experimental tanks at least two hours before food was added. Larvae were observed feeding singly and in groups of six. All observations were made under ambient daylight conditions. Other workers have found that light intensity does not influence fish feeding behaviour until it falls by an order of magnitude from bright daylight to the 100 lux range (Confer et al., 1978; Furnass, 1979); reports of light thresholds of 1 - 20 lux for fish feeding activity have been reviewed by Dabrowski (1982). Prey were hand - sorted by pipetting individuals from Loch Lomond plankton collections into beakers of filtered loch water. Prey were pipetted into the test tank with minimum disturbance to the fish.

In the trials of 1983, larvae were observed and their prey choice recorded from analysis of gut contents. In 1984, larvae were observed in their first encounters with zooplankton.

Eight behavioural units were discerned :

- consideration - a powan larva directed its eyes towards a prey item
and approached to within a body length (approx. 12mm);
- pursuit - a powan larva followed a moving prey item;
- strike - a powan larva's body formed s - shaped curve, then
lunged directly at prey;
- miss - powan larva missed prey item;
- contact - powan larva engulfed prey item;
- ejection - captured prey was ejected from larva's mouth, or
(rarely) escaped;
- handling - powan larva masticated and swallowed ingested prey;
- end - powan larva finished handling ingested prey or
stopped pursuit of or striking at considered item.

RESULTS.

3.1.1 Loch Lomond plankton composition. (Figs. 3.1-3.5)

The plankton was dominated numerically for most of the year by the calanoid copepod Diaptomus gracilis Sars. Of the cyclopoid copepods, Cyclops strenuus abyssorum Sars was abundant during the summer months, while Mesocyclops leuckarti (Claus) could be found in the plankton throughout the year. The cladocerans Bosmina coregoni var. obtusirostris (Sars) and Daphnia hyalina var. galeata Sars were common members of the plankton in spring and summer respectively, with maximal abundances of Bosmina in the spring equalling those of the copepods. The predaceous Cladocera Bythotrephes longimanus (Leydig), Leptodora kindti (Focke) and Polyphemus pediculus (L.) were found in the summer and autumn months but in such low numbers as to make their abundances difficult to determine accurately. Holopedium gibberum Zaddach was also a common member of the Loch Lomond plankton: although its presence was not recorded by Hamilton (1958) or Chapman (1969), it was found in a nearby lochan (Hamilton 1958). Colonial and solitary rotifers were found in summer plankton samples, reaching high densities at times. Of the various insect species which are aquatic for a part of their life cycle, the larvae of Chaoborus flavicans Meigen were taken most frequently in plankton samples. Year to year variation in plankton abundance was considerable in the course of this study. Numbers of zooplankton taken in hauls in May 1985 were particularly low compared to those of May in the previous two years.

Fig. 3.1 Total zooplankton numbers from vertical plankton hauls in Loch Lomond. Counts and medians are shown for each sample date.

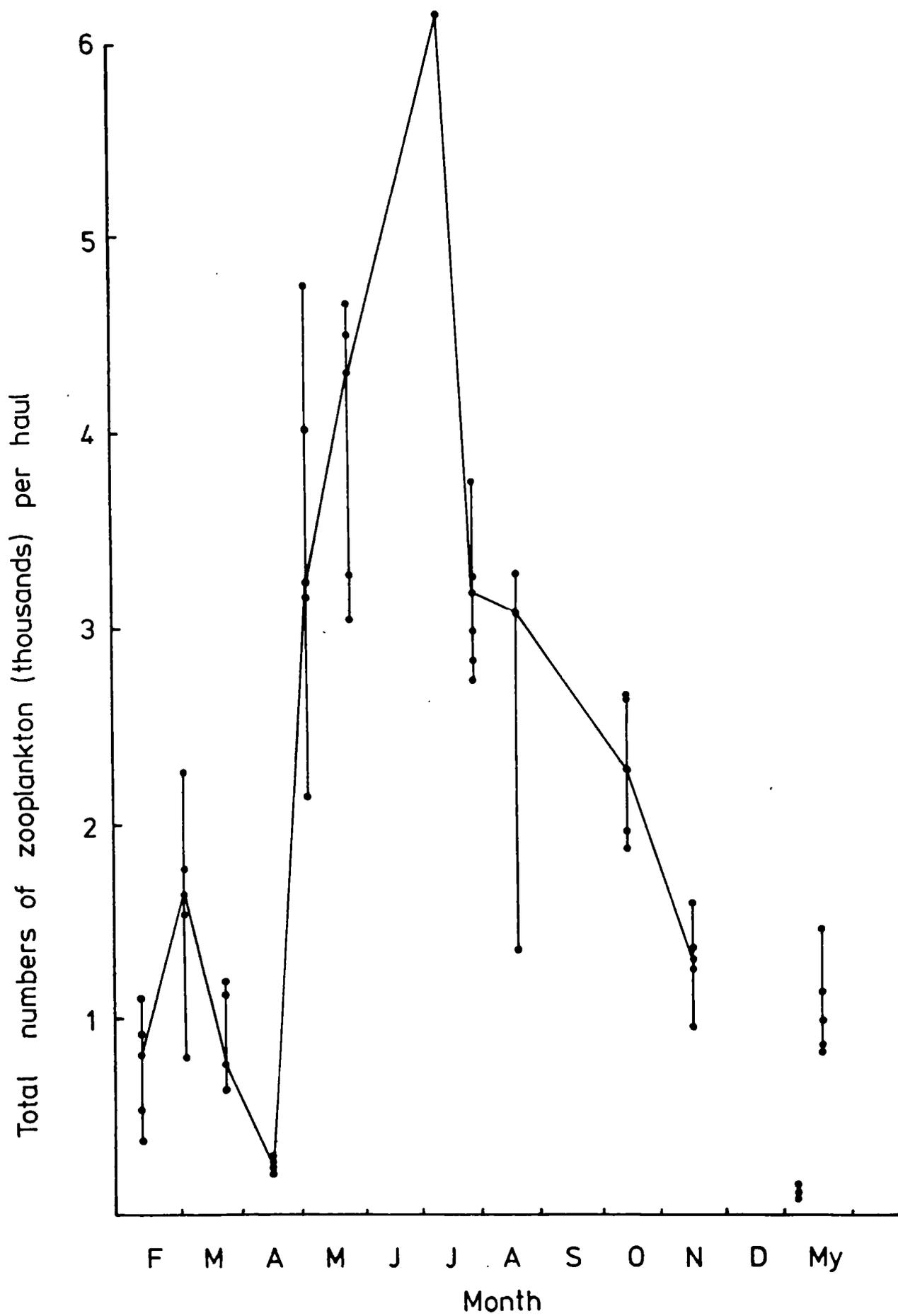


Fig. 3.1

Fig. 3.2 Counts of *Diaptomus gracilis* from plankton samples (includes copepodites and adults). Counts and medians are shown for each sample date.

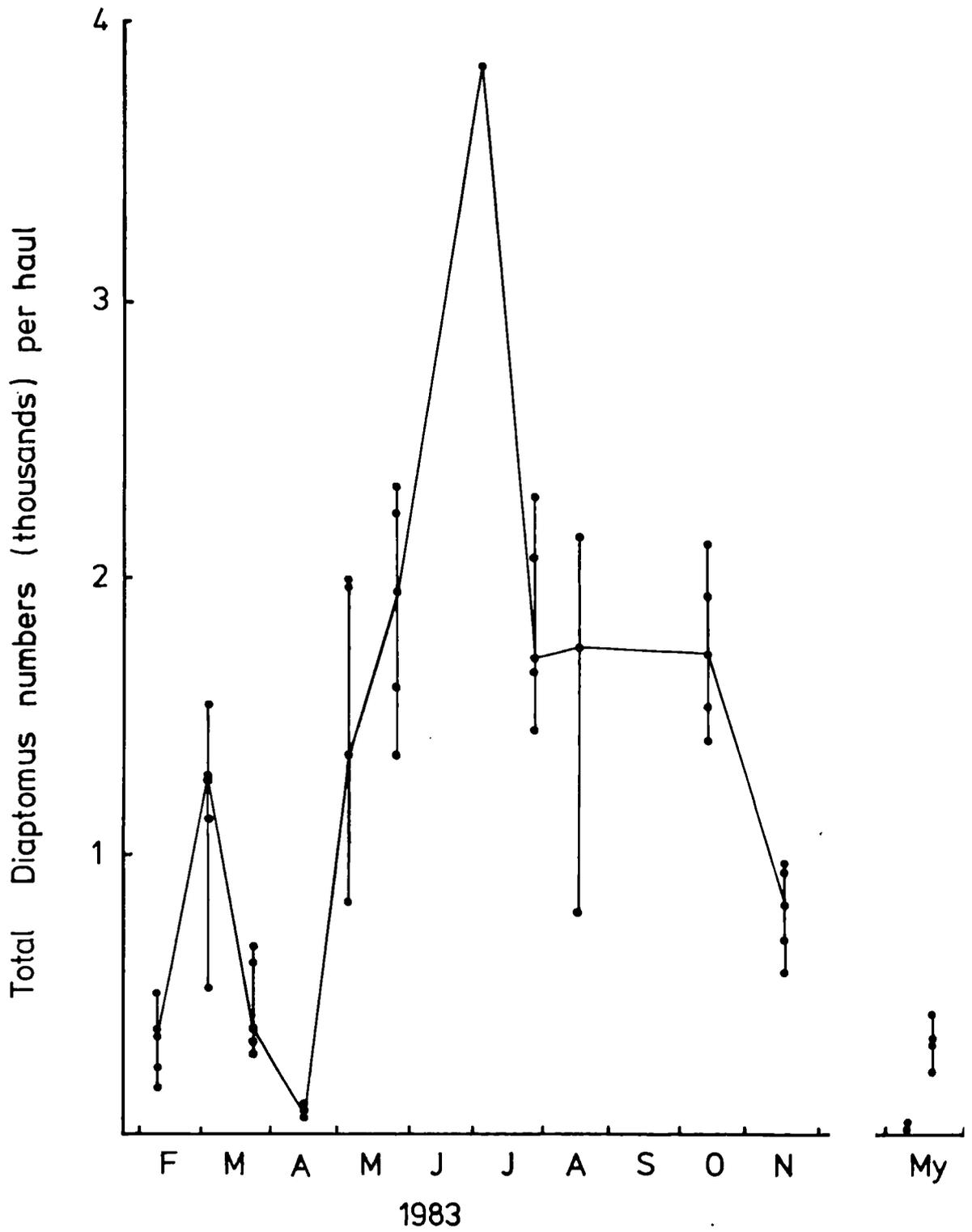


Fig. 3.2

Fig. 3.3 Counts of *Daphnia hyalina* and *Bosmina coregoni* from Loch Lomond plankton samples. Counts and medians are shown for each sample date.

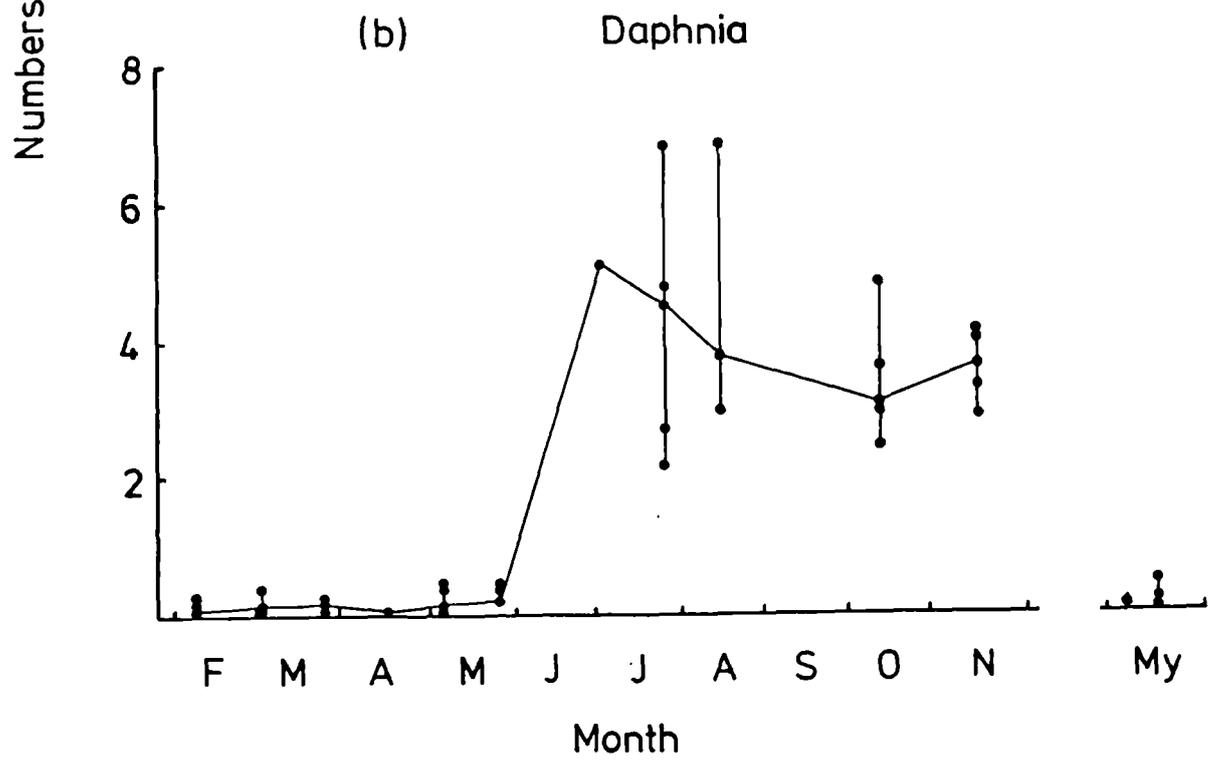
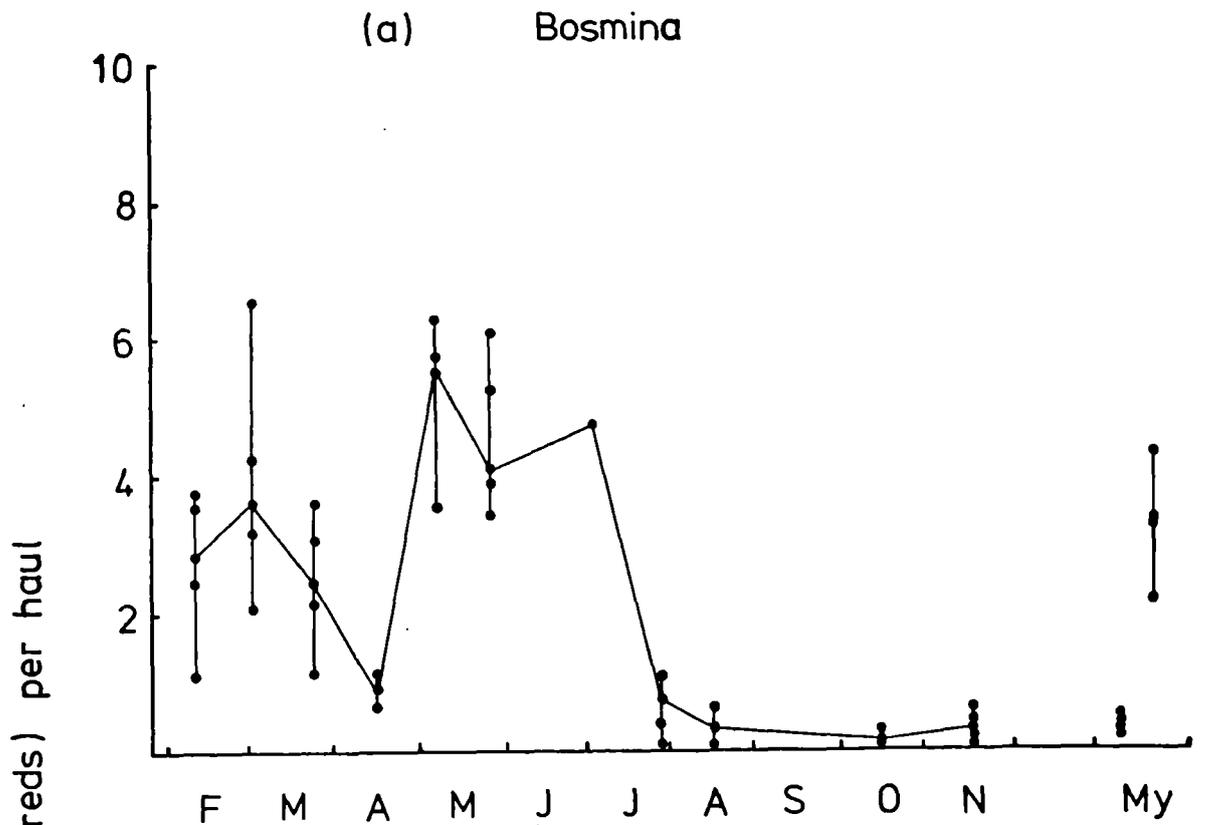


Fig. 3.3 a,b

Fig. 3.4 Counts of *Cyclops strenuus abyssorum* and *Mesocyclops leuckarti* from Loch Lomond plankton samples. Counts and medians are shown for each sample date.

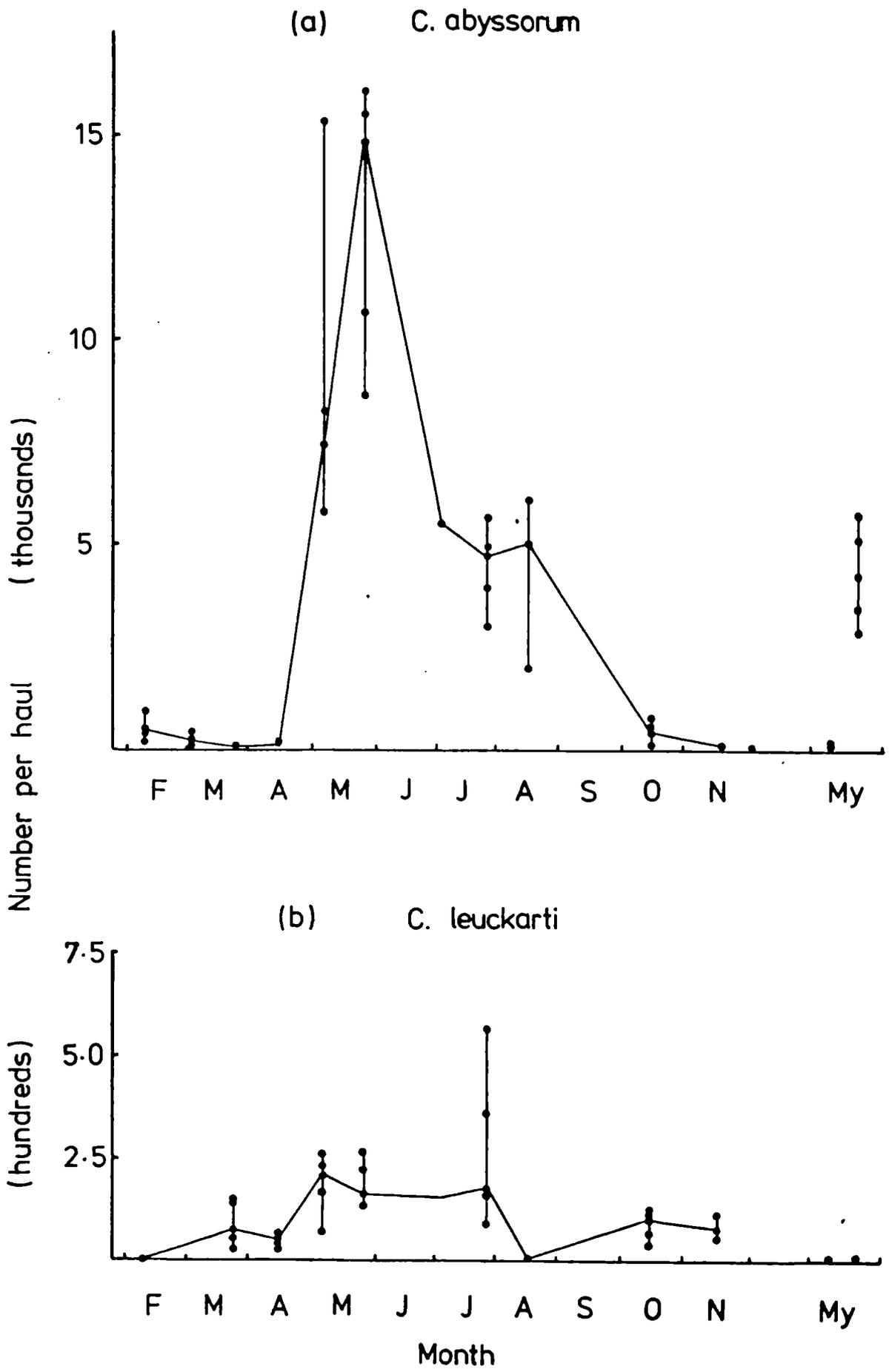


Fig. 3.4 a,b

Fig. 3.5 Counts of Bythotrephes, Leptodora, Polyphemus and Holopedium from Loch Lomond plankton samples. Counts and medians are shown for each sample date.

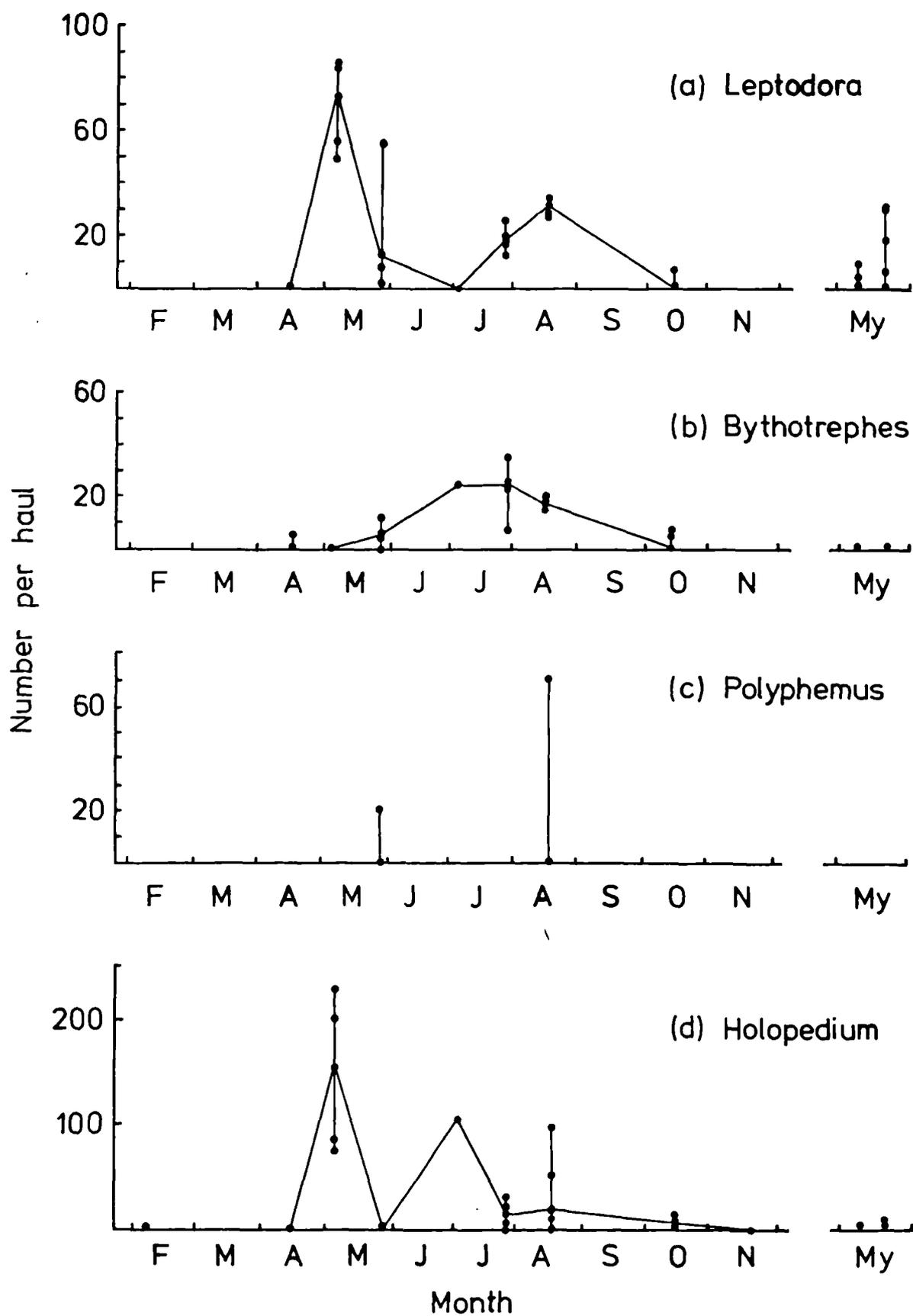


Fig. 3.5 a,b,c,d

3.1.2 Loch Eck plankton composition.

Qualitative plankton samples from Loch Eck in January, February 1984 and August 1985 were generally similar to Loch Lomond plankton. The composition of the samples is shown below.

	counts of individuals		
	12 Jan 84	14 Feb 84	7 Aug 85
Diaptomus gracilis	346	158	291
Bosmina coregoni	17	48	10
Cyclops abyssorum	6	14	83
Daphnia hyalina	2	1	0
Sida crystallina	0	0	47
Bythotrephes longimanus	0	0	2
Leptodora kindti	0	0	4
Holopedium gibberum	0	0	1
Cladocera (other)	0	1	1

Cyclops leuckarti was not found in Loch Eck, and in August Sida crystallina was relatively common. Daphnia hyalina was not numerous in any of the Loch Eck samples. Both Bythotrephes and Leptodora were present in August samples from Loch Eck.

3.2.1 Effect of diel plankton abundance variation on preference.

Preference and electivity values obtained for the stomach and plankton samples of October 1982 and April 1983 are shown in Table 3.1. In the plankton samples of 19 October 1982, relative abundances of the 8 zooplankton species considered were just significantly different in

Table 3.1

Effect of diel variation of relative plankton abundances on calculated preference and electivity values (α_i and ϵ_i), using two methods of calculating α_i and ϵ_i .

	Ri	Ni(1)	Ni(2)	$\alpha_i(1)$	$\alpha_i(2)$	$\epsilon_i(1)$	$\epsilon_i(2)$
19 October 1982							
Dia	0.58	61.10	49.60	0.0001	0.0001	-1.000	-1.000
Bsm	7.30	13.90	1.90	0.0009	0.0018	-0.987	-0.975
Dph	49.70	31.40	4.04	0.0007	0.0006	-0.990	-0.992
Cab	10.30	3.00	2.90	0.0016	0.0017	-0.976	-0.976
Hol	1.65	0.27	0.30	0.0029	0.0026	-0.960	-0.964
Cbr	9.20	0.18	4.90	0.0241	0.0009	-0.706	-0.987
Byt	19.60	0.01	0.01	0.9227	0.9441	0.976	0.983
Lpt	1.00	0.01	0.01	0.0471	0.0482	-0.487	-0.478
17 April 1983							
Dia	3.90	31.70	71.30	0.0010	0.0001	-0.992	-1.000
Bsm	1.20	32.30	25.40	0.0003	0.0001	-0.998	-1.000
Dph	0.05	2.50	0.36	0.0002	0.0001	-0.999	-1.000
Cab	9.00	4.30	1.80	0.0166	0.0013	-0.871	-0.990
Hol	0.00	0.00	0.00	0.0000	0.0000	-1.000	-1.000
Cbr	38.10	0.31	0.01	0.9771	0.9986	0.988	0.999
Byt	0.00	0.00	0.72	0.0000	0.0000	-1.000	-1.000
Lpt	0.00	0.00	0.00	0.0000	0.0000	-1.000	-1.000

Ri = overall percentage composition of species i in powan diet

Ni(1) = percentage composition of species i in plankton at time 1
(noon, October and 1400 April)

Ni(2) = percentage composition of species i in plankton at time 2
(dusk, October and 2100 April)

$\alpha_i(1,2)$ = respective preferences and $\epsilon_i(1,2)$ electivities.

Kolmogorov-Smirnov 2 sample tests on null hypothesis of identical distributions of plankton species abundances at the two times gave:

October Dmax.(570,478) = 0.412, p < 0.001.

April Dmax.(760,279) = 0.396, p < 0.001.

T-test for paired comparisons on preferences obtained using each plankton sample gave :

October t (m-1) = 1.96, p > 0.1

April t (m-1) = 1.95, p > 0.1

Dia = Diaptomus gracilis

Bsm = Bosmina coregoni

Dph = Daphnia hyalina

Cab = Cyclops abyssorum

Hol = Holopedium gibberum

Cbr = Chaoborus flavicans

Byt = Bythotrephes longimanus

Lpt = Leptodora kindti

the noon and dusk sub - surface samples. The two sets of preference values calculated from these abundances and stomach data (using combined percentage composition by number data) were not significantly different :

$$(t(7) = 1.64, p > 0.1).$$

Relative frequencies of the eight plankton species considered in surface plankton samples taken at 1400 and 2200 in April 1983 were not significantly different (Table 3.1). Powan preference values for the plankton species were not significantly different ($t(5) = 1.63, p > 0.1$).

In both the above cases, temporal fluctuations in relative numerical composition of plankton species did not significantly alter calculated powan preference values, given the distribution of individuals amongst prey species in the diet. This may appear surprising, but is largely attributable to the varying contribution to the plankton made by species relatively unimportant to powan as food (Diaptomus).

3.2.2. Variation of preference value α_i with calculation method.

Tables 3.2a,b show preference values calculated from overall percentage composition by number stomach data (Table 3.2a) and by using individual α_i 's for fish to obtain sample mean α_i 's (Table 3.2b). Although calculated preference values differ between calculation methods, significant differences in preference values were detected only for preferences calculated for November 1982 and May 1983. In these samples, a small number of powan stomachs contained large numbers of particular prey item which strongly biased the overall percentage composition by number preference estimate, but had a smaller effect on the mean preference estimate. No significant differences in preference values were obtained for the remaining samples (Table 3.2a).

Table 3.2a

Preference values α_i for overall percentage composition by number stomach contents data compared to plankton samples.

date	Prey species							
	Dia	Bsm	Dph	Cab	Hol	Cbr	Byt	Lpt
Oct	0.000	0.002	0.001	0.002	0.003	0.001	0.944	0.048
Nov	0.000	0.058	0.033	0.062	0.000	0.093	0.431	0.323
Dec	0.000	0.014	0.006	0.000	0.000	0.979	0.000	0.000
Feb	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
Mar	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
Apr	0.000	0.000	0.000	0.001	0.000	0.999	0.000	0.000
May	0.000	0.046	0.533	0.000	0.030	0.034	0.343	0.014
Jul	0.000	0.001	0.004	0.000	0.001	0.062	0.000	0.931
Aug	0.000	0.906	0.003	0.000	0.022	0.000	0.067	0.002
Oct	0.000	0.000	0.001	0.000	0.000	0.996	0.004	0.000
Nov	0.000	0.001	0.013	0.010	0.000	0.977	0.000	0.000
Jan	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
May	0.000	0.106	0.003	0.000	0.442	0.037	0.262	0.150

Prey species as in legend to Table 3.1.

Table 3.2b

Preference values α_i , shown as mean and standard deviations obtained from individual percentage composition by number stomach data compared to plankton samples.

date	Prey species							
	Dia	Bsm	Dph	Cab	Hol	Cbr	Byt	Lpt
Oct	0.000 0.000	0.007 0.023	0.005 0.008	0.018 0.090	0.003 0.005	0.247 0.386	0.647 0.413	0.073 0.185
Nov	0.111 0.292	0.231 0.286	0.153 0.190	0.206 0.212	0.000 0.000	0.072 0.253	0.178 0.348	0.050 0.195
Dec	0.134 0.351	0.261 0.421	0.106 0.266	0.000 0.000	0.000 0.000	0.458 0.502	0.041 0.117	0.000 0.000
Feb	0.167 0.336	0.287 0.430	0.001 0.002	0.000 0.000	0.000 0.000	0.545 0.521	0.000 0.000	0.000 0.000
Mar	0.000 0.000	0.000 0.001	0.000 0.000	0.157 0.180	0.000 0.000	0.843 0.775	0.000 0.000	0.000 0.000
Apr	0.000 0.001	0.006 0.021	0.738 0.406	0.006 0.032	0.000 0.000	0.251 0.398	0.000 0.000	0.000 0.000
May	0.000 0.000	0.303 0.424	0.020 0.043	0.000 0.000	0.045 0.143	0.494 0.521	0.091 0.289	0.046 0.096
Jul	0.001 0.006	0.051 0.128	0.250 0.281	0.002 0.004	0.129 0.189	0.082 0.259	0.256 0.264	0.228 0.377
Aug	0.000 0.000	0.277 0.448	0.089 0.254	0.000 0.001	0.168 0.316	0.001 0.008	0.452 0.430	0.013 0.035
Oct	0.034 0.183	0.005 0.024	0.022 0.075	0.000 0.000	0.000 0.000	0.832 0.379	0.107 0.280	0.000 0.000
Nov	0.004 0.009	0.015 0.036	0.475 0.387	0.255 0.290	0.000 0.000	0.250 0.426	0.000 0.000	0.000 0.000
Jan	0.089 0.266	0.134 0.341	0.135 0.344	0.000 0.000	0.000 0.000	0.643 0.497	0.000 0.000	0.000 0.000
May	0.000 0.000	0.418 0.385	0.002 0.003	0.000 0.000	0.217 0.271	0.034 0.171	0.110 0.230	0.218 0.223

Prey species as in legend for Table 3.1

Table 3.2c

T-tests for paired comparisons on the preference values obtained from the two calculation methods (Tables 4.2a,b) gave :

date	m	t(m-1)	probability level
Oct	8	1.706	p > 0.1
Nov	7	4.775	0.005 > p > 0.001
Dec	6	2.239	0.1 > p > 0.05
Feb	5	2.090	p > 0.1
Mar	5	1.633	p > 0.1
Apr	5	1.633	p > 0.1
May	8	2.716	0.05 > p > 0.025
Jul	8	2.099	0.005 > p > 0.001
Aug	8	1.922	0.005 > p > 0.001
Oct	7	1.960	0.005 > p > 0.001
Nov	6	1.974	p > 0.1
Jan	5	2.429	0.005 > p > 0.001
May	8	2.215	0.005 > p > 0.001

Prey species as in legend to Table 3.1.

3.2.3 Between sample variation in preference - electivity.

Electivity values ϵ_i for samples are given in Table 3.3a,b and Figs. 3.6a,b,c. The seasonal pattern of preference exhibited by powan in Loch Lomond may be summarised as follows :

Date	Preferred prey species (by sample)
.....
Oct 82	Bythotrephes, Chaoborus
Nov 82	Bosmina, Cyclops, Bythotrephes
Dec 82	Chaoborus, Bosmina
Feb 83	Chaoborus
Mar 83	Chaoborus
Apr 83	Chaoborus
May 83	Chaoborus, Bosmina
Jul 83	Bythotrephes, Daphnia, Leptodora
Aug 83	Bythotrephes, Bosmina
Oct 83	Chaoborus
Nov 83	Daphnia, Cyclops, Chaoborus
Jan 84	Chaoborus
May 84	Bosmina, Holopedium, Leptodora

Individual variation in preference within samples.

Standard deviations of the mean preferences shown in Table 3.2b give an indication of preference variation.

Individual preferences shown by fish in the samples of November 82 and August 83 are shown in Table 3.4a,b. Most fish displayed strong preferences for one or two prey species. Of the stomachs in the November 82 sample, preferences were shown for Diaptomus by four fish, twelve preferred Bosmina, eleven preferred Daphnia, Cyclops was preferred by twelve fish, Chaoborus by two fish, Bythotrephes by six

Table 3.3a

Electivities ϵ_i of powan for zooplankton prey species, determined from preference values obtained from pooled percentage composition by number data.

	Dia	Bsm	Dph	Cab	Hol	Cbr	Byt	Lpt
Oct	-1.000	-0.975	-0.992	-0.976	-0.964	-0.987	0.983	-0.478
Nov	-0.997	-0.415	-0.660	-0.432	-1.000	-0.175	0.639	0.482
Dec	-0.999	-0.910	-0.963	-1.000	-1.000	0.986	-1.000	-1.000
Feb	-1.000	-1.000	-0.999	-1.000	-1.000	1.000	-1.000	-1.000
Mar	-1.000	-1.000	-1.000	-0.998	-1.000	1.000	-1.000	-1.000
Apr	-0.992	-0.998	-0.999	-0.871	-1.000	0.988	-1.000	-1.000
May	-1.000	-0.551	0.745	-1.000	-0.687	-0.651	0.516	-0.843
Jul	-1.000	-0.983	-0.953	-1.000	-0.990	-0.432	-1.000	0.976
Aug	-1.000	0.966	-0.965	-1.000	-0.762	-0.998	-0.398	-0.976
Oct	-1.000	-0.999	-0.900	-0.922	-1.000	0.998	-0.968	-1.000
Nov	-0.999	-0.999	-0.900	-0.992	-1.000	0.988	-1.000	-1.000
Jan	-1.000	-1.000	-1.000	-1.000	-1.000	1.000	-1.000	-1.000
May	-0.999	-0.093	-0.959	-0.999	0.694	-0.576	0.426	0.105

Table 3.3b

Electivities ϵ_i of powan for zooplankton prey species, determined from mean preference ai values.

	Dia	Bsm	Dph	Cab	Hol	Cbr	Byt	Lpt
Oct	-1.000	-0.903	-0.937	-0.771	-0.964	0.394	0.856	-0.291
Nov	-0.142	0.288	0.039	0.218	-1.000	-0.367	0.129	-0.521
Dec	-0.753	0.171	-0.356	-1.000	-1.000	0.543	-0.705	-1.000
Feb	-0.249	0.094	-0.995	-1.000	-1.000	0.565	-1.000	-1.000
Mar	-1.000	-0.998	-1.000	-0.457	-1.000	0.830	-1.000	-1.000
Apr	-0.998	-0.956	0.837	-0.956	-1.000	0.146	-1.000	-1.000
May	-1.000	0.370	-0.814	-1.000	-0.616	0.660	-0.331	-0.614
Jul	-0.985	-0.452	0.401	-0.974	0.019	-0.231	0.413	0.348
Aug	-1.000	0.393	-0.264	-0.998	0.096	-0.983	0.663	-0.851
Oct	-0.756	-0.959	-0.834	-1.000	-1.000	0.904	-0.353	-1.000
Nov	-0.964	-0.884	0.566	0.157	-1.000	0.144	-1.000	-1.000
Jan	-0.549	-0.367	-0.362	-1.000	-1.000	0.688	-1.000	-1.000
May	-0.999	0.668	-0.975	-0.999	0.320	-0.602	-0.070	0.323

Prey species as in legend to Table 3.1.

Fig. 3.6 Mean electivities ϵ_i of powan for the eight plankton species considered :

Dia = Diaptomus gracilis
Bsm = Bosmina coregoni
Dph = Daphnia hyalina
Cab = Cyclops spp.
Hol = Holopedium gibberum
Cbr = Chaoborus flavicans larvae
Byt = Bythotrephes longimanus
Lpt = Leptodora kindti.

$$\text{Electivity } \epsilon_i = \frac{m\alpha_i - 1}{(m - 2)\alpha_i + 1}$$

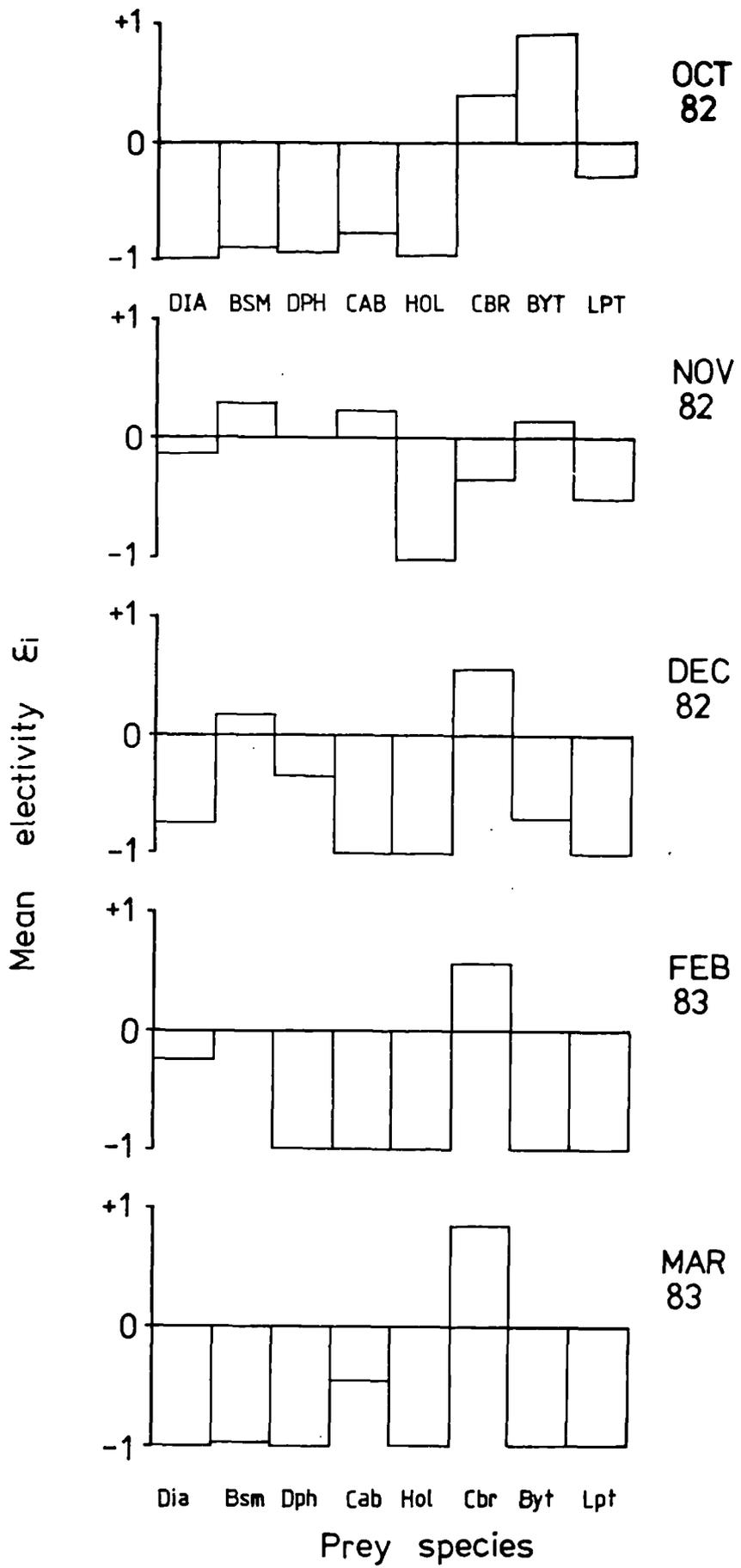


Fig. 36a

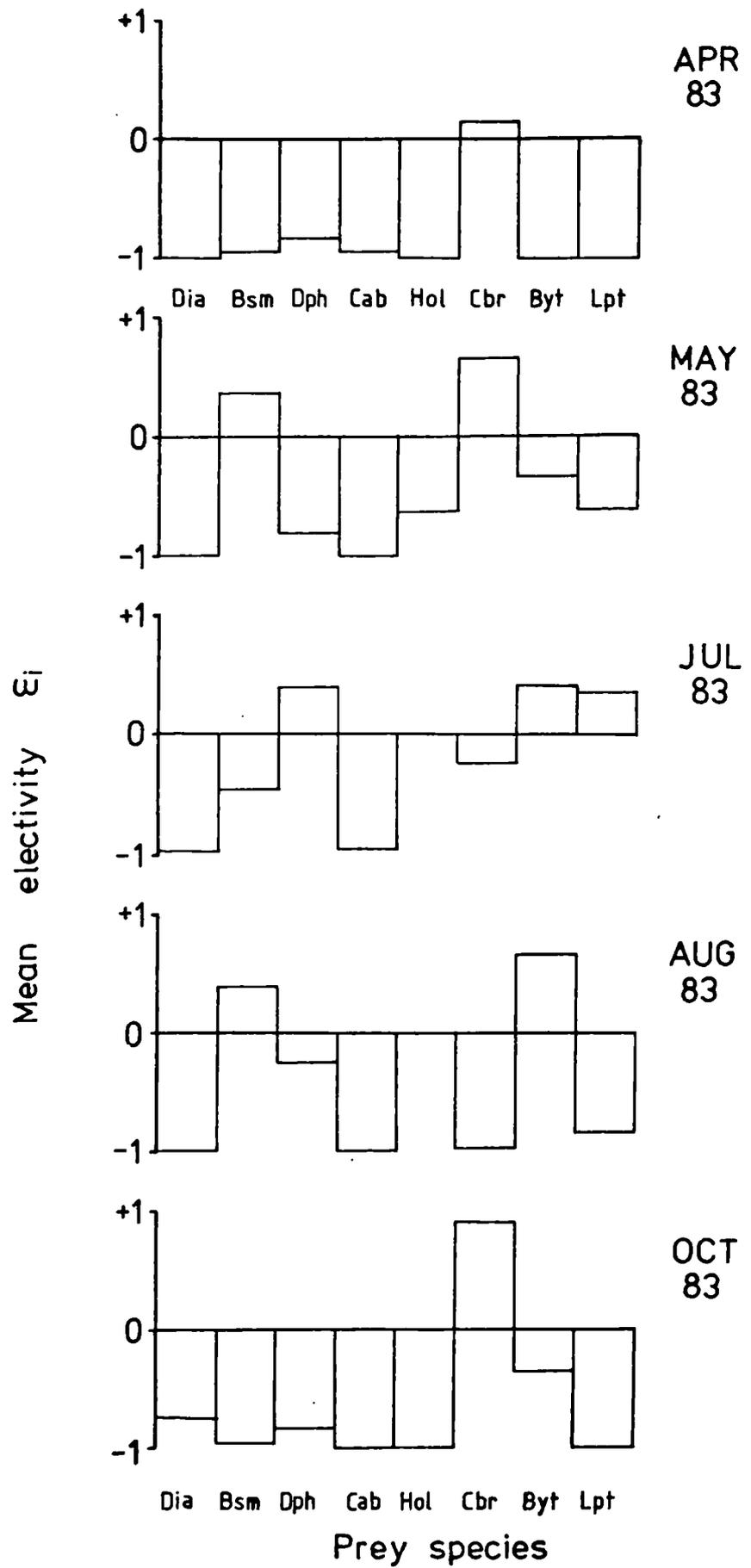


Fig. 3.6b

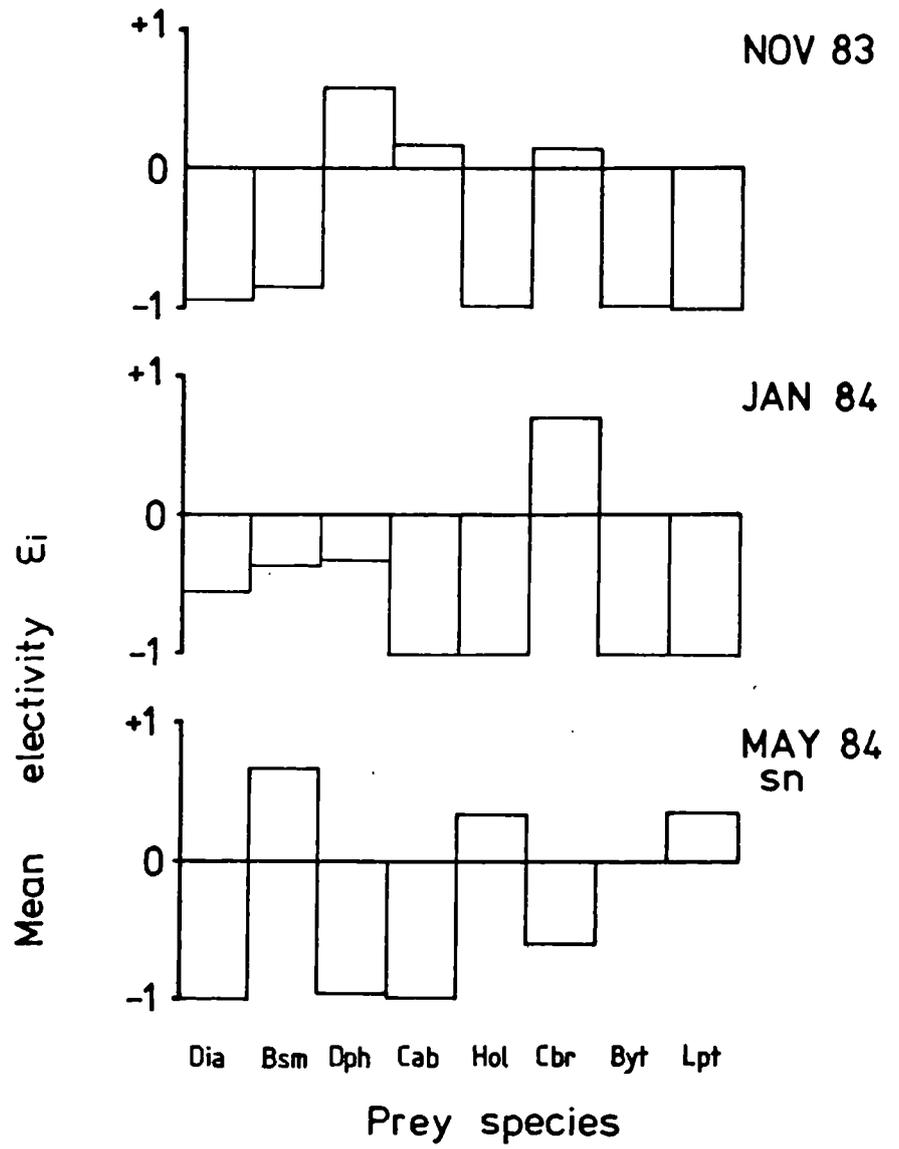


Fig. 3.6c

Table 3.4a

Individual preference values α_i , for plankton prey species for powan from Loch Lomond, 10 November 1982.

fish no.	Prey species							
	Dia	Bsm	Dph	Cab	Hol	Cbr	Byt	Lpt
1.	0.653	0.000	0.000	0.347	0.000	0.000	0.000	0.000
2.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4.	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5.	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6.	0.000	0.025	0.017	0.061	0.000	0.000	0.897	0.000
7.	0.346	0.000	0.654	0.000	0.000	0.000	0.000	0.000
8.	0.004	0.000	0.000	0.000	0.000	0.996	0.000	0.000
9.	0.000	0.300	0.255	0.445	0.000	0.000	0.000	0.000
10.	0.000	0.467	0.533	0.000	0.000	0.000	0.000	0.000
11.	0.000	0.043	0.027	0.083	0.000	0.040	0.403	0.403
12.	0.000	0.000	0.000	0.101	0.000	0.899	0.000	0.000
13.	0.000	0.459	0.206	0.334	0.000	0.000	0.000	0.000
14.	0.000	0.000	0.416	0.584	0.000	0.000	0.000	0.000
15.	0.000	0.183	0.417	0.400	0.000	0.000	0.000	0.000
16.	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
17.	0.000	0.029	0.013	0.063	0.000	0.000	0.895	0.000
18.	0.000	0.386	0.176	0.438	0.000	0.000	0.000	0.000
19.	0.000	0.583	0.098	0.318	0.000	0.000	0.000	0.000
20.	0.000	0.030	0.009	0.017	0.000	0.000	0.000	0.943
21.	0.000	0.159	0.248	0.593	0.000	0.000	0.000	0.000
22.	0.000	0.055	0.031	0.037	0.000	0.000	0.876	0.000
23.	0.000	0.667	0.042	0.291	0.000	0.000	0.000	0.000
24.	0.000	0.018	0.026	0.049	0.000	0.000	0.907	0.000
25.	0.000	0.170	0.330	0.500	0.000	0.000	0.000	0.000
26.	0.000	0.223	0.386	0.390	0.000	0.000	0.000	0.000
27.	0.000	0.090	0.063	0.045	0.000	0.000	0.801	0.000
28.	0.000	0.534	0.000	0.466	0.000	0.000	0.000	0.000
29.	0.000	0.828	0.172	0.000	0.000	0.000	0.000	0.000

Prey species as in legend to Table 3.1.

Table 3.4b

Individual preference values α_i , for plankton prey species for powan from Loch Lomond, 17 August 1983.

fish no.	Prey species							
	Dia	Bsm	Dph	Cab	Hol	Cbr	Byt	Lpt
1.	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
2.	0.000	0.000	0.052	0.002	0.091	0.000	0.843	0.012
3.	0.000	0.000	0.059	0.000	0.027	0.000	0.877	0.037
4.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5.	0.000	0.000	0.005	0.000	0.995	0.000	0.000	0.000
6.	0.000	0.991	0.000	0.000	0.001	0.000	0.007	0.001
7.	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
8.	0.000	0.026	0.021	0.000	0.668	0.000	0.269	0.016
9.	0.000	0.003	0.031	0.000	0.002	0.000	0.937	0.028
10.	0.000	0.000	0.085	0.002	0.040	0.000	0.813	0.059
11.	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
12.	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
13.	0.000	0.000	0.006	0.000	0.963	0.000	0.032	0.000
14.	0.000	0.000	0.121	0.000	0.364	0.000	0.506	0.009
15.	0.000	0.000	0.006	0.000	0.098	0.000	0.896	0.000
16.	0.000	0.000	0.016	0.000	0.000	0.000	0.984	0.000
17.	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
18.	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
19.	0.000	0.000	0.001	0.000	0.113	0.000	0.882	0.005
20.	0.000	0.000	0.038	0.000	0.000	0.000	0.962	0.000
21.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
22.	0.000	0.000	0.022	0.000	0.221	0.042	0.701	0.014
23.	0.000	0.000	0.018	0.000	0.088	0.000	0.894	0.000
24.	0.000	0.000	0.014	0.000	0.000	0.000	0.804	0.182
25.	0.000	0.929	0.001	0.000	0.019	0.000	0.051	0.000
26.	0.000	0.014	0.021	0.000	0.187	0.000	0.778	0.000
27.	0.000	0.997	0.000	0.000	0.000	0.000	0.003	0.000
28.	0.000	0.070	0.035	0.000	0.000	0.000	0.874	0.021
29.	0.000	0.000	0.013	0.000	0.000	0.000	0.987	0.000
30.	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
31.	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000

Prey species as in legend to Table 3.1.

fish and Leptodora by two fish. Those fish which had Chaoborus as the preferred species contained many of the larvae (>50) and ate little else, whilst fish with Diaptomus as the preferred species had only a few animals in the stomach (<20).

Most powan in the August 83 sample showed a high preference value for a single prey species. Bosmina was preferred by eight fish, two preferred Daphnia, Holopedium was preferred by seven fish, Bythotrephes by sixteen fish and Leptodora by a single fish. The remaining species were not preferred, although present in the plankton. Of the fish preferring Bosmina, only two contained more than one other planktonic prey species. Although Daphnia were preferred by only two fish, they were present in twenty-three stomachs. Similarly, Leptodora and Holopedium were preferred by few fish but consumed by most individuals in the sample.

Table 3.5 shows the seasonal variation in the number of prey species preferred by powan (i.e. where $\alpha_i > 1/m$). Where some fish are indicated as having no preferred species, the diet consisted of other (mostly benthic) food : these fish were most frequently observed in winter samples. Summer samples tended to have the greatest number of preferred prey species (May and July samples, Table 3.5).

Table 3.6 lists the prey species preferred by individual fish in samples.

3.3.1 Size - selectivity : interspecific.

Although the maximum body lengths of each prey species considered was found to vary seasonally, the relative sizes of prey species changed little from sample to sample, and rankings of species were changed more by seasonal absences from the plankton than changes in relative body size.

Table 3.5

Number of preferred prey species ($\alpha_i > 1/m$) for
powan stomachs in samples from October 1982 -
May 1984 (effective plankton diet width).

date	n	m	no. prey spp. ($\alpha_i > 1/m$)			
			0	1	2	3
Oct 82	30	8	0	24	6	0
Nov 82	29	7	2	11	9	7
Dec 82	17	6	9	6	2	0
Feb 83	43	5	32	9	2	0
Mar 83	24	5	11	13	0	0
Apr 83	33	5	0	29	4	0
May 83	11	8	1	8	1	1
Jul 83	30	8	1	9	12	8
Aug 83	31	8	2	24	5	0
Oct 83	42	6	12	29	1	0
Nov 83	42	6	12	17	13	0
Jan 84	30	5	16	14	0	0
May 84	25	8	0	7	14	4

n = number of fish stomachs examined

m = number of planktonic prey species considered

Table 3.6

Preferred species ($\alpha_i > 1/m$) for individual fish in samples.

	n	m	Dia	Bsm	Dph	Cab	Hol	Cbr	Byt	Lpt
Oct	30	8	0	0	0	1	0	9	22	4
Nov	29	7	4	12	11	12	0	2	6	2
Dec	17	6	1	3	1	0	0	4	1	0
Feb	43	5	3	4	0	0	0	6	0	0
Mar	24	5	0	0	0	2	0	11	0	0
Apr	33	5	0	0	26	0	0	11	0	0
May	11	8	0	4	0	0	1	5	1	2
Jul	30	8	0	4	17	0	8	3	15	9
Aug	31	8	0	8	2	0	7	0	16	1
Oct	42	6	1	0	1	0	0	25	4	0
Nov	42	6	0	0	21	14	0	8	0	0
Jan	30	5	1	2	2	0	0	9	0	0
May	25	8	0	16	0	0	11	1	5	13

n = number of fish stomachs examined

m = number of plankton prey species available

Prey species as in legend for Table 3.1.

Month Order of maximum prey body length (large - small)

October Cbr > Lpt > Byt, Hol > Cab, Dph > Dia > Bsm

February Cbr > Dph > Cab > Dia > Bsm

May Cbr > Lpt > Byt > Hol > Dph, Cab > Dia > Bsm

August Cbr, Lpt > Byt > Hol, Dph > Cab > Dia > Bsm

Observed

maximum body	Cbr	Lpt	Byt	Hol	Dph	Cab	Dia	Bsm
length (mm)	11.50	10.10	3.10	2.60	2.10	1.70	1.60	1.00

Cbr = Chaoborus Lpt = Leptodora Byt = Bythotrephes

Hol = Holopedium Dph = Daphnia Cab = Cyclops

Dia = Diaptomus Bsm = Bosmina

3.3.2 Intraspecific size - selectivity.

Daphnia (all morphs).

Body length frequency distributions of Daphnia eaten by powan and taken in plankton hauls are shown in Fig. 3.7. In all samples except December '82, the Daphnia in powan stomachs had a significantly different size distribution (composed of larger individuals over the same range of size-classes; K-S one-tailed test) than those in the plankton samples of the same sampling period (Table 3.7a).

Daphnia morphs.

Plankton : in the plankton samples of July '83 the size-frequency distribution of the peaked helmet morph was significantly different to that of the round helmet morph (peaked animals were generally bigger). No significant difference in size

distributions of the two morphs was found in the August and November '83 plankton samples (Table 3.7b).

Stomachs : size distribution of peaked helmet morphs was significantly different (larger individuals) from the round helmet morphs in the July and November '83 stomach samples, but no significant differences were found in morph size distributions for the August '83 stomach samples (Table 3.7c).

Plankton vs. stomachs -

When the size distributions of each morph were compared between plankton and stomach samples, the animals in powan stomachs had significantly different distributions (larger) than the animals in the plankton samples. This was true of both morphs in all samples examined (Table 3.7d).

The proportions of peaked and round helmet Daphnia morphs counted in the plankton and stomach samples were not independent in the samples of July, August, September, October and November '83 (Table 3.8), implying differential predation on the morphs at these times. December's samples did not indicate differential predation (Table 3.8). In July, August and September a greater proportion of round helmets were counted in stomachs than in plankton : in October and November proportionately more peaked Daphnia were counted in stomachs.

Bosmina size frequency distribution (Figs. 3.8a, b, c).

The largest Bosmina measured were in the 1.05mm size class. Comparison of Bosmina body length frequency distributions from powan stomach contents and plankton samples showed that size selection of Bosmina was occurring in all samples tested except those of August and September '83 when no significant differences in size frequency

Table 3.7

Summary of results of Kolmogorov-Smirnov 2 sample tests comparing body length frequency distributions of Daphnia in powan stomachs and plankton samples.

(a) all Daphnia

Sample	n1	n2	Dmax.	Probability
Nov 82	11	468	0.603	p < 0.001
Dec 82	4	117	0.289	p > 0.05
Jul 83	333	342	0.693	p < 0.001
Aug 83	22	460	0.895	p < 0.001
Aug 83	506	460	0.807	p < 0.001
Sep 83	70	460	0.882	p < 0.001
Nov 83	359	279	0.673	p < 0.001
Dec 83	84	279	0.593	p < 0.001

n1, n2 = number of measurements in stomachs(1) and plankton(2)
 Dmax. = largest difference in cumulative relative frequency distributions

Probability = probability of obtaining Dmax. for n1, n2 observations (probability levels are for two-tailed tests).

(b) Daphnia in plankton: peak and round helmet morphs.

Sample	round n1	peak n2	Dmax.	Probability (one-tailed)	direction of relation
Jul 83	218	78	0.339	0.05 > p > 0.01	peak > round
Aug 83	88	345	0.139	p > 0.05	identity
Nov 83	258	21	0.197	p > 0.05	identity

(c) Daphnia in powan stomachs : peak and round helmet morphs.

Sample	round n1	peak n2	Dmax.	Probability (one-tailed)	direction of relation
Jul 83	333	65	0.357	0.05 > p > 0.01	peak > round
Aug 83	230	276	0.121	p > 0.05	identity
Nov 83	216	143	0.483	p < 0.001	peak > round

(d) Daphnia morphs round (r) peak (p) in plankton (n1) and powan stomachs (n2).

Sample	no. in plankton n1	no. in stomachs n2	Dmax.	Probability (one-tailed)	direction of relation
Jul 83 r	218	268	0.784	p < 0.001	stom > plkt
Aug 83 r	88	230	0.815	p < 0.001	stom > plkt
Nov 83 r	258	216	0.643	p < 0.001	stom > plkt
Jul 83 p	78	65	0.661	p < 0.001	stom > plkt
Aug 83 p	345	276	0.874	p < 0.001	stom > plkt
Nov 83 p	21	143	0.661	0.05 > p > 0.01	stom > plkt

Fig. 3.7 *Daphnia hyalina* body length frequencies:
in plankton samples (solid bar histogram),
in powan stomachs (broken line histogram).

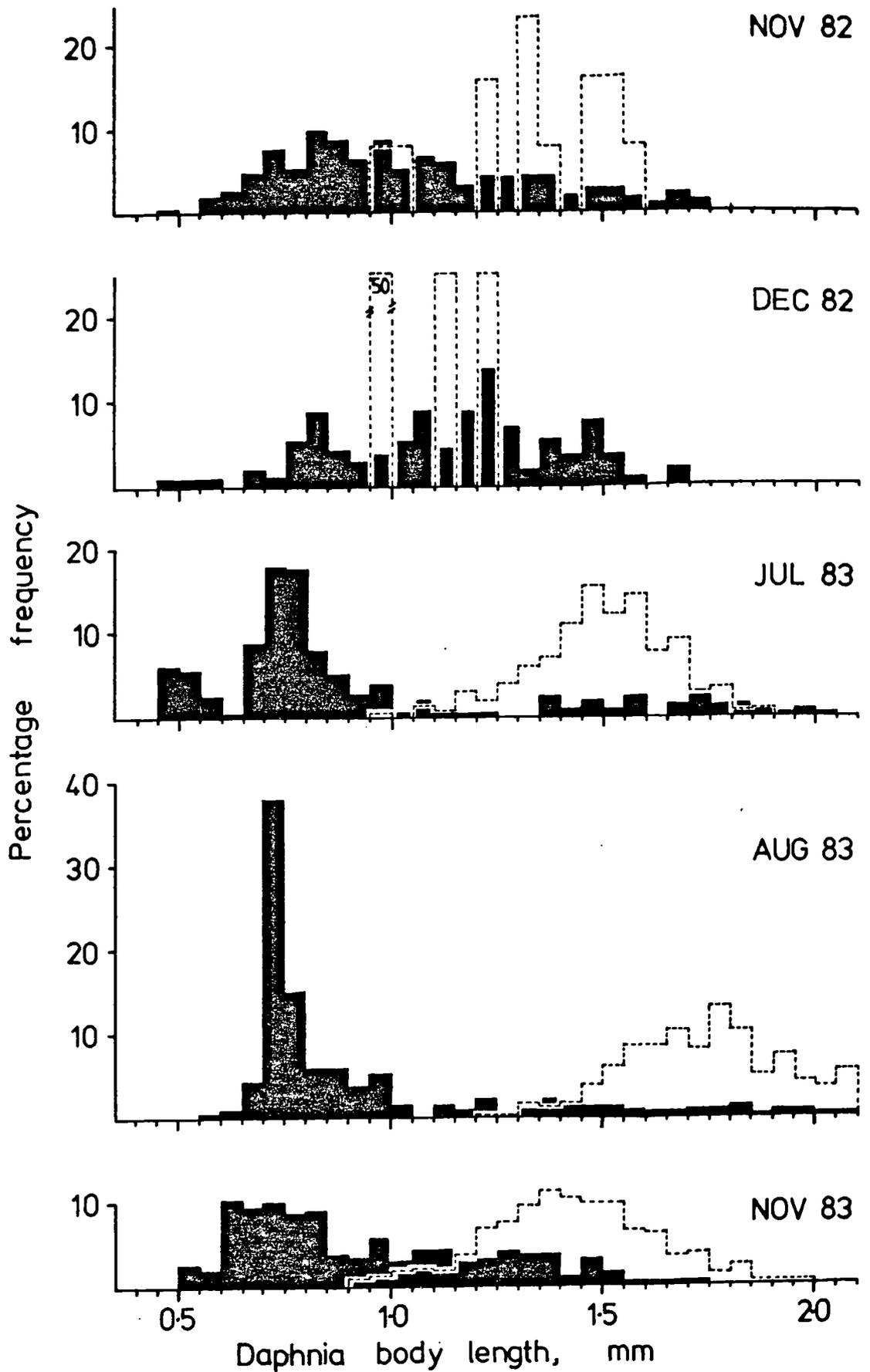


Fig. 3.7

distributions of the two morphs was found in the August and November '83 plankton samples (Table 3.7b).

Stomachs : size distribution of peaked helmet morphs was significantly different (larger individuals) from the round helmet morphs in the July and November '83 stomach samples, but no significant differences were found in morph size distributions for the August '83 stomach samples (Table 3.7c).

Plankton vs. stomachs -

When the size distributions of each morph were compared between plankton and stomach samples, the animals in powan stomachs had significantly different distributions (larger) than the animals in the plankton samples. This was true of both morphs in all samples examined (Table 3.7d).

The proportions of peaked and round helmet Daphnia morphs counted in the plankton and stomach samples were not independent in the samples of July, August, September, October and November '83 (Table 3.8), implying differential predation on the morphs at these times. December's samples did not indicate differential predation (Table 3.8). In July a greater proportion of round helmets were counted in stomachs than in plankton, while from August - November proportionately more peaked Daphnia were counted in stomachs than in plankton.

Bosmina size frequency distribution (Figs. 3.8a, b, c).

The largest Bosmina measured were in the 1.05mm size class. Comparison of Bosmina body length frequency distributions from powan stomach contents and plankton samples showed that size selection of Bosmina was occurring in all samples tested except those of August and September '83 when no significant differences in size frequency

Table 3.8

Relative abundances of *Daphnia* morphs in plankton and powan stomachs.

	count in plankton	count in stomachs (n=29)
Jul 83		
round morph	62	1133
peak morph	15	175
chi-squared value = 28.9, $p < 0.001$		
	count in plankton	count in stomachs (n=18)
Aug 83		
round morph	55	537
peak morph	154	874
chi-squared value = 10.8, $0.01 > p > 0.001$		
	count in plankton	count in stomachs (n=26)
Sep 83		
round morph	55	237
peak morph	154	416
chi-squared value = 7.04, $0.01 > p > 0.001$		
	count in plankton	count in stomachs (n=2)
Oct 83		
round morph	126	6
peak morph	131	20
chi-squared value = 6.39, $0.05 > p > 0.01$		
	count in plankton	count in stomachs (n=23)
Nov 83		
round morph	217	544
peak morph	19	264
chi-squared value = 56.0, $p < 0.001$		
	count in plankton	count in stomachs (n=10)
Dec 83		
round morph	217	845
peak morph	19	76
chi-squared value = 0.01, $p > 0.1$		

Fig. 3.8 *Bosmina coregoni* body length frequencies:
in plankton samples (solid line histogram),
in powan stomachs (broken line histogram).

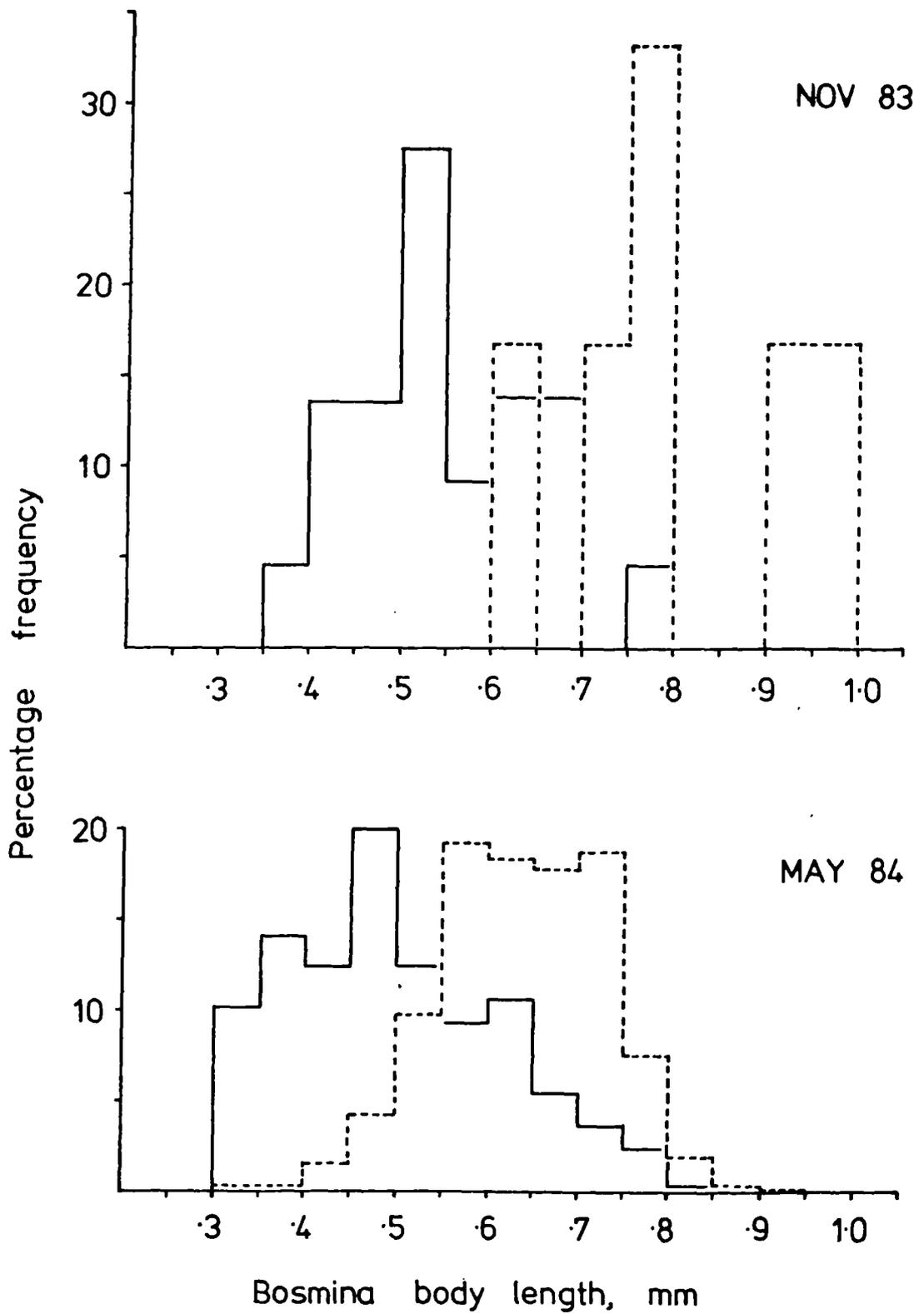


Fig. 3.8a

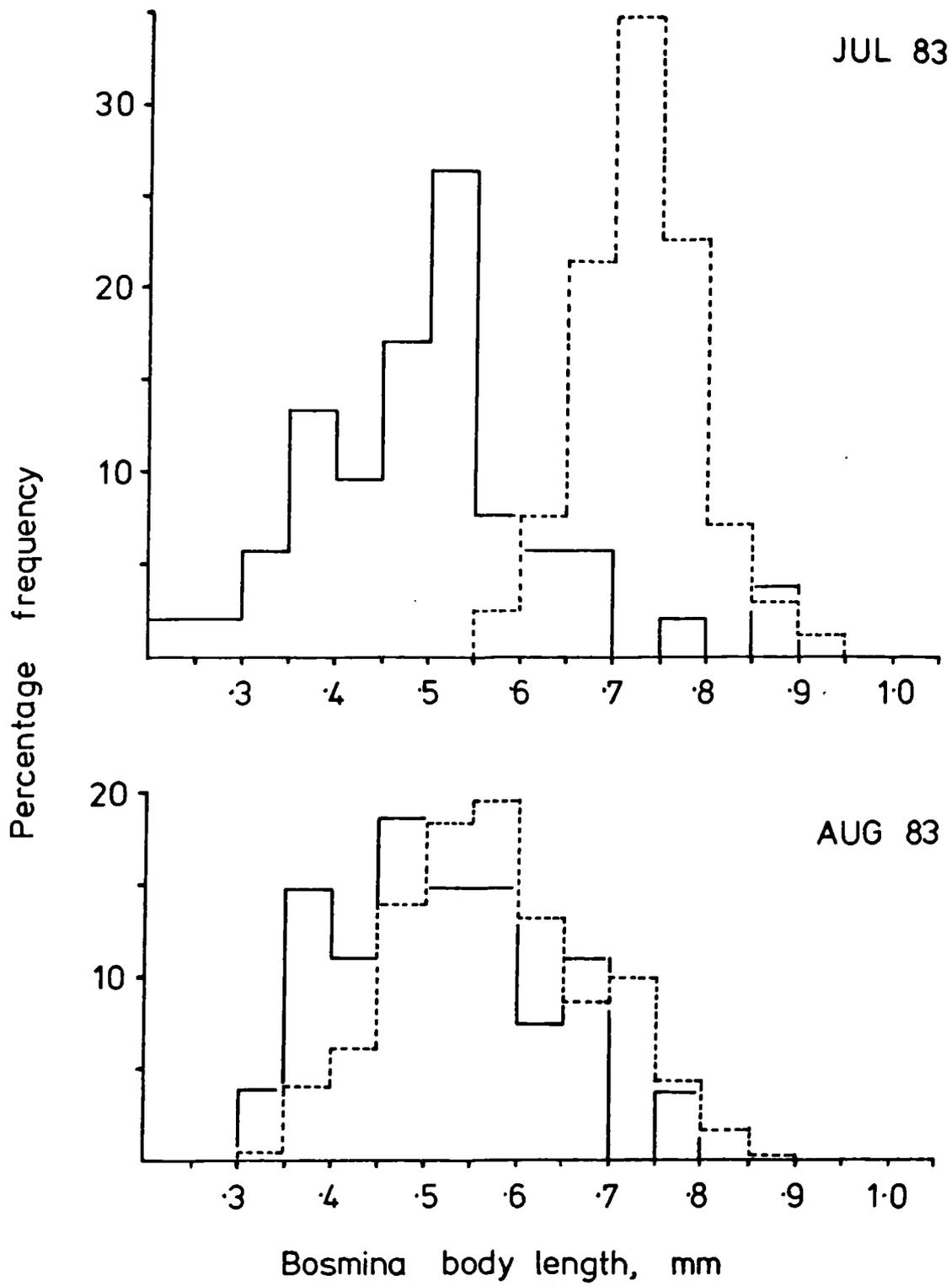


Fig. 3.8b

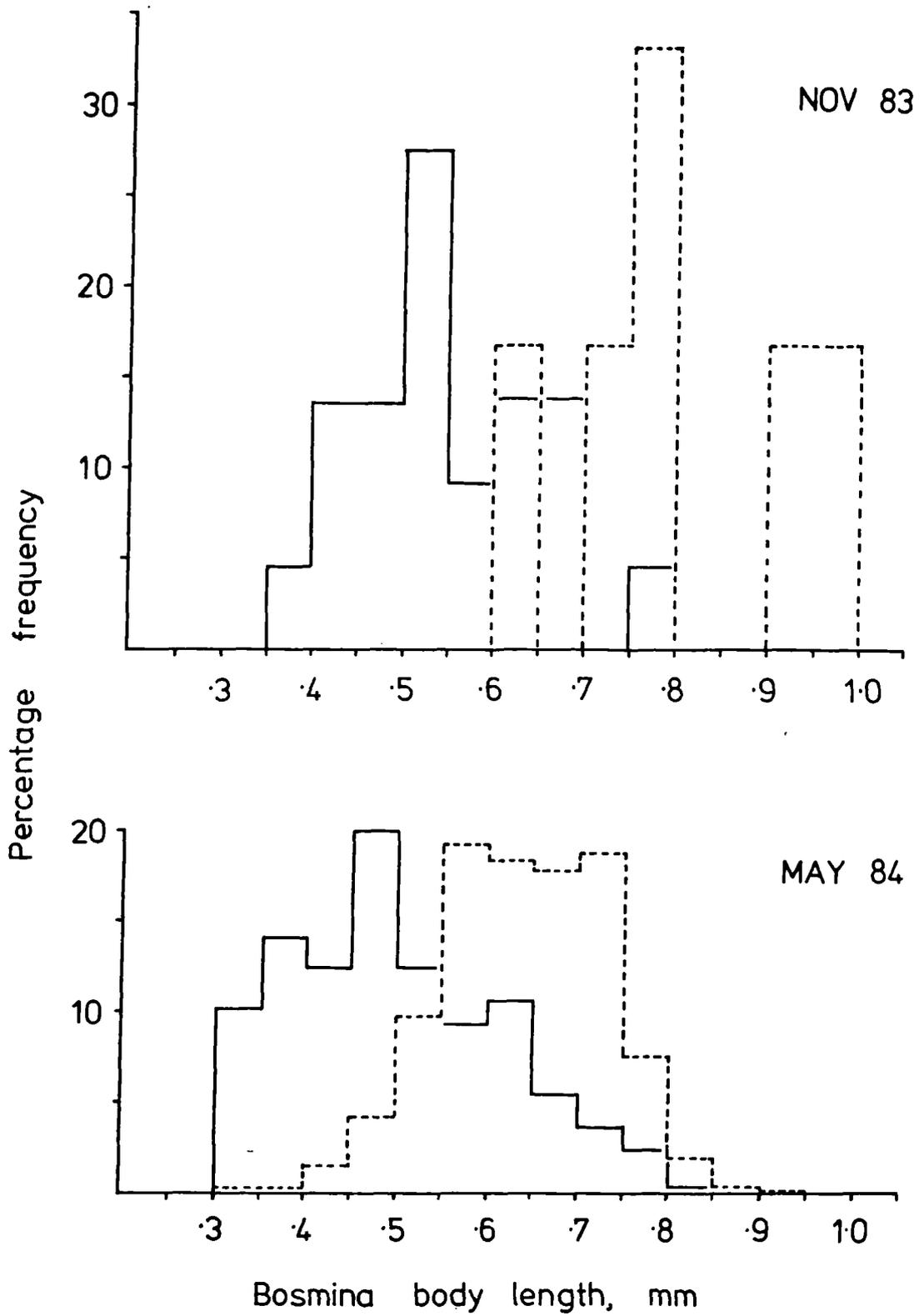


Fig. 3.8c

Table 3.9

Summary of results of Kolmogorov-Smirnov 2 sample tests comparing body length frequency distributions of *Bosmina* in powan stomachs and plankton samples.

Sample	n1	n2	Dmax.	Probability
Nov 82	338	374	0.279	p < 0.001
May 83	725	357	0.681	p < 0.001
Jul 83	168	53	0.807	p < 0.001
Aug 83	596	27	0.236	p > 0.1
Sep 83	98	27	0.162	p > 0.1
May 84 sn 1910		227	0.529	p < 0.001
May 84 st 2425		227	0.511	p < 0.001

n1,n2 = number of measurements in stomachs(1) and plankton(2)
Dmax. = largest difference in cumulative relative frequency distributions
Probability = probability of obtaining Dmax. for n1,n2 observations (probability levels are for two-tailed tests).

distributions could be demonstrated. In the remaining samples Bosmina which had been eaten by pwan were generally larger than Bosmina in the plankton (Table 3.9 and Figs. 3.8a,b,c).

3.3.3 Visibility of prey - fecundity.

Counts of gravid (and non - gravid) Bosmina from plankton and stomach samples were not independent. In all samples examined, gravid animals occurred more frequently in stomachs than in plankton (Table 3.10).

3.4 Feeding trials on Coregonus larva and fry.

Larvae - 1983 trials.

Coregonus larvae eleven days old which had been feeding on Loch Lomond plankton had diets which were numerically dominated by Diaptomus (Table 3.11). Diaptomus were taken more frequently and Bosmina and Daphnia less frequently than would be predicted if random encounters of larvae with prey led directly to ingestion (chi-squared = 16.6, d.o.f. 2, $p < 0.001$).

Larvae - 1984 trials.

Attack success rate (defined as the number of strikes which contacted prey) was low : larvae had a 0.05 attack success rate with Diaptomus on the first day of trials. On the second day, this was increased to 0.19. No strikes on Diaptomus were successful on the third day of the trials. Prey concentrations were lower on the third day. A general decrease in the distance of pursuit of prey was seen over the course of the trials, although this was not constant for all prey species, as Cyclops were pursued further than other prey. When Artemia nauplii were offered to larvae on the third day along with L. Lomond zooplankton, most strikes were directed at Artemia (Table 3.11b), although not in proportion to their abundance.

36-day old larvae (13.5 - 15.5mm total length) offered Artemia larvae

Table 3.10

Relative abundances of gravid and non-gravid
Bosmina in plankton and powan stomach samples.

May 83	count in plankton	count in stomachs (n=24)
gravid	38	1600
non-gravid	321	210
chi-squared value = 981, $p < 0.001$		
Jul 83	count in plankton	count in stomachs (n=3)
gravid	0	325
non-gravid	54	120
chi-squared value = 113, $p < 0.001$		
Aug 83	count in plankton	count in stomachs (n=5)
gravid	2	4003
non-gravid	29	208
chi-squared value = 458, $p < 0.001$		
Sep 83	count in plankton	count in stomachs (n=1)
gravid	1	400
non-gravid	22	0
chi-squared value = 401, $p < 0.001$		
seine May 84	count in plankton	count in stomachs (n=21)
gravid	36	9050
non-gravid	106	960
chi-squared value = 630, $p < 0.001$		
south May 84	count in plankton	count in stomachs (n=30)
gravid	36	13825
non-gravid	106	1134
chi-squared value = 839, $p < 0.001$		

Table 3.11

Summary of feeding trials on Coregonus larvae,
April 1983 - May 1984.

April 1983:

Gut contents from 25 11-day old larvae fed on
Loch Lomond zooplankton, composition :
Diaptomus 250, Bosmina 50, Daphnia 30.

15 empty guts. Total number of prey found = 100.
Diaptomus 93, Bosmina 6, Daphnia 1.

24 April 1984:

Water temperature 9 °C, 100 Diaptomus l.⁻¹
Naive larvae, unfed since hatch, 11-19 days old.

Total observation time = 35 minutes.
Number of larvae trying to feed = 7/12.

Considerations = 52, 17 of which had no further action.

Body lengths pursued : range 0-14 median 5

Total number of strikes = 136, contacts 7, ejections 5.

25 April 1984:

Water temperature 9 °C, 100 Diaptomus,
50 Daphnia, 10 Cyclops l.⁻¹.
Same larvae as previous day, 12-20 days old,
one day's experience of Diaptomus.

Total observation time = 72 minutes.

Number of larvae trying to feed = 7/12.

Total considerations = 101, 22 had no further action.

(59 Diaptomus,
26 Daphnia,
10 Cyclops,
5 debris).

Body lengths pursued : range 0-10 median 3

Total number of strikes = 78, contacts 17, ejections 6.

	strikes	contacts	ejects
Diaptomus	58	11	4
Daphnia	14	5	1
Cyclops	4	0	0
debris	2	1	1

Table 3.11 (cont.)

26 April 1984.

Water temperature 9 °C, 150 Diaptomus,
150 Daphnia, 10 Cyclops l⁻¹.

Same larvae as previous day, 13-21
days old, two days' experience of Diaptomus,
one of Daphnia and Cyclops.

Total observation time = 52 minutes.
Number of larvae trying to feed = 12/12.

Total considerations = 47, 17 had no further action.
(17 Diaptomus,
19 Daphnia,
10 Cyclops,
1 debris).

Body lengths pursued : range 0-7 median 2

Total number of strikes = 36, contacts 2, ejections 0.

	strikes	contacts	ejects
Diaptomus	20	0	0
Daphnia	11	2	0
Cyclops	4	0	0
debris	1	0	0

26 April 1984.

Water temperature 9 °C, 150 Diaptomus,
150 Daphnia, 10 Cyclops + 10 mls Artemia nauplii l⁻¹.

Same larvae as above, 13-21
days old, two days' experience of Diaptomus,
one of Daphnia and Cyclops, naive to Artemia.

Total observation time = 42 minutes.
Number of larvae trying to feed = 12/12.

Total considerations = 54, 13 had no further action.
(9 Diaptomus,
3 Daphnia,
3 Cyclops,
39 Artemia)

Body lengths pursued : range 0-1 median 0.5

Total number of strikes = 54, contacts 10, ejections 2.

	strikes	contacts	ejects
Diaptomus	1	0	0
Daphnia	3	0	0
Cyclops	0	0	0
Artemia	50	10	2

in excess after being starved for twenty-four hours were estimated to have satiation levels of 86 ± 4 nauplii ($n=12$). These were consumed in 14.7 ± 2.1 minutes, after which strike rate (but not consideration rate) fell sharply.

A number of 41-day old larvae were placed in a tank along with a laboratory-reared one year old pohan (130mm total length). Larvae suffered numerous mortalities from strikes by the larger fish, although few larvae were actually consumed as most were ejected after ingestion.

Fry feeding behaviour observations.

1983 : 60-day old fish were seen to attack prey from less than 2cm range by surging at prey with an open mouth. If prey were densely concentrated, fish were often distracted to either side after apparently fixing attention on one item. 80-day fish became noticeably more active when prey were introduced to the tank, but their feeding efficiency did not necessarily increase, as considered prey were ignored and prey within striking distance were by-passed for others further away. The larval behaviour of ejection of an ingested prey was observed in 80-day and older fish, with repeated ingestion and ejection of the same item commonly observed. 240-day fish which had been fed on assorted pond invertebrates (mainly Asellus, Daphnia and Chaoborus) picked out Asellus before turning to Chaoborus larvae and virtually ignoring Daphnia in the initial attacks (first ten minutes) on a fresh batch of food. Attacks on Chaoborus were directed upwards and were not always successful.

DISCUSSION

Fish predation on zooplankton has been studied widely, with considerable effort devoted to evaluating different aspects of the nature of successional force on the zooplankton community by selective piscine predators, (Brooks & Dodson, 1965; Zaret, 1972b; Kerfoot, 1971) and determination of the mechanisms responsible for observed predation patterns (Werner & Brooks, 1968; Hall, 1972; O'Brien et al., 1976; Confer et al., 1978; Mittlebach, 1981; Bence & Murdoch, 1986).

Ivlev's (1961) measure of electivity, E , was shown by Brooks (1968) to be dependent on the prey's body size. Captive alewives (Alosa pseudoharengus, Clupeidae) were shown to remove the largest size classes of the copepod Diaptomus minutus preferentially. Werner & Hall's (1974) study of size-selective predation upon Daphnia magna by juvenile bluegill sunfish (Lepomis macrochirus) demonstrated that where equal numbers of prey size classes were present, electivity was proportional to prey body size. Only when the largest prey size classes declined in abundance did the fish begin significant feeding on the smaller size categories.

Preference can take two forms as defined by Murdoch & Oaten (1975);

- (i) marked preference irrespective of availability,
- (ii) predator switching : preference switching to the most commonly available food, apparently related to experience and learning.

Murdoch et al. (1975) using guppies feeding on fruit flies and worms showed (ii) above. However, although the population of predators showed little preference when offered equal proportions of two prey, individual fish showed considerable variation i.e. the

proportion of specialists in the population changed.

In the situation where the diet of a predator is found to consist entirely of one prey type, then $\alpha_i = 1$. If food type i is not represented in the diet, then $\alpha_i = 0$. Strauss (1979) has criticized α_i for failing to distinguish between cases where food type i is very abundant but not eaten and the situation where food type i is rare and may be absent from the diet by chance. Chesson (1983) has suggested that in both of the above cases $\alpha_i = 0$ is an appropriate measure.

In the situation where prey of the type i are found in the diet but are so rare in the environment as to remain undetected by plankton sampling, accurate enumeration of preference is difficult, particularly if the prey was absent from plankton samples due to sampling selectivity. Chesson (1983) suggests increased sampling effort in cases such as these. However, it is likely that the overall preference pattern will remain unaltered.

Since α_i and ϵ_i are relative measures, the accuracy of comparison between samples will be influenced by absolute sample size. A 10% error in estimation of the most abundant prey would have a smaller effect on the calculated α_i than a 10% estimation error in the least abundant prey.

Feeding modes.

Although most fish planktivores have numerous fine gill rakers on their gill arches, filter feeding has not been demonstrated to be a preferred feeding method. On the contrary, most studies have indicated that freshwater fish are particle selectors. Seghers (1975) recorded feeding frequencies of Coregonus clupeaformis in laboratory feeding experiments using Daphnia magna as prey and found that

particle selection was the only feeding method used for all prey densities tested (up to 44 per litre). Fish fed by taking individual "nips" at prey, with as many as 600 prey consumed in a period of 15 minutes. No relation was found between prey size and gill raker spacing. A similar conclusion was reached by Kliewer (1970) in a study of the food of lake whitefish and gill raker spacing in populations from seven lakes in Manitoba, Canada. Wright *et al.*, (1983) using white crappies, Pomoxis annularis, trained to feed on large Daphnia magna investigated the retention of ingested prey by adding large concentrations of small-bodied items such as Bosmina along with the main prey. Assuming non-selective accidental ingestion of the smaller items in attacks on the Daphnia, they found that gill raker spacing seriously under-estimated the size of prey likely to be retained. Therefore small plankters effectively were immune from predation.

Filter feeding has been observed in clupeids (Blaxter & Holliday, 1958; Janssen, 1978) although particle selection is still the dominant feeding behaviour. Leong & O'Connell's (1969) study and O'Connell's (1972) laboratory studies of feeding in the northern Pacific anchovy showed that fish filter fed when high densities of small prey items (Artemia nauplii) were available, but began particulate feeding when large prey (adult Artemia) were available, even at low densities. This behaviour was thought to accumulate biomass at a greater rate than filter feeding, allowing fish to forage over a greater area per unit time and capture prey which could otherwise escape, particularly larger, mobile plankters. O'Connell (1972) concluded that because of the prey densities encountered in the ocean, particle selection was a necessity even for efficient filter feeders.

A study of the gill rakers of powan from Loch Lomond and Loch Eck

(Miller, 1984) indicated that fish from L. Eck had approximately two more gill rakers per gill arch than powan in Loch Lomond although individual gill raker spacing was not significantly different. Of the important planktonic prey species in Loch Lomond, Bosmina is the smallest, reaching a maximum length of 1.05mm. Bosmina less than 0.5mm in length were rarely eaten by powan, although Miller (1984) found that gill raker spacing was in the order of 0.7 - 0.9mm. The smallest Bosmina were eaten when there were few Bosmina in the plankton (August '83) and the clearest evidence of size selectivity occurred at maximum plankton abundance.

As in this study, Northcote & Clarotto (1975) found that the contents of the stomachs of the salmonid species of six lakes in British Columbia did not always tally with the species taken in contemporaneous plankton samples. Species which appeared in fish stomachs were absent from plankton samples. Bluegill sunfish (Lepomis macrochirus) were shown to detect ehippial Daphnia magna at greater distances than non-gravid Daphnia (Tucker & Woolpy, 1984). The eye-spot diameter of Bosmina and other cyclomorphic Cladocera has been proposed as the critical determinant in differential predation rates by planktivores (Zaret, 1972; Zaret & Kerfoot, 1975). Confer et al. (1978) were unable to detect any change in reactive distance of fish to differing eye spot pigmentation and concluded that the magnitude of the change was insufficient. Kettle & O'Brien (1978) showed that pigmented pond zooplankton were more susceptible to lake trout predation than typically non-pigmented lake forms. Species such as Daphnia in which morphs with peaked and elongate helmets occur are thought to reduce invertebrate predation without increasing their detectability to vertebrate predators (O'Brien et al., 1978). In the present study, both Daphnia morphs suffered size selective predation by powan. In the one sample where the peaked morph was larger than

the round helmeted morph (July '83) the size distribution of Daphnia in powan stomachs reflected this. In November '83 peaked Daphnia in powan stomachs were larger than those in the plankton.

Zooplankton in Loch Lomond has been studied by Chapman (1965, 1969, 1972) and Maitland et al., (1981). Reference is made to the zooplankton of the loch in Slack et al., (1957), Hamilton (1958) and Goldspink & Scott (1971). Goldspink & Scott (1971) described the vertical migration patterns exhibited by the instars of Chaoborus in the Lochan Dubh beside Loch Lomond. Similar migrations of Chaoborus larvae have been observed in Loch Lomond in this study and by Scott (pers. comm.).

The problem was to accurately estimate what prey was available to fish in the environment. Counts from qualitative plankton samples generally reflected the seasonal abundances of the zooplankton species recorded by other workers (Chapman, 1969, 1972; Maitland, 1981). Unpublished data (Hamilton, pers. comm.) also reflects the same general seasonality, with the only anomaly being the failure of these samples to detect large numbers of Daphnia in December 1983. The composition and abundance of the loch plankton changes in a cyclical manner, with exact timing depending on environmental factors.

The spatial discontinuity of plankton has been described for some freshwater systems (Hutchinson, 1967; George 1972,1981). Any short term benefit to predators in energy gain per unit time of feeding on patches must be offset by the cost of locating the patches (increased searching time). Detailed information on zooplankton distribution is required to allow reliable estimates of foraging effectiveness of powan in Loch Lomond. The volume of water "searched" by fish will be directly proportional to their swimming speed, irrespective of the

irrespective of the model of visual field used.

Other workers have reported that the first food of Coregonus larvae consisted of copepods and particularly Diaptomus in the first few weeks after hatching (Bronisz, 1979; Marciak, 1979; Dabrowski, 1981; Teska & Behmer, 1981; Salojarvi, 1982). Bronisz (1979) observed that coregonine larvae selected the largest diaptomids and daphnids from the plankton. However, Kokova (1978) found that C. lavaretus larvae feeding on large Daphnia died as a result of gut blockage. Kokova's (1978) larvae took Moina, Paramecium and rotifers. Drenner et al., (1981) have suggested that the escape ability of Diaptomus is superior to that of many Cladocera, and the reason for the predominance of this species in the diet of newly-hatched Coregonus larvae may lie in the relative scarcity of alternative zooplankton prey at hatching time. Most larvae hatch with a reserve of food in the yolk sac. In Lough Neagh, early hatching larvae of C. autumnalis pollan were found to survive for a longer period with little food than late hatching, but did not start exogenous feeding until 3-4 days after hatching, while late hatching began to feed immediately (Dabrowski, 1981). Larvae of C. autumnalis pollan were found to require a greater threshold of light intensity than fry for feeding activity to take place, with the result that in Lough Neagh's heavily coloured water, the limits of visual feeding for larvae were estimated to be in the 1.6-2.8m depth range in March and 3-4m in April. By May, although the fish had a lower visual threshold, the light attenuation had increased to reduce the feeding depth to 3-3.5m (Dabrowski, 1982, 1984). Hartmann (1983) found that C. fera larvae could ingest Artemia nauplii in the dark, but at concentrations which they were unlikely to encounter in natural conditions. Powan in Loch Eck apparently do not eat zooplankton as adults. The question of their larval feeding habits is one which deserves attention.

CHAPTER 4. A consideration of bioenergetic relations for
powan from Loch Lomond and Loch Eck.

INTRODUCTION

Despite the economic importance of coregonines to many northern latitude freshwater fisheries, little is known about the seasonal interaction between food intake, reproduction, metabolism and somatic growth. Dabrowski's studies on pollan C. autumnalis pollan Thompson from Lough Neagh, N. Ireland and vendace C. albula in Polish lakes are the exception (Dabrowski, 1982a,b, 1983, 1985).

The steady accumulation of information on the biology of powan C. lavaretus in Loch Lomond has reached the stage at which a consideration of the fishes' energy budget is feasible, provided that certain assumptions are made. The cyclical nature of reproduction and associated events has either been described (Fuller et al., 1976; Scott, 1979; McCulloch, 1981; Brown, 1983; Rashid, 1984; O'Connell, 1984) or is under investigation (McCulloch, in prep.; Brown, in prep.) and can be included in the overall consideration of the seasonal cycle. The purpose of this chapter is to provide the basis for a reasonable estimate of the daily food intake of powan from Loch Lomond and Loch Eck using information from previous chapters and additional information from the literature on closely related species. Bioenergetic studies of fish populations require the quantification of a number of parameters which may be difficult to measure even under laboratory conditions. Previous studies in this area have followed either a laboratory based approach using species which were easily maintained in the laboratory (Wootton, 1977; Wootton et al., 1980a; Allen & Wootton, 1982a, 1984) or by combining laboratory and field

studies on annually reproducing wild populations to determine the allocation of energy into growth, reproduction and metabolism (Elliott 1975a,b,c 1976; Adams *et al.*, 1982; Jobling, 1982; Dabrowski, 1983, 1985; Basimi & Grove, 1985a,b,c). A general energy budget for a specified time period is given by Ricker (1978):

$$C = F + U + \Delta B + R$$

$$\text{and : } R = R_s + R_a + R_d$$

where :

C is the total energy content of the food, F is the energy value of the faeces, U is the energy value of the excretory products, ΔB is the total change in energy value of body materials (growth or depletion of energy content) including reproductive products released by the fish, R is the total energy of metabolism made up of ;

R_s , the energy released in the course of metabolism in unfed and resting fish, R_a , the energy required for locomotion and other activity; R_d , the energy required for the digestion, mobilisation and deposition of food materials (including the post-prandial increase in oxygen consumption).

In most cases, a number of assumptions are included in the model. Verification of the estimates used in the analysis can be achieved by estimating food consumption directly from changes in the weight of food found in powan stomachs over a period of time, determining the "value" of the food and comparing this to observed growth, reproduction and metabolism. A comparison of the consequences of the observed diets in the two lochs is then possible by examining condition and reproductive activity of the two powan populations.

MATERIALS & METHODS.

Components of the energy budget were assessed as follows.

4.1 Total energy content of food. C.

Consideration of the ingested food's value to the fish may be in terms of total food energy (KJ), particular dietary components which have a measurable energetic content available for anabolism or catabolism (protein, carbohydrate, lipid), or constituents of the diet which do not contribute significantly to the energy content of the food but are essential (minerals, vitamins, water). Total calorific content of food was used as a measure of food value in this analysis.

Calorific value of prey items.

Fresh samples of powan prey organisms were obtained from Loch Lomond plankton and preserved in 4% formaldehyde solution. If fresh specimens were not available prey were taken from preserved fish stomach contents, taking only whole undamaged individuals for analysis. Sorted material was washed in distilled water, dried in an oven for 24 hours at 60°C, cooled and ground into a homogeneous powder with a mortar and pestle. Compacted pills were made from the ground powder using a pill press. The pills were cooled to -20°C and freeze-dried for a minimum of 12 hours. On removal the pills were stored in a desiccator. The number of pills made was governed strictly by the amount of material available subject to the selection criteria above, but an optimum of ten pills was required for each prey type and sample date for calorific and ash determination. Ash values were obtained by combustion of weighed pills in a muffle furnace at 550°C for five hours. After cooling in a desiccator weights were

recorded to the nearest 0.0001mg on a Mettler Me22 electronic balance.

Calorific values were determined using a Phillipson-type microbomb calorimeter (Gentry Instruments, Aiken, S. Carolina) connected to a Vitatron pen recorder. The calorimeter is a non-adiabatic type, but in a room of constant temperature and with shielding, errors due to heat loss by convection from the bomb are negligible (Phillipson 1964). The bomb was charged to 25 atmospheres oxygen and checked for leaks by immersing in cold water. This also served to equilibrate the temperature of the bomb and the cold junction of the thermocouple. Pre-fire and post-fire corrections together with the wire correction (associated with the small heat change due to ignition) were applied to all calculations as applicable in accordance with the manufacturers' recommendations. No correction was made for the effect of nitric acid formation in combustion as this was assumed to be negligible. The apparatus was calibrated using pills of benzoic acid (26.440 KJg^{-1}) and the calibration was checked prior to each set of firings.

Additional corrections to the observed heat rise were applied since the material combusted contained appreciable amounts of calcium carbonate and in some cases silicates. The maximum endothermy observed when calcium carbonate is combusted can be calculated as 1.79912 Jmg^{-1} and 0.174 Jmg^{-1} for vitrification of silica (Weast 1976). Major element analysis of Pisidium and debris samples was carried out by X-ray fluorescence (St. Andrews University Geology Department, Philips PS 1212), calibration achieved by reference to a monitor (H12) and 25 international rock standards.

Calorific values were expressed as Joules per milligram dry weight of

food material, corrected for endothermy. This includes the ash dry weight.

Mean dietary energy was calculated for each sample date by using the relative dry weight proportions of prey items in the 'average' diet (Chapter 2) and the appropriate calorific values obtained. 'Average' diet was assumed to consist of the median counts of prey types for each sample as recorded in Chapter 2, Table 2.4. This necessarily implies considerable variation around the 'average' value, due to individual variation in prey composition and quantity of food consumed.

Note that only the feeding fish in a sample are included in the analysis.

Dry weights of prey groups sorted from earlier analyses were obtained by drying known numbers of whole prey items to constant weight. Samples were oven dried at 60°C for 24 hours, cooled in a desiccator and weighed to the nearest 0.0001g. Mean weight estimates of prey groups were obtained from:

$$\text{mean individual weight} = \text{total dry weight of } n \text{ items}/n$$

Since the variability in the individual mean weights obtained is unknown, but particularly influenced by small numbers of exceptional prey items, the range of means is given as a variability estimate along with the overall mean for that group in a sample.

4.2 Daily ration estimation.

Although direct measurements of gastric evacuation rate, k (the amount of food evacuated from the stomach in unit time), for captive adult powan were not possible, preliminary estimates of k were

obtained from Windell (1978) for related species (mainly Salmo trutta) feeding on similar foods over the temperature range 5 - 15 °C, and Enderlein (1981b) for Coregonus albula feeding on zooplankton at temperatures of 8-14 °C. These estimates assume an exponential function for gastric evacuation, i.e. :

$$S_t = S_o e^{-kt}$$

where: S_t, S_o are the weights of food in the stomach at times t and o respectively and k is the gastric evacuation rate.

Estimates of k used :

Water temperature °C	Windell estimate k1	Enderlein estimate k2
5	0.12	0.25
7.5	0.14	0.33
10	0.18	0.45
15	0.30	0.68

A check on the validity of the evacuation rate estimates, k , was possible by examining the data for diel catches of powan in Loch Lomond outlined in Chapter 2 and assuming that decreases in stomach contents over non-feeding periods (generally the hours of darkness) followed an exponential decay.

Data obtained from the routine nettings in this study were used to estimate the population daily mean dry weight of food in stomachs, S , by S' , the observed mean dry weight of food in stomachs for a sample.

The validity of this estimate is likely to vary seasonally. For a fish which feeds primarily by sight, the principal determinant of available feeding time will be environmental light conditions. The potential daily period available for feeding was calculated, based on the assumption that the hours between -12° solar altitude (nautical twilight) at 56° N (i.e. before dawn to after dusk) indicate the approximate limits of visual predation in powan. This serves as a rough indication of potential feeding time (t), since the light environment in fresh water can change drastically both quantitatively and qualitatively over a small change in spatial and temporal dimensions. Three feeding time values were used to calculate estimates of the average daily food intake.

The first was half the estimated potentially available feeding period (t/2), the second used all the potentially available feeding period (t) and the third used the full 24-hour period. The latter would be realistic only if;

- (i) S' , the observed mean dry weight of food in stomachs is close to the true value of S, the daily population mean dry weight of food in stomachs;

or

- (ii) fish are able to feed throughout the 24-hour period because of light conditions (eg in late May-early June) or by using non-visual means of detecting food.

The above assumptions were used to calculate daily food consumption according to the following models:

1. Modified Bajkov method, (Eggers 1979, Pennington 1985).

$$D = 24Sk$$

where: S = population daily mean dry
weight of food in stomachs, g
k = stomach evacuation rate
D = daily food ration, g dry weight

2. Maximum meal estimate.

$$D = (\text{max. wt.})n$$

where: max. wt. = maximum dry weight of food
calculated from regressions
in Table 2.15
n = number of meals in a
24 hour period (Elliott 1973)

The maximum dry weights of food material in powan stomachs on sample dates (found from regressions obtained in Chapter 2) were used as an indication of meal size to give another estimate of daily food consumption. The number of meals in a day was obtained from Elliott (1973).

Therefore the estimates of daily food intake used were :

$$D1 = (t/2)S'k1 \qquad D2 = tS'k1$$

$$D3 = (t/2)S'k2 \qquad D4 = tS'k2$$

$$D5 = n(\text{maximum meal}) \qquad D6 = 24S'k2$$

As well as overall daily ration estimates for the whole catch at sampling time, direct comparisons of food consumption for fish of the same sex and age classes were made for female 3+ and 4+ powan from Loch Lomond and Loch Eck, since analysis of covariance of data for females from the two lochs had indicated parallel slopes for the separate regressions of the dry weight of food on corrected fish weight (Chapter 2). Fish were aged by A. McCulloch and E.A.R. Brown and access to their data is gratefully acknowledged. Mean weight changes within the cohorts were determined for each sample. Spawning output was assessed similarly.

Maintenance ration C_{main} was calculated for powan of given body weights according to the equations in Elliott (1976c) for brown trout, defined in Elliott (1976c) as the daily energy intake required to satisfy all metabolic demands including activity but with no net growth or loss of total body energy, i.e. :

$$C_{\text{main}} = F + U + R_s + R_d + R_a .$$

Water temperatures within the distribution of powan were taken from Table 1.3 and surface water temperatures recorded at sampling time.

An estimate of metabolic rate was given by the multiple regression equation of Wohlschag (1957) relating log of oxygen uptake to fish weight, swimming speed and water temperature for Canadian whitefish.

Swimming speeds of powan were assumed to be similar to those recorded by Wohlschag (1957) and used by Dabrowski (1985) for pollan and vendace. Total energy of respiration (Resp) was therefore :

$$\text{Resp} = \text{Rs} + \text{Rd} + \text{Ra} .$$

Energy excreted as faeces and urine (F + U) was assumed to account for 30% of the total energy ingested over the range of temperatures encountered (Elliott, 1976; Giussani & De Bernardi, 1977; Dabrowski, 1985).

4.3 Feeding rates.

In the special case where rate of food intake, a , equals stomach evacuation rate, k , there should be no net change in amount of food in the stomach. Feeding rates necessary to balance stomach evacuation rate were calculated for a variety of powan prey organisms using the individual dry weights obtained in the previous section. Results were expressed in numbers of prey required per minute to maintain stomach contents at an equilibrium level.

4.4 Somatic growth : length/weight relationship.

Growth may be described in terms of body length or weight. Somatic growth may be defined as the growth of all body tissues and is accumulative over an animal's life cycle, while non-somatic growth (of gonads and storage materials) may be accumulated and lost in a cyclical process. Under certain circumstances body tissues may be catabolised, making the distinction less certain. Powan length and weight data were analysed by the following methods to determine changes in somatic relationships.

4.4.1 Condition factors.

In order that results from this study might be directly compared to previous studies (Rashid, 1984; O'Connell, 1984) the mean monthly "Condition Factor", CF and the "Somatic Condition Factor" SCF were computed for each sex as follows:

$$CF = \frac{\text{corrected total weight (g)} \times 10^2}{\text{total length (cm)}^3}$$

$$SCF = \frac{(\text{corrected total weight} - \text{gonad weight}) \text{ (g)} \times 10^2}{\text{total length (cm)}^3}$$

where:

corrected total weight = (total weight - weight of gut contents).

Somatic condition factor may be more useful than condition factor since the large changes in weight associated with gonad development are removed. However, indices such as the above have been the subject of some discussion in the past, (Iles, 1984) largely because the index is a ratio derived from two dependent variables. It is important to note that changes in "condition" may arise in a number of ways. Increases in length (somatic growth) and changes in weight resulting from deposition, mobilisation and shedding of somatic material may be occurring at the same time, giving a net result which is difficult to interpret. Thus condition factors CF can be influenced by major changes in any or all of the body organs and do not indicate growth directly, but describe the relative relationship between the variables in question.

4.4.2 Condition estimated by regression.

For any stage in the life history of a fish, its weight (W) will vary as a power of the length (L):

$$W = aL^b$$

Where $b = 3$, isometric growth is described. Since W and L are measured with some error and a functional regression is required, the recommendations of Ricker (1973) were followed to produce geometric mean (GM) regressions of log weight on log length. The data was separated by sex and loch. Although a geometric mean regression as described by Ricker (1973) may estimate the functional relationship between weight (W) and length (L) without bias, at present no statistical technique analogous to analysis of covariance exists for simultaneous comparison of several regressions. Analysis of covariance was carried out on the log transformed weight and length data.

4.5 Non-somatic growth : the reproductive cycle.

The reproductive state of fish was determined by two methods :

4.5.1. Visual assessment of gonads.

The reproductive state of fish could be judged by inspection of the gonads during dissection. This method was adequate for separating mature and immature fish at most times of year and could discern different stages of gonadal maturation in females around spawning time.

testes - creamy white when mature, becoming deep pink/red
in post-spawning and early maturation stages;

ovaries - yellow/orange, compact granular appearance in early maturation stages;
 immediately pre-ovulating - opaque yellow/orange oocytes enclosed by mesovarium;
 ovulating - translucent yellow/orange oocytes within mesovarium (ovulated fish - ova free in body cavity);
 spent - most ova lost from body cavity;
 atretic - ovary resorbing unshed oocytes of various sizes, numerous blood vessels ramify the organ.

4.5.2 Somatic Gonadosomatic Index (SGSI). The ratio of gonad weight to somatic weight was expressed as a percentage by calculating:

$$\text{SGSI} = \frac{\text{gonad weight g.}}{(\text{corrected total weight} - \text{gonad weight}) \text{ g}} \times 100$$

The mean monthly somatic gonadosomatic index was calculated for males and females. The index indicates changes in the gonad weight relative to the somatic weight of the fish and is thus preferred to the commonly used gonadosomatic index. Although somatic gonadosomatic index is subject to all the criticisms outlined for condition factors, the method successfully follows the gross reproductive changes in powan and allows assessment of that portion of non-somatic growth produced as gonad in females.

RESULTS.

4.1 Calorific value of prey items.

Calorific values obtained for the prey groups tested ranged from 15.96 - 28.32 corrected Jmg^{-1} ash-free dry weight for Loch Eck material, and 17.34 - 25.95 corrected Jmg^{-1} ash-free dry weight for Loch Lomond material (Table 4.1). Chaoborus larvae and some of the September '83 stomach contents gave highest corrected calorific values (Jmg^{-1}). Chironomid larvae of the genus Procladius gave the highest corrected Jmg values for Loch Eck prey. When calorific values for prey species were converted to Jmg^{-1} ash-free dry weight, most prey items, both benthic and planktonic, fell into the 23-25 Jmg^{-1} range.

All the Loch Eck prey groups showed evidence of seasonal changes in calorific value. The two main chironomid prey groups, C. anthracinus and Procladius spp. gave the highest ash-free calorific values in May samples, with the lowest values recorded from February samples. Values for Pisidium showed less seasonal fluctuation. The highest calorific values for Cyclops were obtained for the February and May samples which contrasted strongly with low August/September values. Debris burned to give calorific values comparable to those obtained for Pisidium. Calorific values for planktonic prey collected from Loch Lomond were in some cases higher than the values obtained for Loch Eck prey groups (eg Chaoborus). Samples of material taken from preserved stomach contents combusted to give calorific values higher than those obtained from comparable plankton samples.

Table 4.1

Variation of calorific value of prey groups from Loch Lomond and Loch Eck.

Sample date	no. dets.	J mg ⁻¹ dry wt. mean ± s.d.		mean % ash	mean wt pill mg	Corrected J mg ⁻¹ ash-free dry wt. mean ± s.d	
L. Eck : Pisidium							
Feb 84	3	8.17	0.13	57.3	10.75	21.55	0.32
Sep 84	1	7.10		70.9	7.10	24.38	
Jan 85	3	7.14	0.22	70.0	7.34	23.80	0.74
Feb 85	2	7.75	0.23	67.4	8.61	23.78	0.75
Mar 85	2	7.47	0.04	67.9	6.93	23.28	0.13
May 85	3	8.02	0.34	-	8.97	22.91	1.03
Aug 85	3	6.55	0.26	74.9	9.99	26.09	1.10
L. Eck : Chironomus anthracinus larvae							
Feb 84	2	12.28	1.87	-	12.81	20.45	3.23
Sep 84	3	13.12	0.27	42.8	6.22	22.94	0.49
Jan 85	5	12.38	0.20	45.0	5.39	22.51	0.38
Feb 85	3	13.40	0.08	43.5	6.42	23.72	0.15
Mar 85	2	15.21	0.43	34.8	7.94	23.32	0.68
May 85	3	16.86	0.15	38.5	7.14	27.42	0.25
Aug 85	3	12.58	0.17	46.6	7.33	23.56	0.33
L. Eck : Chironomus anthracinus pupae							
May 85	3	17.01	0.66	37.7	7.20	27.30	1.09
L. Eck : Procladius spp.							
Feb 84	3	19.30	0.79	14.8	12.85	22.65	0.94
Sep 84	3	20.06	0.48	-	6.23	23.60	0.57
Jan 85	5	20.54	0.91	15.0	5.39	24.16	1.08
Feb 85	3	21.71	0.08	-	7.51	25.54	0.09
Mar 85	3	21.14	0.54	10.1	6.88	23.49	0.61
May 85	3	24.07	0.55	-	7.43	28.32	0.65
Aug 85	3	18.97	0.24	20.6	7.91	23.89	0.31
L. Eck : Cyclops viridis							
Feb 84	3	17.31	0.51	22.3(?)	7.15	22.35	0.66
Sep 84	1	12.56		-	0.95	16.16	
Jan 85	2	16.56	0.49	-	3.23	21.17	0.63
Feb 85	1	17.72		-	3.15	22.69	
Mar 85	2	16.57	0.16	-	3.90	21.28	0.21
May 85	1	18.02		-	4.15	23.47	
Aug 85	3	12.50	0.14	-	4.71	15.96	0.18

Table 4.1 (cont.)

Variation of calorific value of prey groups from Loch Lomond and Loch Eck.

Sample date	no. dets.	J mg ⁻¹ dry wt.		mean % ash	mean wt. pill mg	J mg ⁻¹ ash-free dry weight.	
		mean	± s.d.			mean	± s.d.
L. Eck : Debris							
Feb 84	1	8.96		60.2	9.95	22.48	
Sep 84	3	9.27	0.16	56.0	12.51	21.06	0.36
Jan 85	4	8.74	0.04	61.3	8.65	22.58	0.10
Feb 85	2	9.12	0.01	60.1	9.69	22.87	0.03
Mar 85	2	9.78	0.85	60.9	7.08	25.00	2.18
May 85	2	9.29	0.58	55.5	11.00	20.87	1.31
Aug 85	3	6.34	0.20	68.5	8.35	20.12	0.64

L. Lomond : September '83

Chaoborus	2	23.66	0.05	-	6.51	25.58	0.05
Daphnia	3	20.82	0.91	-	1.21	22.51	0.99
H'pedium m	1	22.18		-	1.69	23.97	
H'pedium w	1	16.04		-	3.33	17.34	
Leptodora	1	19.83		-	1.79	20.23	
Byt'phes	2	20.27	0.90	-	2.56	21.92	0.98
Stomach 1	3	24.01	0.89	7.56	4.65	25.95	0.97
Stomach 2	2	23.18	0.04	7.45	7.65	25.06	0.04
Stomach 3	2	22.48	0.21	7.53	3.57	24.30	0.23
Stomach 4	2	21.42	1.18	6.48	4.49	23.15	1.27
Stomach 5	1	23.78		4.49	4.34	25.70	

Loch Lomond : May 83

Stomach 1	2	22.15	0.62	-	5.73	23.94	0.67
Stomach 2	2	20.63	0.41	-	8.28	22.30	0.67
Stomach 3	2	21.54	0.30	8.59	9.50	23.56	0.33

H'pedium m,w = Holopedium with matrix (m), without matrix (w).

Byt'phes = Bythotrephes

Numerical composition of stomach contents analysed:

- September 83
1. Bosmina, Bythotrephes, Leptodora 40:1:1
 2. Bythotrephes, Leptodora, Daphnia 1:1:1
 3. Bythotrephes, Leptodora, Holopedium 17:2:1
 4. Daphnia, Leptodora, Bythotrephes 3:2:1
 5. Cyclops spp.

- May 83
1. Bosmina
 2. Bosmina, Holopedium 12:1
 3. Bosmina, Bythotrephes 8:1

Ash accounted for between 4.49-8.59% of the total dry weight of planktonic prey groups, while for Procladius and Cyclops in Loch Eck samples, ash was determined as 10 - 22% of the dry weight. C. anthracinus and Pisidium were composed of approximately 40% and 70% ash respectively. Therefore the energy values (expressed as Jmg^{-1} corrected for endothermy) indicate that planktonic prey have a higher energetic profitability per unit dry weight than most of the prey groups found in stomachs of powan from Loch Eck.

4.2 Estimates of daily food consumption. It should be emphasised that few fish in winter samples from Loch Lomond had much food in their stomachs. The highest proportions of full or nearly-full stomachs occurred in powan caught in May and July. Powan in Loch Eck had little food in their stomachs in January and February samples, but most fish had relatively full stomachs in the other samples from the rest of the year (see also Chapter 2). This analysis deals with feeding fish.

4.2.1 Mean calorific energy of food found in powan from Loch Lomond ranged from 19-26 corrected Jmg^{-1} dry weight. The highest energy values occurred around spawning time when powan eggs made up most of the diet and the lowest values occurred in the pre-spawning period when benthic food including Pisidium made up the bulk of the diet (Table 4.1). In Loch Eck, the mean powan diet energy (excluding debris) ranged from 8.09-14.78 corrected Jmg^{-1} since prey with a high ash content were eaten throughout the year. The diet with the highest energy content per unit dry weight was taken in May when many chironomid pupae were eaten (Table 4.2).

Table 4.2

Analysis of diet : mean composition of L.Eck stomach contents as determined by calorimetric analysis. Data for prey groups are expressed as Joules.

Date	Jan4	Feb4	Sep4	Jan5	Feb5	Mar5	May5	Aug5
ntot.	27	15	16	24	16	19	18	20
mean food dry wt. mgs	39.6	107.4	49.5	55.5	70.0	66.5	102.0	173.9
st. dev.	31.7	46.4	37.9	59.5	51.3	79.4	95.0	124.0
Procladius spp.	-	371	132	152	182	89	77	360
Chironomus anthracinus	-	668	194	433	595	587	497	111
chironomid pupae	-	-	-	-	-	-	611	-
chironomid (others)	345*	11	0	0	5	12	14	11
Pisidium spp.	146	246	196	88	126	162	256	942
Cyclops spp.	28	97	6	13	11	20	15	19
Miscell.	0	11	0	5	1	7	5	13

ntot = number of fish examined

mean dfwt = mean dry weight of food material (mg)

st. dev. = standard deviation of the mean

(Miscell. = Trichoptera, Plecoptera, Hirudinea, Ostracoda)

* = all chironomids.

4.2.2 Comparison of estimated stomach evacuation rates with the data obtained from diel catches (Table 4.3) was limited by the small number of fish taken. Stomach evacuation rates in the diel samples were examined below.

May 1983 sample.

Assuming the fall in stomach contents during non-feeding periods follows :

$$\ln S_0 - \ln S_t = kt$$

all fish had full stomachs before being caught and were caught at the same time, with a stomach evacuation rate of 0.33, the fishes whose mean weight of stomach contents at 1100 was 0.038g had been in the net for 2.5 hours.

August 1983 diel samples.

The highest mean dry weight of stomach contents occurred in the sample from 2130-0000 hours, the lowest occurred from 0000-0530 hours. Nautical twilight (-12° solar altitude) occurred at 2200 and 0400 hours (approximately). Assuming an exponential fall in stomach contents (as above) for the period of darkness, it may be seen that ;

the highest dry weight of stomach contents at 0000 hours was 0.190g in a 206g fish, which would give 0.0045g remaining at 0530, assuming no further feeding between 0000 and 0530 hours. The observed dry weights of stomach contents at 0530 were 0.0001g from a 262g fish and 0g from a 363g fish.

Since most fish were feeding in August, it is likely that feeding ceased sometime after nautical twilight. Estimated stomach evacuation

Table 4.3

Diel changes in dry weights of stomach contents of powan in Loch Lomond.

Sample date	surface water temp. °C	net soak	observed mean dry wt. food g	n	mean fish weight g	predicted max. mean dry wt. food g
26 May 83	8.0	2100-1100	0.038	87	186.1	0.085
22 Aug 83	14.5	2130-0000	0.034	12	230.0	0.173
23 Aug 83	14.5	0030-0530	0.000	2	140.7	0.101
23 Aug 83	14.5	0600-1000	0.001	5	269.6	0.206
23 Aug 83	14.5	1030-1230	0.025	2	91.4	0.063
6 Dec 83	7.3	1230-1530	0.009 mal	3	227.4	0.099
			0.003 fem	5	262.8	0.116
	7.3	1600-1930	0.002 fem	1	244	0.107
			0.001 fem	1	310	0.139
7 Dec 83	7.3	0030-1130	0.000 fem	1	278	0.123
14 May 84	8.0	seine 2200	0.091	25	209.5	0.097
15 May 84	8.0	south	0.089	31	184.5	0.085
10 May 85	9.5	2200-1000	0.014	12	209.5	0.112
11 May 85	9.5	1900-2300	0.013	13	186.6	0.098
12 May 85	9.5	0000-0730	0.012	13	230.0	0.123
12 May 85	9.5	0800-1315	0.004	10	210.4	0.112
12 May 85	9.5	1345-1800	0.029	3	171.3	0.090

mal = males, fem = females

predicted maximum dry weights of food from Table 2.15;

$$(\log y = -4.2625 + 1.0907 \log W + 0.735 \log T)$$

net soak = time of net set - time of net lift

(seine approx. 20 mins., south 1630-1030)

rate of 0.68 was of the correct magnitude for observed data.

December 1983 diel samples.

Highest mean dry weight of food in stomachs occurred from 1230-1530 hours. The mean dry weight food in males' stomachs was greater than that in females', despite males being smaller on average (but only 11 fish taken). Very little food was recorded from fish caught between 1600 hours on the 5th and 1130 hours the following day. Feeding activity was greatest during the hours of daylight.

May 1984.

Seine-netted sample 14 May 1984 taken at 2200 hours;

mean dry weight food observed = .091g (mean fish weight =209.5g)

max. dry weight food predicted = .097g.

South basin sample 15 May 1984 taken from overnight gill net raised 1030 hours;

mean dry weight food observed = .089g (mean fish weight =184.5g)

max. dry weight food predicted = .085g

(darkness may not occur at this time of year).

It may be inferred that peaks in stomach fullness occurred after dusk and about mid-morning in May 1984. It is unknown if powan maintained the observed stomach fullness throughout the day.

May 1985.

No significant differences were observed between the mean weights of food in powan stomachs from catches taken at 1000, 2300 and 0730 hours. Mean weight of food in stomachs was significantly lower in the 1315 hours catch. The highest mean weight of food recorded in this sampling period was from three fish taken between 1345 and 1800 hours.

At no time did the weights of stomach contents approach the predicted maxima for the weight of fish caught (Table 4.3). Plankton samples from this date had the lowest counts of zooplankton recorded during the study.

4.2.3 Daily food consumption estimates (D1-D6) were obtained using the data summarised in Table 4.4. The monthly estimates of daily ration varied considerably (Table 4.5). Initial comparisons between different estimates of daily food consumption (D1-D6) and daily maintenance requirement (Cmain.) indicated that estimates D1, D2, D3 and D5 were insufficient to balance the maintenance energy required in any month (Table 4.5). Food consumption estimates D4 and D6 can be considered further. D4 gave a net annual energy deficit for Loch Lomond powan while Loch Eck fish had a net surplus. D6 indicated a net surplus of energy for both lochs compared to the maintenance requirement. D6 was used as the estimate of daily energy intake, Cest., in compiling the consumption estimates for the 3+ and 4+ age-classes of female powan in the two lochs.

4.2.4 The daily energy budgets of female powan assigned to the 3+ and 4+ age classes from the two lochs are indicated in Tables 4.6, 4.7 and Figs. 4.1, 4.2. In Loch Lomond from January until April the food ingested was lower in energy value than that required by routine maintenance. From May until October an excess of energy was provided by the food, with maximum rations providing approximately twice the energy required for maintenance (Table 4.6). Energy intake from October to December was insufficient to meet maintenance needs. Powan in Loch Eck were estimated to exceed their maintenance energy requirements from January to August inclusive, with the remaining

Table 4.4

Summary of information used to construct estimates of food consumption for powan in the wild.

	Mean fish Mo wet wt. g	Mean water temp. °C	Stomach evacuation rate k1 k2		meals per day n	t hours	mean dry wt. food g	max. dry wt. food g
Loch Lomond								
J	223.1	6.0	0.12	0.25	1	10.5	0.0313	0.0829
F	177.0	5.1	0.12	0.25	1	12.0	0.0168	0.0566
M	187.7	5.0	0.12	0.25	1	14.2	0.0203	0.0594
A	219.5	6.8	0.14	0.33	1	17.3	0.0334	0.0899
M	186.1	7.5	0.14	0.33	2	21.2	0.0378	0.0812
J	190.0	11.0	0.18	0.45	2	23.0	0.0450	0.1127
J	193.3	13.5	0.30	0.68	2	21.2	0.0579	0.1351
A	230.6	14.5	0.30	0.68	2	17.4	0.0508	0.1734
S	244.0	14.0	0.30	0.68	2	14.6	0.0777	0.1793
O	216.1	11.0	0.18	0.45	2	12.7	0.0094	0.1296
N	215.7	10.5	0.18	0.45	1	10.9	0.0235	0.1247
D	230.6	7.3	0.14	0.33	1	10.3	0.0304	0.1004
Loch Eck								
J	218.5	5.0	0.12	0.25	1	10.5	0.0809	0.1195
F	191.6	3.0	0.12	0.25	1	12.0	0.0796	0.1186
M	202.1	4.0	0.12	0.25	1	14.2	0.0605	0.1168
A	215.0	6.5	0.14	0.33	1	17.3	0.0750	0.1111
M	232.2	8.0	0.14	0.33	2	21.2	0.0949	0.1139
J	215.0	12.0	0.18	0.45	2	23.0	0.1200	0.0970
J	215.0	14.0	0.30	0.68	2	21.2	0.1200	0.0938
A	204.2	14.0	0.30	0.68	2	17.4	0.2118	0.0894
S	193.9	13.5	0.30	0.68	2	14.6	0.0386	0.0860
O	235.0	11.0	0.18	0.45	2	12.7	0.0500	0.1073
N	278.3	9.5	0.18	0.45	1	10.9	0.0771	0.1295
D	270.6	7.5	0.14	0.33	1	10.3	0.0707	0.1330

Mo = month of sample. Lomond (June) and Eck (April, June, July and October) food figures were estimated.

k1, k2 estimated from data in Windell (1978), Enderlein (1981).

n = Number of meals per day estimated from Elliott (1975).

Maximum dry weight of food calculated from regressions of maximum stomach contents vs. fish weight (Table 2.15).

t = maximum available time for feeding, using nautical twilight (-12° solar altitude) as light threshold for feeding.

Table 4.5

Estimates of daily ration for powan from routine samples. Elliott's (1976) values of the maintenance ration, C_{main} , for brown trout of the same weight and at the same temperature are shown for comparison.

Mo	Mean diet energy Jmg^{-1}	Daily food consumption (Joules)					max. meal	S. trutta (Elliott) C_{main} .
		modified Bajkov method		k2		D5		
		D1	D2	D3	D4	D5	D6	
Loch Lomond								
J	26.00	513	1016	1068	2136	2154	4883	4754
F	22.00	266	533	554	1108	1245	2218	3292
M	22.00	380	760	793	1585	1306	2679	3358
A	20.50	829	1658	1954	3908	1844	5422	5465
M	21.50	1195	2390	2843	5686	3492	6437	5208
J	21.50	2003	4005	5007	10014	4845	10449	7637
J	21.50	3959	7918	8973	17946	5810	20316	10057
A	22.00	2917	5834	6612	13224	7628	18240	12721
S	22.50	3828	7657	8678	17357	8069	27445	12584
O	19.40	209	419	521	1042	5030	1969	8397
N	19.00	438	876	1095	2190	2369	4822	7957
D	19.00	416	833	981	1963	1908	4575	5973
Loch Eck								
J	11.91	607	1214	1346	2691	1423	5781	3743
F	13.04	747	1494	1557	3114	1546	6228	2177
M	13.02	671	1243	1398	2796	1521	4726	2830
A	13.60	1236	2472	2911	5823	1511	8078	5178
M	14.78	2082	4164	4906	9812	3367	11109	6462
J	13.50	3353	6705	8384	16767	2619	17496	9292
J	11.00	4198	8396	9515	19029	2063	21542	11463
A	8.09	4472	8944	10137	20274	1447	27964	11036
S	10.90	921	1841	2089	4177	1875	6867	10088
O	12.00	686	1373	1714	3429	2756	6480	8933
N	12.00	908	1815	2269	4538	1554	9992	8644
D	12.00	612	1223	1442	2884	1595	6719	6863

Mo = month of sample.

Mean dietary energy (corrected Jmg^{-1} dry weight of food) calculated from composition of diets using calorimetric determinations given in Table 4.1.

D1-D4 = estimated daily energy intake, using modified Bajkov method, with :

$$D1 = (t/2)S'k1, D2 = tS'k1, D3 = (t/2)S'k2, D4 = tS'k2$$

D5 = estimated daily energy intake using maximum dry weight of food regressions as meal size indicator and number of meals per day as in Table 4.1.

D6 = maximum modified Bajkov estimate, = $24S'k2$

C_{main} = Maintenance daily ration determined for hatchery-reared brown trout, *S. trutta*, (Elliott 1976).

Table 4.6

Energy budget for female 3+,4+ powan in Loch Lomond.

	Mean fish weight	Mean dry wt. food	D6 dry wt. intake	food energy intake Cest.	Elliott daily energy Cmain	Wohlschag daily resp.1 energy	net weight change	total wet wt. food
Mo	g	g	g day ⁻¹	J day ⁻¹	J day ⁻¹	J day ⁻¹	g mo ⁻¹	g mo ⁻¹
Loch Lomond 3 +								
J	150	0.0228	0.1368	3557	3577	5370	-31	31.6
F	142	0.0143	0.0858	1888	2812	4699	-8	18.5
M	139	0.0142	0.0852	1874	2708	4596	-4	20.3
A	140	0.0206	0.1632	3345	3924	5180	1	37.7
M	143	0.0346	0.2740	5892	4289	6384	3	65.3
J	157	0.0316	0.3413	7338	6636	9699	14	81.4
J	195	0.0319	0.5206	11193	10122	14246	38	124.1
A	235	0.0290	0.4733	10413	12900	17365	40	112.9
S	243	0.0760	1.2403	27908	12546	17609	8	286.2
O	246	0.0146	0.1577	3059	9239	14471	3	37.6
N	252	0.0145	0.1566	2975	8924	14552	6	36.1
D	254	0.0324	0.2566	4876	6414	10583	2	61.2
Loch Lomond 4 +								
J	225	0.0359	0.2154	5600	4783	7707	-55	51.4
F	217	0.0230	0.1380	3036	3809	6857	-8	29.7
M	214	0.0230	0.1380	3036	3686	6751	-3	32.9
A	200	0.0300	0.2376	4870	5103	7117	-14	56.7
M	198	0.0498	0.3944	8480	5452	8531	-2	94.0
J	205	0.0427	0.4612	9915	8077	12301	7	106.4
J	225	0.0703	1.1473	24667	11248	16183	20	273.6
A	255	0.0317	0.5173	11382	13700	18676	30	123.4
S	283	0.0902	1.4721	33121	14037	20170	28	339.4
O	296	0.0180	0.1944	3771	10589	17064	13	46.7
N	307	0.0181	0.1955	3714	10321	17350	11	45.1
D	308	0.0403	0.3192	6064	7411	12566	2	76.1

Table 4.7

Energy budget of 'small' 3+ and 'large' 4+ female powan in Loch Eck.

	Mean	Mean	D6	food	Elliott	Wohlschag		
	fish	dry wt.	dry wt.	intake	daily	daily	net	total
	weight	food	intake ₋₁	Cest. ₋₁	energy	energy	weight	wet wt.
Mo	g	g	g day ⁻¹	J day ⁻¹	Cmain. ₋₁	resp 2	change	food
					J day ⁻¹	J day ⁻¹	g mo ⁻¹	g mo ⁻¹
Loch Eck 'small'								
S	100	0.0252	0.4113	4388	6187	5616	*	69.3
O	111	0.0250	0.2700	3240	5139	5383	11	33.5
N	128	0.0260	0.2808	3370	4877	5828	17	33.7
D	144	0.0410	0.3247	3897	4312	5431	16	33.6
J	150	0.0661	0.3966	4938	2859	4651	6	41.0
F	150	0.0683	0.4098	5385	1827	4244	0	42.7
M	115	0.0349	0.2094	2762	1885	3556	-35	26.0
A	124	0.0450	0.3564	4847	3492	4234	9	48.8
M	138	0.0655	0.5188	7501	4403	5312	14	48.2
J	145	0.0850	0.9180	12393	6951	7457	7	110.2
J	149	0.1050	1.7136	18850	8749	8141	4	212.5
A	155	0.1274	2.0792	17403	9007	8432	6	261.0
Loch Eck 'large'								
S	295	0.0524	0.8552	9125	13733	14726	*	168.5
O	310	0.0450	0.4860	5832	10956	13442	15	60.3
N	325	0.0489	0.5281	6337	9691	13368	15	63.4
D	334	0.0724	0.5734	6881	8015	11493	9	59.3
J	337	0.1145	0.6870	8553	5105	9567	3	71.0
F	284	0.1052	0.6312	8294	2886	7496	-53	65.7
M	290	0.0653	0.3918	5168	3664	8107	6	48.6
A	307	0.0850	0.6732	9156	6682	9496	17	80.8
M	315	0.1146	0.9076	13124	8090	11083	8	85.3
J	320	0.1450	1.5660	21141	10956	15096	5	187.9
J	327	0.1800	2.9376	32314	15614	16399	7	364.3
A	332	0.2134	3.4827	29150	15790	16623	5	436.8

Fig. 4.1 Estimated daily ration (D6) in KJ for female powan in Loch Lomond = solid line and symbols.
Elliott's maintenance ration (Cmain.) is shown by the broken line and empty symbols.
Fish aged 3+ = circles , 4+ = squares.
x = D6 ration estimate for 4+ females from seine (sn) and south (st) catches of May '84.
All estimates adjusted to mean cohort weight for sample.

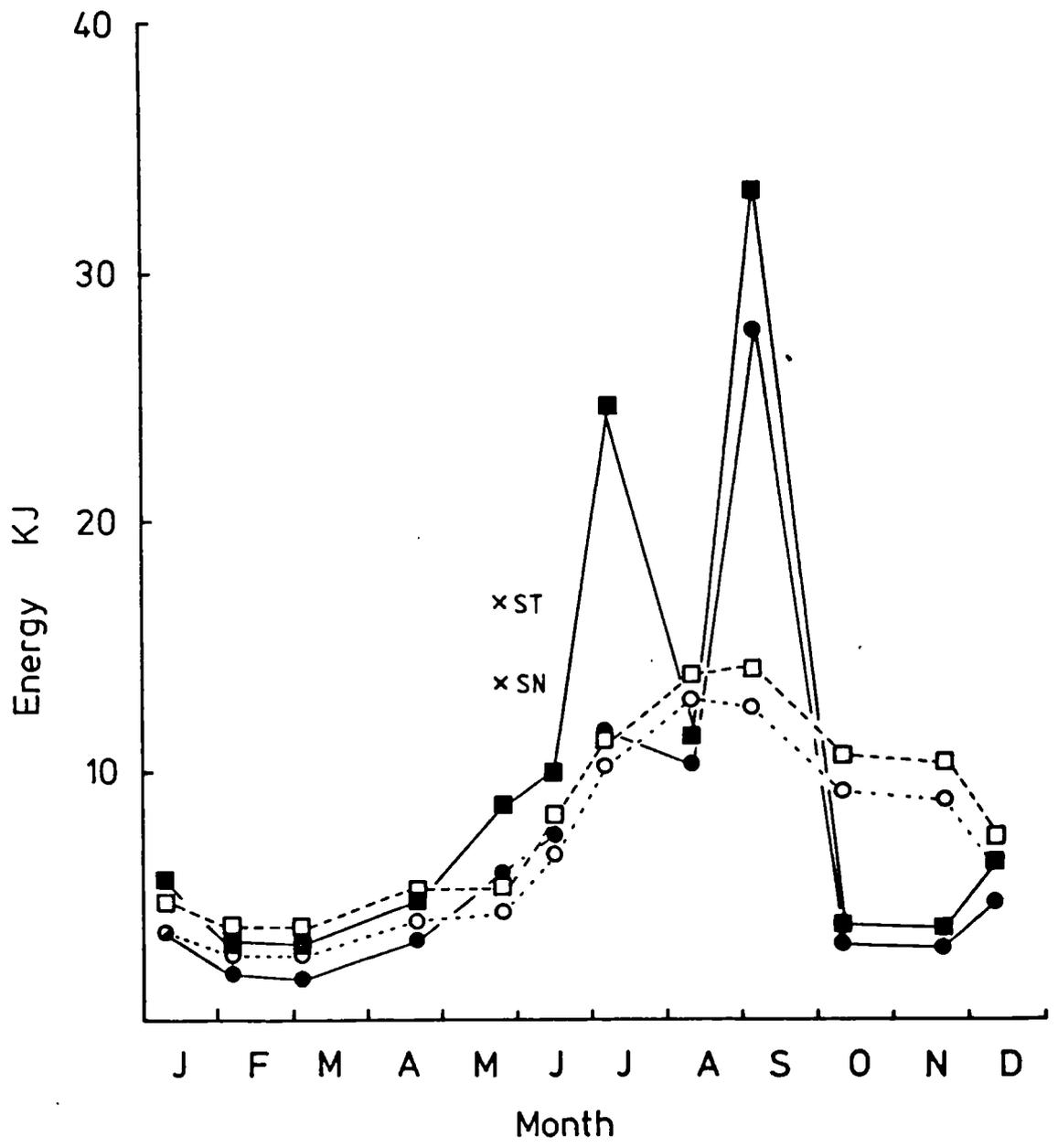


Fig. 4.1

L. Lomond, females

Fig 4.2 Estimated daily ration (D6) in KJ for female powan in Loch Eck = solid line and symbols.
Elliott's maintenance ration (Cmain.) is shown by the broken line and empty symbols.
Fish aged 3+ = circles, 4+ = squares.

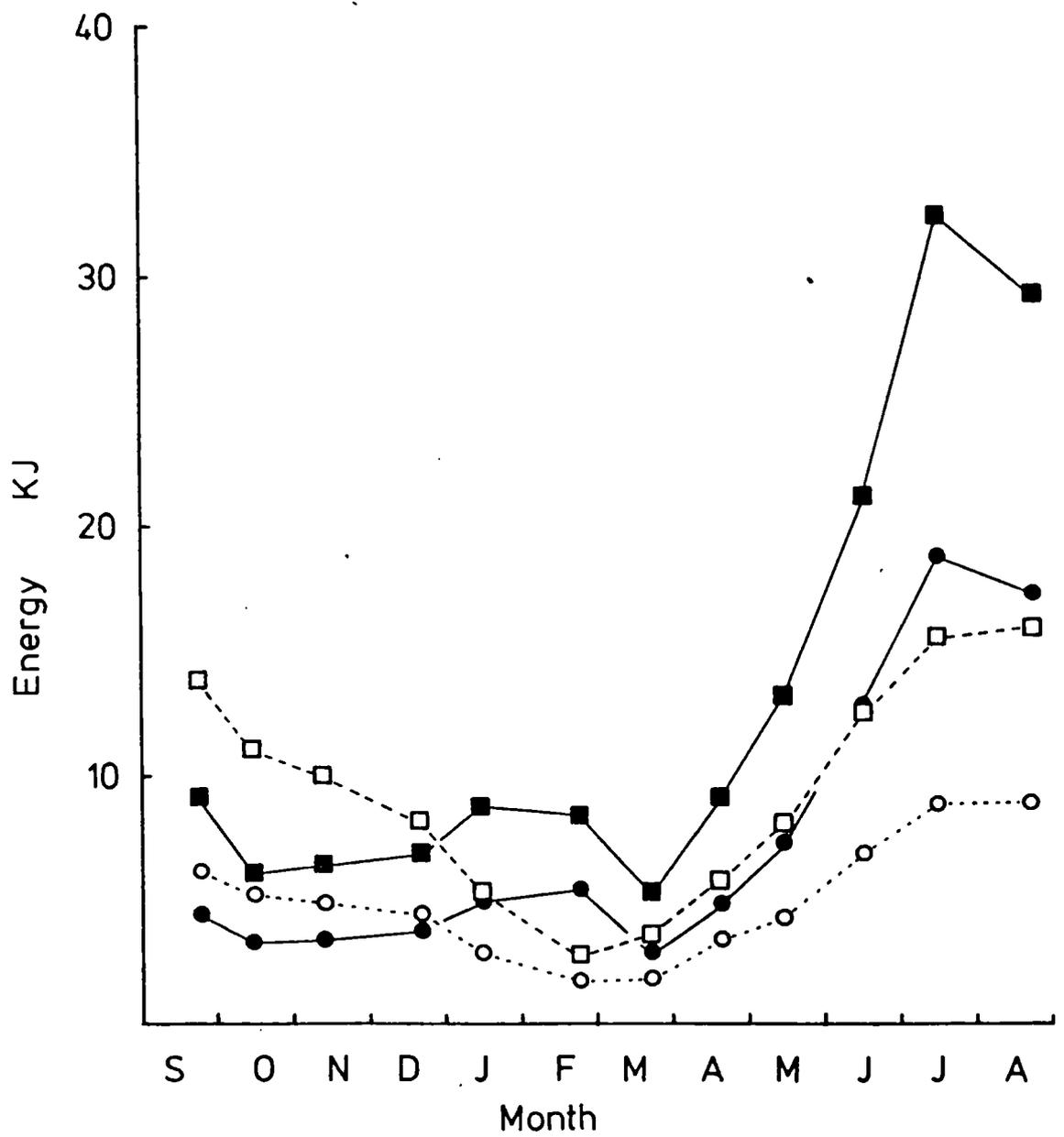


Fig. 4.2

L Eck, females

months requiring more energy for maintenance requirements than was obtained from ingested food (Table 4.7).

4.2.5 Maintenance and respiration energy (Cmain., resp. and Rmax.).

In Loch Lomond, calculated maintenance energy values (Cmain.) were consistently lower than calculated total respiratory energy (resp.) for the water temperatures and swimming speeds used (Table 4.8). This is an anomalous situation since maintenance energy supposedly includes total respiration energy plus energy excreted and egested. Wohlschag's respiration estimates (resp. 1) for Canadian whitefish exceeded Elliott's estimates of the maximum respiratory energy, Rmax., in hatchery trout for all but the higher water temperatures (June to October) when the Wohlschag total respiration estimate tended to be less than Elliott's maximum respiration estimate (Table 4.8). If similar average swimming speeds for powan in Loch Eck were assumed at the corresponding temperatures, energy of respiration was much greater than estimated maintenance energy (resp 1, Table 4.9 and Cmain., Table 4.7). However if swimming speeds were lower than those estimated in Loch Lomond (arbitrarily taken as approximately half the Loch Lomond swimming speeds) the respiration energies fall to levels of similar magnitude to maintenance requirements (resp. 2, Table 4.7 and 4.9). Annual consumption and production estimates are summarised in Table 4.10. For powan in Loch Lomond, annual food consumption for females in the 3+ and 4+ year classes was 913g and 1275g wet weight respectively. In Loch Eck the corresponding totals were 961g and 1692g. In view of the estimates used and their potential errors it would be wrong to say that large differences in total annual energy

Table 4.8

Energy equivalent of oxygen consumption rate for povan feeding in Loch Lomond calculated according to Wohlschag's (1957) multiple regression equation :

$$Y = 0.891 x_1 + 0.0243 x_2 + 0.0138 x_3 - 0.8687$$

Mo	mean fish wt. g	mean water temp. °C	mean swimming speed m min ⁻¹	total energy (Wohlschag) resp.1 KJ day ⁻¹	Elliott (1976) Rmax. KJ day ⁻¹
Loch Lomond 3+					
J	150	6.0	3	5.370	2.5
F	142	5.1	2	4.699	1.9
M	139	5.0	2	4.596	1.8
A	140	6.8	3	5.180	2.5
M	143	7.5	6	6.384	3.2
J	157	11.0	10	9.699	8.5
J	195	13.5	12	14.246	15.5
A	235	14.5	12	17.365	21.0
S	243	14.0	12	17.609	21.0
O	246	11.0	10	14.471	14.0
N	252	10.5	10	14.552	11.0
D	254	7.3	6	10.583	5.0
Loch Lomond 4+					
J	225	6.0	3	7.707	3.2
F	217	5.1	2	6.857	2.7
M	214	5.0	2	6.751	2.2
A	200	6.8	3	7.117	3.0
M	198	7.5	6	8.531	4.3
J	205	11.0	10	12.301	10.5
J	225	13.5	12	16.183	18.0
A	255	14.5	12	18.676	22.6
S	283	14.0	12	20.170	23.0
O	296	11.0	10	17.064	16.8
N	307	10.5	10	17.350	12.5
D	308	7.3	6	12.566	5.5

Y = log O₂ consumption rate, mgs per hour,
 x1 = log weight, g, x2 = swimming speed,
 metres per min, x3 = water temperature, °C.

Table 4.9

Energy equivalent of oxygen consumption rate
for povan feeding in Loch Eck
calculated according to Wohlschag's
(1957) multiple regression equation :

$$Y = 0.891 x_1 + 0.0243 x_2 + 0.0138 x_3 - 0.8687$$

	mean fish wt. Mo g	water temp. °C	swimming speed		Tot. resp. energy (Wohlschag, 1957)		Elliott (1976) Rmax. KJ day ⁻¹
			1 m min ⁻¹	2 m min ⁻¹	resp 1 KJ day ⁻¹	resp 2 KJ day ⁻¹	
Loch Eck 'small'							
S	100	13.5	12.0	6.0	7.857	5.616	8.4
O	111	11.0	10.0	5.0	7.121	5.383	6.2
N	128	9.5	10.0	5.0	7.709	5.828	4.2
D	144	7.5	6.0	3.0	6.423	5.431	3.2
J	150	5.0	2.0	1.0	4.919	4.651	2.1
F	150	3.0	1.0	0.5	4.365	4.244	1.0
M	115	4.0	2.0	1.0	3.760	3.556	1.0
A	124	6.5	3.0	1.5	4.605	4.234	2.2
M	138	8.0	6.0	3.0	6.283	5.312	3.5
J	145	12.0	12.0	6.0	10.431	7.457	8.4
J	149	14.0	12.0	6.0	11.389	8.141	13.8
A	155	14.0	12.0	6.0	11.796	8.432	13.5
Loch Eck 'large'							
S	295	13.5	12.0	6.0	20.600	14.726	22.5
O	310	11.0	10.0	5.0	17.781	13.442	13.0
N	325	9.5	10.0	5.0	17.683	13.368	9.5
D	334	7.5	6.0	3.0	13.593	11.493	6.5
J	337	5.0	2.0	1.0	10.118	9.567	3.5
F	284	3.0	1.0	0.5	7.708	7.496	1.5
M	290	4.0	2.0	1.0	8.574	8.107	1.6
A	307	6.5	3.0	1.5	10.328	9.496	4.2
M	315	8.0	6.0	3.0	13.109	11.083	6.0
J	320	12.0	12.0	6.0	21.118	15.096	16.5
J	327	14.0	12.0	6.0	22.942	16.399	23.4
A	332	14.0	12.0	6.0	23.254	16.623	23.6

Y = log O₂ consumption rate, mgs per hour,
x₁ = log weight, g, x₂ = swimming speed,
metres per min, x₃ = water temperature, °C.

Table 4.10

Annual energy budget for female powan 3+,4+ from
L. Lomond and L. Eck.

	Lomond		Eck	
	3+	4+	'small'	'large'
D6 estimate annual ration wet wt. food g	913	1275	961	1692
D6 estimate annual ration KJ per year	2580 (3253)	3600 (4702)	2723	4745
Maintenance ration Cmain. KJ per year	2573	3005	1826	3402
Physiologically useful energy ($\Delta B = C - F - U - R$) KJ per year	7 (680)	595 (1697)	896	1343
.....				
Observed mean 'growth' of age class per year	3+	4+	'small'	'large'
total length mm	35	20	*?	*?
somatic weight g	60	31	60	35
gonad spawned g	32	55	35	53
energy content of mature ovaries KJ	236	405	258	390

Loch Lomond figures in brackets indicate estimates based on projected consumption assuming similar feeding levels to those observed in July and September 1983.
Loch Eck calculations were based on the same stomach evacuation rates as L. Lomond, i.e. assuming no effect of debris on stomach evacuation rate.
Energy content of ovaries based on 115 oocytes per g ovary and energy equivalent of 64 J per oocyte.

input exist between the two populations. Rather, a difference in the rate at which food is available over the year can be seen (Figs 4.1-4.2).

4.3 Feeding rates.

The feeding rates required to maintain stomach contents at equilibrium levels are inversely proportional to individual prey dry weight (Table 4.11). At a stomach evacuation rate of 0.18 and assuming sub-satiation constant feeding rate, 417 Bosmina must be consumed per minute if the stomach contents are not to decline (Table 4.12). Feeding on Chaoborus at the same rate requires the capture of 8.4 animals per minute, while fish eating larger items such as Pisidium or C. anthracinus larvae require 3 - 4 such items per minute.

4.4 Length/weight relationship.

4.4.1 Condition factors.

Differences between condition and somatic condition factors largely reflect gonad development, although other factors (principally lipid mobilisation and deposition) are also involved. Seasonal variation of condition factors is shown for mature males and females from Loch Lomond (1982-1984) and Loch Eck (1984-1985) in Figs. 4.3-4.6.

Condition factor, CF.

Loch Lomond females showed highest condition in November 1982 and in August 1983 (Fig. 4.3). A slight decrease in condition factor occurred until spawning time in January when condition fell steeply. This decline in condition continued in post-spawning females to

Table 4.11

Estimates of prey dry weights in samples.
Means and ranges of weights are shown (mgs).

Loch Eck benthos.

Sample date	Pisidium	Cyclops	Procladius	C. anthracinus
Jan 84	1.786	0.300		
	1.052	0.083	-	-
	0.100	0.033		
Feb 84	1.350	0.114	0.590	1.612
	0.887	0.037	0.340	1.145
	0.160	0.022	0.069	0.842
Sep 84	1.336	0.133	0.333	0.400
	0.740	0.095	0.228	0.161
	0.050	0.078	0.114	0.083
Jan 85	1.800	0.167	0.698	0.927
	0.970	0.077	0.332	0.715
	0.183	0.024	0.057	0.182
Feb 85	1.975	0.100	0.558	1.128
	1.002	0.067	0.361	0.804
	0.043	0.050	0.129	0.213
Mar 85	2.486	0.175	0.636	1.245
	1.143	0.081	0.300	0.799
	0.700	0.050	0.100	0.383
May 85	1.885	0.300	1.630	6.040
	1.331	0.079	0.331	(1.048) 1.255
	0.200	0.056	0.125	(pupa) 0.100
Aug 85	2.021	0.100	0.421	2.375
	1.031	0.072	0.327	1.033
	0.490	0.048	0.100	0.300

Table 4.11 (cont.) Estimates of individual prey dry weights. Means and ranges of weights are shown (mgs).

Loch Lomond plankton.

Sample date	Prey species or group	mean dry wt. (mg)	
May 83	Bosmina as main (>90%) component,	0.0072	n=1329
Sep 83	Combinations of (Bythotrephes, Leptodora, Daphnia)	0.060	n=3500
	Cyclops viridis	0.0103	n=6680
Nov 83	Daphnia	0.0364	n= 22
		0.0138	n=2774
		0.0053	n= 76
	Chaoborus larvae	0.371	n= 600
		0.348	n=1305
		0.305	n= 250
Cyclops viridis	0.065	n= 67	
Jan 84	Chaoborus larvae	0.373	n= 790
		0.326	n=2756
		0.234	n= 200
	Pisidium	1.000	n= 2
		0.600	n= 39
		0.440	n= 14
Cyclops viridis	0.110	n= 10	
	0.062	n=1607	
	0.005	n= 4	

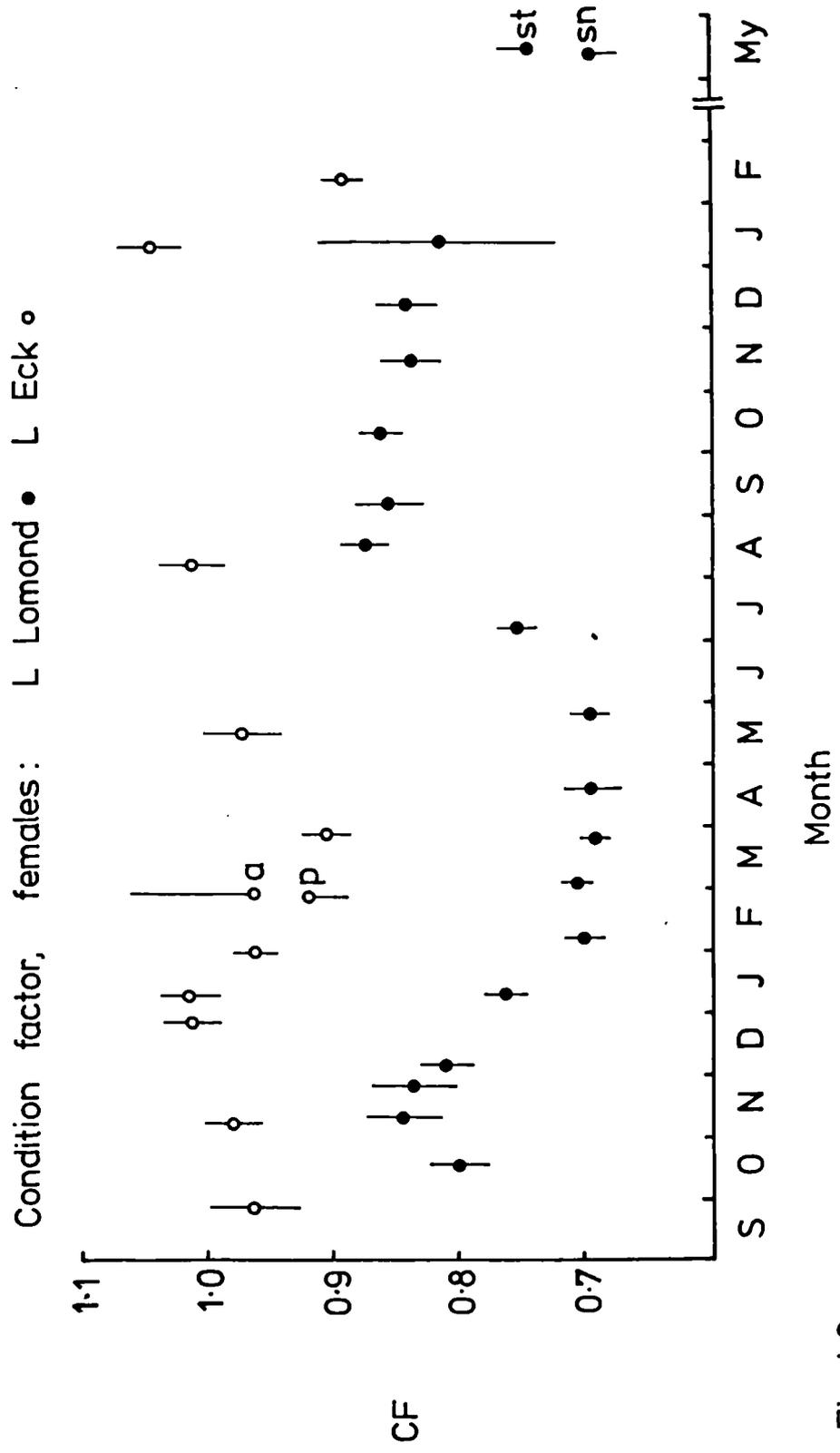
Table 4.12

Feeding rate of powan. When the rate of food intake, a , is equal to the rate of stomach evacuation, k , there is no net change in the weight of stomach contents.

The numbers of prey required per minute to satisfy the equilibrium condition described above, assuming a constant feeding rate are shown for values of (k, a) .

Prey	Individual dry weight mgs.	Absolute value of ingestion and evacuation rate k, a					
		0.12	0.18	0.30	0.45	0.68	0.8
Chaoborus	0.330	6.1	8.4	14	21	32	-
Cyclops viridis	0.065	31	46	77	116	174	-
Chaoborus/ C. viridis	mix. (2:1)	8.3	12.5	21	31	47	-
Bosmina	0.007	278	417	695	1042	1574	-
By' trephes	0.100	20	30	50	75	113	-
Bosmina/ By' trephes	mix. (20:1)	173	259	432	647	978	-
Leptodora	0.040	50	75	125	188	283	-
Daphnia	0.014	145	217	362	543	821	-
Byth/Lept/ Daphnia	mix. (1:1:1)	33	50	83	125	188	-
Pisidium	1.000	2	3.5	5	7.5	11.3	13.3
Chironomus anthracinus	0.900	2.2	3.3	5.6	8.3	12.6	14.8
Procladius	0.320	6.3	9.4	16	23	35	41
C. viridis	0.075	27	40	67	100	151	178
'typical' L. Eck diet	0.668	3	4.5	7.5	11.2	17	20

Fig 4.3 Condition factors for female powan in Loch Lomond (solid circles) and Loch Eck (open circles). Means and 95% confidence limits. a,p = catches from nets across width and parallel to shore of loch respectively. sn,st = seine and south catches from May '84 respectively.



February, after which no significant changes were recorded until after late May. In Loch Eck, female condition factor appeared to increase from September to early January. A significant decrease occurred between early and late January followed by a further fall by February for spawning females. Spent females showed no significant differences in condition factors between late January and February. A significant increase in condition was observed between March and May with a further increase by August. Values for January and February 1984 (pre- and post-spawn samples respectively) showed a highly significant decrease in condition factor.

Condition factor of males in Loch Lomond decreased gradually from October towards spawning time in early January, remaining at a low level until late spring (Fig 4.4). Significant increases occurred between May-July and July-August. Maximum condition for males in 1983 occurred in September. A steady decline was recorded between September and January. Loch Eck males had maximal condition factor in September but no significant differences were observed between September and late December. By January condition had decreased. Considerable variation in condition of males was recorded in late January, but by late February condition was at a minimum. No significant differences could be shown between condition factors of inshore (spawning ground) males and offshore males. Condition remained low in March but significant increases were recorded for May and August. January and February samples from 1984 showed a significant post-spawning decrease in condition factor.

Somatic condition factor.

Seasonal variation in somatic condition factor was apparent for females in both lochs (Fig. 4.5). The major differences between

Fig 4.4 Condition factors for male powan in Loch Lomond (solid circles) and Loch Eck (open circles). Means and 95% confidence limits. a,p = catches from nets across width and parallel to shore of loch respectively. sn,st = seine and south catches from May '84 respectively.

Condition factor, males: L. Lomond • L. Eck ◦

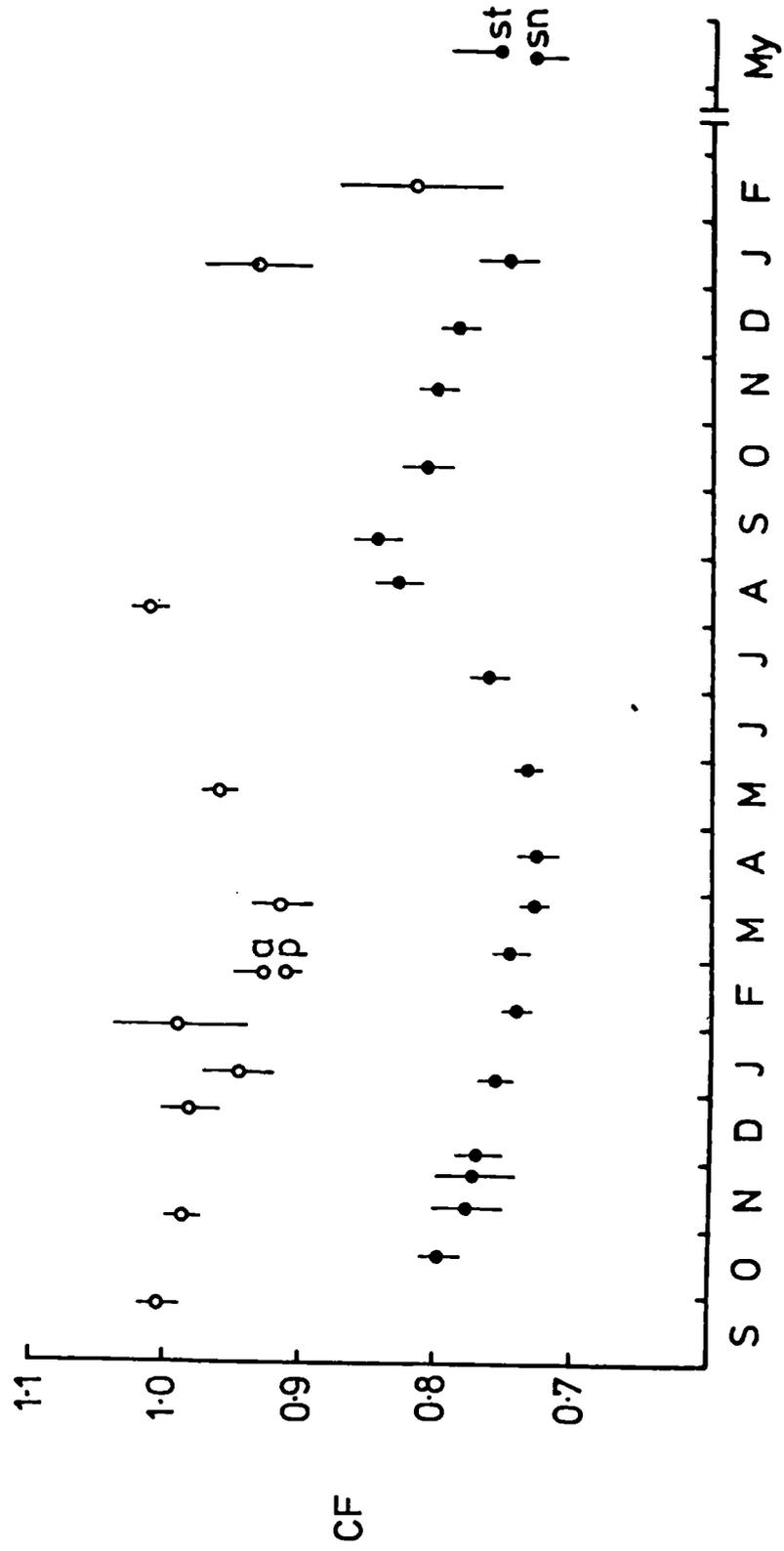
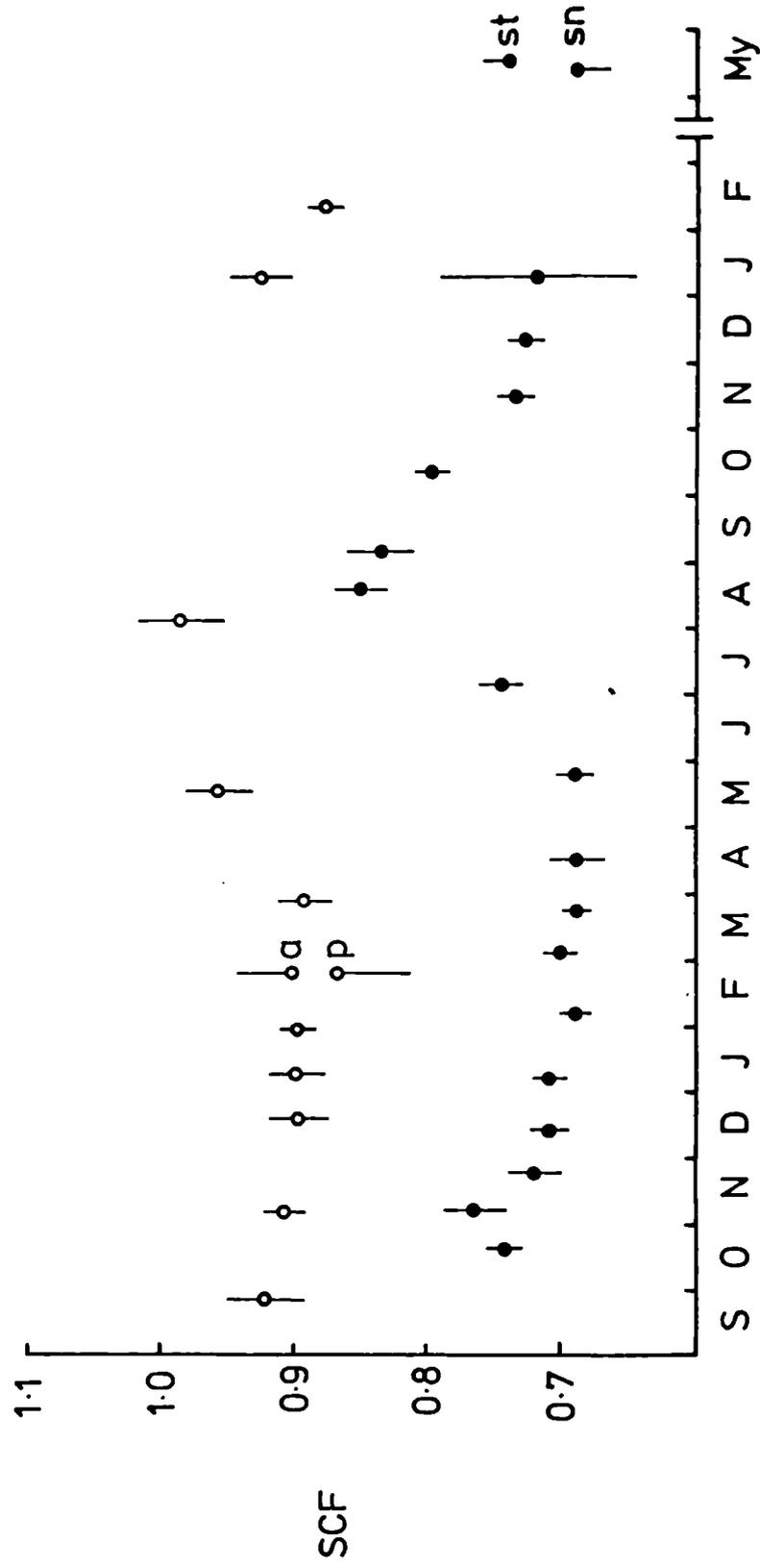


Fig. 4.4

Fig 4.5 Somatic condition factors for female powan
in Loch Lomond (solid circles) and Loch
Eck (open circles).
Means and 95% confidence limits.
a,p = catches from nets across width and
parallel to shore of loch respectively.
sn,st = seine and south catches from
May '84 respectively.

Somatic condition factor, females: L Lomond • L Eck ◊



Month of sample

Fig. 4.5

lochs were that females in Loch Eck consistently had higher somatic condition factors than powan in Loch Lomond and increase of somatic condition factor was more rapid after spawning in Loch Eck. Amplitude of seasonal variation was smaller in Loch Eck than Loch Lomond. In Loch Lomond females reached maximum somatic condition factor in late August - early September. As spawning approached, the somatic condition factor fell to a minimum, about which there was little oscillation until an increase in late spring. Loch Eck females showed much less variation in somatic condition factor over the course of the year. A minimum was reached at spawning time, followed by a rapid recovery during the next few months.

Male somatic condition factor in Loch Lomond showed greatest increase between late May and September after which a significant fall was observed to October's value (Fig. 4.6). After November, somatic condition factor declined through December and January. No significant differences were observed between January and April when somatic condition factors were minimal. In Loch Eck somatic condition factor showed a smaller seasonal change than in Loch Lomond. The observed fall in somatic condition factor for Loch Eck fish after spawning in 1984 was of greater magnitude than that observed the following year or for females in the same year.

Overall, condition of powan in Loch Eck (estimated by condition and somatic condition factors) was significantly higher than that of fish of the same sex from Loch Lomond at similar times of year. Fish in Loch Eck recovered condition quicker and earlier after spawning than those in Loch Lomond. However, the cyclical fluctuation in condition appears to follow a broadly similar pattern in the two lochs.

Fig 4.6 Somatic condition factors for male powan
in Loch Lomond (solid circles) and Loch
Eck (open circles).
Means and 95% confidence limits.
a,p = catches from nets across width and
parallel to shore of loch respectively.
sn,st = seine and south catches from
May '84 respectively.

Somatic condition factor, males: L. Lomond • L. Eck ◊

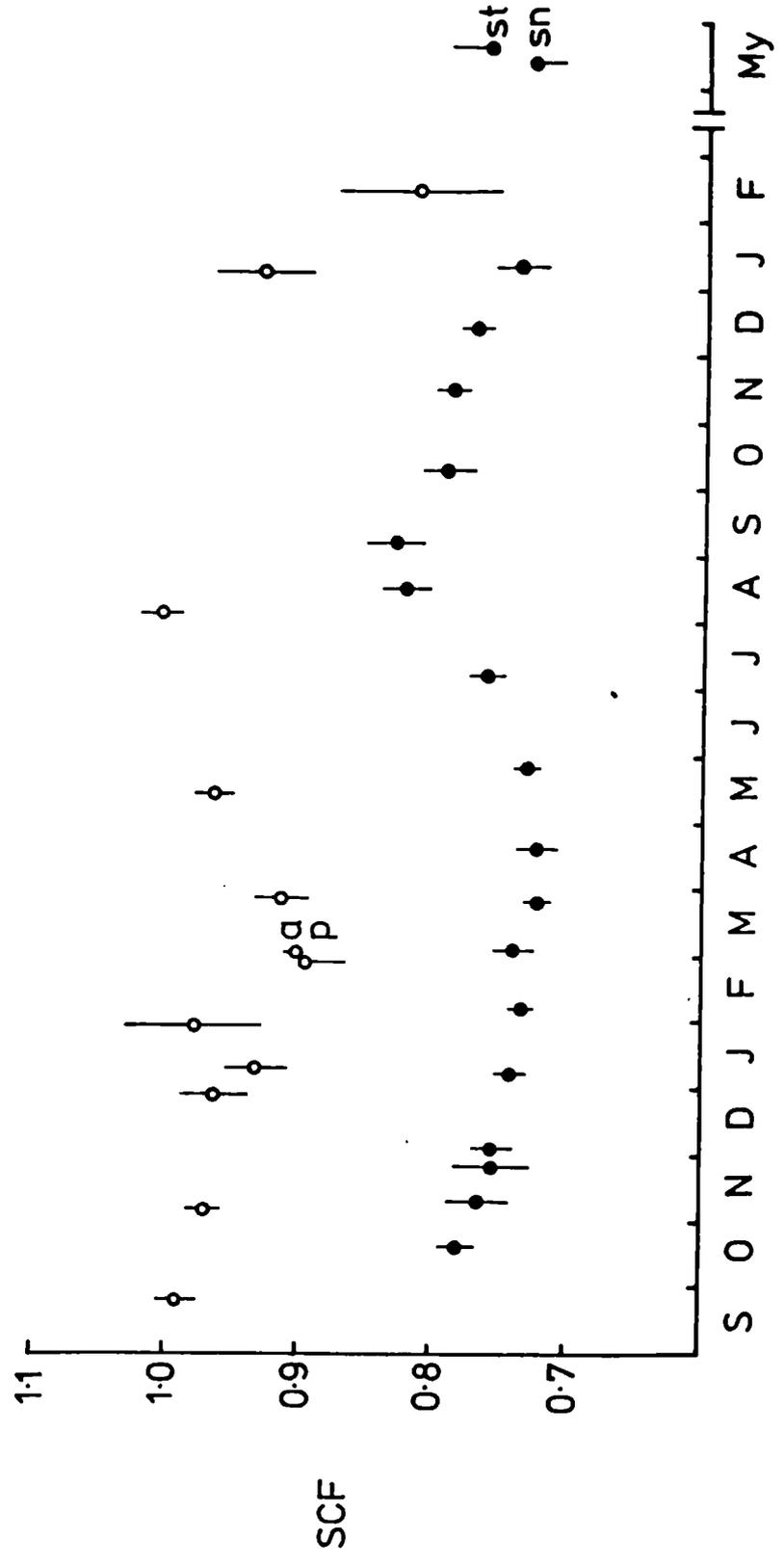


Fig 4.6

4.4.2 Condition estimated by regression.

The geometric mean regression statistics for slope ($V_{y.x}$) and intercept (a_v) for the regressions of log weight on log length are shown in Table 4.13, along with the least squares regression estimate of slope, b , for comparison. Preliminary analysis of variance suggested there were significant differences between the mean weights of both male and female fish for the samples from Lochs Lomond and Eck. Analysis of covariance on the log transformed weight-length data indicated that these differences remained significant even after adjustment to common length and common regression slope. However, individual regressions showed significant heterogeneity between slopes for the different sample dates. These results are summarised in Table 4.14. Under these conditions, intercept values, a_v , may serve only as a rough indication of condition.

4.5.1 Variation in timing of spawning.

Spawning times of powan in Loch Lomond are available from data collected from 1976-1986 and have been infrequently recorded since 1966 (Table 4.15). Year-to-year variation in spawning time is small, with most spawning activity concentrated in the period from late December to mid-January. Samples obtained from two spawning sites approximately 5 km apart in Loch Lomond in January 1985 indicated synchronised spawning behaviour.

In Loch Eck, data has been collected since 1984. Catches in that year indicated that Loch Eck powan were spawning up to a month later than in Loch Lomond. The following year, maximum spawning activity in Loch Eck was estimated to be 3-6 weeks later than in Loch Lomond. In 1986,

Table 4.13

Least-squares and geometric mean regression analysis of condition.

yrmody	n	Males				Females				
		r ²	b	Vy.x	av	n	r ²	b	Vy.x	av
L. Lomond										
821019	42	.991	3.109	3.176	.00434	47	.993	3.324	3.345	.00253
1110	24	.996	3.263	3.275	.00309	34	.992	3.259	3.285	.00325
1125	13	.957	3.262	3.410	.00189	14	.986	3.408	3.456	.00175
1201	46	.987	3.151	3.198	.00385	69	.985	3.331	3.381	.00220
830107	78	.992	3.194	3.220	.00357	76	.989	3.248	3.285	.00295
0208	69	.995	3.241	3.261	.00308	46	.991	3.025	3.083	.00533
0302	36	.989	3.114	3.131	.00475	48	.995	3.050	3.064	.00569
0323	51	.996	3.228	3.252	.00307	39	.996	3.015	3.026	.00653
0416	30	.993	3.256	3.258	.00304	22	.989	2.815	2.845	.01185
0526	47	.993	3.092	3.124	.00480	31	.994	2.915	2.944	.00845
0705	49	.993	3.045	3.073	.00596	43	.990	3.049	3.079	.00578
0817	33	.988	2.990	2.989	.00858	30	.986	2.896	2.936	.01082
0905	31	.992	2.954	2.977	.00907	36	.981	3.069	3.129	.00549
1012	52	.997	3.242	3.252	.00346	35	.994	3.147	3.184	.00465
1116	53	.993	3.210	3.262	.00330	44	.989	3.308	3.345	.00257
1213	39	.990	3.115	3.138	.00484	39	.993	3.441	3.465	.00170
840110	20	.985	3.080	3.128	.00486	33	.835	2.968	3.641	.00091
0514	14	.970	3.055	3.149	.00438	11	.977	2.608	2.671	.02127
0515	29	.962	3.079	3.181	.00417	31	.971	2.800	2.884	.01098
L. Eck										
	n	r ²	b	Vy.x	av	n	r ²	b	Vy.x	av
1984:										
Jan	23	.996	3.271	3.288	.00375	92	.989	3.305	3.361	.00314
Feb	15	.956	2.756	2.911	.01054	70	.995	3.045	3.130	.00570
Sep	64	.994	3.189	3.216	.00485	34	.979	2.910	2.979	.01037
Nov	97	.991	3.145	3.172	.00546	47	.993	3.066	3.115	.00676
Dec	62	.990	3.104	3.134	.00623	50	.989	3.056	3.088	.00751
1985:										
Jan 10	32	.994	3.118	3.137	.00599	59	.990	3.225	3.257	.00431
Jan 30	6	.997	3.215	3.223	.00467	80	.985	2.992	3.036	.00856
Feb a	28	.995	3.097	3.113	.00631	21	.966	3.248	3.362	.00297
Feb p	59	.995	3.100	3.116	.00616	6	.983	2.712	2.757	.02080
Mar	64	.987	3.119	3.160	.00532	39	.993	2.984	3.004	.00894
May	74	.993	3.041	3.062	.00782	35	.982	2.739	2.788	.01922
Aug	92	.983	2.980	3.032	.00907	31	.983	2.882	2.931	.01280

a, p refer to nets set across the width (a) and parallel to the shore (p) of Loch Eck on 26th February 1985.

Vy.x, av are the geometric mean regression slope and intercept, b is the least-squares regression slope.

Table 4.14

Analysis of covariance on log weight and length data.

category	males L. Lomond	females L. Lomond	males L. Eck	females L. Eck
Preliminary anova of weights by sample	F 18,827	F 18,709	F 11,552	F 11,608
F value	2.64	3.55	8.07	19.56
p value	p<0.001	p<0.001	p<0.001	p<0.001
F value parallel slopes	2.357	3.213	5.466	2.612
p value	p<0.001	p<0.001	p<0.001	0.01>p>0.001

N.B. since parallel slopes are not indicated, the pooled regression slopes may be a poor description of the data.

ancova	F 18,826	F 18,708	F 11,551	F 11,607
F value (with adjusted means and common slope)	19.47	21.93	15.57	15.40
	p<0.001	p<0.001	p<0.001	p<0.001
Pooled regression with 95% C.I.	(3.1627) (3.1348) (3.1905)	(3.1537) (3.1090) (3.1989)	(3.0817) (3.0419) (3.1215)	(3.1044) (3.0694) (3.1394)

Table 4.15

Variation in timing of powan spawning: female reproductive condition.

Year	date	Loch Lomond						Loch Eck						
		imm	st	pov	ov	sp	at	imm	st	pov	ov	sp	at	
1982	16 Jan			1	2	11	1							
1982	1 Dec			(none ovulating)			2							
1983	7 Jan				2	27								
1983	13 Dec			(none ovulating)			1							
1984	10 Jan	5	3	18	0	7	1							
	12 Jan				-			9	11	69	0	0	5	
	14 Feb				-			14	9	1	0	48	0	
1984	20 Dec				-			(none ovulating)					2	
1985	10 Jan				-			0	11	46	1	0	1	
	11 Jan	1	3	1	4	2	0							
	30 Jan				-			3	33	23	7	14	2	
	26 Feb a				-			2	11	1	0	26	0	
	26 Feb p				-			0	1	2	1	1	0	

im = immature fish (negligable gonad) ov = ovulating fish
 st = starting fish (gonad in early maturation) sp = spent fish
 pov = pre-ovulating fish at = atretic fish
 [26 Feb a,p = catches from nets set across loch width in deep water (a) and parallel to shore in shallow water (p) of Loch Eck.]

Summary of spawning data and lunar cycle given by O'Connell (1984):

Year	Time of spawning	Full moon
1966-67 :	spawning began at end of December.	27 Dec.
69-70 :	spawning in progress at end of December.	23 Dec.
71-72 :	spawning began in early January.	31 Dec.
76-77 :	spawning began in early December.	6 Dec.
77-78 :	spawning in progress 22nd December.	25 Dec.
78-79 :	spawning in progress 16th December.	14 Dec.
79-80 :	spawning not begun 29th December, under way 12th January.	3 Jan.
80-81 :	spawning not begun 21st December, almost complete 18th January.	21 Dec.

(spawning data collected during this study)

81-82 :	Lomond - mostly finished 16 Jan.	11 Dec., 10 Jan.
82-83 :	Lomond - almost finished 7 Jan.	31 Dec., 29 Jan.
83-84 :	Lomond - in progress 10 Jan.	19 Dec., 18 Jan.
	Eck - between 12 Jan.-14 Feb.	
84-85 :	Lomond - in progress 11 Jan.	7 Jan., 8 Feb.
	Eck - in progress 30 Jan.-26 Feb.	
85-86 :	Lomond - almost finished mid-Jan.	27 Dec., 26 Jan.
	Eck - in progress mid-Jan.	
86-87 :	Lomond - finished by 1 Feb.	15 Dec., 16 Jan.
	Eck - almost finished 1 Feb.	

Loch Lomond powan were spawning in mid-January and Loch Eck fish had completed spawning between late December and mid-February and in 1987 powan in Loch Eck had just finished spawning at the end of January whereas the Loch Lomond population had clearly spawned earlier (Brown, pers. comm.).

4.5.2 Seasonal variation in somatic gonadosomatic index.

Males : Loch Lomond. (Fig. 4.7)

The somatic gonadosomatic index for male powan decreased from spawning time in January 1983 and reached a minimum of 0.26% of somatic weight in May. From July to August a rapid increase in somatic gonadosomatic index was observed, followed by a maximum value of 1.9% of somatic weight in October. Thereafter a slight decline was observed although a temporary non-significant increase at spawning time was observed.

Males : Loch Eck. (Fig. 4.8)

Male powan in Loch Eck show a broadly similar cyclical pattern of change in their somatic gonadosomatic index to that of Loch Lomond males. However, in August 1985 a considerable range of SGSI's were shown by males with some fish displaying SGSI's of $1.87 \pm 0.38\%$ (n=8) while others showed SGSI's of $0.70 \pm 0.2\%$ (n=7). All these fish were large males, 350-550g total weight.

Females : Loch Lomond. (Fig. 4.9)

A fall in the SGSI of female powan was observed after spawning. From March to early July the gonad weighed around 1% of the somatic weight of female powan. The SGSI began to increase after mid-summer, reaching a maximum of 16.7% in December prior to spawning.

Fig. 4.7 Seasonal variation of somatic gonadosomatic index (SGSI) for Loch Lomond males.

$$\text{SGSI} = \frac{\text{gonad weight g} \times 100}{(\text{total weight} - \text{gonad weight}) \text{ g}}$$

Means and 95% confidence limits are shown.

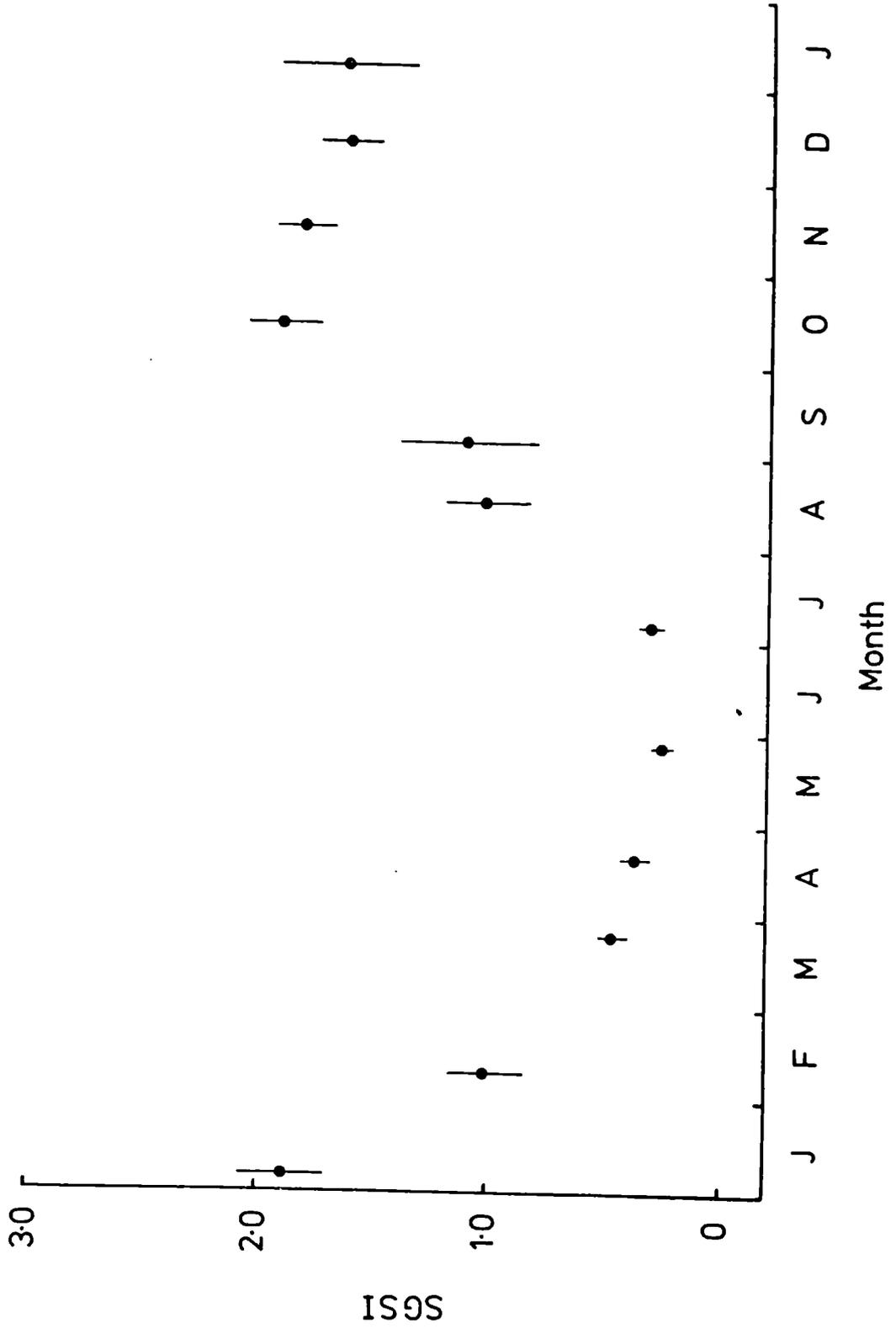


Fig. 4.7

Fig. 4.8 Seasonal variation of somatic gonadosomatic index (SGSI) for Loch Eck males.

$$\text{SGSI} = \frac{\text{gonad weight g} \times 100}{(\text{total weight} - \text{gonad weight}) \text{ g}}$$

Means and 95% confidence limits are shown.

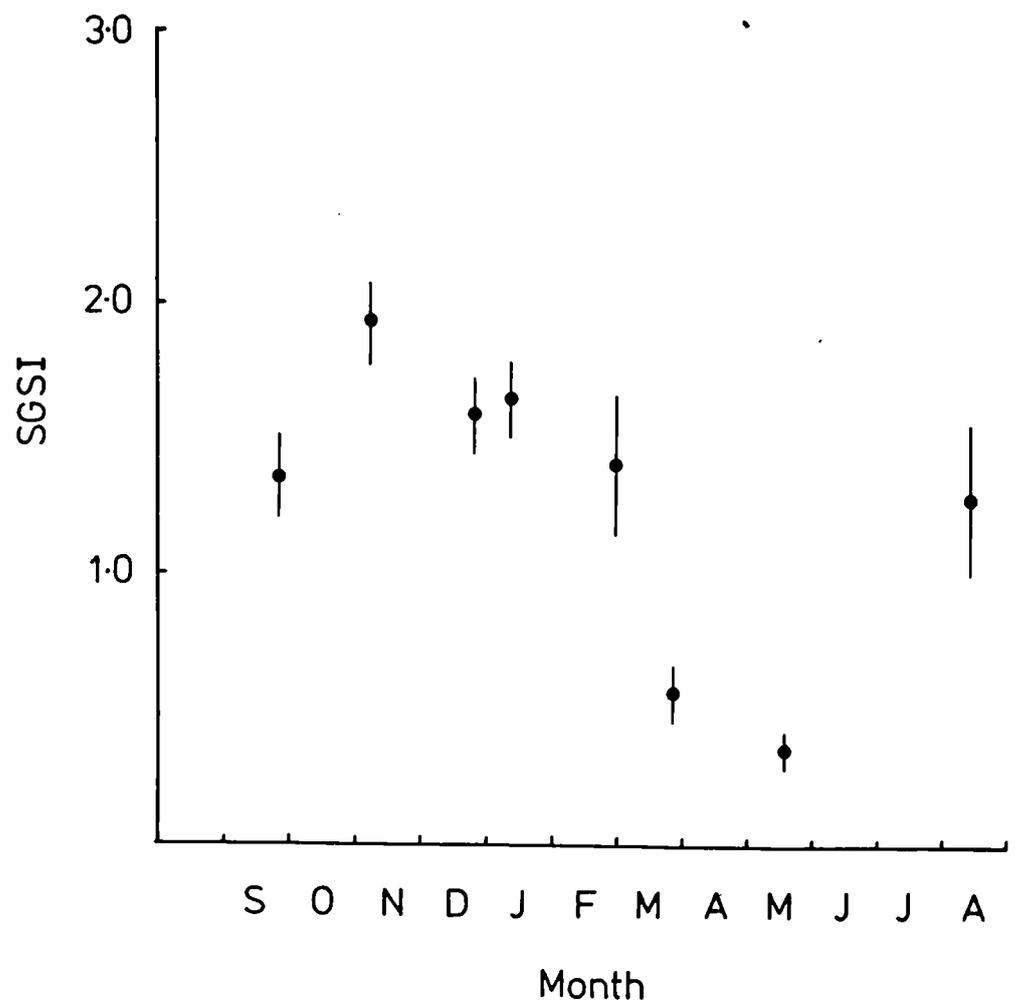


Fig. 4.8

Fig. 4.9 Seasonal variation of somatic gonadosomatic index (SGSI) for Loch Lomond females.

$$\text{SGSI} = \frac{\text{gonad weight g} \times 100}{(\text{total weight} - \text{gonad weight}) \text{ g}}$$

Means and 95% confidence limits are shown.

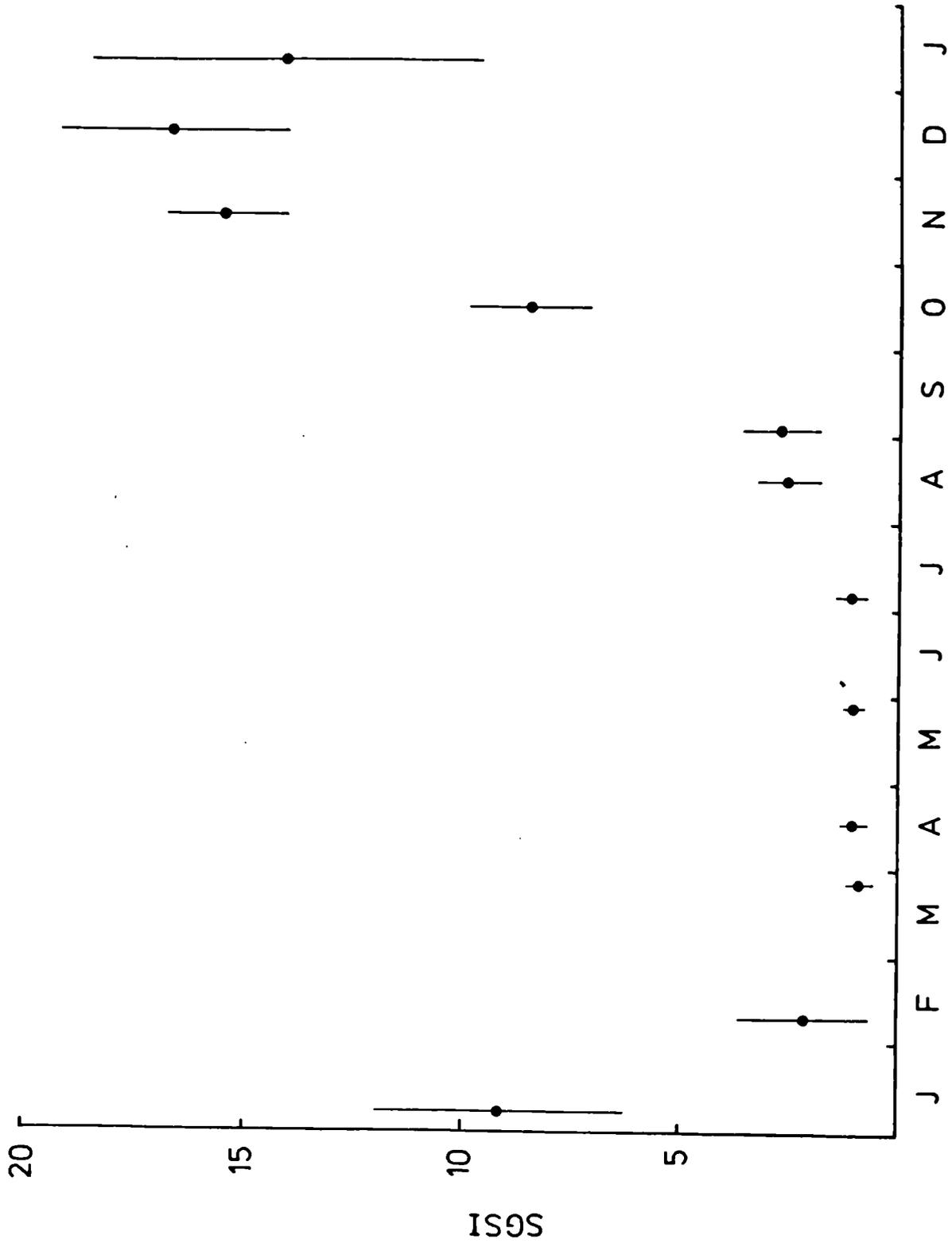


Fig. 4.9
Month

Females : Loch Eck. (Fig. 4.10)

The variation in female somatic gonosomatic index followed the same pattern as in female powan from Loch Lomond, with a fall after spawning and a relatively low value (1-2%) until after mid-summer, followed by a gradual increase to 18% of somatic weight in late January. The later spawning time of powan in Loch Eck compared to powan in Loch Lomond seems to have little effect on the overall cyclical pattern of gonadal recrudescence. Fish grouped into different age classes could not be discerned on the basis of SGSI alone.

Fig. 4.10 Seasonal variation of somatic gonadosomatic index (SGSI) for Loch Eck females.

$$\text{SGSI} = \frac{\text{gonad weight } g \times 100}{(\text{total weight} - \text{gonad weight}) g}$$

Means and standard errors are shown.

sp = approximate spawning period.

solid squares = 'large' 4+

empty squares = 'small' 4+

solid circles = 'large' 3+

empty circles = 'small' 3+

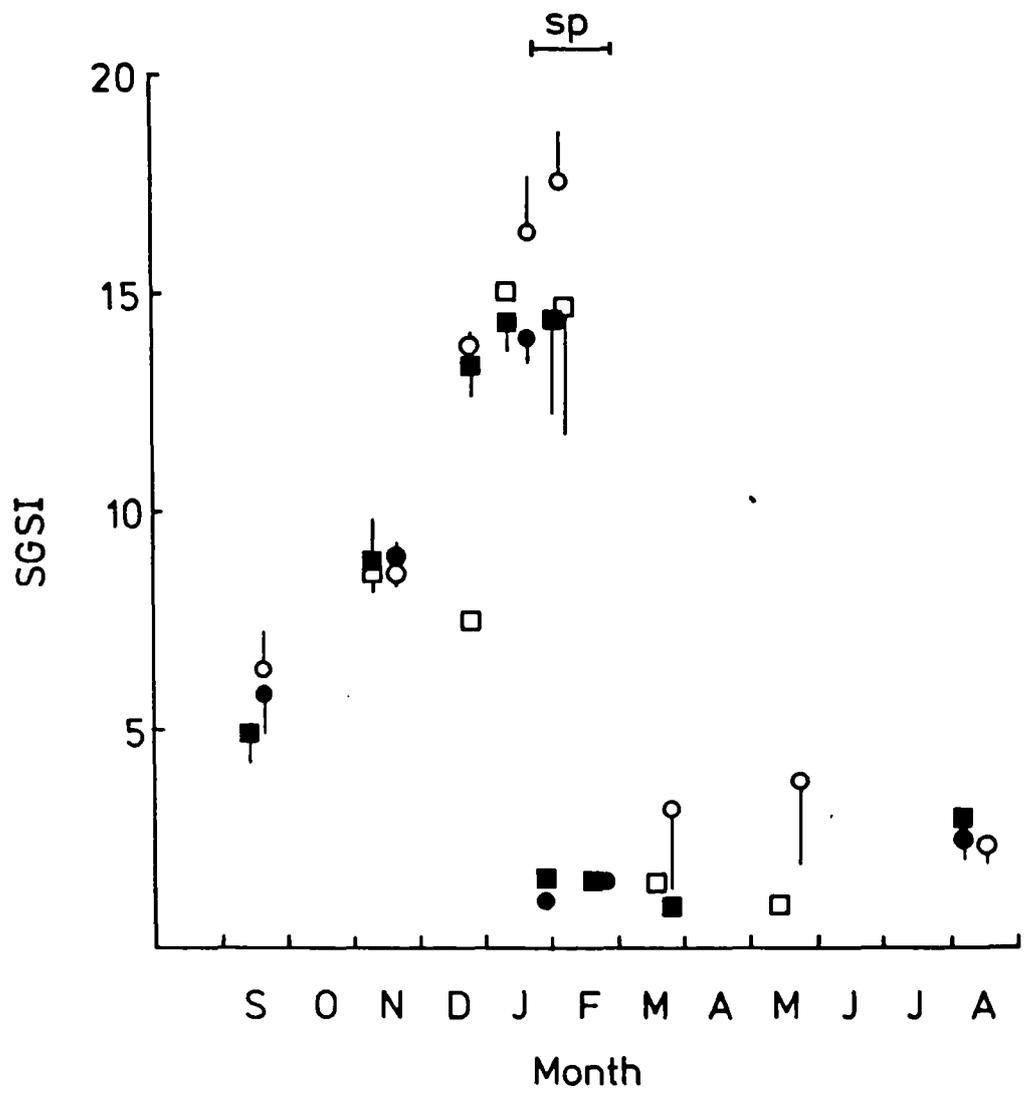


Fig. 4.10

DISCUSSION

Until comprehensive measurements on each component of the energy budget of powan are obtained the accuracy of such studies is limited by the included assumptions and estimations. Wootton *et al.*, (1980) suggested that food consumption and respiration were the most critical components of the energy budget to be assessed. Bartell *et al.*, (1986) confirmed this conclusion suggesting that excretion and egestion parameters contributed little to prediction errors. Accurate estimation of food consumption by fish in the wild is difficult. Ideally, large random samples of fish should be obtained at regular short (3 hours) intervals over an extended time period (24-48 hours) to determine diel feeding periodicity and individual variation in feeding. These samples should be repeated seasonally. Field samples rarely satisfy all these optima.

Methods proposed for the calculation of daily food intake are of two types: (i) where stomach evacuation is modelled by a mathematical function derived from observed data, either from experimentally fed captive fish or from field observations (Elliott, 1972, 1975, 1976; Thorpe, 1977; Elliott & Persson, 1978; Eggers, 1979; Jobling, 1981; Allen & Wootton, 1984; Pennington, 1985; Sainsbury, 1986) and (ii) where simple differences in diel feeding peaks are used to estimate consumption (Keast & Welsh, 1968; Nakashima & Leggett, 1978). The latter methods effectively ignore gastric evacuation and frequently lead to underestimations of daily food consumption (Elliott & Persson, 1978; Allen & Wootton, 1984).

To date the most widely applied method is that of Elliott & Persson (1978) where the rate of gastric evacuation is assumed to be an exponential function of the quantity of food in the stomach and feeding rate is assumed to be constant. Non-constant feeding may be modelled if satiation ration is known. Jobling (1981) used a square-root decay function to model evacuation rate. Allen & Wootton (1984) assumed that 50% of the daily ration of Gasterosteus aculeatus was eaten within 4 hours of sunrise in order to estimate the daily food consumption. They also assumed that the decline in weight of food in stomachs during the hours of darkness would give an estimate of gastric evacuation rate which could be checked against an independent estimate for sequentially slaughtered fish. Thorpe (1977) suggested estimation of evacuation rate from the observed stomach fullness over some part of the diel feeding cycle. Sainsbury (1986) described methods for following the trajectories of stomach fullness over feeding and non-feeding intervals. Elliott & Persson's (1978) method and that of Thorpe (1977) require information on the amount of food in fish stomachs at two times, preferably not more than 3 hours apart. These models are designed to estimate consumption over a (short) period for which observations on stomach contents are available at the beginning and end of the period and assume a constant feeding rate over that period (hence the desirability of short sampling intervals). The more recent methods of Sainsbury (1986) require quantification of several feeding parameters. These more complex methods were felt to be unsuitable for the current data.

Assessment of daily food consumption estimates.

Calorific values obtained for the food organisms available were generally in good agreement with published values for zooplankton and invertebrates (Moshiri & Cummins, 1969; Schindler *et al.*, 1971; Giussani & De Bernardi, 1977). Schindler *et al.*, (1971) found that material preserved in formaldehyde gave lower calorific values than freshly frozen samples, the difference amounting to approximately 5%. Calorific values do not necessarily reflect the food energy assimilated by fish. Indigestible fractions of the prey's body and partially digested material almost certainly complicate the issue. Webb (1978) quotes absorption efficiencies of 96-99% for ingested protein and 80-90% for ingested lipid in a variety of species.

It is possible that the mean weight of stomach contents (S') from gill-netted catches will not be a good indicator of mean feeding levels within the powan population. Since the variability of feeding levels in contemporaneous catches was high, that of an overnight gill netting can be similarly variable at best (e.g. seine and south samples of May '84). It may be that because of high stomach evacuation rates the highest weight of stomach contents observed in a (summer) sample more closely represented the feeding level in the population while smaller amounts indicated fish held captive longer. In addition, winter catches rarely contained more than 50% of feeding fish, so the mean monthly intake of food for the population at this time may be closer to D3 estimates of food consumption than D6.

The estimates of powan stomach evacuation rate which gave reasonable daily consumption estimates were higher than those given for other species (Windell, 1966; Elliott, 1972; Allen & Wootton, 1984) but tended to confirm Enderlein's (1981b) proposition that coregonines have comparatively high stomach evacuation rates.

Talbot & Higgins (1984) showed that starvation could have a significant effect on the size of meal eaten and on gastric evacuation in juvenile Atlantic salmon with differing effects observed for pre- and post-prandial starvation. Meal size has been shown to affect gastric evacuation rate, with increases in meal size as a proportion of body weight increasing the residence time of food in the stomach and the evacuation rate (Jobling *et al.*, 1977).

Basimi & Grove (1985) found an increased rate of gastric evacuation when the energy content of ingested materials fell below 0.5 kcal g⁻¹ (2.142 Jmg⁻¹) gastric evacuation time decreased to 55-70% of its original value. Jobling (1986) found that as the energy content of ingested material was reduced from 5.021 to 0 Jmg⁻¹, gastric evacuation time fell gradually to 55% of its initial value. The mean overall value of material ingested by Loch Eck fish varied seasonally, but the composition of the debris fraction was such that values of 8 Jmg⁻¹ were routinely recorded for its combustion. If all this energy was available to fish, when the calorific value of all ingested material is considered, values did not fall below 7.5 Jmg⁻¹ dry weight. In this situation it is unlikely that gastric evacuation rate was significantly elevated in Loch Eck fish, despite the debris intake. However if only a small fraction of the debris component of the diet contributed to the total energy ingested, the calorific

"dilution" of the diet may have led to increased stomach evacuation rates. It may be assumed that the mean dry weight of debris was approximately three times the mean dry weight of food eaten and if just 1% of energy available in debris was utilised by fish, this would give the following extra diet energy :

daily weight of					
debris ingested mgs	300	600	1200	2400	

(mean calorific value of debris = 8.5 Jmg^{-1})

1% energy equivalent

Joules	25.5	51	110	220
--------	------	----	-----	-----

In addition, mean energy value of the ingested material drops to 3.0 Jmg^{-1} , which may decrease the gastric evacuation time. If the above figures are expressed in terms of the energy budgets considered in Table 4.5, the energy of the daily ration would be increased by an additional 5.1% in March and 2.0% in August. In the annual budget this becomes a additional 18.9 KJ per year for small fish and 32.9 KJ for large fish. The metabolic demands of processing this material and passing it through the alimentary tract are unknown.

The parity between maximum dry weights of food from powan in Lochs Lomond and Eck, despite a debris:food dry weight ratio of 3:1 in stomach contents from Loch Eck is difficult to explain (Table 2.15). Stomach fullness level will be determined by a number of factors. Measures of the volumes of material consumed would help to clarify the situation, since the densities of the material differ.

Although some physiological effects of gill and seine netting on powan

are known (Fuller, 1974; Fuller et al., 1976) the effects of capture on stomach evacuation rate are unknown. Allen & Wootton (1984) found that field estimates of stomach evacuation rate had large confidence limits.

Accurate determination of evacuation rates of natural foods, distribution of feeding time and satiation levels obtained from captive powan would be extremely useful for future daily ration estimates.

Diel feeding cycles.

In this study serial nettings to establish diel feeding regimes did not yield sufficient numbers of powan to allow accurate determination of feeding peaks. Diel variation in feeding intensity was observed, with feeding ceasing over hours of darkness in December and August (possibly continuing in May). Netted fish could not be maintained in a sufficiently normal environment to simulate natural feeding. The relations described by Elliott (1976a,b,c) for trout were obtained for hatchery raised fish which were experimentally co-operative. Wild fish were found to be unsuitable for experiments because of their unwillingness to feed.

Elliott's (1973, 1975a, b) field and laboratory studies found that trout feeding at 4.7 - 7.3°C had full stomachs once a day, at 0130 - 0230. At 10.8°C two peaks occurred, at 0130 - 0230 and 1330 - 1430. In laboratory studies fish with freely available food had elevated gastric evacuation rates, allowing consumption of up to three meals per day. Powan obtained from a seine net haul of the Salloch beach in May 1984, showed considerable individual variation in the amount of food consumed. Scott (pers. comm.) noted that seine-netted powan

taken at dawn had little if any stomach contents. Asynchrony of feeding in the fish population could confound interpretation of stomach content data, especially where assumptions on beginning and end of feeding periods and their duration are required. Year-to-year variation in feeding was noted, particularly in May, possibly as a result of timing of zooplankton increases.

Energy required for respiration.

Wohlschag (1957) measured oxygen uptake rates of fish in a field situation. His multiple regression equation may have limited application and applying it to the annual range of conditions encountered in the present study may be unjustified. Alternatively, coregonines may have higher respiratory demands at low temperatures than trout, or some of the estimates of parameters may be excessive. Elliott (1976) derived his equation for maximum respiratory energy, $R_{max.}$, from trout feeding on maximum rations. The agreement between Elliott's $R_{max.}$ and Wohlschag's resp.1 at summer water temperatures when food is most abundant increases the likelihood that these are realistic estimates of powan respiratory energy requirements, if only at these times. Since surface water temperatures were used in the estimation of respiration rates during the summer months it may be assumed that these estimates will approximate the upper limit of powan respiration at this time.

Loch Lomond powan movements.

Limited evidence exists for diel vertical migration patterns throughout the year (Maitland, 1970b; O'Connell, 1984). Powan ascended from a depth of 20-30m or deeper to the upper water layers in response to decreasing light levels and returned to deeper water as light levels increased. O'Connell (1984) suggested that the onset of nautical twilight (-12° solar altitude) was the cue for appearance of fish in the surface waters, therefore the time spent by powan in the upper water layers varied seasonally. Vertical migration of fish in summer was associated with shoaling. No shoals were observed in winter. when fish were dispersed throughout the water column at night. Fish were found in shallower inshore water in summer, particularly at night, but also during the day (O'Connell, 1984). Slack et al. (1957) stated that in Loch Lomond "powan shoal in littoral shallows in the summer".

Vertical migration may have considerable consequences for the overall energy budget of powan. In Loch Lomond, the thermal characteristics of the three main basins can be considered as following a predictable annual cycle, with small year-to-year fluctuations in timing (Fig. 1.3). Typically, thermocline formation takes place from late May and lasts until November in the mid-basin. In the deep northern basin stratification may prevail into December (Slack, 1957). Diel vertical migrations of powan in Loch Lomond during the period of stratification may involve a change in water temperatures of as much as 7°C in the mid-basin. Stratification of the shallower southern basin is of a temporary nature, involving a smaller temperature gradient, although the rate of temperature change

and annual range of temperature are greatest in this part of the loch. Elliott's (1976) estimate of maximum respiratory energy requirements for a 150g trout increase from 3.2 KJ per day at 7.5°C to 14 KJ per day at 14.5 °C. Wohlschag's (1957) respiration equation for a 150g whitefish predicted an increase from 6.4 KJ per day at 7.5°C to 11.2 KJ per day at 14.5°C. Elliott (1976) found that the maximum growth efficiency of trout occurred in the temperature range 7.5 - 11°C when the average daily food consumption was 5 - 8.5 KJ (close to maximum rations).

Vendace, C. albula, did not cross the thermocline in their diel vertical migrations in the Mazurian lakes of north-east Poland (Dembinski 1971). Persson (1986) has indicated that roach and perch occupy the thermal regions of lakes best suited to their foraging abilities which were shown to change with temperature. Dabrowski (1985) presented a seasonal energy allocation budget for the coregonines C. albula (vendace) in a Polish lake and C. autumnalis pollan Thompson (pollan) in Lough Neagh, Northern Ireland. The calculations were based on the published data of Wohlschag (1957), Giussani & De Bernardi (1977), Enderlein (1981b) and Wilson (1984). Vendace were shown to achieve high growth rates in summer by heavy feeding on zooplankton combined with favourable water temperatures in the deeper Polish lake. Pollan were observed to display similar feeding activity, but because of high water temperatures in the shallower Lough Neagh, a greater proportion of the ingested food was used in routine metabolism rather than growth.

Feeding rates.

Detection of prey by fish can be related to fish swimming speed and encounter rates. Determination of encounter rates requires information on prey density. Absolute densities of planktonic prey vary over small and large scale gradients. George (1981) outlined the causes and nature of patchiness of typical freshwater zooplankton distributions. Behavioural responses of Daphnia were thought to result in small scale patches (0.5 x 1m), while advective factors produced a gradient of Bosmina density ranging from 50 - 1000 animals per litre across a small reservoir (George, 1981).

In Loch Lomond, the density of benthic animals was estimated to range from 25 to 400 per square metre at depths of 180 and 13m respectively (Weerekoon, 1956). Densities of Chaoborus larvae may be in the order of several hundreds per cubic metre in late autumn if their abundances are similar to those in the neighbouring Lochan Dubh (Goldspink & Scott, 1971).

The reproductive cycle.

Ultimately the reproductive process will have evolved to maximise the chances of survival of the offspring. Seasonality of reproduction is usual for many fish species, including some tropical and deep sea species where seasonality takes the form of river flooding or food availability (Bye 1984). In Loch Lomond the timing of spawning of Coregonus lavaretus varies from mid December to early or mid January. In each of the past four years, powan in Loch Eck have been observed to spawn up to a month later than the Loch Lomond population (Scott, pers. comm.). Both populations were characterised by a high degree

of synchronisation in spawning time of individuals. Zuromska (1982) noted that European coregonine populations showed considerable variation in spawning times but the duration of the spawning period was short. Timing of reproduction has been observed to vary little in Loch Lomond over the course of the past twenty-five years. Although there are records of powan spawning in October-November (Brown, 1897) extruded oocytes from injured fish may have been mistaken for naturally running fish. Scott (1979) and O'Connell (1984) have suggested that the beginning of spawning may be initiated by the lunar cycle as few other environmental variables change with sufficient amplitude to be detected at the time of year favoured for spawning. Evidence for the role of moonlight in determining powan spawning time over the past few years is inconclusive (Table 4.15).

Gonadal recrudescence monitored by the somatic gonosomatic index provides no information on the developmental processes occurring in the gonads (see Rashid 1984), but indicates that powan gonadal recrudescence begins in late spring and continues through summer and autumn. This coincides with the maximum production of plankton in Loch Lomond (and probably in Loch Eck); growth in length also occurs at this time (McCulloch, 1981, in prep.; Brown, 1983, in prep.).

Fluctuations in somatic condition factor were used by Rashid (1984) as indicators of protein catabolism and anabolism. During winter, catabolism of muscle was noted particularly in females (Rashid, 1984). Although tissue hydration and lipid mobilisation may mask the true extent of protein metabolism, elevated plasma cortisol levels around spawning were recorded by Fuller (1974). Dabrowski (1982) found high levels of free amino acids in the blood of vendace

C. albula in the spawning period and noted sex-related differences in the amounts and identity of amino acids and cholesterol in the blood. Males had different free amino acids in the plasma and had much higher levels of blood cholesterol than females. Males apparently remain on the spawning grounds for extensive periods while females move onto the spawning grounds as they ovulate. Behavioural interactions are known for other spawning salmonids and cannot be ruled out for powan. Many fish become infected with fungal lesions around spawning time and the location of these lesions and their frequency of occurrence on the body may be sex-specific (Pomeroy, 1982). The loss of condition shown by both sexes at spawning time is an indication of the high energy costs involved in reproduction.

Water temperature may have an important secondary role in the spawning process. Kamler *et al.* (1982) found that European coregonine populations spawned at water temperatures 2.5-8.0°C, and at different temperatures in different years. Similar observations have been made for powan in Loch Lomond (Scott, 1979; O'Connell, 1984). The annual cycle of water temperature in Loch Lomond is subject to weather fluctuations but shows a regular yearly pattern. It is probable that this fluctuation in water temperature is intimately connected to the spawning cycle, but its precise relationship is unclear at present. Bye (1984) suggests that temperature probably has an insignificant effect on gametogenesis in salmonids provided that physiological limits are not exceeded, but may have a greater effect on the later stages of maturation, ovulation and spawning.

Growth in length and weight.

Changes in condition of fish can be attributed to a number of causes. Growth in length of powan in Loch Lomond occurs from mid-summer up until October or later (McCulloch, 1981; Brown, 1983). This is also the period in which the main gonadal recrudescence is occurring (Fuller *et al.*, 1976; Scott, 1979; Rashid, 1984) and condition is at a maximum at this time (Fig. 4.7). Loch Eck fish display similar trends in condition factors and somatic gonadosomatic indices to Loch Lomond fish for much of the year: their growth patterns remain unclear at present. Brown (pers. comm.) found that growth of Loch Lomond powan follows the back-calculated growth pattern according to scale annulus readings and follows a regular annual pattern. However, powan in Loch Eck show much greater variation in somatic growth patterns with checks formed on scales from May to September. The condition factors calculated above would indicate a significant difference between the "fatness" of fish from the two lochs, although the precise reason for this is unclear.

Chapter 5. General discussion.

The two Scottish populations of powan Coregonus lavaretus (L.) live in lochs less than 40km apart. They are assumed to have originated from the same stock about 10,000 years ago and show a cl genetic relationship (McEwan, 1985). Nevertheless the populations differ in a number of fundamental respects.

- (i) Feeding habits of the two populations differed widely, both in terms of food type and feeding behaviour.
- (ii) "Condition" of powan in Loch Eck was higher than in Loch Lomond throughout the year.
- (iii) The peaks of spawning activity occurred at different times in the two lochs, Loch Eck being the later. This is despite the populations being subjected to the same physical environmental cues.
- (iv) There is limited evidence to suggest that mean gill raker number may differ between lochs (Miller, 1984).

Powan in Loch Lomond are primarily planktivores, showing evidence of inter- and intra-specific size-selectivity. Some fish showed preferences for prey which could not be explained totally by relative prey abundances. The high numbers of items in stomachs during late spring and summer indicated high rates of prey capture which implied either very efficient selective "nip" predation or some form of non-selective gulp or filter feeding at high prey densities. Benthic food made up the greater part of the winter and early spring diet. In Loch Eck, powan fed on benthic material throughout the year.

Although seasonal fluctuations in the quantity of food consumed were similar to those observed in Loch Lomond, few instances of non-feeding fish were recorded in comparison. Feeding rates of powan largely depend on their ability to detect prey. Detection of planktonic and benthic prey may involve different mechanisms. Benthic prey may be taken with less discrimination than are planktonic prey, as large amounts of debris material were found in stomachs of powan from Loch Eck. The manner of ingestion of this non-food material is a matter for conjecture. It may be eaten actively for some unknown reason, acquired as a result of feeding on food of similar appearance (e.g. fish eggs), or ingested while fish struggled in the net. Observations of laboratory raised powan have confirmed that fish will feed off the bottom and frequently were seen to ingest gravel and debris for a short while, then expel it from the mouth. Such fish were 6-18 months old and greater than 50mm total length.

Powan fecundity.

Maitland (1967) found the mean fecundity of powan in Loch Lomond to be 5516 eggs for a fish of 246g total weight. In a subsequent study, Finnigan (1983) confirmed this finding mean fecundity was 5906 eggs for fish weighing 285g. Recalculation of the above data to compare with data from Loch Eck gave the following :

where: (log gonad weight, g) $y = a + b$ (log Fork Length, mm)

Loch Lomond :

Maitland, 1967 $y = -5.346 + 2.8384 \text{ F.L.}$ $r^2 = 0.508$ $n = 88$

Finnigan, 1983 $y = -6.468 + 3.3296 \text{ F.L.}$ $r^2 = 0.471$ $n = 28$

Loch Eck :

this study $y = -4.056 + 2.2836 \text{ F.L.}$ $r^2 = 0.714$ $n = 49$

There was no evidence of significant differences in gonad weight/fork length relationship between Maitland's data and those from Loch Eck over the size range of fish examined. Finnigan (1983) found no evidence of size-related changes in relative fecundities although a small number of fish were examined. Highest partial correlation was shown between fecundity and total fish weight, as was the case for pollan in Lough Neagh (Wilson, 1984). No differences in mean fecundities were found for pollan of different ages, but there was evidence of a decline in specific fecundity over a period of six years while somatic growth rates over the same period were not different (Wilson, 1984). It was suggested that a smaller proportion of ingested energy was allocated to gonad production in later years. Both pollan and powan showed considerable variation in fecundity within populations and year classes.

The lipid cycle.

Mobilisation and deposition of lipid in powan from Loch Lomond has been investigated by Rashid (1984). Total body lipid was maximal in September for adult females and October for adult males. Both sexes and immature fish showed a decline in total body lipid by spawning time with no significant increase until spring. Throughout the year the bulk of total lipid was stored in muscle, although the percentage of lipid in muscle was low and an unknown proportion of this was structural rather than "reserve". The viscera and gonads contained most of the remaining lipid with a small amount in the liver. The main mobilisable lipid store was in the viscera (including the visceral fat body) which accounted for up to 32% and 23% of the total body lipid in mature males and females respectively in September. Thereafter, a steady decline in lipid level was observed.

Directly after spawning, a small temporary rise in lipid level in the viscera was observed. Low levels of lipid occurred in March before the main lipid accumulation over the summer and early autumn. Prior to spawning, mature females lost lipid from muscle, liver and fat body, accompanied by a general decline in lipid levels in the body. However, some of this lipid was assumed to be incorporated in the ovaries. Males maintained a high overall lipid content prior to spawning, but during the spawning period a large loss of lipid was observed, which was not attributable to loss of gonad in spawning but was thought to be activity-related (Rashid, 1984). Lipid levels were low for the period between spawning and the resumption of planktonic feeding in late spring. A gradual increase of lipid occurred reaching a peak in August/September, which then declined to spawning time.

Kissack (1986) performed preliminary lipid studies on powan from Loch Eck. The available data for powan lipids in Loch Eck are difficult to compare directly with fish from Loch Lomond since Loch Eck fish were probably heavier than those from Loch Lomond. Therefore the data are complicated by allometric problems and the fact that they were recorded from different years. General trends may suffice. The overall pattern for lipid mobilization and deposition in gonad and liver was similar for the adult sexes from the two lochs, but in Loch Eck females showed an earlier fall in visceral fat levels (between August and September) compared to Lomond females (September-November). Visceral fat levels were higher in Loch Lomond males than Loch Eck males in September but similar in both lochs around spawning time. Lipids in the muscle of adult females in Loch Eck declined from November to February whilst in Loch Lomond, a gradual decline was observed from September to early spring. In Loch Eck the muscle lipid content of males remained at approximately similar levels over the

August-January period, whilst in Loch Lomond lipid levels of male fish fell from a peak in October to a minimum at spawning time.

Dabrowski (1982,1985) found that both adult sexes of C. pollan in Lough Neagh lost lipid to the same extent but over different times. Lipid in females declined from August to November, while males lost lipid directly before spawning (November to December). Vendace C. albula in Polish lakes lost lipid as gonad was grown, with more lipid depletion in females than males. Total body lipid reached a maximum in September. The catabolism of protein in both species was maximal in the pre-spawning period, but vendace relied on this source of metabolites to a greater extent than pollan, as vendace food intake during this period was lower than that of pollan. Assessment of reproductive energy allocation in coregonines may be misleading unless the seasonal energy budget is considered.

Sympatric species and feeding interactions.

Charr, whitefish, trout.

Studies on interactions of introduced populations of the above species in Swedish lakes suggested that competitive replacement of arctic charr Salvelinus alpinus by whitefish Coregonus species should occur in the early stages of interaction when all are planktivorous (Nilsson & Pejler, 1973). Charr are planktivorous up to a length of 400mm (Nilsson & Pejler, 1973). Frost (1977) described the diet of charr in Lake Windermere as consisting mainly of planktonic Cladocera and the larvae and pupae of chironomids and Chaoborus. No overlap of diet was observed with the seven other fish species in the lake. Sparholt (1985) found the diets of "small" and "large" charr to differ considerably, with the smaller fish feeding in the littoral and larger fish feeding on plankton in the pelagic zone. Studies of fish diets

have shown that both species, like many other fish, tend to eat the largest most abundant food. It is possible that where charr and whitefish co-exist the ability to exploit food at the smaller end of the available prey size range may be critical, as Zaret (1980) suggests. In Nilsson & Pejler's (1973) classification of lakes by their fish fauna and hence main vertebrate predators, lakes with whitefish and trout or whitefish only were thought to have the most intense fish predation on plankton (state 4), while lakes with trout, charr and whitefish were considered to have less intense plankton predation. The largest zooplankton species and individuals within species were intensely predated, while the smallest zooplankton species were found in lakes dominated by whitefish. These observations agreed with the work of Dodson (1970). Dwarfed Austrian charr fed more intensively than larger forms in other lakes, but did not feed in the pelagic zone in the presence of whitefish.

In Loch Lomond powan appear to feed on zooplankton in a similar way to that which has been described for other whitefish populations (Haram & Jones, 1971; Nilsson & Pejler, 1973; Jacobson, 1974; Guissani & De Bernardi, 1977; Enderlein, 1981b). However in Loch Eck powan were never found to feed on plankton, feeding exclusively on benthic material throughout the year. Charr fed on zooplankton and littoral invertebrates (Table 5.1a,b). The population of charr in Loch Eck appears to be a dwarfed form similar to that found in Loch Rannoch and has been suggested to be a sub-species (Friend, 1956)(Table 5.2, Plate 3).

Loch Eck is unique in being the only Scottish loch to have a salmonid fish fauna comprising salmon, sea trout, brown trout, charr and powan.

Table 5.1a

Comparison of powan and charr diets in Loch Eck.
 Percentage frequency of occurrence.

	27 September 84		27 March 85		17 May 85	
	powan	charr	powan	charr	powan	charr
	n=17	n=7	n=18	n=22	n=20	n=10
debris	100	0	100	31.8	95	0
vegetation	94.1	14.3	100	4.5	95	0
Pisces	0	0	0	9.1	0	0
Leptodora	5.9	28.6	0	0	0	0
Hirudinea	0	0	0	4.5	5	0
Ostracoda	23.5	0	0	4.5	30	0
Cyclops spp.	52.9	0	73.7	36.4	65	0
Trichoptera	0	0	5.3	9.1	0	0
Plecoptera	0	0	0	4.5	0	0
chironomids	100	57.1	100	27.3	95	20
Insecta pupae	0	85.7	0	0	100	75
Chaoborus	5.9	42.9	15.8	4.5	20	20
Pisidium	82.4	0	94.7	0	75	0
Ephemeroptera	0	0	0	4.5	0	0
Insecta adults	5.9	0	0	0	0	0

Table 5.1b

Comparison of powan and charr diets from Loch Eck.
 (b) Percentage composition by number.

	27 September 84		27 March 85		17 May 85	
	powan n=17	charr n=7	powan n=18	charr n=22	powan n=20	charr n=10
Pisces	0	0	0	2.7	0	0
Leptodora	0.04	79.2	0	0	0	0
Hirudinea	0	0	0.9	0	0.05	0
Ostracoda	0.2	0	0	45.0	1.1	0
Cyclops spp.	3.0	0	14.2	29.0	9.2	0
Trichoptera	0	0	0.05	1.8	0	0
Plecoptera	0	0	0	0.9	0	0
chironomids	77.0	1.1	66.8	12.6	37.5	2
Insecta pupae	0	19.0	0	0	30.7	93
Chaoborus	0.5	0.04	0.2	0.9	0.2	1
Pisidium	19.6	0	18.8	0	21.2	0
Ephemeroptera	0	0	0	1.8	0	0
Insecta adults	0.04	0	0	0	0	0

Table 5.2

Numbers of charr caught and feeding
with size distribution, Loch Eck .

Species, sample date	total catch	number feeding	T.L. range mm	T.Wt. range g
charr, <i>Salvelinus alpinus</i>				
14 Feb 84	7	4	200 - 261	62 - 122
27 Sep 84	13	7	144 - 243	22 - 108
10 Jan 85	3	0	168 - 242	36 - 112
30 Jan 85	3	0	200 - 234	62 - 102
26 Feb 85	12	0	158 - 240	30 - 106
27 Mar 85	62	22	134 - 262	16 - 136
17 May 85	10	10	175 - 245	42 - 90

Overall log length/log weight regression for charr was

$$\log \text{ weight} = -4.999 + 2.945 \log \text{ total length}$$

(s.e. of b = 0.318, r-squared = 0.963
G.M. regr. coeff. = 3.055)

trout, *Salmo trutta*

26 Feb 85	10	10	186-244mm T.L.
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Loch Lomond

ruffe, *Gymnocephalus cernua*

16 Nov 83	2	2	102-118mm T.L.
9 May 85	17	17	61-124mm T.L.

Whitefish and ruffe.

Since the appearance of ruffe in Loch Lomond in 1982, the abundance of this previously exotic percid has increased dramatically (Maitland *et al.*, in press). At present only limited information is available on the interaction of this species and the other fish in Loch Lomond (Table 5.3). Ruffe preyed upon littoral invertebrates and showed some evidence of feeding on powan eggs, although not to the same extent as powan themselves.

Pokrovskii (1960) documented the effect on production of Russian whitefish *C. albula* populations of predation by ruffe *Gymnocephalus cernua*. Many whitefish species spawn on shallow gravel banks or shores of lakes in exactly the habitat favoured by ruffe. Largely as a result of their predation on the ova of whitefish, ruffe were estimated to have reduced the abundance of whitefish in some lakes to half their previous numbers. In Lake Syamozero, Karelia predation on the fertilised eggs continued from spawning right through till hatching, with ruffe estimated to consume 80-90% of the total eggs deposited (Pokrovskii, 1960). In a lake where whitefish production was high, ruffe numbers had been decimated by the parasite *Tetracotyle*. Adult pike and perch are known to feed on ruffe.

Growth, age structure and survivorship.

Studies on growth of powan in Loch Lomond have been extended to consider aspects of somatic growth, year class variation and distinct populations (McCulloch 1981;in prep.; Brown 1983;in prep.). Mean weights of powan assigned to age classes by McCulloch (pers. comm.) in each sample of 1983 are shown in Fig. 5.1 (Loch Lomond) and those aged by Brown (pers. comm.) for 1984-1985 in Fig. 5.2 (Loch Eck). The possibility of erroneous ageing must be considered particularly in

Table 5.3

Comparison of ruffe and powan diets, Loch Lomond.

	Prey	Percentage frequency of occurrence		Percentage composition by number	
		powan n = 24	ruffe n = 2	powan n = 24	ruffe n = 2
16 Nov 83	Asl	0	50	0	2.6
	Trl	0	100	0	26
	Krl	10	100	7	71.4
	Cbr	19	0	24	0
	Psd	7	0	3	0
	Cvr	5	0	3	0
	Bsm	17	0	1	0
	Dah	55	0	60	0
10 Jan 85		n = 17	n = 3	n = 17	n = 3
	Egg	41.2	33?	23.6	0.9
	Clu	17.6	0	3.1	0
	Dah	52.9	0	25.7	0
	Bsm	5.9	0	0.5	0
	Ery	5.9	0	2.6	0
	Asl	11.8	0	5.2	0
	Dia	52.9	0	15.7	0
	Cvr	29.4	0	11.0	0
	Iul	0	33	0	0.9
	Pll	0	33	0	0.9
	Trl	11.8	33	1.0	1.9
	Krl	23.5	100	3.7	89.7
	Cbr	5.9	33	1.0	5.6
	Lim	5.9	0	0.5	0
	Psd	29.4	0	5.8	0
9 May 85		n = 37	n = 17	n = 37	n = 17
	Dah	43.2	0	38.1	
	Bsm	16.2	0	31.4	0
	Byt	2.7	0	0.4	0
	Dia	24.3	0	3.6	0
	Iup	48.6	17.1	5.9	4.5
	Psc	5.4	0	0.2	0
	Trl	8.1	35.3	0.3	5.8
	Krl	24.3	82.3	1.1	44.5
	Cbr	37.8	11.8	17.4	1.9
	Psd	2.7	0	0.1	0
	Asl	0	94.1	0	36.1
	Cvr	0	23.5	0	3.9
	Pll	0	5.9	0	1.0

Prey categories as in Chapter 2.

Fig. 5.1 Mean corrected total weights of age classes
2+ - 5+ , Loch Lomond 1983 for both sexes.
Means and 95% confidence limits,
solid circles = males empty circles = females.

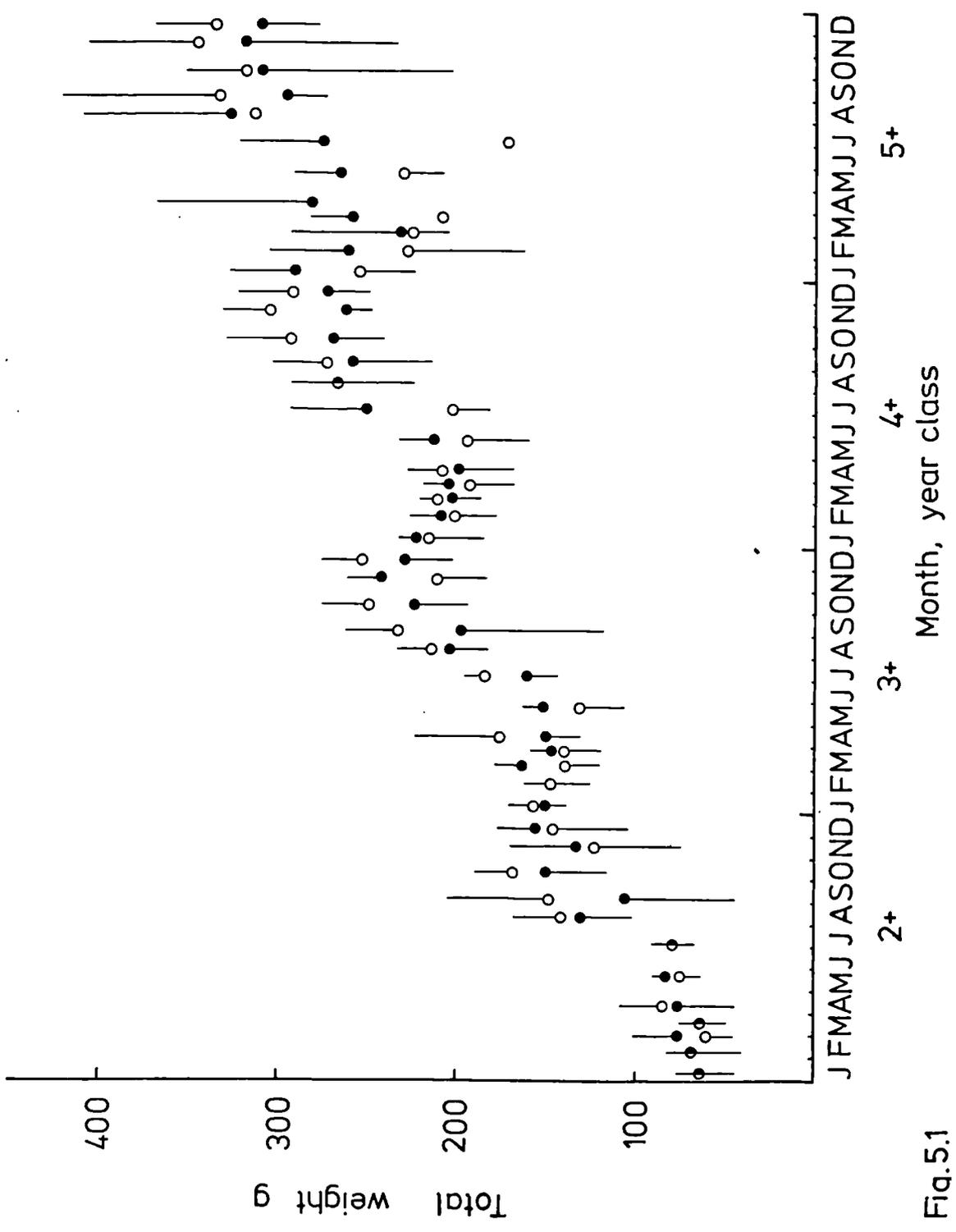


Fig.5.1

Fig. 5.2 Mean corrected total weights for females aged 3+, 4+ in Loch Eck 1984-1985.
Means and standard errors,
solid squares = 'large' 4+ unspawned
empty squares = 'small' 4+ unspawned
solid squares = 'large' 3+ unspawned
empty squares = 'small' 3+ unspawned
+ = spent 4+ x = spent 3+
sp = approximate spawning period.

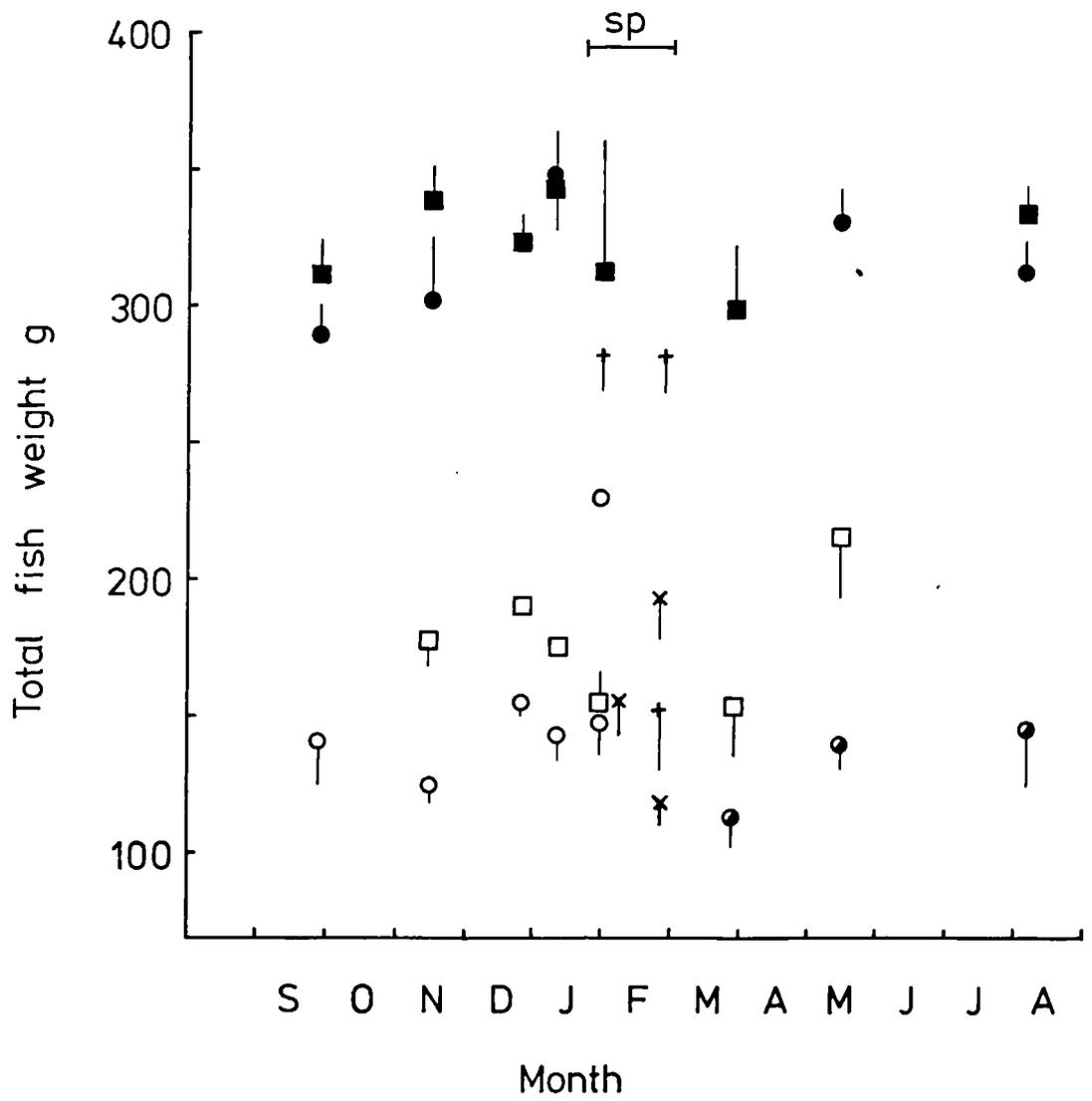


Fig. 5.2

the case of powan from Loch Eck (Brown, pers. comm.). The catch age composition of powan in Loch Lomond data are plotted as catch curves in Fig. 5.3 and total number of fish aged for that year is given in Table 5.4. For the three years for which data is shown, there is considerable variation around the classic catch curve form. This would appear to be due to variations in year class strength. It can be seen that the 4+ year class of 1981, subsequently the 6+ year class of 1983, was poorly recruited. If the data for three years is combined to stabilise recruitment variation, (Fig. 5.3, catch curve D), a more general estimate emerges. Recruitment to the fishery (in this case the composite gang of gill nets) is not complete for fish in age classes less than 3+, hence the slope at age 6+ on the catch curve reflects the survival rate (6 - 3) years previous to 1983. Survivorship of the older age classes falls steeply beyond age class 7+. Survivorship is almost constant over the year classes 4+ to 7+ if major recruitment variations are ignored (Table 5.5, Fig. 5.3). Year to year recruitment variation may affect individual year class strength but not the overall trend of survivorship.

The causes of variation in year class strength may be closely related to the quality of feeding conditions. There is evidence to suggest that egg quality (measured as size and biochemical content) is variable and directly related to the condition of the spawning population (Kamler & Zuromska, 1979; Kamler *et al.*, 1982). When the spawning population experiences relatively good feeding, survival of eggs may be better than usual in the absence of major fluctuations in other factors affecting egg survival. Dabrowski (1982) quoted eight-fold variations in vendace year class abundances in eutrophic Polish lakes, although individual growth rates were similar between years. Pollan showed large fluctuations in year class

Table 5.4

Numbers of fish used in mean weights of age classes and survivorship, Loch Lomond samples, (Figs. 5.1 and 5.3).

mo	Year class							
	males				females			
	2+	3+	4+	5+	2+	3+	4+	5+
J	6	25	17	7	14	24	14	11
F	7	29	21	7	5	13	7	4
M	4	14	15	3	5	17	7	9
M	6	13	16	13	9	9	9	2
A	5	16	11	5	2	4	6	0
M	10	21	17	7	5	9	7	5
J	11	26	6	4	8	17	9	2
A	9	13	5	3	6	8	7	2
S	5	5	8	7	6	7	9	6
O	12	10	12	3	6	12	6	3
N	9	19	14	3	7	12	11	4
D	9	11	12	4	5	11	8	6

Fig. 5.3 Catch curves for powan in Loch Lomond
1982-1984.
A = 1982 B = 1983
C = 1984 D = combined data.

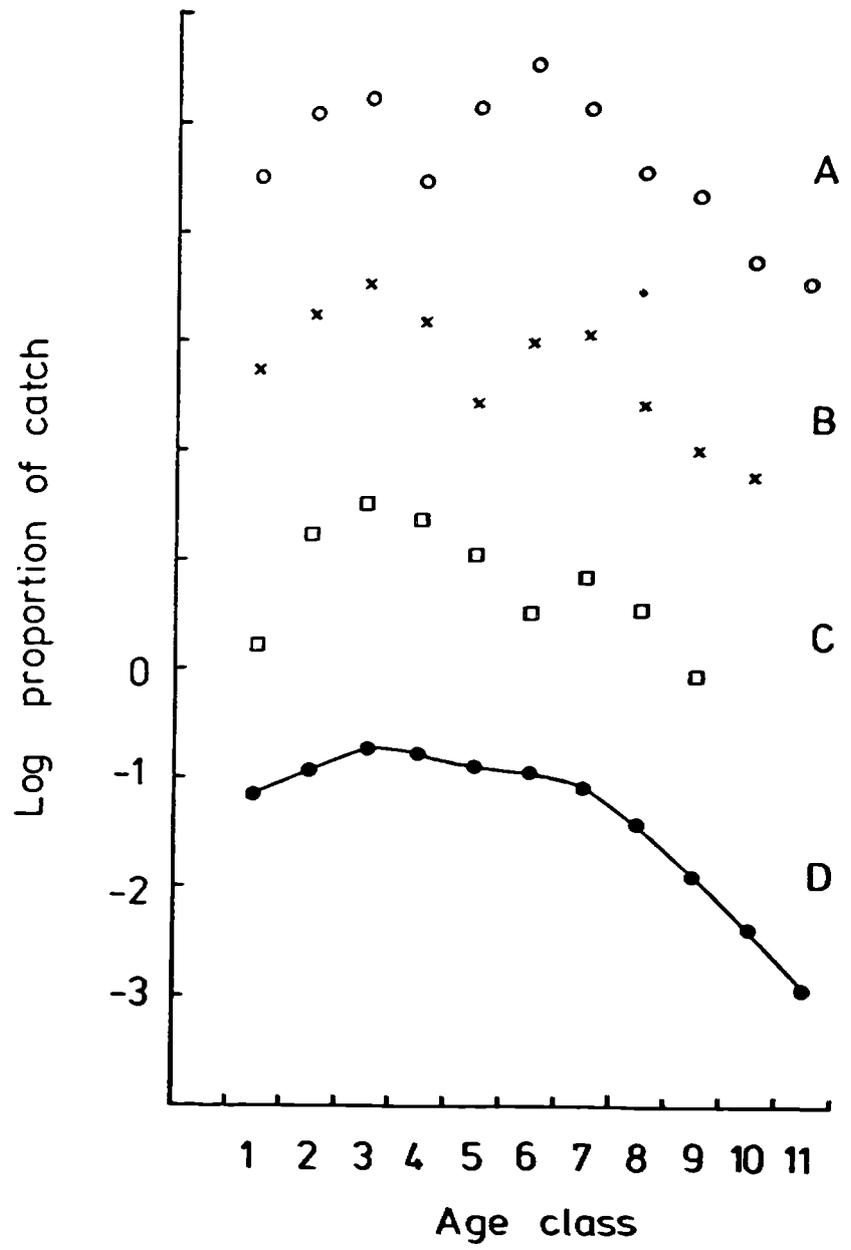


Fig. 5.3

Table 5.5

Estimation of instantaneous mortality rate Z , and survival rate S , for year classes from the catch curve in Fig. 5.3.

year class	year hatched	Z	S
11+	1974	2.625	0.072
10+	1975	2.395	0.091
9+	1976	1.842	0.159
8+	1977	1.082	0.339
7+	1978	0.414	0.661
6+	1979	0.207	0.813
5+	1980	0.299	0.742
4+	1981	0.414	0.661

strengths in Lough Neagh (Wilson, 1984).

Parasites.

Powan in Loch Lomond are host to a number of parasite species (Copland, in Slack, 1957) the effects of which are difficult to assess. In Loch Eck, powan appear from subjective observation to have a considerably lighter parasitic load, although at some times of year heavy infestations of tapeworms were recorded from the pyloric region of the intestine. Specific identification of parasites and their vectors would produce further information on the dietary differences between the two populations. The role of parasitic infestation in powan energy budgets requires investigation.

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APPENDIX 1.

Sub-sampling.

For a considerable portion of the year (spring to late autumn) powan in Loch Lomond feed almost exclusively on small planktonic Crustacea. At such times, stomachs taken from feeding fish may contain thousands of individual prey items. The enumeration of these prey species presents some difficulty, depending on the information required. In this study, a reasonable estimate of the total number of prey animals ingested and their representation by the different prey taxa or operational taxonomic units were of major importance. Numbers of prey individuals in stomachs vary by several orders of magnitude even within a single catch, and may include a range of prey species whose composition and abundances change with season.

Contents of stomachs collected from winter and early spring when little food was found were analysed in toto. Stomachs collected from the remainder of the year were analysed by sub-sampling the total stomach contents. The specific timing of the change of analysis method was determined by subjective examination of stomach contents from each sample, not by a pre-arranged schedule.

In general, where sub-samples were taken, the procedures described by Elliott (1977) were followed and tested for powan stomach data. Initially several methods of sub-sampling the total stomach contents were compared.

Method 1: Random squares.

With the total stomach contents placed in 10% ethanol solution in a counting cell, random squares (identified by marking the underside of the cell) were chosen and organisms within them counted. Animals lying on the perimeters of each chosen square were counted for two of the four sides. Immediate problems occurred because of the sheer number of prey items encountered in some stomachs. Side effects of the cell and surface tension effects caused considerable disturbance of the items present. An alternative method was used.

Method 2: Volumetric.

The total stomach contents were made up in a known volume of preservative and agitated thoroughly. The agitated mixture was sub-sampled by pipette. If the prey items were distributed randomly when sub-sampled and a small proportion of the total removed in each sub-unit, then the counts of the sub-sample should have a Poisson distribution. This was checked using a chi-squared test on a sub-sample of five sub-units. Where there was agreement with a Poisson distribution, a random distribution was assumed and a single sub-unit used to estimate the total numbers. The accuracy of this estimate depends on the size of the count of the sub-unit, ie: 95% confidence limits are $\pm 50\%$ for a count of 16, $\pm 20\%$ for a count of 100, and $\pm 10\%$ for a count to 400. Therefore the accuracy of the count is improved by counting more items if the Poisson distribution is a suitable model. If the counts of the sub-samples indicate that the organisms were contagiously distributed in the sampling container, transformation of the original counts may be necessary. Small variations in the implementation of this technique were tested to determine the best method of taking sub-samples from the sampling

vessel. Where samples consisted of many small items, eg Bosmina and a few larger items, eg: insect pupae, the larger items were removed and counted separately before sub-sampling took place. Trials of sub-sampling methods were carried out on old plankton samples.

Method(2a): 10 plankton samples taken at dusk 19th October 1982 were each made up to 300mls with 10% ethanol solution. The flask containing each sample was thoroughly agitated by repeated inversion for 20 seconds. Five sub-samples of 20mls each were removed by pipette from the sampling vessel. This process lasted 20 - 25 seconds, during which time there was no further agitation of the vessel other than that caused by sub-sampling. The copepod Diaptomus gracilis was counted in each sub-sample. The sub-samples were replaced, and the process repeated for each plankton sample.

Method(2b): The above procedure was repeated, using the same plankton samples, but with the additional precaution of inversion of the sampling vessel between sub-samples.

One of the ten samples examined was found to have a contagious distribution of sub-sample counts. This second method was used in all further sub-sampling.

It has already been stated that the reliability of the estimate of total numbers in the sample increases with total count. For this reason, Elliott (1977) recommended the use of the total count of five sub-units (having established their agreement with the Poisson distribution) as the estimate of the original number of animals in the sample, using 95% confidence intervals obtained from Crow & Gardiner (1959).

Sub-sample size.

In determining the size of sub-sample used in this study to estimate total numbers of prey and prey species contained in fish stomachs, trials were carried out on stomach samples collected by D.B.C. Scott and the late H.D. Slack from Loch Lomond in the 1960's. Five sub-units were sub-sampled from the total volume of stomach contents for each case. Different fractions of the total volume of contents were compared as suitable sub-units. The counts were tested for agreement with a Poisson series, estimates of the total counts for each stomach obtained and the number of prey species encountered during the sub-sampling was recorded.

For the three stomachs examined, counts for each numerous species were in agreement with a Poisson series (Table A.1). Since the precision of the total estimate depends on the magnitude of the counts obtained from sub-sampling, the total fraction of the original sample counted is not as important as the total number of items counted (Table A.2).

The occurrence of prey species in the sub-units is shown in Table A.2. More species are detected as the fraction of the total contents examined increases. However, the counting effort involved in detecting the rarer species is disproportionate to their importance in the diet, unless these rare items are relatively large, in which case the technique of sub-sampling will not be required for their detection. It was decided that where sub-sampling was necessary, counts of one sixth of the total volume of preservative plus stomach contents would fulfil the requirements of numerical accuracy and prey species composition. This standard sub-sample aliquot was used for all stomachs sub-sampled.

Table A.1

Sub-sampling method selection.

(a) Total volume of each sample = 300mls
Volume of sub-samples = 5 x 20mls

Sample number	Counts of individuals per 20 ml. sub-sample					mean x	variance s	chi-squared	Poisson accepted
1.	140	157	163	172	261	178.6	2258.3	50.6	no
2.	163	199	166	180	200	181.6	308.3	6.8	yes
3.	275	191	183	177	202	205.6	1592.8	40.0	no
4.	157	189	166	140	181	166.6	377.3	9.1	yes
5.	93	111	120	103	99	105.2	111.2	4.2	yes
6.	157	177	194	139	175	168.4	441.8	10.5	yes
7.	198	219	179	188	200	196.8	224.7	4.6	yes
8.	141	93	131	118	99	116.4	417.8	14.4	no
9.	190	166	136	192	144	165.6	658.8	15.9	no
10.	175	144	154	166	148	157.4	165.8	4.2	yes

(b) Sampling volumes as in (a).

Sample number	Counts per 20 ml sub-sample					mean x	variance s	chi-squared	Poisson accepted
1.	147	171	166	153	144	156.2	139.7	3.6	yes
2.	206	187	181	199	190	192.6	98.3	2.0	yes
3.	177	184	167	159	190	175.4	157.3	3.6	yes
4.	133	107	146	117	120	124.6	229.3	7.2	yes
5.	85	108	81	98	108	96.0	159.5	6.6	yes
6.	172	155	146	138	158	153.8	165.2	4.3	yes
7.	173	198	191	154	200	183.0	379.7	8.3	yes
8.	161	104	131	149	132	135.0	464.3	13.8	no
9.	116	130	112	124	131	122.6	70.8	2.3	yes
10.	186	163	170	161	181	172.2	120.7	2.8	yes

Table A.2

Determination of sub-sample size for fish stomach contents.

	Fish A. prey species			Fish B. prey species			Fish C. prey species		
	Bosm	Daph	Byth	Bosm	Lept	Byth	Bosm	Byth	Holo
Sub - 1	81	9	20	232	17	0	109	11	16
sample 2	77	11	22	220	20	2	97	9	12
number 3	70	12	20	199	17	1	122	14	15
4	74	14	23	230	16	4	106	10	15
5	78	14	28	243	15	2	111	11	10
Total count	380	60	113	881	85	9	545	55	68
Mean	76	12	22.6	220.3	17	1.8	109	11	13.6
Chi-squared Poisson accepted	3.6 yes	7.6 yes	6.0 yes	4.15 yes	0.82 yes	4.9 yes	2.99 yes	0.5 yes	1.85 yes
95% C. I.									
Lower	353	45	93	840	67	4	513	41	52
Upper	467	76	134	922	104	17	577	71	85
Whole sample estimate (Mean & CI)	1059 1140 1321	135 180 228	279 339 402	4032 4229 4426	322 408 499	19 43 82	1539 1635 1731	123 165 213	156 204 255

Sub sample sizes : Fish A - total volume = 30 mls, aliquot = 2 mls.
 Fish B - total volume = 120 mls, aliquot = 5 mls.
 Fish C - total volume = 150 mls, aliquot = 10 mls.

95% confidence interval obtained from Crow and Gardiner (1959).
 Prey species : Bosm = *Bosmina coregoni*, Daph = *Daphnia hyalina*,
 Byth = *Bythotrephes longimanus*.

Table A.3

Cumulative occurrence of new species in sub-units.

		Aliquot				
		1	2	3	4	5
Cumulative proportion of sample examined	Fish A	2/30	4/30	6/30	8/30	10/30
Number of prey species counted	Fish A	5	6	6	6	6
Cumulative proportion of sample examined	Fish B	5/120	10/120	15/120	20/120	25/120
Number of prey species counted	Fish B	4	5	5	6	6
Cumulative proportion of sample examined	Fish C	10/150	20/150	30/150	40/150	50/150
Number of prey species counted	Fish C	3	4	4	5	5

All monochrome plates taken using a Zeiss photomicroscope,
Optovar 1.25, Planapo x4, x2.5 or Plan x1 objectives,
calibrated with stage micrometer.
Pan F rated at 7 or Panatomic-X rated at 5 volts.
Acutol 1:10 6.5 minutes at 20°C.
Colour plates are from Kodakchrome-25 and VR100
transparencies.



Plate 1. Loch Lomond.
Mid-basin, looking north, January 1984.

Plate 2. Loch Eck.
Approximately 3km from northern end of loch,
showing shallows of east shore, looking north.



Plate 3. Catch from Loch Eck, February 1984:

powan, *Coregonus lavaretus*
charr, *Salvelinus alpinus*
three-spined sticklebacks, *Gasterosteus aculeatus*
(lens cap diameter is 57mm).



Plate 4. *Daphnia hyalina* var. *galeata* from Loch Lomond,
round helmeted morph, showing measurement of
body length (bl).

Plate 5. As above, but showing peaked helmet morph.

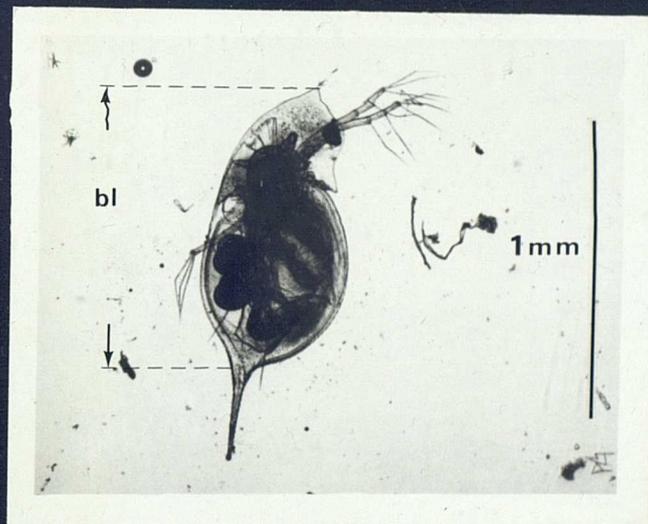
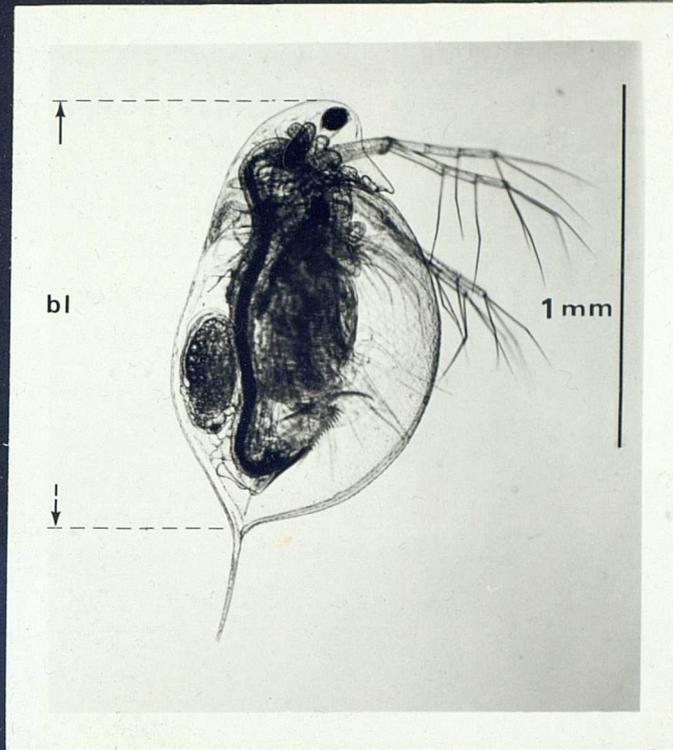


Plate 6. *Bosmina coregoni* var. *obtusirostris*,
showing measurement of body length (bl).

Plate 7. *Diaptomus gracilis*.

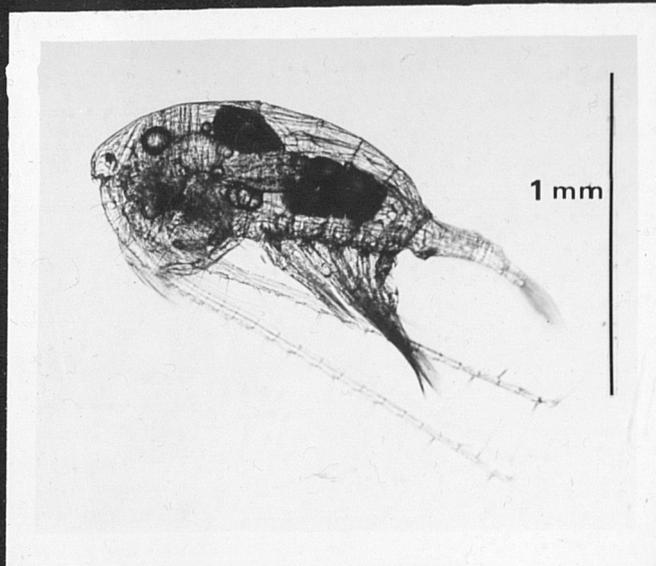
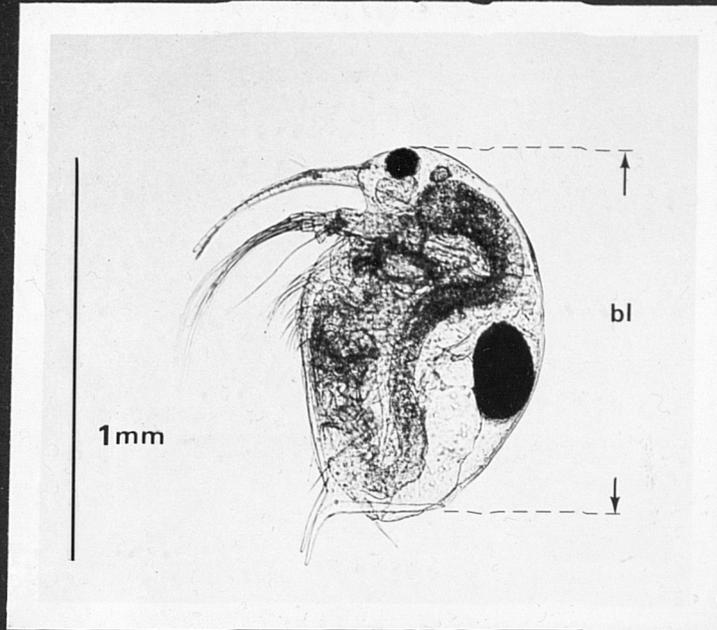


Plate 8. *Cyclops strenuus abyssorum*, female.

Plate 9. *Cyclops strenuus abyssorum*, male.

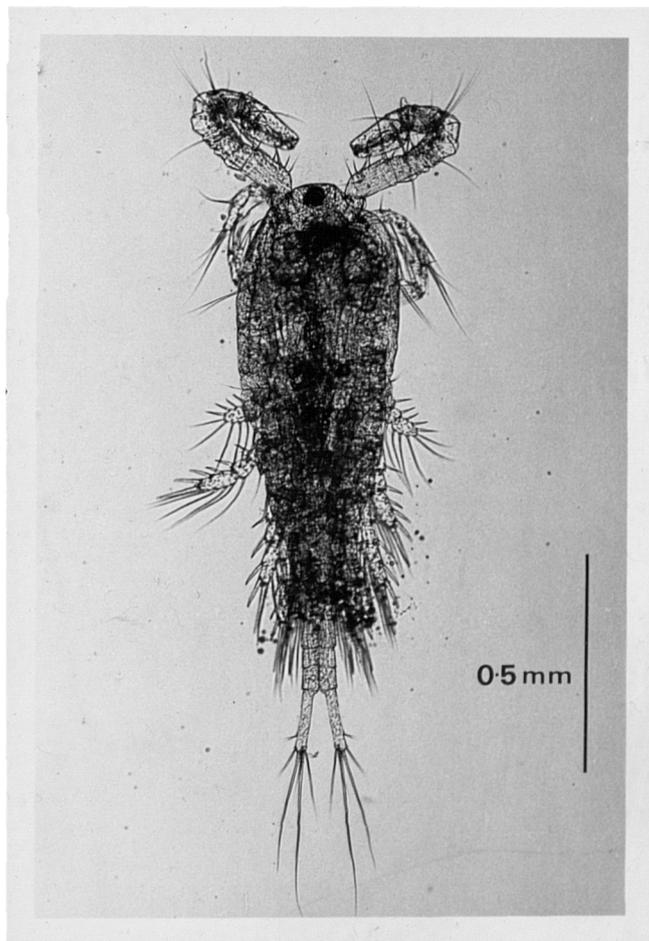
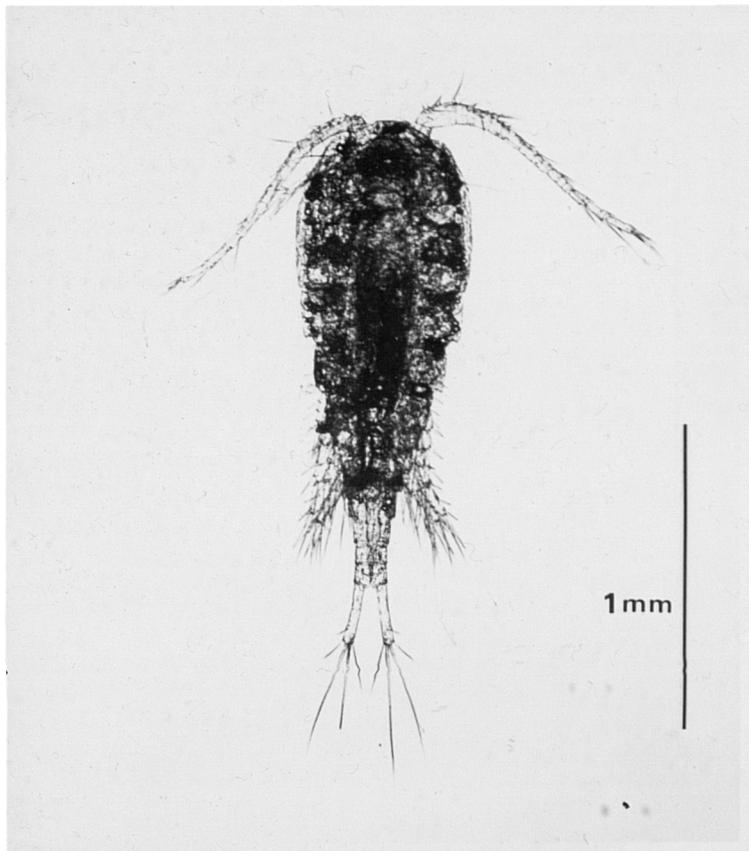


Plate 10. *Bythotrephes longimanus* (with
damaged caudal spine).

Plate 11. *Polyphemus pediculus*.

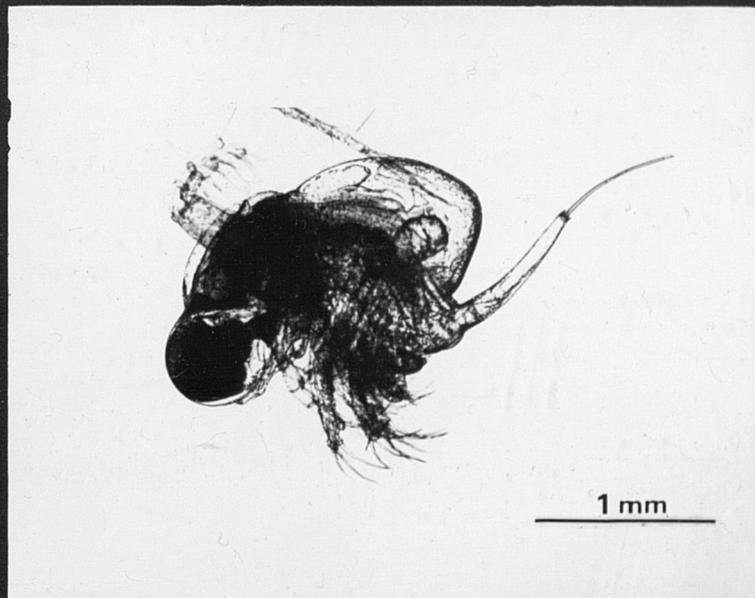
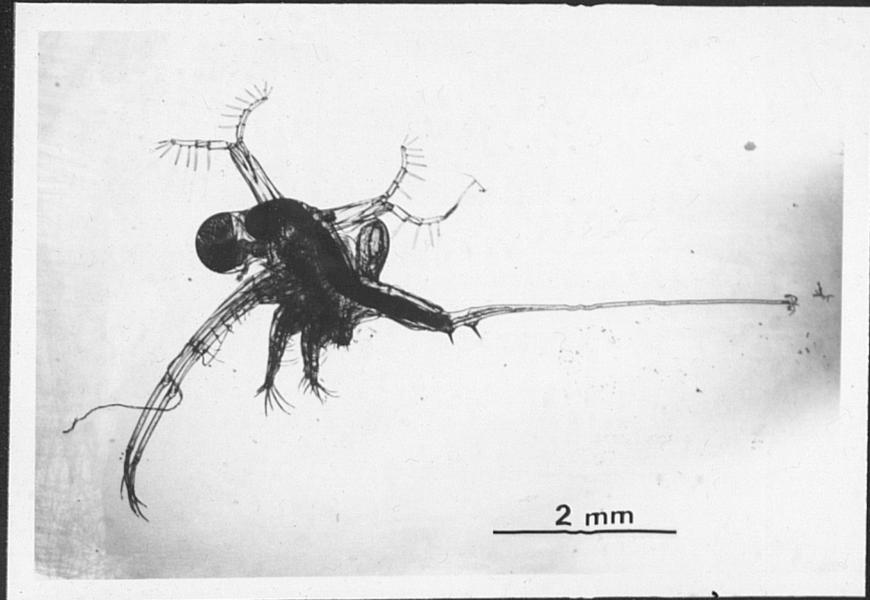
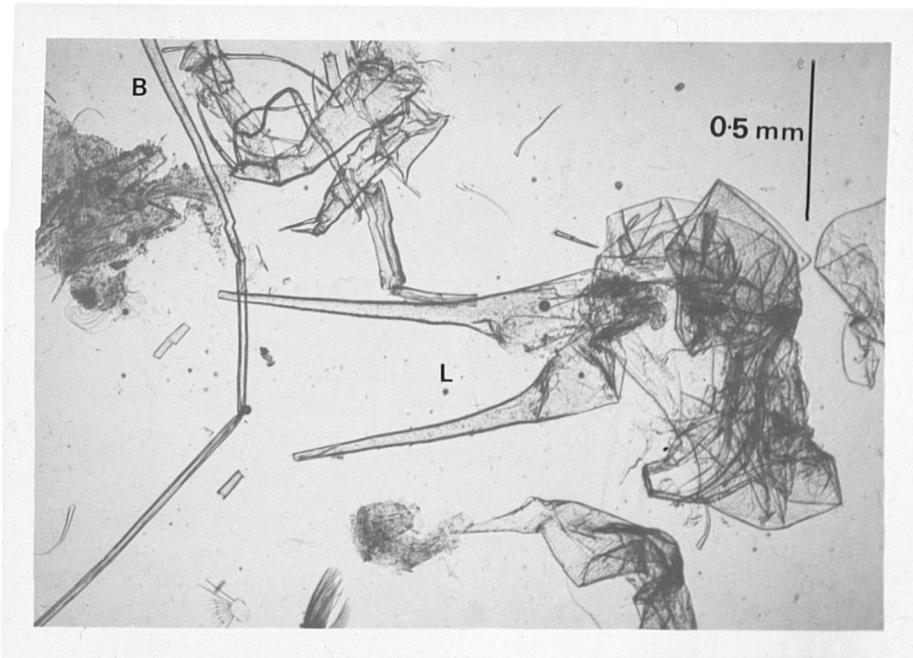
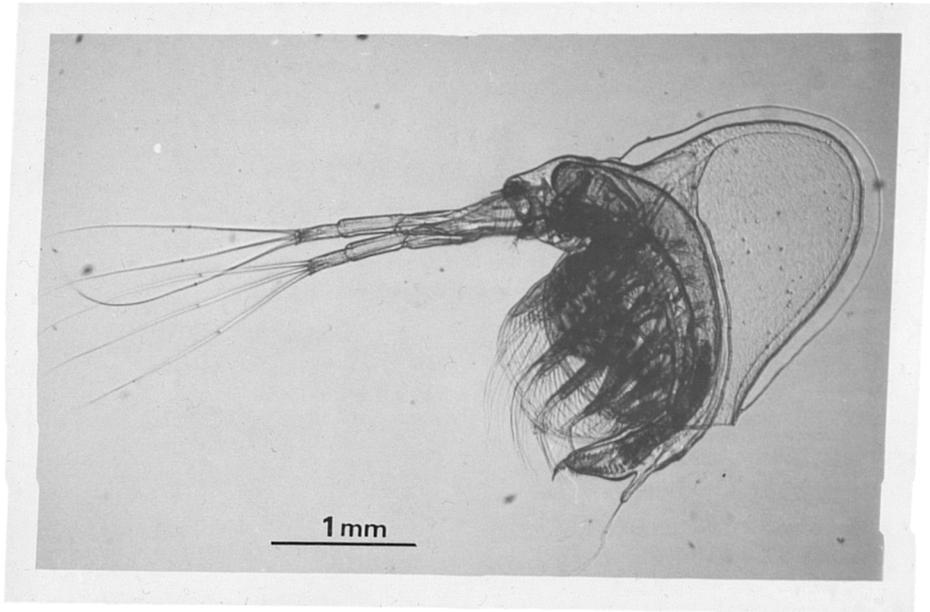


Plate 12. *Holopedium gibberum* (without
gelatinous matrix)

Plate 13. Stomach contents of powan, July 1983,
showing remains of *Leptodora* (L) and
Bythotrephes (B).



Plates 14,15. Laboratory raised powan, 150 days old
(total length = 65mm).

