THE BIOLOGY OF THE BRITISH ATHERINIDAE, WITH PARTICULAR REFERENCE TO *ATHERINA PRESBYTER* CUVIER OF LANGSTONE HARBOUR, HAMPSHIRE

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CONTENTS

ABSTRACT

The study has recorded the presence of two members of the Atherinidae in British waters, the common sandsmelt, *Atherina presbyter* Cuvier and Boyer's sandsmelt, *A. boyeri* Risso. The latter is a notable find and only the fourth record of the species from British waters. A systematic analysis of samples from eight localities suggests that British atherinids support the present accepted taxonomic scheme for the Atlantico-Mediterranean silversides.

Aspects of the biology of the two species have been recorded. Individual fish in samples of *A. presbyter* from Langstone Harbour and Fawley and *A. boyeri* from Oldbury-upon-Severn were measured, weighed, sexed, and aged, by counting the growth zones in the saccular otoliths. These data were used to determine age and length structure of the population, annual mortality, growth in length and weight, length-weight relationship and sex ratio. Certain phenological parameters were also followed: condition, mesenteric lipid reserves, hepatosomatic index, intestine weight, and gonadosomatic index. The ecology of the two species was also investigated and included an analysis of diet and infection by parasites.

The gonadosomatic index, fecundity counts, and oocyte size-frequency distributions were used to describe the sexual cycle. Adult *A. presbyter* were spawned in the laboratory which enabled the ovum to be described and established the pattern of embryo development, time to hatching with respect to temperature, and pattern of postlarval development. The life-histories of the two species were considered in the context of current views concerning the evolution of life-history strategies of small fishes.

The study gives a detailed account of the ecology and biology of *A. presbyter*, a little studied fish species, and also provides information on an isolated and unstudied population of *A. boyeri*.

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SECTION I

GENERAL INTRODUCTION

The silversides (Atherinidae) are a large family of atheriniform teleost fishes inhabiting tropical, sub-tropical and temperate waters of both hemispheres. The family includes about 29 genera of some 156 species (Nelson 1976) which are found in a variety of conditions representing a full range of salinities. Thus, there are inshore marine, estuarine and freshwater species and even some which are able to live in very high salinities. Most atherinids are small but some species grow to almost 60cm. The body form is characterised by two widely separated dorsal fins, the anterior one being composed entirely of spines; a broad silvery lateral band (black in preserved specimens); no lateral line; and relatively large scales. In feeding niches, active carnivores, plankton, algal and detritus feeders are all represented.

Although most members of the Atherinidae are abundant shoaling species their economic importance is mainly on a local basis, often as a subsistence fishery. However, the world landings have averaged just over twelve thousand metric tons during the last six years (FAO 1978). Of this figure more than a half is contributed by the South American countries and one third by the Mediterranean and Black Sea fisheries (Table 1.1). In addition, certain members of the family are of limited importance as aquarium fishes, e.g. *Pseudomugil signatus* (Günther) and the Celebes rainbow fish, *Telmatherina ladigesi* Ahl, (Frey 1961) and as sportfish (Woodling 1968, Frey 1971, Wilton 1974).

Members of the Atherinidae in North American waters have received most attention from fish biologists. Here there are both marine and freshwater representatives. The grunions, *Leuresthes tenuis* (Ayres) and

Table 1.1. Commercial catches of members of the Atherinidae, in metric tons (FAO 1978).

		1972	1973	1974	1975	1976	1977
Atlantic, N.W.	Total	100	0	38	36	30	15
	U.S.A.	100	0	38	36	30	15
Atlantic, N.E.	Total	0	0	0	6	0	0
	France	0	0	0	6	0	0
Mediterranean	Total	4300	4900F	4245F	3779F	3683F	3562F
and Black Sea	Egypt	200	200	179	141	79	182
	France	0	0	155	112	238	229
	Italy	3700	4100	3621	3156	3112	2782
	Romania	200	300	3	83	15	85
	Turkey	100	100F	100F	100F	100F	100F
	Yugoslavia	100	200	187	187	139	184
Atlantic, S.W.	Total	1700	2000	2274	2415	1581	735F
	Argentina	1300	1700	1100	680	1169	323
	Brazil	400	300	1174	1735	412	412F
Pacific,	Total	1100	1300	1175	1281	1335	942
W. Central	Fiji	0	0	1	1	6	7
	Philippines	1100	1300	1174	1280	1329	935
Pacific, S.E.	Total	2400	1300	7006	11216	4240	3554
	Chile	600	400	953	919	902	240
	Peru	1800	900	6053	10297	3338	3314
Africa,	Total	0	0	0	165	96	94
inland waters	Egypt	0	0	0	165	96	94
	Total	9600	9500F	14738F	18898F	10965F	8902F

(F = FAO estimate)

L. sardina (Jenkins and Evermann), Pacific coast species have been much studied because of their unusual tide-controlled spawning habits which has given rise to a unique sport fishery (Clark 1925, Thompson and Thompson 1919, Walker 1952, Hubbs 1965, Woodling 1968, May 1971, Reynolds and Thomson 1974a,b,c, Thomson and Muench 1974, 1976, Moffatt and Thomson 1975, Reynolds *et al* 1976). Clark (1929) also published data on the fishery, spawning and growth rates of another West Coast species, the California jacksmelt, *Atherinopsis californiensis* Girard. The third Pacific Coast genus, *Atherinops*, has received particular attention owing to the occurrence of several forms which have been given specific and subspecific status (Jordan and Snyder 1913, Hubbs 1918, Schultz 1933). The tolerance of one of these, the topsmelt *Atherinops affinis* (Ayres), to variations in temperature and salinity has also been investigated (Doudoroff 1945, Carpelan 1955, Hubbs 1965).

The largest atherinid genus within North America, with regard to the number of species, is *Menidia* Bonaparte. This genus is basically of Atlantic coastal origin although members are found in both the marine and freshwater environments (Kendall 1902, Gosline 1948). The spawning and subsequent development (Hubbs *et al* 1971, Fisher 1973, Hubbs and Bryan 1974, Hubbs 1976), the diet (Saunder 1959) and general ecology (Mense 1967) of the Mississippi silverside *M. audens* Hay have been studied. This species has been established in some Californian lakes in an attempt to control, biologically, chaoborid midge populations (Cook 1968, Cook and Moore 1970). These introductions have had an effect on the endemic fish fauna (Li *et al* 1976) and have led to the species extending its geographical range (Moyle 1974, Meinz and Mecum 1977). Another freshwater atherine investigated in this context was

Labidisthes sicculus (Cope) (Cook 1968). The ecology and breeding habits of this species are also well documented (Hubbs 1921).

At present, four marine and euryhaline species of the genus *Menidia* are recognised along the eastern coastline of the United States (Johnson 1973, 1974, 1975). This has led to cases of hybridization where their ranges overlap (Rubinoff and Shaw 1960). The most euryhaline of these is the tidewater or waxen silverside, *M. beryllina* (Cope) which has been recorded from freshwater impoundments (Tilton and White 1964). Hildebrand (1924) described and figured the egg and larval development of this species and of *M. menidia* (L.), the reproduction of which has since been further investigated (Rubinoff 1958, Austin *et al* 1975, Middaugh and Lempesis 1976).

The Pacific, Indian and South Atlantic Oceans and the fresh waters which flow into them contain many genera of atherine fishes, the majority of which have been little studied. However, a review of the atherine fishes of Japan was carried out by Jordan and Starks (1901) whilst the feeding habits and digestive systems of two of these species, *Atherina bleekeri* (Günther) and *Atherina tsurogal* (Jordan and Starks) were investigated by Suyehiro (1942). In addition, Smith (1965) reviewed the atherine fishes of the Western Indian Ocean and Red Sea.

North-East Atlantic and Mediterranean waters contain three species of the genus *Atherina* Linnaeus and a single species of the genus *Pranesus* Whitley (Kiener and Spillmann 1973). However, the latter species, *Pranesus pinguis* (Lacepède), is a recent immigrant from the Red Sea and at present is only found in the coastal waters of Israel. Of the three *Atherina* species, *A. boyeri* Risso and *A. hepsetus* L. are essentially Mediterranean and Black Sea species with only occasional populations in North-East Atlantic waters, the area to which *A. presbyter*

Cuvier is confined. Only *A. presbyter* (the sandsmelt) and *A. boyeri* have been recorded from British waters and it is these two species which form the basis of this investigation.

At present the biology and ecological requirements of these two species, particularly *A. presbyter*, is little understood. (The information presently available is not reviewed here as this will be done in the introduction to the relevant section). As small fish of little economic or sporting value they have apparently been much neglected by fish biologists. This investigation, although raising many unanswered problems provides information concerning the basic biology of the British Atherinids, particularly with respect to the *A. presbyter* population in Langstone Harbour, Hampshire, the major study area.

SECTION II

STUDY AREAS AND GENERAL METHODS

2.1. Study areas and methods of sample capture

Atherinid samples have been collected by a variety of methods from eight localities (Fig. 2.1), seven around the coast of Britain and one in the Channel Islands. The distribution of these samples is set out in Table 2.1.

2.1.1. Langstone Harbour, Hampshire

The greatest number of samples has been obtained from within Langstone Harbour (Fig. 2.2), which thus forms the main study area. This is an almost enclosed tidal basin of 19.4km^2 between Portsmouth Harbour to the west and Chichester Harbour to the east. The three harbours are physically connected by channels at the north through which slight exchanges of water take place (Dunn 1972, Portsmouth Polytechnic 1976). Langstone receives relatively small amounts of fresh water from a number of streams, land drains, and two sewage outfalls. The inflows have, of course, localised effects on the salinity of the harbour water. On the whole, however, the harbour can be considered fully saline with readings of 33.0 to 34.0$^{o}/_{oo}$ over most of its area throughout the year. Indirect temperature records of harbour water are kept by the Portsmouth Polytechnic's Marine Laboratory. The temperature of water pumped from the harbour for its seawater system is monitored by a pen recorder. Mean monthly seawater temperatures over the study period are given in Table 2.2.

At high tide, the sheet of water is interrupted by Farlington Marshes, a reclaimed peninsula of pasture and marsh forming an extension of the northern mainland, and four islands which lie to the east of the

Fiqure 2.1.

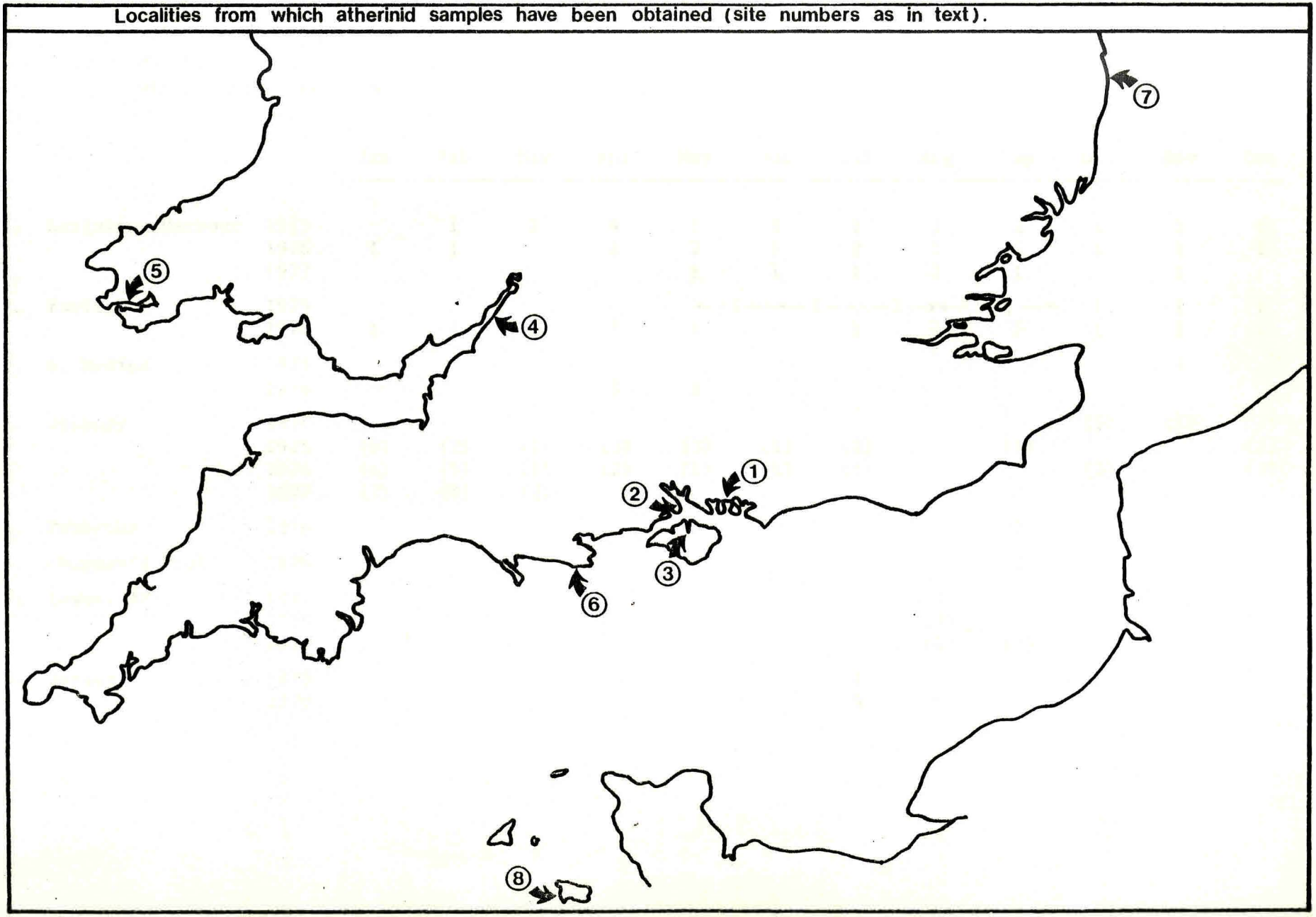

Localities from which atherinid samples have been obtained (site numbers as in text).
1
2
3
4
5
6
7
8

Table 2.1. Monthly distribution of samples obtained from each site (numbers in parantheses refer to actual fish where numbers were small).

			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1.	Langstone Harbour	1975		1	1	4	1	2	1	1	2	1	1	1
		1976	1	1		1	2	1	2	2	2	1	1	1
		1977					1	1	1	1	1		1	
2.	Fawley	1975					←1	→←1	→←1	→←1	→←	1	1	1
		1976	1	1	1	1	1	1	1	1	1	1	1	1
3.	R. Medina	1975											1	
		1976				1	1							
4.	Oldbury	1974										(1)	(1)	(7)
		1975	(8)	(2)	(1)	(3)	(3)	(1)	(2)		(1)			(2)
		1976	(4)	(1)	(1)	(2)	(1)	(1)	(1)			(3)		(3)
		1977	(7)	(8)	(2)									
5.	Pembroke	1976									1			
6.	Chapman's Pool	1976									2			
7.	Lowestoft	1975								(3)				
		1976								(3)				
		1977								(4)	(2)			
8.	Jersey	1975							1					
		1978							4					

Figure 2.2.

Langstone Harbour - Sampling sites

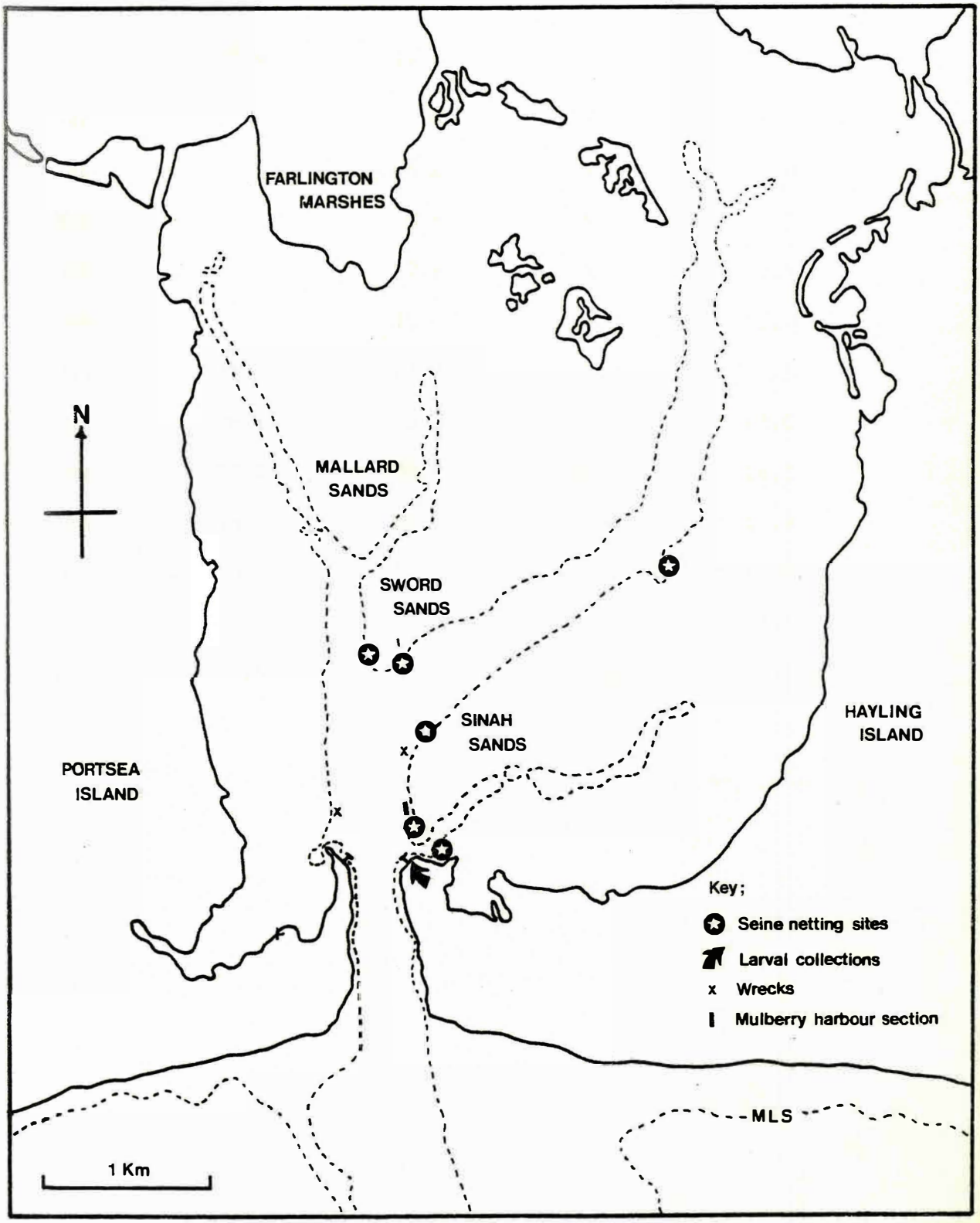


Table 2.2. Langstone Harbour - mean monthly seawater temperatures (^{o}C)

	1974	1975	1976	1977
Jan		7.0	6.2	4.5
Feb		5.8	4.3	6.0
Mar		5.6	5.4	7.5
Apr		7.8	8.3	8.5
May		11.0	12.2	12.0
Jun	15.3	15.9	17.3	14.5
Jul	16.5	18.4	20.1	18.0
Aug	17.5	20.2	20.0	18.3
Sep	13.9	16.2	16.6	15.9
Oct	10.2	12.1	14.0	14.0
Nov	8.2	8.5	9.5	9.8
Dec	7.6	5.8	6.0	7.0

marshes. However, at low water three sandbanks of considerable area are exposed situated at the junctions of the main drainage channels. The remainder of the harbour bottom is composed of a variety of deposits from gravel through to fine silt and mud, the dominant substrate being mud.

The samples were most frequently obtained from the south-western edge of Sinah Sands in the proximity of a Mulberry Harbour section marooned during World War II (Fig. 2.3). Fish were captured at low water using a sandeel seine. This was 25m long with a depth of 1.5m at the wings increasing to 2.5m at the bunt where the mesh was 6mm bar. Sufficient sandsmelt were usually caught at this site to provide a sample. However, particularly in winter, the fish were sometimes scarce and other localities within the harbour were tried but seldom with more success.

Samples of postlarvae too small to be retained by the seine-net were captured by a plankton meshed dipnet in the vicinity of the Hayling ferry pontoon and from various shore pools.

2.1.2. Fawley, Hampshire

Nineteen monthly samples have been obtained off the intake screens at Fawley Power Station situated on the south-western shore of Southampton Water (see Acknowledgements). Here water is drawn from a deep water offshoot of the main channel. Sea water temperatures at the nearby Calshot Jetty are recorded by the British Transport Docks Board and the monthly maximum and minimum thermograph readings, for 1975 and 1976, are presented in Table 2.3. Unfortunately, no salinity data was obtainable.

2.1.3. Medina Estuary, Isle of Wight

Three samples of atherinids were seined from the lower middle

Figure 2.3.

The Mulberry Harbour section viewed from Sinah sands at mean low water spring tide level.

Table 2.3. The maximum and minimum seawater temperatures (^{o}C) for Calshot Jetty (British Transport Docks Board)

	1975		1976	
	Max	Min	Max	Min
Jan	10.2	6.7	8.0	4.6
Feb	8.5	6.0	7.5	2.9
Mar	8.0	5.6	7.9	4.6
Apr	12.1	8.9	11.1	6.7
May	13.9	10.0	14.9	9.1
Jun	18.3	11.1	22.2	13.3
Jul	18.9	15.6	23.9	19.8
Aug	22.8	17.8	22.3	18.7
Sep	22.0	14.1	20.0	15.4
Oct	15.6	9.8	17.9	12.4
Nov	12.2	7.8	13.5	8.9
Dec	8.8	6.0	9.9	5.0

reaches of the River Medina Estuary, in conjunction with a Medina survey instigated by the Nature Conservancy Council (Tubbs 1975, Withers 1979).

This is a narrow estuary never exceeding 0.4km in width and extending from Newport to Cowes which is a distance of some 6.8km. At low water a single shallow channel remains flanked by mud banks except through Cowes where it is lined by docks, boatyards and marinas.

In addition to the freshwater entering the Estuary from the River Medina above Newport there are two major sewage discharges. From salinity readings taken at various sites on four different occasions it is suggested that salinity is dependent on rainfall (Withers 1979). Unfortunately, no salinity readings were taken at the time of sample collection. However, the low water salinity was recorded from the sampling site on the day following the first dated sample and gave a value of $32^{o}/oo$.

No record of the temperature régime within the estuary appears to exist. Kingston Power Station just above Cowes abstracts and returns warmed seawater. However, this is now only intermittant and probably has little effect on estuary temperatures.

2.1.4. Oldbury-upon-Severn, Gloucestershire

Thirty eight dated samples of atherinids have been obtained from the intake screens of Oldbury-upon-Severn Power Station. Here water is drawn from a 1.6 km^2 tidal reservoir that has been constructed over the intertidal mud flats and is isolated from the Severn Estuary for from 6 to 7 hours in each tidal cycle. These atherinids were collected as part of an investigation into the ecology of the fish populations of the Middle Severn Estuary (Claridge and Gardner 1976, 1978) (see Acknowledgements). Mean monthly water temperatures and salinities at the intake screens were monitored as part of this investigation and are

presented in Table 2.4 with the mean monthly seawater temperature at Hinkley Point for comparison.

2.1.5. Pembroke Power Station

One sample of fish was obtained by seine net in the autumn of 1976 (see Acknowledgements).

2.1.6. Chapman's Pool, Dorset

Two samples of O-group fish were collected from a large shore pool. A technique documented by Gibson (1967) utilising anaesthetic quinaldine was employed.

2.1.7. Lowestoft, Suffolk

Three fish were obtained by beam trawl from the Newcombe Bank while the remainder were caught on rod and line from Hamilton Dock (see Acknowledgements).

2.1.8. Jersey, Channel Islands

One large fish, standard length 141mm, was found dead on the beach near Gorey, in July 1975. The remainder were postlarvae captured by dipnet from shore pools at St. Aubins (July 1975), and St. Brelades, Petit Port and L'Etaq (1978). Postlarvae were also collected at Maitresse Ile, Les Minquiers (1978).

2.2. Preservation of material

Fish from Langstone Harbour and the Medina Estuary were frozen as soon as possible after capture. All other fish were preserved in 4% formol-saline solution. The effects of both these methods of preservation on the lengths and weights of individual fish have been

Table 2.4. Mean monthly water temperatures and salinities.

	a) Oldbury Power Station (intake screens)		b) Hinkley Point
	°C	°/oo	°C
1974			
Oct	10.8	17.0	12.0
Nov	8.5	14.6	9.2
Dec	7.8	11.7	9.0
1975			
Jan	8.1	10.0	8.6
Feb	6.9	9.5	7.4
Mar	6.6	12.4	6.9
Apr	8.4	16.1	9.4
May	12.8	18.7	13.7
Jun	15.8	22.2	16.6
Jul	18.8	23.6	19.4
Aug	20.9	27.7	20.5
Sep	17.2	28.5	17.4
Oct	13.0	28.4	14.9
Nov	10.3	24.5	10.8
Dec	7.2	21.0	7.8
1976			
Jan	7.7	17.8	7.8
Feb	4.7	20.3	7.0
Mar	6.6	21.1	
Apr	9.6	21.2	
May	12.5	24.5	
Jun	16.7	26.3	
Jul	21.1	27.5	
Aug	19.6	28.8	
Sep	16.3	27.8	
Oct	13.9	15.0	
Nov	9.8	15.8	
Dec	5.9	11.3	
1977			
Jan	4.1	9.8	
Feb	6.4	5.9	
Mar	7.4	9.7	

investigated against time. Changes in these parameters are effected in both cases but the error is under 5%. In the case of 4% formol-saline the error is reduced if the fish are not examined for a minimum of one week. The effect of preservation on individual body components has not been investigated.

2.3. Age convention

Throughout this study atherinids have been assigned to particular age-groups, for example 0 group, I group, II group, III group etc. The changeover from one group to the next takes place on 1 January each year. This 'age convention' is regularly used in fish biology and is particularly applicable to British atherinids for three reasons:-

1. the exact age cannot be determined accurately because the spawning period is spread over several weeks;
2. 1 January lies within the winter period of minimal growth;
3. 1 January immediately follows the period of hyaline ring formation in the otoliths.

Thus a fish spawned in the early summer of one year is an 0 group fish until 1 January the following year when it becomes a I group fish. This it remains until entering group II on the following 1 January. During this study 1+ refers to age-group I together with all older age-groups and similarly II+ refers to age-group II together with all older age-groups.

2.4. Body length and weight

Body length was measured to the nearest millimetre (mm), from the tip of the lower jaw to the caudal extremity of the lateral silver stripe, using a pair of vernier calipers. This is the body or standard length (SL) and was chosen to eliminate the effect of damaged caudal fin

rays which could influence total length (TL). The relationship between standard length and total length in *A. presbyter*, derived from a regression analysis of 100 fish (42 to 137mm SL), was SL = 0.8693 TL - 0.6790 (r = 0.9996).

Body weight was obtained by first removing any external moisture with tissue paper and then weighing on a single pan analytical balance to the nearest 0.01 gram. Carcass weight refers to the body weight minus the weight of the gonad, mesenteric fat deposits, liver and alimentary canal.

2.5. Statistical treatments

Throughout this study basic statistical functions have been calculated for descriptive and comparative purposes. Means ($\bar{x}$) have regularly been calculated. To these 95% Confidence Limits (CL) have been applied where the sample number (n) is 5 or greater. Lack of overlap in 95% CL in two sample comparisons has usually been relied upon for a significant difference between the respective means. Throughout this study "significant difference" refers to significance at this probability level ($p < 0.05$) unless otherwise stated. The 95% CL have been calculated as follows:-

$$\bar{x} \pm t^{0.05} \times \text{standard error}$$

or

$$\bar{x} \pm t^{0.05} \times \frac{\text{standard deviation (S) n-1}}{\sqrt{n}}$$

In some borderline cases the student's t - test has been used.

$$t = \frac{\bar{x}_1 - \bar{x}_2}{S\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}$$

No transformation of the raw data has been undertaken and thus it has

been assumed throughout that distribution is normal. According to Simpson, Roe and Lewontin (1960) in practice the t - test is quite insensitive to deviations from normality and it was considered by Reay (1972) that the same presumably applied to the use of the t - statistic in the calculation of confidence limits.

Occasional use has also been made of regression analysis to determine the relationship between two variables. The gradient or slope (b) of the best line for this relationship has been determined by the least squares method:

$$b = \frac{\Sigma xy - \frac{\Sigma x . \Sigma y}{n}}{\Sigma x^2 - \frac{(\Sigma x)^2}{n}}$$

and its intercept (a) on the Y axis as:-

$$a = (\bar{y} - b\bar{x})$$

Where applicable, 95% CL have been applied to b for comparative purposes. These were determined as follows:-

$$b \pm (t^{0.05} \text{ x standard error of b})$$

The extent of correlation between the two variables was determined by calculating the Correlation Coefficient (r).

$$r = \frac{\Sigma xy - \frac{\Sigma x . \Sigma y}{n}}{\sqrt{(\Sigma x^2 - \frac{(\Sigma x)^2}{n})} \sqrt{(\Sigma y^2 - \frac{(\Sigma y)^2}{n})}}$$

or

$$r = \frac{\text{corrected sum of products}}{\sqrt{(\text{sum of squares of x})} \sqrt{(\text{sum of squares of y})}}$$

Where "significant correlation" exists it is correlation at the 95% probability level ($p < 0.05$) unless otherwise stated.

SECTION III

TAXONOMY OF THE BRITISH ATHERINIDAE

3.1. Introduction

Before investigating the biology and ecology of British atherinid populations it was considered essential to establish the specific identity of each of these populations. The systematics of North-Eastern Atlantic, Mediterranean and Black Sea silversides was until recently confused and often contradictory due to the proliferation of generic and specific names. A history of this nomenclature was presented by Kiener and Spillmann (1969) who went on to revise the systematics of the Atherinidae within these waters. Their findings will be summarised here as the only recent authoritative systematic work on the Atlantico-Mediterranean silversides. Indeed they are also the authors of the Atherinidae section in the Checklist of the fishes of the North-Eastern Atlantic and of the Mediterranean (Kiener and Spillmann 1973).

Historically, only two genera were used: *Atherina* Linnaeus (type: *Atherina hepsetus* L.) and *Hepsetia* Bonaparte (type: *Atherina boyeri* Risso). Schrieken and Swennen (1969) could find no reason to separate these. However, Kiener and Spillmann suggested that *Hepsetia* should be retained but as a sub-genus and that this could be separated from the other sub-genus *Atherina* on certain characteristics of mouth structure.

From examining type specimens, museum collections and their own collections Kiener and Spillmann concluded that there are in fact only three species present in the general area. These being *Atherina (Hepsetia) boyeri* Risso, *Atherina (Hepsetia) presbyter* Cuvier, and *Atherina (Atherina) hepsetus* Linné. *A. boyeri* in particular exhibits considerable variability owing to the diversity of ecological

conditions in which it is found in the Atlantico-Mediterranean zone. They suggest that this variation gave rise to the prolific generic and specific nomenclature.

Specific identity can be determined both meristically and morphometrically. Of the former the vertebral and lateral scale counts were considered the most important and reliable specific determinents. Extensive meristic and morphometric data for various North-East Atlantic, Mediterranean, and Black Sea localities were given by Kiener and Spillmann concerning the three species. A key has been compiled for separating these three species based on the information from Kiener and Spillmann (1969) (Table 3.1). It is this key which has been used to identify British atherinids to specific level. However, Kiener and Spillmann did not include fish from British localities in their meristic and morphometric data and so it was felt that the present study would be useful in determining where British atherinids would fit into the existing, accepted taxonomic scheme.

3.2. British literature

Only *A. presbyter* and *A. boyeri* have been recorded from Britain. A review of the meristics and morphometrics given for these two species in British waters is presented in Table 3.2. Only the data given by Bowers and Naylor (1964) refers to a specific locality; Queen's Dock, Swansea.

From the Table it is evident that little previous data exists. This is particularly so when it appears that Kennedy (1954) used the data from Day (1880-84) and that Lythgoe and Lythgoe (1971) obtained theirs from Wheeler (1969). The authors quoted gave little morphometric data only head size and the size of the eye compared with

Table 3.1. Key for the separation of species of the genus *Atherina* in Atlantico-Mediterranean waters (after Kiener and Spillmann 1969).

A. Very small teeth localised in the middle of the vomer and fine teeth on the palatines (Fig. 3.1.a). The elevated median process of the premaxillar slender and very long (Fig. 3.1.b) extending past a line joining the anterior margins of the eyes and equal to or longer than the horizontal process. Lateral blade of the mandible elevated. Shape index $\frac{\text{Depth}}{\text{S.L.}} \times 100$ of around 16 (measurements not made on females swollen with eggs).

Sub-genus *Atherina* (1 species)

1. Scales in lateral series 61 to 65, vertebral count 53 to 57, head elongated and mouth little inclined, no teeth on the ectopterygoids, maximum length attained 20cm.

Atherina (Atherina) hepsetus L.

B. Many vomerine and palatine teeth. Median process thicker and not so long, shorter than the horizontal process (Fig. 3.1.b). Lateral blades of the mandibles little elevated. Shape index $\frac{\text{Depth}}{\text{S.L.}} \times 100$ higher than 18.

Sub-genus *Hepsetia* (2 species)

1. Teeth on the ectopterygoids found divided into two small groups (Fig. 3.1.a), median process short not extending past the line joining the anterior eye margins. Scales in lateral series 41 to 49, vertebral count 40 to 47, maximum length attained about 13cm.

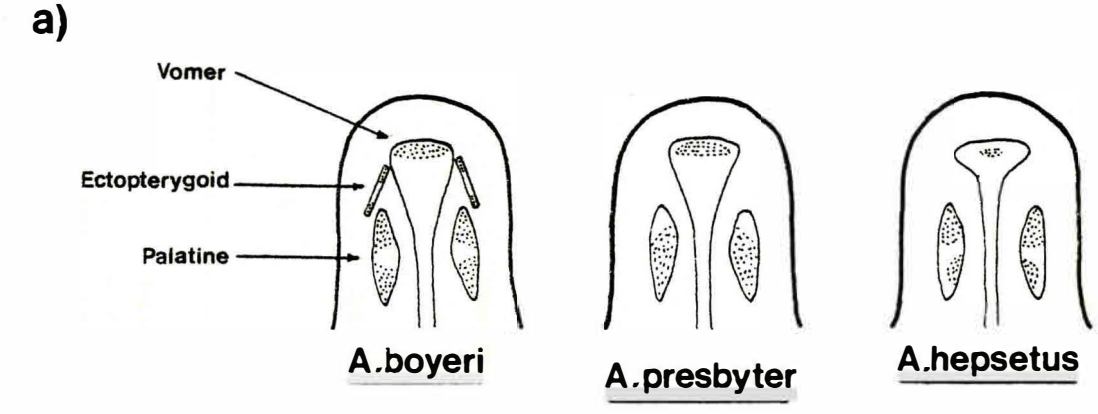
Atherina (Hepsetia) boyeri Risso

2. Teeth absent on the ectopterygoids (Fig. 3.1.a) median process slightly exceeds the line joining the anterior margins of the eyes. Scales in lateral series 52 to 56, vertebral count 47 to 51, maximum length attained 20cm.

Atherina (Hepsetia) presbyter Cuvier

Figure 3.1

Characteristics of mouth structure used in the separation of species of the genus Atherina in Atlantico-Mediterranean waters (Kiener and Spillmann 1969).



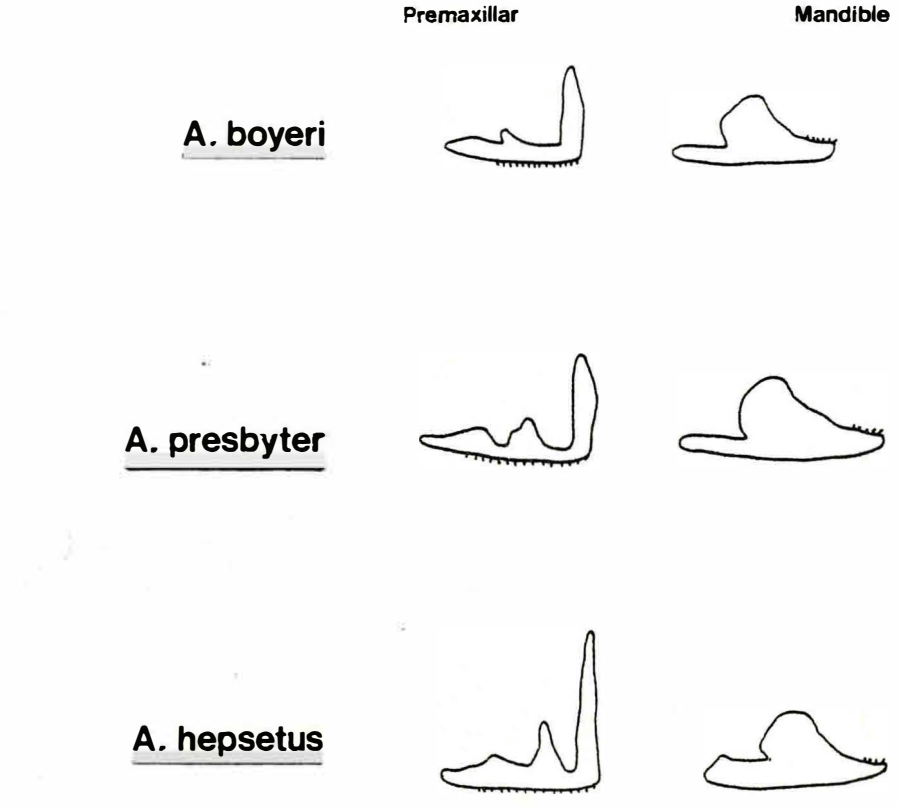


Table 3.2. Atherinid meristic and morphometric data previously presented for fish from British waters

	1D	2D	A	Pect.	P	C	Lat. scale count	Vert.	Gill Rakers	H/S.L x 100%	E/Hd
A. presbyter											
Yarrell 1836	8	1/12	1/14	15	1/5	17		50			28.6
Günther 1861	7-8	1/12	1/15-16				60	50			
Couch 1868	8	13	17	14	6	18					
Day 1880-84	7-9	1/11-13	1/14-18	13-15	1/5	17	57-62	51			33.3-36.4
Kennedy 1954	7-9	1/11-13	1/14-18				57-62	51			
Wheeler 1969	7-8	II/10-13	II/13-16				53-57	48-52	27-30	≤ 22.2	
Lythgoe & Lythgoe 1971							53-57			22.2	
A. boyeri											
Günther 1861	6-8	1/12	1/13-14				55-60	47			
Day 1880-84	7-8	1/11-12	1/12-14	14-15	1/5	17	50-57	44-46			40.0
Kennedy 1954	7-8	1/11-12	1/12-14				50-57				40.0
Bowers & Naylor 1964	7-9	12-14	1/11-14	13-14	1/5	15-17		43-46			
Wheeler 1969	7-9	II/9-11	II/11-13				44-48	43-45	21-26	25.0-26.8	

it were used. These were invariably presented as fractions and have been converted here to percentages to make them directly comparable with Kiener and Spillmann's work.

3.2.1. Comparison with Kiener and Spillmann's key

a) Vertebrae

Except for the upper limit of the range given by Wheeler (1969) all values for *A. presbyter* presented by the authors lie within the key range, as do those presented for *A. boyeri*.

b) Lateral scale count

The lateral scale counts given by three of the authors (Gunther 1861; Day 1880-84; Kennedy 1954) are high for both *A. presbyter* and *A. boyeri*, outside the key ranges. In contrast, Lythgoe and Lythgoe (1971) and Wheeler (1969) agree closely with the key ranges for both species.

3.2.2. Other meristics and morphometrics

Data presented by Kiener and Spillmann (1969) for the two species in north-eastern Atlantic waters is presented in Table 3.3. They gave only meristic means but these invariably lie within the ranges given in the British literature especially when the latter are corrected in respect of second dorsal and anal spines. In contrast, only the ratio of head to standard length for *A. presbyter* given by Wheeler (1969) and Lythgoe and Lythgoe (1971) is in morphometric agreement.

3.3. Methods and materials

For this study it was considered important to use the same morphometrics as Kiener and Spillmann (1969) so that direct comparisons

Table 3.3. Data presented by Kiener and Spillmann (1969) for *A. presbyter* and *A. boyeri* in North Eastern Atlantic waters

	1D	2D	A	Gill Rakers	Lat. scale count	V	Hd/SL	E/Hd	D-D/S.L.	LD1/S.L.	LD2/S.L.	Ped.c/Hd	Depth/S.L.	T.L. max. mm
							x 100%							
A. presbyter														
Netherlands	8.4	Ii/11.0	Ii/13.4	30.5	54.8	50.5	20.2	32.4	16.9	44.5	67.2	34.2	19.8	148
Bassin D'Arcachon						49.6								
Biarritz	8.4	Ii/11.5	Ii/14.4	30.5	54.1	50.0	21.3	33.1	16.2	44.2	65.7	30.4	18.3	139
Morocco	8.2	Ii/11.0	Ii/13.8	31.4	54.3	47.5	22.6	31.7	15.5	45.2	66.3	32.7	19.2	146
A. boyeri														
Netherlands	7.0	Ii/11.6	Ii/12.8	25.2	46.2	45.1	21.9	29.2	13.8	42.0	63.4	27.6	17.6	101

could be made with the populations that they examined. Those morphometrics used are given in Fig. 3.2. All specimens examined morphometrically had been preserved in 4% formol-saline. This method of preservation has been shown to have little effect on standard length but eye diameter in particular seemed to be affected by shrinkage.

Kiener and Spillmann did not state whether their vertebral counts included the urostyle, however in this study it has been included.

A minimum of thirty fish from each site were examined meristically and morphometrically if sufficient specimens were available. A greater number of Langstone Harbour and Oldbury-upon-Severn fish were examined so that sexual dimorphism and the effect of size on morphometrics could be investigated.

For each sample the mean ($\bar{x}$) and 95% confidence limits were calculated for each character. Regression analysis has been used to establish the extent of correlation between morphometric ratio and S.L. This procedure has already been outlined in 2.3.

3.4. Results and discussion

The meristic and morphometric characters of atherinids from the seven British and one Channel Island locality are shown in Table 3.4.

3.4.1. Specific identity

In Kiener and Spillmann's species key, given in 3.1, the vertebral and lateral scale counts were singled out as the most important specific determinants. On this basis the atherinids at all localities other than Oldbury were identified as *A. presbyter*. At all these localities the mean values of the vertebral and lateral scale counts lie within the key ranges of 47 to 51 and 52 to 56 respectively. In addition, as seen overleaf, the ranges at these seven localities are

Figure 3.2.

The measurements recorded for the morphometric analysis of British atherinids.

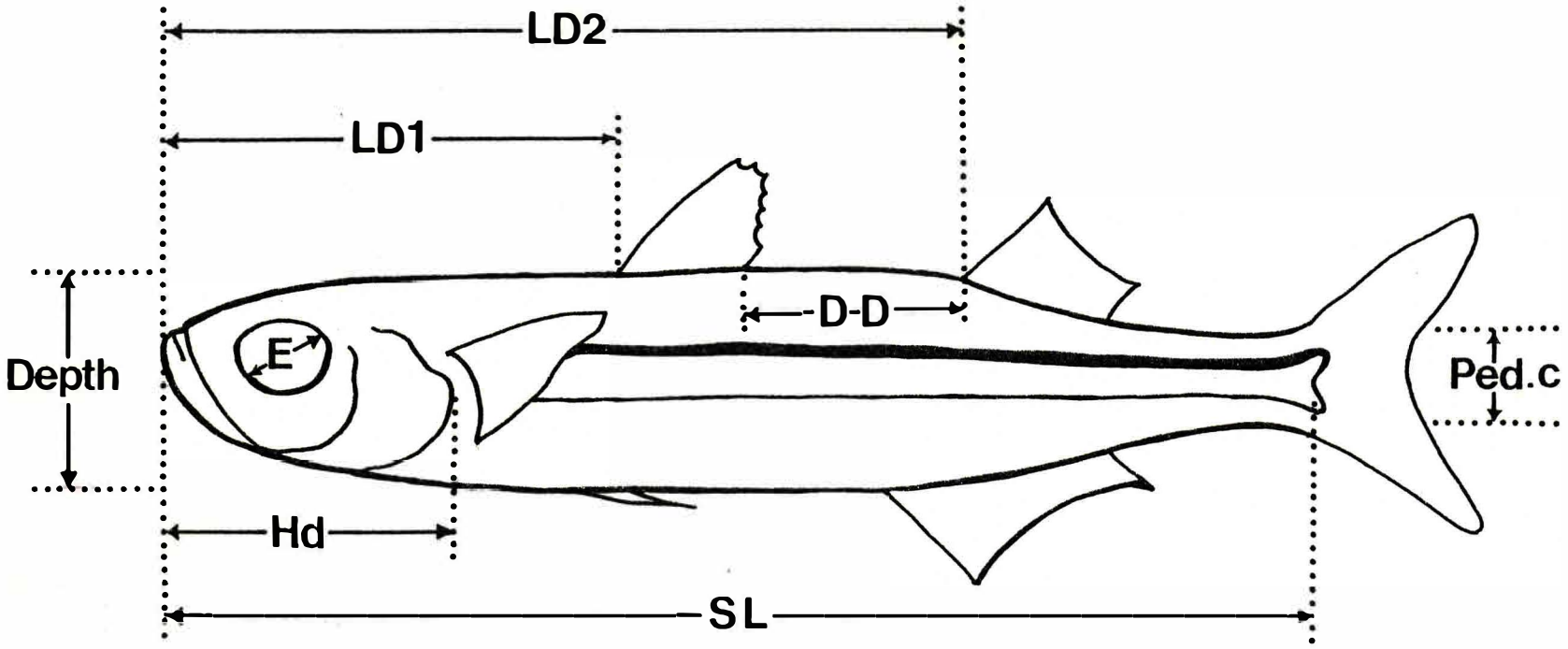


Table 3.4. Meristics and morphometrics of *A. presbyter* and *A. boyeri* at the localities investigated

		1D	2D rays	A rays	Pect.	P	C	Lat. scale count	Vert	Hd / S.L	E / Hd	D-D / S.L	LD1 / S.L	LD2 / S.L	Ped.c / S.L	Depth / S.L	S.L. mm
										x 100%							
A. presbyter																	
Lowestoft	$\bar{x}$	8.67	11.25	14.67	15.33	1/5	17.08	55.58	51.08	20.74	32.52	16.28	43.44	65.83	30.31	19.36	
	N	12	12	12	12	12	12	12	12	12	12	12	6	6	6	6	86-131
	95%C.L.±	0.56	0.55	0.68	0.31	-	0.18	0.50	0.63	0.66	1.09	0.55	1.47	1.98	1.35	0.94	
Langstone Harbour	$\bar{x}$	8.32	11.48	14.56	15.86	1/5	16.96	55.34	50.88	22.22	33.92	16.02	43.77	65.78	29.05	17.95	
	N	50	50	50	50	50	50	50	48	65	65	65	65	65	65	65	41-130
	95%C.L.±	0.18	0.26	0.29	0.16	-	0.08	0.28	0.24	0.29	0.46	0.37	0.32	0.31	0.57	0.23	
Fawley	$\bar{x}$	8.18	11.34	14.62	15.46	1/5	16.98	55.44	50.78	21.50	33.84	16.16					
	N	50	50	50	50	50	50	50	50	50	50	50					51-125
	95%C.L.±	0.22	0.25	0.28	0.17	-	0.07	0.31	0.24	0.28	0.41	0.30					
R. Medina	$\bar{x}$	8.15	11.15	14.55	15.70	1/5	16.98	54.75	50.60	22.14	36.10	15.37	44.61	65.87	28.97	17.17	
	N	40	40	40	40	40	40	40	40	40	20	40	20	20	20	20	43-89
	95%C.L.±	0.19	0.22	0.31	0.18	-	0.05	0.35	0.33	0.21	0.60	0.35	0.50	0.50	0.59	0.41	
Chapman's Pool	$\bar{x}$	7.91	10.73	13.91	14.91	1/5	17.00	55.64	50.73	22.60	34.58	15.26					
	N	11	11	11	11	11	11	11	11	11	11	11					36-63
	95%C.L.±	0.56	0.43	0.47	0.47	-	0.30	0.69	0.68	0.69	0.61	0.68					
Pembroke	$\bar{x}$	8.60	11.97	15.17	15.60	1/5	16.97	55.13	50.87	21.18	33.92	15.66	42.71	64.53	30.18	16.99	
	N	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	58-133
	95%C.L.±	0.23	0.27	0.44	0.23	-	0.07	0.30	0.34	0.36	0.47	0.44	0.49	0.56	0.69	0.36	
Jersey	$\bar{x}$		11.80	14.90					51.00								
	N		10	10					10								16-23
	95%C.L.±		0.45	0.53					0.75								
Combined (excluding Jersey)	$\bar{x}$	8.29	11.39	14.64	15.60	1/5	16.98	55.24	50.80	21.72	34.08	15.90	43.63	65.49	29.38	17.67	
	N	193	193	193	193	193	193	193	191	238	208	238	121	121	121	121	
	95%C.L.±	0.10	0.12	0.15	0.09	-	0.04	0.15	0.13	0.14	0.23	0.17	0.25	0.26	0.38	0.20	
A. boyeri																	
Oldbury-upon-Severn	$\bar{x}$	7.58	10.36	12.14	14.48	1/5	17.08	46.12	44.48	23.19	32.75	15.72	43.74	65.77	23.52	16.36	
	N	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50-86
	95%C.L.±	0.18	0.22	0.21	0.22	-	0.17	0.38	0.28	0.48	0.48	0.36	0.44	0.40	0.46	0.37	

in close agreement, although in each case the upper and lower limits of the range are elevated.

Locality	Vertebral count inc. urostyle	Lateral scale count
Lowestoft	50-53	54-57
Langstone Harbour	49-53	54-57
Fawley	49-52	54-59
River Medina	49-53	53-57
Chapman's Pool	48-52	54-57
Pembroke	48-52	54-57
Jersey	50-53	not available

If this had been apparent in only the vertebral count it might have been assumed that it was due to the urostyle not being included in the key count. However, it is probably best explained by the fact that Kiener and Spillmann based their ranges on only four *A. presbyter* collections, Holland, Brittany and the Bay of Biscay, Biarritz and Morocco. Of these, only Holland is on a similar latitude to Britain, the rest are further south. Thus, for more northerly waters, less data is available and the true ranges are probably not represented. A modified key incorporating British data is presented in 3.4.4.

From the data for these four localities, Kiener and Spillmann suggested that a trend existed. As one progresses northward, the mean number of vertebrae increases. A similar situation for lateral scales can be envisaged. As *A. presbyter* reaches the northern limit of its range within British waters an elevated lower limit, similar to that observed, due to this trend might well have been anticipated.

The concept applied by Kiener and Spillmann is not new. As early as the last century, Jordan (1891) suggested that a relationship existed

between temperature and the number of vertebrae. Hubbs (1922) demonstrated that such variations in the number of vertebrae and other meristic characters in fish were more strictly correlated with the temperature of water during development. Later, Gabriel (1944) showed that under laboratory conditions the temperature prevailing during development of *Fundulus heteroclitus* (L.) had a pronounced effect on the vertebral number. High temperatures were associated with low counts but significantly higher counts could be achieved by reducing water temperature during development. Subsequent studies demonstrated that in addition to temperature other environmental factors could also influence meristic characters (Taning 1950, 1952; Weisel 1955; Morris and Scheer 1957; Garside 1970).

Kiener and Spillmann gave no water temperature data to support their assumption but presumably they reasoned that the lower water temperature of more northerly latitudes is associated with the higher vertebral counts observed. It will be noted that the highest mean vertebral count found in this study was from Lowestoft on the North Sea coast.

The atherinids at the remaining locality, Oldbury-upon-Severn, were identified as *A. boyeri*. According to the key *A. boyeri* should have a lateral scale count of 41-49 and a vertebral count of 40-47. The *A. boyeri* from Oldbury had ranges of 43-49 and 43-47 respectively. Thus very close agreement with the key exists. As this record is from the northern extremities of the present known distribution for this species the elevated lower range limits observed were anticipated from the trend suggested by Kiener and Spillmann (1969).

In addition to vertebral and lateral scale counts, the Oldbury *A. boyeri* differ significantly ($P < 0.05$) from the combined British *A. presbyter* data (Table 3.4) on all meristic counts other than caudal

and pelvic fins and on all morphometric ratios investigated other than origins of the dorsal fins and the dorsal interspace.

There seems to be some confusion amongst workers concerning the number of spines preceding the second dorsal and anal fin rays. In the present study, two, or occasionally three spines were noted in each case for both *A. presbyter* and *A. boyeri*. It is convention to represent spines using Roman numerals. However, in this study this has been neglected so that decimal places may be used to express the mean more clearly in particular for the first dorsal fin.

Throughout this study the same morphometrics as employed by Kiener and Spillmann (1969) have been used. However, on reflection the caudal peduncle depth and eye size would probably be better expressed as a percentage of the standard length. This would have given greater uniformity and not required the introduction of a further independent variable.

It will be noted that except for the Lowestoft atherinids, the mean shape index ($\frac{\text{Depth}}{\text{S.L.}} \times 100$) does not exceed 18.0 in either species. According to Kiener and Spillmann this is one of the criteria separating the sub-genus *Hepsetia* from that of *Atherina*. This would seem to question the validity of using this characteristic. Such a ratio must also be affected by condition which as will be seen later (6.3.4) undergoes annual fluctuations.

The population of *A. boyeri* at Oldbury is only the fourth recorded from British waters and, as such, is a significant find. It is also important because it is a discrete population easily identified from the more common *A. presbyter* in surrounding waters. Thus it not only supports the basis of Kiener and Spillmann's key for specific determination but in a more general context their taxonomic scheme for atherinids in the Atlantico-Mediterranean zone.

3.4.2. Geographical variation in *A. presbyter* around the British Isles

From Table 3.4 it will be noted that no significant differences ($P < 0.05$) occur between the means for the following characters; first dorsal, pelvic and caudal fins, lateral scale count, vertebral count and dorsal interspace. For the other characters investigated certain significant differences do occur. This suggests that biogeographical parameters may bring about certain variations in these characters. However, as will be seen later (3.4.3), such differences in the morphometrics may also be brought about by differences in the size range of the sample investigated.

Most of the fin ray counts of the *A. presbyter* from Chapman's Pool are noticeably lower than for the other localities although not significantly so. This may be due to the small sample size; the presence of only one age group; or conceivably, as they were 0-group fish from a shore pool, they may have been the offspring of the same parents and thus not truly representative of the population at this locality.

3.4.3. Sexual dimorphism and the effects of age and length on morphometrics

It was considered important to investigate the possibility of sexual dimorphism as, if present, it would bring about significant variation in character means due solely to variation in the sex ratio of the sample rather than to any biogeographical parameter.

a) *A. presbyter* - Langstone Harbour (Tables 3.5 and 3.6).

From these results there is no evidence of sexual dimorphism in the meristic characters and morphometric ratios investigated.

In analysing the morphometrics by age-groups in this way it

Table 3.5. Analysis of meristic sexual dimorphism in *A. presbyter* from Langstone Harbour.

		1D	2D soft rays	A soft rays	Pect.	P	C	Lat. scale count	Vert	N
♂♂	$\bar{x}$	8.36	11.68	14.71	15.75	1/5	16.93	55.43	50.88	28
	95% C.L.±	0.24	0.38	0.39	0.23	0.00	0.15	0.36	0.33	
♀♀	$\bar{x}$	8.27	11.18	14.36	16.00	1/5	17.00	55.23	50.86	22
	95% C.L.±	0.31	0.26	0.46	0.24	0.00	0.00	0.47	0.39	

became evident that significant differences existed between these groups. The pooled means of males and females for each of the three age-groups are also presented in Table 3.6. From these means certain trends correlated with age but more strictly with standard length can be noted. The proportionate length of head, eye diameter, and distance from snout to first dorsal fin decrease whilst the depth, dorsal interspace and distance to the origin of the second dorsal fin all increase with respect to increased standard length. The caudal peduncle as a proportion of the head increases but this might be expected due to the relative decrease in the size of the head. Significant differences ($p < 0.05$) between 0 and II+ age-groups occur in all morphometric ratios investigated except for the origin of the second dorsal fin. Each ratio has also been subjected to regression analysis in order to determine the extent of correlation between change in ratio and the increase in standard length (Table 3.7). It will be noted that all ratios are correlated either positively or negatively to

Table 3.6. Analysis of morphometric sexual dimorphism in *A. presbyter* from Langstone Harbour

Age	Sex	Hd/S.L. x 100% $\bar{x}$	95% C.L.±	E/Hd x 100% $\bar{x}$	95% C.L.±	D-D/S.L. x 100% $\bar{x}$	95% C.L.±	LD1/S.L. x 100% $\bar{x}$	95% C.L.±	LD2/S.L. x 100% $\bar{x}$	95% C.L.±	Ped.c/Hd x 100% $\bar{x}$	95% C.L.±	Depth/S.L. x 100% $\bar{x}$	95% C.L.±	N.
	♂♂	23.03	0.77	36.25	0.69	15.18	0.70	44.23	0.66	65.28	0.58	26.61	1.26	17.03	0.24	13
0	Com.	23.28	0.48	36.04	0.53	15.11	0.55	44.48	0.48	65.38	0.40	26.86	0.82	17.08	0.26	22
	♀♀	23.63	0.37	35.74	0.90	15.01	0.99	44.83	0.70	65.53	0.58	27.22	0.93	17.16	0.58	9
	♂♂	22.43	0.38	33.46	0.48	15.85	0.33	43.41	0.91	65.21	0.56	29.07	0.90	17.97	0.49	10
I	Com.	22.31	0.26	33.52	0.30	15.77	0.26	43.57	0.56	65.58	0.46	29.11	0.46	18.12	0.33	20
	♀♀	22.18	0.39	33.57	0.41	15.68	0.43	43.73	0.72	65.95	0.70	29.16	0.37	18.28	0.46	10
	♂♂	21.02	0.44	32.26	0.84	17.18	0.97	43.22	1.52	66.31	0.95	30.66	1.32	18.35	0.53	8
II+	Com.	21.14	0.23	32.23	0.39	17.11	0.69	43.28	0.59	66.34	0.68	31.10	0.68	18.64	0.33	23
	♀♀	21.20	0.28	32.22	0.45	17.06	0.96	43.31	0.55	66.36	0.95	31.33	0.82	18.80	0.42	15

Table 3.7. Linear regression of standard length against morphometric ratios for *A. presbyter* from Langstone Harbour

Ratio (x 100%)	Coeff. of correlation (r)	Slope	Intercept	For Graph S.L. mm	
				41	130
$\frac{Hd}{SL}$	-0.8321	-0.0376	25.3265	23.7813	20.4270
$\frac{E}{Hd}$	-0.8055	-0.0579	38.6919	36.3153	31.1561
$\frac{D-D}{SL}$	0.5390	0.0307	13.4817	14.7442	17.4848
$\frac{LD1}{SL}$	-0.3991	-0.0201	45.4285	44.6042	42.8150
$\frac{LD2}{SL}$	0.2896	0.0140	64.6256	65.2016	66.4518
$\frac{Ped.c.}{Hd}$	0.7569	0.0679	23.4535	26.2405	32.2903
$\frac{Depth}{SL}$	0.6033	0.0220	16.1358	17.0407	19.0048
	$\pm$0.2500	Value of r to be exceeded for significance ($p < 0.05$)			

standard length ($p < 0.05$).

b) *A. boyeri* - Oldbury-upon-Severn.

Here the same procedure has been applied. Age-groups have not been separated for morphometric analysis due to reduced numbers. Also the size range investigated was much narrower (50-86) and so even if morphometrics are correlated with standard length this will bring about much less change in the morphometric means than for the *A. presbyter* data.

From Table 3.8 it is evident that no sexual dimorphism with respect to either meristics or morphometrics occurs in *A. boyeri*. For those characters investigated there are no significant differences between male and female character means. Only one morphometric ratio is significantly correlated with standard length ($\frac{E}{Hd} \times 100$) (Table 3.9). However, whether lack of correlation for other characters is an attribute of the species or is merely a result of the narrow size range investigated requires further investigation.

c) The validity of using morphometrics in atherinid systematics

The discovery that morphometrics in *A. presbyter* and the eye:head ratio in *A. boyeri* are correlated with S.L. has important implications. It suggests that a significant difference in a morphometric ratio, when two localities are compared, may not necessarily be due to biogeographical parameters. It may be brought about by variation in the size range of the two samples investigated. This implies that the value of morphometrics for comparative purposes, both intra- and inter-specifically for members of the sub-genus *Hepsetia* is called into question as too many variables are present.

The validity of morphometrics in taxonomic studies of the

Table 3.8. Analysis of meristic and morphometric sexual dimorphism in *A. boyeri* from Oldbury-upon-Severn

	1D	2D	A	Pect.	P	C	Lat. scale count	Vert.
$\bar{x}$	7.68	10.16	12.20	14.68	1/5	17.16	46.28	44.56
95% C.L.±	0.29	0.33	0.34	0.31	0.00	0.23	0.57	0.45
$\bar{x}$	7.48	10.56	12.08	14.28	1/5	17.00	45.96	44.40
95% C.L.±	0.24	0.29	0.29	0.30	0.00	0.27	0.53	0.38

Hd / S.L.	E / Hd	D-D / S.L.	LD1 / S.L.	LD2 / S.L.	Ped.c. / S.L.	Depth / S.L.	N	S.L. mm
				x 100%				
23.28	33.29	15.65	43.48	65.67	23.40	16.51	25	50-81
0.25	0.49	0.49	0.63	0.58	0.55	0.40		
23.10	32.20	15.80	44.00	65.87	23.63	16.20	25	51-86
0.41	0.80	0.58	0.65	0.62	0.78	0.64		

Table 3.9. Linear regression of standard length against morphometric ratios for *A. boyeri* from Oldbury-upon-Severn

Ratio (x 100%)	Coeff. of correlation (r)	Slope	Intercept	For Graph S.L. mm	
				50	86
$\frac{Hd}{SL}$	-0.2402	-0.0223	24.7509	23.6315	22.8256
$\frac{E}{Hd}$	-0.5505	-0.1052	40.0918	34.8270	31.0363
$\frac{D-D}{SL}$	0.0994	0.0144	14.7130	15.4370	15.9583
$\frac{LD1}{SL}$	0.0022	0.0003	43.7126	43.7323	43.7466
$\frac{LD2}{SL}$	0.0377	0.0061	65.3394	65.6480	65.8702
$\frac{Ped.c.}{Hd}$	-0.0118	-0.0021	23.6706	23.5622	23.4841
$\frac{Depth}{SL}$	-0.1762	-0.0258	18.1595	16.8670	15.9363
	$\pm$0.273	Value of r to be exceeded for significance ($p < 0.05$)			

Atherinidae in general should also be examined because in the past morphometrics have been widely used in the description of species and for separating closely related species and sub-species (Kendall 1902, Jordan and Snyder 1913, Hubbs 1918, Gosling 1948, Schultz 1948, Rubinoff and Shaw 1960, Smith 1965, Moffatt and Thomson 1975). As far as can be ascertained these authors did not consider the question of such a correlation and certainly no allowances were made for it. However, in recent years the use of biochemical and genetical techniques (Johnson 1973, 1974, 1975) for investigating speciation and geographical variation may well clarify the situation. Such an investigation involving the atherinids of the N.E. Atlantic, Mediterranean and Baltic would prove invaluable particularly for establishing the origins of possible immigrant *A. boyeri* populations.

3.4.4. Key modifications

The species key proposed by Kiener and Spillmann (1969) and used in this study for identification was constructed with limited data on *A. presbyter* and without reference to this species in British waters. Data accumulated in this study has suggested slight modifications in this key are desirable in order to encompass fish within British waters. In particular the validity of the "shape index" in the separation of sub-genera has been called into question by the morphometric analysis of British *A. presbyter* and *A. boyeri* populations. In view of this it has been dropped from the modified key in Table 3.10.

3.4.5. Species descriptions

Presentation of synonyms follows Kiener and Spillmann (1973)

Table 3.10. Modified key for the separation of species of the genus *Atherina* in Atlantico-Mediterranean waters

A. Very small teeth localised in the middle of the vomer and fine teeth on the palatines (Fig. 3.1.a). The elevated median process of the premaxillar slender and very long (Fig. 3.1.b) extending past a line joining the anterior margins of the eyes and equal to or longer than the horizontal process. Lateral blade of the mandible elevated.

Sub-genus *Atherina* (1 species)

1. Scales in lateral series 61 to 65, vertebral count 53 to 57, head elongated and mouth little inclined, no teeth on the ectopterygoids, maximum length attained 20cm.

Atherina (Atherina) hepsetus L.

B. Many vomerine and palatine teeth. Median process thicker and not so long, shorter than the horizontal process (Fig. 3.1.b). Lateral blades of the mandibles little elevated.

Sub-genus *Hepsetia* (2 species)

1. Teeth on the ectopterygoids found divided into two small groups (Fig. 3.1.a), median process short not extending past the line joining the anterior eye margins. Scales in lateral series 41 to 49, vertebral count 40 to 47, maximum length attained about 13cm.

Atherina (Hepsetia) boyeri Risso

2. Teeth absent on the ectopterygoids (Fig. 3.1.a), median process slightly exceeds the line joining the anterior margins of the eyes. Scales in lateral series 52 to 59, vertebral count 47 to 53, maximum length attained 20cm.

Atherina (Hepsetia) presbyter Cuvier

but with additional references for British waters.

ATHERINA (HEPSETIA) PRESBYTER CUVIER, 1829 (Fig. 3.3)

Atherina presbyter Cuvier, 1829, 235 (La Rochelle). (Lectotype: MNHN no. 4337, by subs. design of Blanc & Hureau, 1972)

Atherina presbyter: Valenciennes in Cuvier & Valenciennes 1835: 439, pl. 305/ Yarrell, 1836: 214, fig. 1/ Günther, 1861: 392/ Day 1880-84: 225, pl. 65 (fig. 1)/ Moreau, 1881: 202, fig. 170/ Borsieri, 1904: 18, pl. 6/ Le Danois, 1913: 55/ Jordan & Hubbs, 1919: 36/ Nobre, 1935: 322, fig. 14/ Fowler, 1936: 581, fig. 268/ Jenkins, 1936: 121, pl. 51/ Lozano Rey, 1947: 712, fig. 187/ Poll, 1947: 323, fig. 210/ Schultz, 1948: 17/ Kennedy, 1954: 194, fig. vii-4/ Duncker & Ladiges, 1960: 289, fig. 116/ Wheeler, 1969: 469, fig. / Lythgoe & Lythgoe 1971: 189, fig. / Muus and Dahlstrom 1974: 136, fig. 99/ Maitland 1977: 204, fig.

Atherina (Hepsetia) presbyter: Kiener & Spillmann 1969: 66, pl. 1-2

Body moderately elongate and slender, subcylindrical but with some degree of lateral compression. Snout shorter than eye diameter; head dorsally flattened and laterally compressed; eyes large and lateral. Jaws strongly oblique, extending laterally almost to anterior margin of the eye; lower jaw slightly in advance; teeth small numerous on jaws, vomer, palatines and in median patch along tongue. Anus about mid way between origins of pelvic and anal fins. Dorsal fins well separated, the first composed entirely of spines and situated just

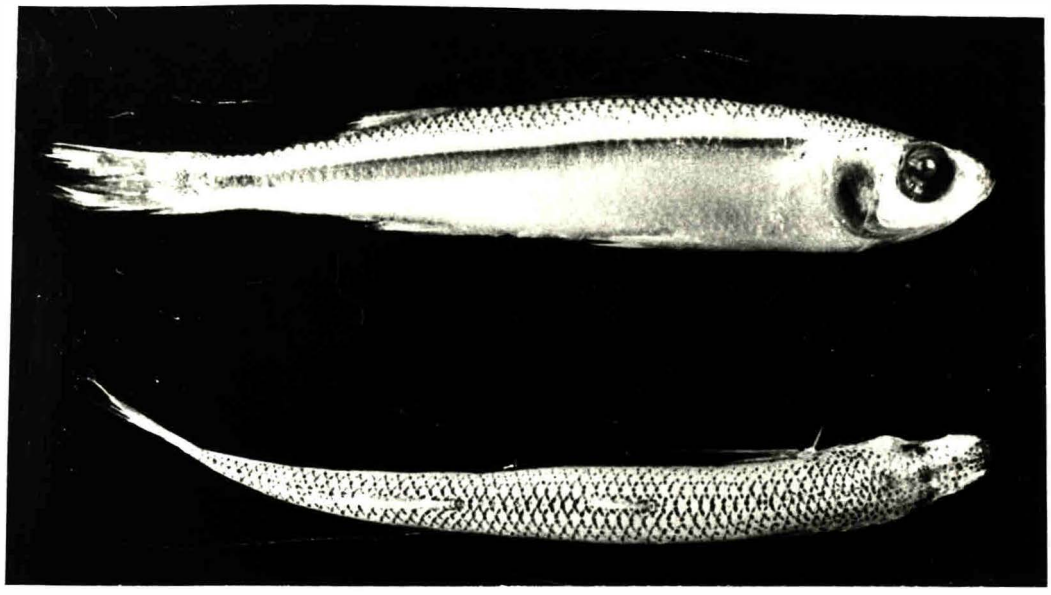
Figure 3.3. *Atherina presbyter.*

a. Male, 69mm SL, captured at Fawley during September 1976 (scale = 10.0mm).

b. Radiograph of a male, 88mm SL, captured in Langstone Harbour on 9 May 1977 (scale = 10.0mm).

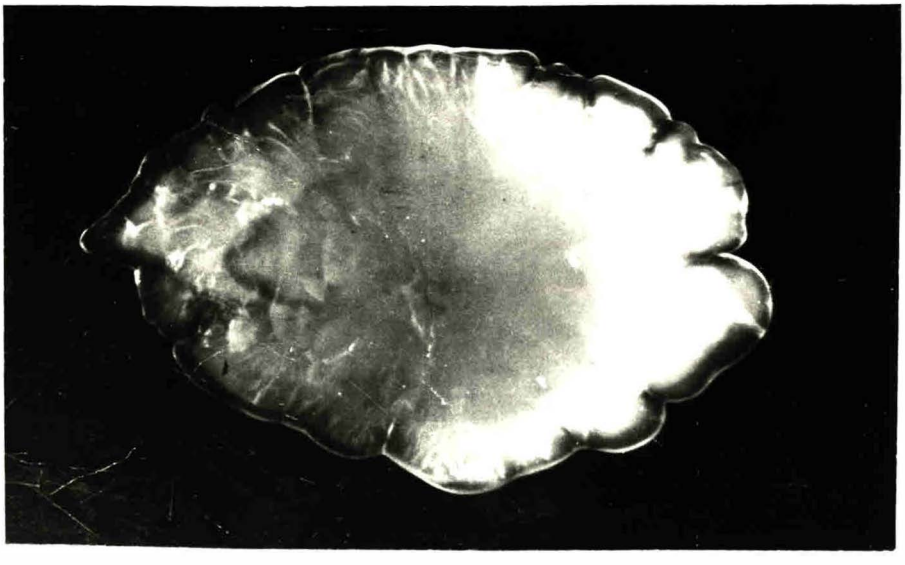
c. Saccular otolith from a male, 108mm SL, captured in Langstone Harbour on 23 June 1977 (scale = 1.0mm).

a



b

c



behind the posterior edge of the pectoral and the origin of the pelvic fins. Second dorsal and anal opposite one another; caudal fin forked. Body covered with large cycloid scales, decreasing in size on head. Colour brown or green above, silvery on the sides and below, with a prominent silver band along the lateral midline from pectoral base to caudal fin; above the silver band, translucent muscle shows through skin. On back occasional large melanophores in dermis, beneath scales. In larger fish, particularly females, fins also with black spots. Otoliths (Fig. 3.3) relatively large, elongated anterioposteriorly, flattened, outer surface slightly concave; posterior end bluntly rounded, anterior end pointed.

*Body proportions (as percentage of standard length)		
head length (Hd)	19.31 - 25.12	(21.72 ± 0.14, 238)
trunk depth (Depth)	15.22 - 21.03	(17.67 ± 0.20, 121)
first dorsal origin (LD1)	40.09 - 46.29	(43.63 ± 0.25, 121)
second dorsal origin (LD2)	60.28 - 68.56	(65.49 ± 0.26, 121)
dorsal interspace (D-D)	12.79 - 20.00	(15.90 ± 0.17, 238)
(as percentage of head length)		
eye diameter (E)	29.14 - 23.72	(34.08 ± 0.23, 208)
caudal peduncle (Ped.c.)	23.26 - 34.42	(29.38 ± 0.38, 121)
*Meristic characters		
first dorsal fin	VII - X	(8.29 ± 0.10, 193)
second dorsal fin	II (III) / 9 - 14	(11.39 ± 0.12, 193)
caudal fin	15 - 18	(16.98 ± 0.04, 193)
anal fin	II (III) / 12 - 19	(14.64 ± 0.15, 193)

*range ($\bar{x}$, 95% confidence limits, number examined)

pelvic fin	I / 5	
pectoral fin	14 - 17	(15.60 ± 0.09, 193)
scales in lateral series	53 - 59	(55.24 ± 0.15, 193)
vertebrae (including urostyle)	48 - 53	(50.80 ± 0.13, 191)

ATHERINA (HEPSETIA) BOYERI RISSO 1810 (Fig. 3.4)

Atherina boyeri Risso, 1810: 338 (Nice)

Atherina hepsetus var. 2 Delaroche, 1809: 358 (Iviça, Baléares)

Atherina hepsetus var. 3 Delaroche, 1809: 358 (Iviça)

Atherina mochon Cuvier, 1829: 235 (Iviça)

Atherina presbyter var. *pontica* Eichwald, 1831: 72

Atherina risso Valenciennes in Cuvier & Valenciennes, 1835: 354 (Nice)

Atherina sarda Valenciennes in Cuvier & Valenciennes, 1835: 435 (Sardaigne)

Atherina lacustris Bonaparte, 1836: 279, pl. 118 (fig. 3)

Atherina boyeri: Bonaparte, 1836: 281, pl. 118 (fig. 4)/ Günther, 1861: 394/ Canestrini, 1872: 116/ Day, 1880-84: 227, pl. 65 (fig. 2)/ Moreau, 1881: 205/ Borsieri, 1904: 31, pl. 8/ Lo Bianco, 1909: 420/ Nobre, 1935: 324/ Jenkins 1936: 121, pl. 51/ Šoljan 1948-63: 211, fig. / Kennedy 1954: 198/ Dieuzeide *et al.*, 1955: 250 fig. / Zei, in Riedl, 1963: 564, pl. 214/ Bowers & Naylor 1964: 318/ Lythgoe & Lythgoe 1971: 190.

Atherina boieri: Valenciennes, in Cuvier & Valenciennes, 1835: 432, pl. 303/ Guichenot, 1850: 66/ Depèret, 1883: 82.

Atherina mochon: Valenciennes, in Cuvier & Valenciennes 1835: 434, pl. 304/ Günther, 1861: 396 (*mocho*, altered spelling)/ Moreau, 1881: 209/ Borsieri, 1904: 39, pl. 9/ Lo Bianco, 1909: 429/ Slastenenko, 1939: 53/ Lozano Rey, 1947: 706, fig. / Šoljan, 1963: 211/ Berg,

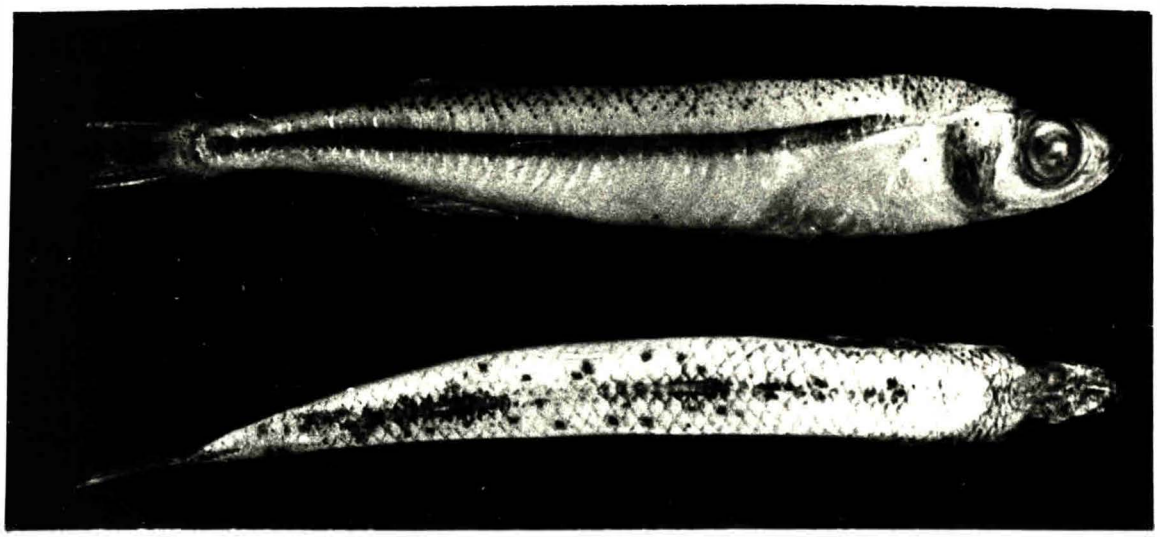
Figure 3.4. *Atherina boyeri*.

a. Female, 66mm SL, captured at Oldbury-upon-Severn during January 1976 (scale = 10.0mm).

b. Radiograph of a female, 66mm SL, captured at Oldbury-upon-Severn during January 1976 (scale = 10.0mm).

c. Saccular otolith from a female, 76mm SL, captured at Oldbury-upon-Severn on 15 April 1975 (scale = 1.0mm).

a



b

c

1949: 1001, fig. / Dieuzeide *et al.*, 1955: 251, fig. / Riedl, 1963: 564, pl. 214/ Bănărescu, 1964: 624, fig. 269/ Svetovidov, 1964: 226, fig. 66/ Bini, 1965: 102, fig. / Tortonese, 1967: 3, fig. 2/ Wheeler, 1969: 470, fig. / Lythgoe & Lythgoe, 1971: 190/ Maitland, 1977: 204, fig.

Atherina pontica Eichwald, 1838: 137

Atherina pontica Günther, 1861: 393

Atherina hyalosoma Cocco, 1885: 239

Atherina sarda Carus, 1893: 704

Atherina Riqueti Roule, 1902: 262, 4 fig. (canal du Midi)

Atherina Rissoi Borsieri, 1904: 175, pl. 10/ Lo Bianco, 1909: 424

Atherina Bonapartii Boulenger, 1907: 426

Hepsetia boyeri Jordan & Hubbs, 1919: 31/ Schultz, 1948: 18, pl. 1-2, from Borsieri, 1904/ Albuquerque, 1954-56: 614

Atherina caspia Fowler, 1936: 582

Hepsetia rissoi Schultz, 1948: 18

Hepsetia mochon Schultz, 1948: 18.

Atherina caspia Albuquerque, 1954-56: 612

Atherina bonapartei Svetovidov, 1964: 220, fig. 68/ Tortonese, 1967: 3, fig. 2

Atherina (Hepsetia) boyeri Bini, 1965: 104, fig. / Kiener & Spillmann, 1969: 66, pl. 1-2; 1972: 563-580, fig. 1-2.

Essentially similar to *A. presbyter* but body less laterally compressed, narrower caudal peduncle and wider less tapering in dorsal view. Also the head slightly larger although eye relatively smaller. Snout and eye subequal; jaws more strongly oblique, lower jaw more advanced; teeth as in *A. presbyter*, but with an additional patch on the

ectoterygoids (Fig. 3.1). Fin arrangement as in *A. presbyter;* scales larger and fewer in lateral series; basic colouration (preserved) as in *A. presbyter* but with pronounced black spots and blotches on dorsal surface even in small specimens. Otoliths similar to *A. presbyter* but anterior end less pointed (Fig. 3.4).

*Body proportions (as percentage of standard length)		
head length (Hd)	21.11 - 25.44	(23.19 ± 0.48)
trunk depth (Depth)	13.90 - 21.09	(16.36 ± 0.37)
first dorsal origin (LD1)	40.14 - 47.59	(43.74 ± 0.44)
second dorsal origin (LD2)	62.73 - 68.42	(65.77 ± 0.40)
dorsal interspace (D-D)	13.49 - 18.90	(15.72 ± 0.36)
(as percentage of head length)		
eye diameter (E)	29.27 - 35.40	(32.75 ± 0.48)
caudal peduncle (Ped.c.)	20.25 - 26.40	(23.52 ± 0.46)

*Meristics		
first dorsal fin	VI - IX	(7.58 ± 0.18)
second dorsal fin	II (III)/ 8 - 11	(10.36 ± 0.22)
caudal fin	15 - 18	(17.08 ± 0.17)
anal fin	II (III)/11 - 14	(12.14 ± 0.21)
pelvic fin	I / 5	
pectoral fin	13 - 16	(14.48 ± 0.22)
scales in lateral series	43 - 49	(46.12 ± 0.38)
vertebrae (including urostyle)	43 - 47	(44.48 ± 0.28)

*range ($\bar{x}$, $\pm$ 95% confidence limits) of 50 specimens

3.5. Summary

1. *A. presbyter* were found to be the most numerous and widespread British atherinid occurring at six of the seven stations examined.

2. *A. boyeri* were found only at Oldbury-upon-Severn.

3. At no time have mixed populations of the two species been found in British waters.

4. The use of the 'shape index' ($\frac{\text{Depth}}{\text{S.L.}} \times 100$) to separate the two sub-genera *Atherina* and *Hepsetia* appeared to be of little value.

5. Morphometric ratios were often correlated with standard length.

SECTION IV

ECOLOGY

4.1. *Atherina presbyter*

4.1.1. Distribution

A warm temperate species which reaches its northern limit of distribution within British waters. It has been recorded from most North Eastern Atlantic coastal waters, between latitudes 30° and 58° north, with the exception of the North Sea, where it has only been recorded as far north as latitude 54°N. The species is only rarely found in the Mediterranean, and only then, near the Strait of Gibralter (Kiener and Spillmann 1973).

In British waters the species is only occasionally captured in the North Sea north of the Wash. Day (1880-84) recorded captures at Aberdeen, St. Andrews and at Bridlington Bay, Yorkshire. Along south eastern, southern and western coasts it is more frequently captured (Wheeler 1969). *A. presbyter* has been recorded from Great Yarmouth and Lowestoft (Day 1880-84); the Medway Estuary (van den Broek 1978); Dungeness, Kent (Yarrell 1836); Sussex, Hampshire and the Isle of Wight coastline (Day 1880-84, Anon 1900, Morey 1909, Culley and Palmer 1978, Langford *et al* 1978); Weymouth, Dorset (Day 1880-84); Exmouth (Allen and Todd 1902); Salcombe (Allen and Todd 1900); Plymouth area (Plymouth Marine Fauna 1957); Cornwall (Day 1880-84) in particular Falmouth (Günther 1861); the Bristol Channel (Lloyd 1941, Hardisty and Huggins 1975); the Menai Straits (Herdman and Dawson 1902); Morecambe Bay (Gledhill 1978); the Isle of Man (Miller 1962, Bruce *et al* 1963); Loch Etive, Argyll (Kislalioglu and Gibson 1977); and the lochs of North Uist, Outer Hebrides (Nicol 1936). This last record was for juvenile

Atherina sp. but, presumably, these were *A. presbyter*. Sites where *A. presbyter* have been recorded during this investigation are given in Section 3.4.

In Ireland, *A. presbyter* has been recorded from all parts of the coastline (Kennedy 1954). During the present century it has apparently disappeared from some of its former haunts which may be associated with the decline of the *Zostera* beds (Bracken and Kennedy 1967). However, in 1953 it was still a component of the fauna in Strangford Lough (Williams 1954) and in 1959 one larva was recorded from Kilkieran Bay, Co. Galway (Fives 1970). More recently, June 1978, specimens were also captured at Sherkin Island, Baltimore, Co. Cork (Forster 1978).

Outside the British Isles *A. presbyter* has been recorded from a number of localities; the Waddenzee, Netherlands (Schrieken 1964); the Veerse Meer, Netherlands (Vaas *et al* 1975); in the dock basins of Zeebrugge, Blankenberge, Ostend and Nieuport, Belgium (Poll 1947); in the ports of Dieppe, St. Valery-en-Caux and Fécamp (Moreau 1881); around both Guernsey (Sinel 1905, Wheeler 1970) and Jersey (Le Sueur 1967) in the Channel Islands; at Concarneau, Brittany (Fabre-Domergue and Béatrix 1897); at D'Arcachon (Moreau 1881, Bauchot *et al* 1959, Cazaux and Labourg 1973) and Biarritz (Moreau 1881, Kiener and Spillmann 1969) in South West France; in North West Spain (Chesney and Iglesias 1979); along the coastline of Portugal (Albuquerque 1956); around Madeira (Günther 1861, Maul 1949, Albuquerque 1956); and the Atlantic coastline of Morocco (Kiener and Spillmann 1969).

4.1.2. Habitat

The species is typically found in inshore and coastal waters

frequenting bays, harbours and estuaries. Wheeler (1969) considered it to be attracted to waters of low salinity. However, Kiener and Spillmann (1969) suggested that the species was not really euryhaline and preferred areas where marine conditions prevailed. This was based on a review of localities where populations flourished at which salinities varied between 17 and 45°/oo.

The results of five experiments carried out to investigate certain aspects of the salinity tolerance in *A. presbyter* are presented in Appendix A1. These experiments were parts of student projects (Moore 1976, Watson 1978) and the results were not subjected to statistical analysis. They suggest that although some *A. presbyter* can withstand fairly low salinities (less than 10°/oo) such conditions cause stress and usually eventual death if the fish are maintained in them. The $L.C._{50}$ was between 5 and 10°/oo, for a slow decrease in salinity. During a more rapid decrease, even a reduction to a concentration of 75% seawater (23.3°/oo) caused an increase in activity. Such observations support the assumption of Kiener and Spillmann that *A. presbyter* is not a euryhaline species, preferring marine conditions.

When the salinity was slowly increased normal activity was maintained until 46.6°/oo when activity increased. This was close to the upper limit of 45°/oo suggested by Kiener and Spillmann. However, in this experiment two fish survived a slow increase to 69.3°/oo followed by a faster decrease to normal salinity (31.4°/oo) without any apparent permanent damage. The $L.C._{50}$ in this experiment was between 52 and 55°/oo.

At all sites where *A. presbyter* were recorded during this investigation the salinities where known were close to fully marine. This even applied in the Medina Estuary at the sites and times of sample

capture (Section 2.1.3).

4.1.3. Migrations

As *A. presbyter* is essentially a warm temperate species, it shows seasonal fluctuations in abundance, apparently dependent on temperature. Wheeler (1969) considered the species to be distinctly more common along all coasts in the summer months, an occurrence which could only be caused by a northerly migration of the stock in the western Channel and Biscay areas.

During this investigation, *A. presbyter* were only recorded from the North Sea (Lowestoft) during the summer months. In Langstone Harbour all age-groups (I+) were abundant during the spring and early summer months. During late summer the II+ fish apparently left the harbour as they were no longer a component of the catches, to be followed in autumn by the I group fish. Only 0 group fish seemed to overwinter in the harbour and even then only in low numbers. The migration pattern of fish in the Medina Estuary was probably similar to Langstone for although only three samples were collected these contained only 0 group fish in November 1975 but I, II, III and V group fish in April 1976.

In complete contrast are the records for *A. presbyter* impinged on the cooling water intake screens at Fawley. During recent years the species has been common all year round but has reached massive peaks during autumn and winter (Langford *et al* 1978). During March 1973, 27,444 *A. presbyter* were impinged on the screens out of a total for the whole year of 115,887 (Holmes 1975). Later, in Section 5.4., it will be seen that these winter catches contained all age-groups, not only 0 group fish as they did at Langstone.

The information obtained from a site such as that at Fawley may indicate that migrations to overwintering areas are on a more local scale than was suggested by Wheeler (1969). Although a conspicuous gregarious fish during the summer months, swimming near the surface in large shoals and congregating around pier piles, jetties and alongside boats, it may well be that, as the water temperature drops, *A. presbyter* seek localised areas of relatively deep sheltered water in the vicinity where they remain comparatively inactive. Such areas, if not close to a cooling water intake, would probably remain undiscovered as commercial mesh sizes are normally too large to retain them and sandeel seine-nets are rarely used during the winter months even if they were to fish deep enough or in the right area.

During December 1976 there was a sudden influx of small 0 group fish into Langstone Harbour which remained throughout the winter. From their size these fish must have been spawned late in the summer of 1976. There was no indication of such a late spawning having taken place in Langstone or at any other site investigated in this context. One possible explanation is that *A. presbyter* along the east and south-east coasts of Britain spawn slightly later than those in Langstone or at Fawley, and the young 0 group fish (as well as the adults) migrate west along the English Channel to overwinter. The surface water temperatures of the southern North Sea during January are generally colder than those experienced in the central English Channel. *A. presbyter* are normally captured in the North Sea only during the summer months and thus, they probably need to make comparatively long migrations to overwintering areas.

4.1.4. Diet and feeding habits

Introduction

Until recently, no systematic gut analysis of *A. presbyter* had been undertaken. Over the period October 1971 to October 1972, Kislalioglu (1975) examined the gut contents of 334 specimens taken from Loch Etive, Scotland and found the principal food groups to be amphipods, calanoid copepods, and cladocerans (Kislalioglu and Gibson 1977). Thirty nine *A. presbyter* caught from Oxwich Bay, South Wales between June 1976 and November 1977 were examined by Al-Abdul-Jabbar (1978). Here the main food items were amphipods, isopods, calanoid copepods, ostracods and harpacticoid copepods. In addition, Forster (1978) examined the gut contents of 15 *A. presbyter* caught at Baltimore, County Cork, Eire during June 1978 and found the principal food groups to be harpacticoid copepods, brachyuran larvae, and calanoid copepods.

No description of the alimentary canal appears to exist for Atlantico-Mediterranean silversides, although Alexander (1967) described the jaw mechanics of food capture in *A. presbyter*. However, Al-Hussaini (1947) described and figured the anatomy of the alimentary tract in *Pranesus pinguis* Lacépède (as *Atherina forskali* Rupp) from the Red Sea while Suyehiro (1942) completed similar work on *A. bleekeri* (Günther) and *A. tsuragae* (Jordan and Starks).

An investigation concerning the food and feeding habits of *A. presbyter* in Langstone Harbour was formulated prior to the publication of the surveys outlined above. As such, it was intended to be the first systematic analysis of the gut contents of *A. presbyter* within British waters. However, it should still prove to be a useful contribution and an interesting comparison to the data already made available.

Methods and Materials

During 1977 the gut contents of 80 *A. presbyter* from Langstone Harbour were examined. Samples from other locations were not examined in this context. Identification of frozen material was found to be easier than that preserved in formol-saline.

The gut was removed by dissection and attached mesenteries, mesenteric fat and gonad were removed before weighing. Other data recorded included age-group, sex, standard length, carcass weight and gut weight after removal of contents.

A similar procedure to that employed by Halliday (1969) was used for the gut contents analysis. The gut was first assigned a fullness index on the scale 0-20. This index was then divided by eye between the items in the gut including unrecognisable material in an advanced state of digestion. Numbers of each food item present were also recorded, as was the frequency of occurrence.

The identification of gut items was to species wherever possible, but, owing to the varying states of digestion, sometimes only to genus, family or order. Occasionally, specialist help for identification was sought (see Acknowledgements).

Casual observations on feeding behaviour both in the field and in the artificial environment were recorded.

Results and Discussion

Table 4.1 gives the general results of the analysis of the gut contents of *A. presbyter* based on the examination of 80 fish, with a variation in standard length of 40-120mm, over the period May-November 1977. The combined results over this period are presented in three different ways by numerical abundance, by percentage occurrence and by

Table 4.1. Gut content analyses of *Atherina presbyter* from Langstone Harbour

		Date	9.5.77		13.6.77		7.7.77		22.8.77		20.9.77		20.9.77		10.11.77		10.11.77		Combined 80 fish		
		Age group	2+		1		1		1		0		1		0		1				
		/10 fish	No.	Pts.	No.	Pts.	No.	Pts.	No.	Pts.	No.	Pts.	No.	Pts.	No.	Pts.	No.	Pts.	No.	Pts.	%Oc
Algae	Al												1	0.1					1	0.1	1.3
Foraminifera	Fm				2	+									1	+			3	+	2.5
Trematoda	Tm	19	+	86	0.3	11	+	31	+	39	0.2	12	+	52	0.2			250	0.7	48.8
Nematoda	Nm	51	1.5	11	0.4			3	+	1	0.2	2	+					68	3.1	22.5
Annelida																					
Polychaeta	Po					1	2.0	4	8.1			2	1.1					7	11.2	7.5
Mollusca																					
Gastropoda	Ga																				26.3
Littorina sp.		8	+	20	+	73	+	181	0.1	30	+	3	+					315	0.1		
Hydrobia sp.		43	0.7					1	+									44	0.7		
Bivalvia	Bv																				18.8
Mytilus spat		63	0.1			3	+	1	+	12	+			1	+			80	0.1		
Cerastoderma spat		?	15.6									1	0.1					?	15.7		
Crustacea																					
Copepoda	Cd	525	1.4	45	+	5	+	55	+	863	5.0	88	0.1	220	1.0			1801	7.5	62.5
Cirripedia larvae	Ci	62	0.1	1	+	8	+	25	+	30	+	1	+			4	+	131	0.1	23.8
Mysidacea	My	1	0.1															1	0.1	1.3
Cumacea	Cu	7	0.3															7	0.3	3.8
Amphipoda	Am	55	6.8	10	1.1	59	9.6	25	4.0	1	+	65	22.3	4	0.6	23	5.0	242	49.4	53.8
Decapoda - larvae	Dl	34	0.4	4	+			455	6.3	102	5.6	70	0.3	1	+			666	12.6	37.5
- adults	Da	1	+															1	+	1.3
Arachnida - Acarina	Ac													2	+			2	+	1.3
Insecta - adults	Ia	2	1.6	11	0.4	3	0.4	6	0.2	3	0.8	6	0.1	23	2.6			54	6.1	28.8
- larvae	Il	3	0.1															3	0.1	3.8
Vertebrata																					
Teleostei - juveniles	Tj					20	50.5											20	50.5	10.0	
- eggs	Te					2	+	2	+									4	+	2.5	
Unidentified material			64.6		10.8		29.5		43.3		153.3		36.0		60.6		15.0		413.1		
Fullness $\bar{x}$			9.9		1.3		9.2		6.2		16.5		6.0		6.5		2.0				

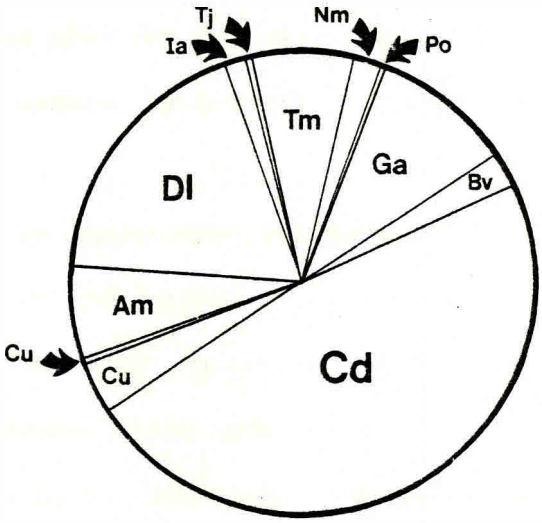
volume (Figure 4.1).

The numerical abundance was simply the number of each particular item found within the combined eighty guts, irrespective of size or the number of guts in which they occurred. By this method of analysis, copepods were by far the most important food item. Of less importance were decapod larvae, juvenile *Littorina* species, amphipods and barnacle larvae; of lower numerical importance were *Mytilus* spat, insects (Diptera), *Hydrobia* sp. and fish. *Cerastoderma* spat may also have been of importance but these were impossible to count as they occurred in the gut as broken shell fragments. All the above were considered to be food items but also fairly abundant in the gut was a digenean trematode, and, of less importance numerically, a larval nematode, both of which are parasitic species (see also Section 4.1.5).

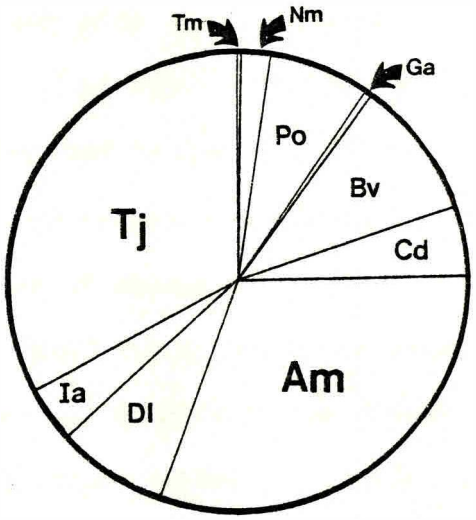
The percentage occurrence method recorded the presence of a particular item, irrespective of its size or abundance, and thus gave equal importance to large and small, common and rare organisms in any one gut. However, its advantage lay in the fact that it gave an overall picture of the frequency with which each item occurred in the population. Again copepods were the most important food item occurring in 62.5% of the guts examined. They were followed in importance by amphipods (53.8%), decapod larvae (37.5%), adult insects (28.8%), gastropods (26.3%), barnacle larvae (23.8%), bivalve molluscs (18.8%) and fish (10.0%). The two parasitic species were also of frequent occurrence.

The points method took actual volumes of food items into account and as such was more a measure of the real importance of each group present. This method is open to criticism on several counts not least that the points were assigned by eye. As a check on the validity and consistency of this method, a regression analysis was carried out to

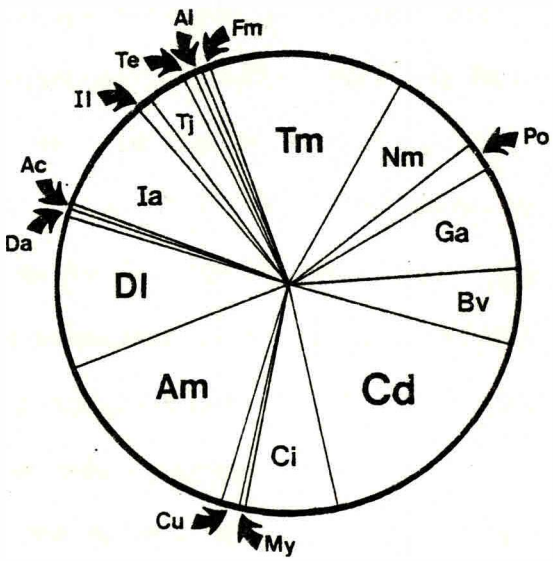
Figure 4.1.
A.presbyter Pie diagrams of the gut contents of 80 fish (abbreviations from Table 4.1.)



Number



Points



Percentage occurrence

test the relationship of the fullness index ascribed to each of the eighty fish with its corresponding gut content weight to somatic weight ratio. The result of this analysis is given in Appendix A2, from which it will be apparent that the fullness index and the ratio of the gut content weight to somatic weight showed a high degree of correlation ($P < 0.001$).

By volume the most important food item was fish (50.5). This highlights a flaw in this method as fish occurred only in one sample and yet, due to size dominated the combined points result. The fish were in a late stage of decomposition thus making identification difficult. However, most were almost certainly juvenile clupeoids and one or two juvenile *A. presbyter* may also have been present.

Close behind in importance volumetrically were amphipods (49.4). These tended to be dominated by *Gammarus locusta* (L) but *Jassa* sp. and *Caprella* sp. were also recorded. Surprisingly, the next most important were the shell fragments of cockle spat (15.7) which were followed by decapod larvae (12.6), polychaetes (11.2), copepods (7.5) and insects (6.1). The latter were all members of the Diptera which presumably were taken dead off the water surface or as they sank. Volumetrically the two parasite species were fairly unimportant.

Thus, in Langstone Harbour perhaps the most important component of the diet overall were amphipods which figured highly in all three methods of analysis. Also of general importance were decapod larvae, copepods, juvenile molluscs, insects and fish. Therefore, this investigation is in agreement with the studies of Kislalioglu and Gibson (1977) and Al-Abdul-Jabbar (1978), in both of which amphipods were found to be the most important food group.

Because *A. presbyter* has no distinct stomach, it was necessary

to examine the contents of the whole alimentary canal. Therefore, the points allotted to unidentified material were always high. None of the 80 guts were completely empty and the variation in mean fullness index of the samples showed no clear seasonal pattern which could be linked with changes in feeding activity.

From observations of *A. presbyter* feeding, both in their natural environment and in tanks under laboratory conditions, it was apparent that the species feeds actively by sight within the water column. Under laboratory conditions captive fish 'tested' most items which fell through the water column eating a wide variety of the animal food that was small enough. Once the food particle settled on the bottom of the tank, however, it usually ceased to be of any interest. Only starved fish would take food off the floor of the tank and only then if it was a clean bottom or consisted of flat sand.

These observations initially seem to contradict some of the evidence from the gut analyses where such basically benthic species as *Gammarus locusta* and the various molluscs recorded were of substantial importance in the diet. However, *G. locusta* is quite an active amphipod (Dr. R.G. Withers, pers. comm.) which not only takes cover on the seabed but also amongst floating algae and debris, and no doubt is frequently forced into the water column due to the strong tidal currents within Langstone Harbour. These currents might also account for the large numbers of small juvenile littorinids, *Hydrobia, Mytilus* and *Cerastoderma* spat which were perhaps swept up into the water column before being eaten.

From this and previous investigations, it may be concluded that *Atherina presbyter* is an active pelagic feeder eating a wide variety of food organisms but not plant material. Although it seems to have a

preference for various amphipods it is apparently an opportunist feeder taking advantage of whatever prey species are most abundant.

4.1.5. Parasites

These were not specifically searched for in *A. presbyter* but two different parasites were found and identified (see Acknowledgements).

Phylum: Nematoda

Class: Secernentea

Order: Ascaridida

Family: Heterocheilidae

Thynnascaris adunca (Rudolphi 1902)

This nematode species was found as the third stage larvae in the mesenteries of 17.8% and 29.8% of *A. presbyter* at Langstone and Fawley respectively. It also occurred in the gut of 22.5% of *A. presbyter* at Langstone (see Table 4.1) usually again as third stage larvae but some were in the process of moulting to the fourth (pre-adult) stage.

This nematode species is obtained by fish when they feed upon copepods, other small crustaceans or chaetognaths which harbour the parasite (Dr. D.I. Gibson, pers. comm.). The third stage larvae occurs in the body-cavity of almost all species of marine teleost around the British coast. Pre-adults occur in the gut of a wide range of teleost hosts, but it only appears to moult into the adult stage in a small number of fishes, particularly gadoids.

Phylum: Platyhelminthes

Class: Trematoda

Order: Digenea

Family: Fellodistomidae

Bacciger bacciger (Rudolphi 1819)

This digenean species was recorded in 48.8% of *A. presbyter* guts from Langstone Harbour (see Table 4.1). It has previously been recorded from the guts of *A. presbyter* at several localities; North Uist, (Outer Hebrides, Scotland), Port Erin (Isle of Man) and Salcombe, Devon (Bray and Gibson, in press); and at Plymouth, Devon (Nicoll 1914). All of the records of the adult parasite from North East Atlantic waters have been from *A. presbyter*. However, elsewhere it infects other *Atherina* species, in fact the type-host and locality are *Atherina hepsetus*, Naples, Italy. According to Dawes (1968) and Bray and Gibson (in press) the first host is a bivalve mollusc (*Donax, Venerupis*) and the second an amphipod, *Erichthonius difformis* Milne-Edwards 1830.

4.2. *Atherina boyeri*

4.2.1. Distribution

Characteristically a Mediterranean and Black Sea species. However, *A. boyeri* is occasionally found in North-East Atlantic waters, but particularly in the north, only at isolated stations.

In British waters *A. boyeri* has been recorded from four separate localities; Penzance, Cornwall (Couch 1849); Swansea, South Wales (Bowers and Naylor 1964); Cavendish Dock, Barrow-in-Furness, Lancashire (Wheeler 1969); and, during this investigation, at Oldbury-upon-Severn, Gloucestershire (Palmer *et al.*, 1979).

The only other localities in North-Eastern Atlantic waters from which it has been recorded are the Veerse Meer and the adjoining Kanaal door Walcheren and Binnenhaven of Vlissingen in South-West Netherlands (Kiener and Spillmann 1969, Schrieken and Swennen 1969, Velde and Polderman 1972, 1976, Vaas *et al* 1975); D'Arcachon, South-West France (Casaux and Labourg 1973); and Madeira and the Atlantic coastline of

Morocco (Kiener and Spillmann 1969).

4.2.2. Habitat

As previously discussed (Palmer *et al* 1979), it is interesting to consider why *A. boyeri*, an essentially Mediterranean species, is found, and is able to maintain itself, at Oldbury, when it is not, as far as is known, found elsewhere around the coasts of the British Isles. When conditions at Oldbury are compared with other northern European sites there seem to be three important ecological parameters which need to be considered. These are temperature, salinity and wave action.

At Oldbury, cooling water is drawn from a 1.6km^2 tidal reservoir that has been constructed over the intertidal mud flats and is isolated from the Estuary for six or seven hours in each tidal cycle. During isolation, warmed water, up to 10°C above ambient, is discharged downstream of the reservoir, resulting in no thermal enrichment of the compound. When the incoming tide surmounts the reservoir wall, a certain degree of warm water contamination must occur in the reservoir, although the rise in temperature is probably minimal as a result of the large tidal volume and the extremely rapid currents which are part of the famous Severn tidal régime, one of the highest in the world.

Maximum intake water temperatures of from 18 to 21°C are reached in July and August, minimum temperatures in the range of from 4 to 7°C occur during the winter (Table 2.4). The temperature régime at Oldbury thus covers a range normal for coastal waters of the area, and does not appear to show any large artificial heating effects. This is probably because the tidal volume of the Severn is so relatively large compared with the cooling waters that the heating potential of the effluent is

insignificant. Temperature values compare with those, for example, from Mumbles Pier (Swansea Bay) which has a range from 4 to 18°C (Withers 1972) and Hinkley Point (Table 2.4).

Three of the records were associated with raised water temperatures due to thermal pollution, at Queen's Dock, Swansea (Naylor 1965); Cavendish Dock, Barrow-in-Furness (Markowski 1966); and the Binnenhaven of Vlissingen (Velde and Polderman 1972). The gradual reduction and final termination of thermal pollution in Queen's Dock has resulted in the loss of *A. boyeri* from this locality (Bullimore et al 1978). However, the Veerse Meer and probably Oldbury are not thermally polluted.

A. boyeri was most commonly caught on the screens at Oldbury during December, January and February when both temperature and salinity are at their lowest. It was not recorded during August.

Large seasonal fluctuations occur in the salinity of the water in the holding reservoir with a peak in August of 28 or 29°/oo (Table 2.4). The winter salinity appears to be dependent upon rainfall. During the dry winter of 1975/76 the salinity only dropped to 17.8°/oo whereas in the winter of 1976/77, it dropped rapidly after September and reached a minimum of 5.9°/oo in February. Salinities over a tidal cycle tend to be relatively stable, however, as the reservoir tends to buffer the effects of freshwater discharge experienced at low tide.

Kiener and Spillmann (1969) suggested that *A. boyeri* is found in a wider range of salinities (1-77°/oo) than *A. presbyter* (18-45°/oo), although the most important populations are in brackish water. The Veerse Meer in South West Netherlands has a lowered salinity of between 20 and 29°/oo (Vaas *et al* 1975) as does Cavendish Dock, Barrow-in-Furness, where values of from 1.3 to 14.3°/oo have been recorded

(Markowski 1966). However, Queen's Dock, Swansea can be considered fully marine with a salinity of 30°/oo ± 3°/oo (Naylor 1965). At Oldbury, as mentioned above salinity is less than fully marine and when the fish is most commonly caught on the screens it is definitely brackish.

Kiener and Spillmann (1969) suggested that populations of *A. boyeri* were usually associated with calm water. This certainly seems to be justified as all localities so far described are either docks, lagoons or reservoirs. So too is the record for the Bassin d'Arcachon, South West France where *A. boyeri* has been observed in meso-polyhaline pools which are set aside for fish culture (Cazaux and Labourg 1973).

However, although *A. boyeri* in the Severn are associated with calm compounded waters at low tide, rapid and turbulent conditions will be experienced on the incoming tide. The possibility must be considered that the reservoir walls provide some degree of local shelter which enables *A. boyeri* to survive in this tidal reservoir.

Thus it is suggested that calm water with increased temperature or decreased salinity, or possibly both, are conditions which *A. boyeri* favours. It is interesting that no *A. presbyter*, the common British atherinid, have been recorded from the tidal reservoir whilst *A. boyeri* has been present. The lowering of the salinity is not marked enough in itself to inhibit *A. presbyter*, but it may be possible that the lowered salinity combined with competition from the more euryhaline *A. boyeri* prevents the establishment of a population of *A. presbyter*. In the Veerse Meer both species are present although as the numbers of *A. boyeri* have increased there has been a corresponding reduction in the numbers of *A. presbyter* (Vaas *et al* 1975).

Whether *A. boyeri* is a genuine immigrant, as suggested for the

population of the South West Netherlands (Velde and Polderman 1976) or not, remains a matter for conjecture. Clearly more long term ecological investigations might help to establish the criteria necessary for successful colonisation of areas by *A. boyeri*. The problem is a complex one and we may be witnessing a genuine example of a species extending its range by natural marginal dispersion.

4.2.3. Diet and feeding habits

During this study the gut contents of *A. boyeri* at Oldbury were not recorded because of the poor state of preservation of such material in the specimens examined. However, Markowski (1966) examined the gut contents of one hundred and two specimens from the population in Cavendish Dock, Barrow-in-Furness. Of these twenty four were empty whilst the remainder contained six different species (*Nereis diversicolor, Merceierella enigmatica, Balanus improvisus, Sphaeroma hookeri, Gammarus* species, *Amnicola taylori*?) of which the amphipods were considered to be the most important constituent.

In the Prevost lagoon, Montpellier, France, *Atherina boyeri* were found to feed essentially on amphipods (*Gammarus* and *Corophium*) the feeding level varying with body size and time of year (Kohler 1976). Duka (1973) investigated the food of adult and larval *Atherina boyeri* (as *A. mochon pontica*) separately, in the Black Sea. Both were found to utilise a wide variety of food organisms. The most important consumed by larvae were diatoms, cladocerans, copepods, various crustacean nauplii and molluscan larvae and by adults diatoms, harpacticoid copepods, various crustacean nauplii, gammarids and molluscan larvae. In the freshwater environment of Lake Trasimeno, Italy *A. boyeri* (as *A. mochon*) was considered to be a pelagic fish, eating ostracods,

copepods, cladocerans and considerable numbers of adult and larval chironomids (midges) and hydracarinids (water mites) (Moretti *et al* 1959).

4.2.4. Parasites

These were not specifically searched for in *A. boyeri* but the third stage larvae of the nematode *Thynnascaris adunca* (Section 4.1.5) were found in the mesenteries of 33.9% of fish examined.

At Cavendish Dock, Barrow-in-Furness, Markowski (1966) found that *Atherina boyeri* (as *Atherina* sp.) were parasitised by the larval nematodes of a *Contracaecum* species. According to Yamaguti (1961) *Contracaecum* (Rud.) is a synonym of *Thynnascaris* (Rud.) so this may well have been the same species as that recorded at Oldbury.

In the Mediterranean and Adriatic *Atherina boyeri* have been found to be parasitised by the cimothoid isopod *Mothocya epimerica* Costa (Brian 1921, Mosella 1920, Kiener and Spillmann 1969, Boscolo 1970), and in Lake Trasimeno, Italy, by various unnamed Platyhelminthes (Moretti *et al* 1959).

SECTION V

AGE

5.1. Introduction

No major investigation of the age structure of *A. presbyter* or *A. boyeri* populations appears to have been previously undertaken. The small amount of data that does exist presents a rather confusing picture.

Kristensen (1956) found that *A. presbyter* from Dutch waters could be divided into three year classes of different age by counting winter rings on the scales. In contrast, Bracken and Kennedy (1967) considered that the scales showed rather vague growth zones which were difficult to interpret. However, on examining opercular bones, they were found to show growth zones but only in the outer portions. The larger atherines examined showed eight or nine such annuli and the authors considered *A. presbyter* to be a relatively long-lived species.

Kohler (1976) constructed length-frequency distributions for samples of *A. boyeri* from the Prevost Lagoon, Montpellier, France but made no attempt to age the fish by this method.

At the start of this investigation both scales and opercular bones were examined to assess their suitability for ageing. Neither was considered reliable, and indeed, scales rarely showed conspicuous annuli (Appendix B.1). This was considered rather surprising as previous ageing studies on other members of the Atherinidae had invariably used scales in addition to length-frequency distributions (Clark 1925, 1929, Schultz 1933, Walker 1952). The saccular otoliths, however, showed distinct growth zones. These are regularly used for age determination in a variety of fishes and they are often considered to be better than scales, particularly for older fish (Lux 1971). The

otoliths of *A. presbyter* and *A. boyeri* have previously been described in terms of their detailed morphology (Scott 1906, Frost 1929, Chaine 1958). However, there is no account of the seasonal deposition of material which produces the growth zones used in ageing.

Therefore, the aim of this section of the study has been to determine the age-structure and mortality rates of the *A. presbyter* populations at Langstone and Fawley and the *A. boyeri* population at Oldbury, by counting the zones in the otoliths and, to a more limited extent by referring to length-frequency histograms. By measurements and observations the deposition of material in forming these zones has been followed to check the validity of using these zones for ageing. In addition, otolith growth has been followed and the relationship between otolith length and body length determined. This has been presented separately in Appendix B.2.

5.2. Methods and materials

The saccular otoliths were extracted from the inner ear by making an anterio-oblique cut into the skull. After removal they were cleaned by immersion in 70% ethanol, rubbed between the fingers to remove any extraneous matter and, if not to be examined immediately, stored dry. Preparation of otoliths for examination by grinding and polishing (Johnston 1938), or by burning (Christensen 1964), was found to be unnecessary. Thus, examination and measurement was carried out on the intact structure and on which ever otolith of the pair showed the clearest growth zones. Microscopic examination took place with the otoliths immersed in 70% ethanol in a watch glass on a black tile and viewed through a binocular microscope using reflected light. Measurements (Fig. 5.1) were made with an eye-piece graticule, to the nearest

Figure 5.1.
Otolith from a II group A.presbyter in late-June to show dimensions measured.

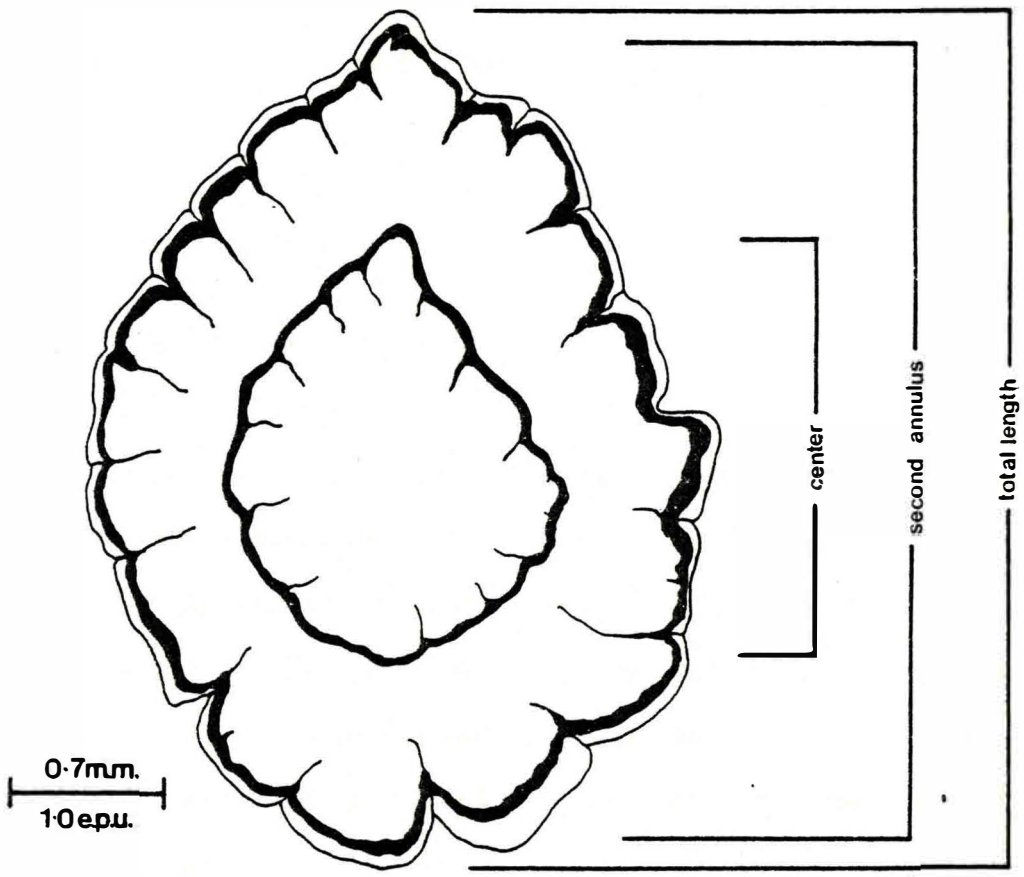
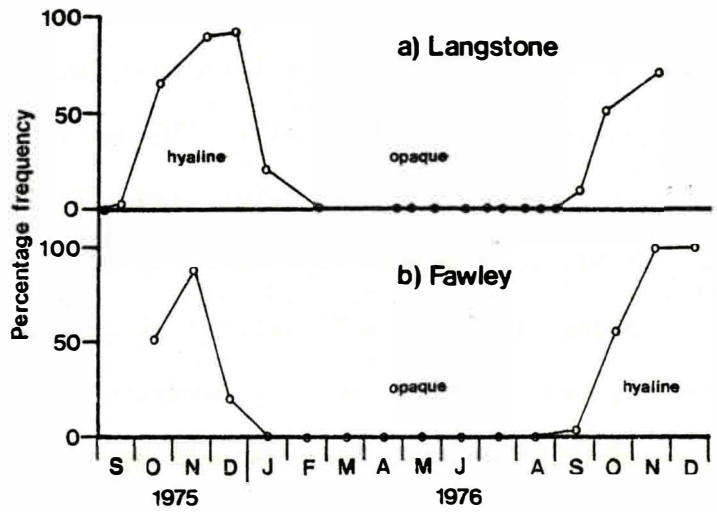


Figure 5.2.
Percentage of A.presbyter otoliths with hyaline margins.



0.1 eye-piece unit (epu) where 1.0 epu = 0.7 mm. The outward extremity of each opaque zone was measured as this formed a more distinct boundary than the outward extremity of the corresponding hyaline zone. In addition, it was recorded whether the otolith edge was opaque or hyaline.

5.3. Otolith studies

5.3.1. *Atherina presbyter*

A. Otolith Structure

The general morphology of the sacculer otoliths in *A. presbyter* has already been described in some detail (Scott 1906, Frost 1929, Chaine 1958) and they are illustrated in Fig. 3.3 and by the photographs in Appendix B.3. They are relatively large structures, elongated anterioposteriorly, flattened and slightly concave on their outer surface. The posterior end is bluntly rounded while the anterior end is quite pointed.

When the saccular otoliths of large *A. presbyter* are viewed against a dark background they show a structure of dark and light rings. These rings may be separated into hyaline (dark) and opaque (light) zones (Blacker 1974).

The chemical composition of fish otoliths has received much attention (Hickling 1931, Irie 1955, 1960, Dannevig 1956, Mina 1968, Blacker 1969). Blacker (1974) in his review paper considered fish otoliths to be composed mainly of crystals of calcium carbonate embedded in an organic matrix. The evidence suggests that the two types of zonation observed are due to variations in the organisation of this matrix, although Blacker concluded that the basic difference between the hyaline and opaque zones is still not fully understood.

B. Deposition of material at the otolith edge

The 'seasonal' nature of deposition of the opaque and hyaline rings in fish otoliths has been investigated in a variety of species (Molander 1947, Kelly and Wolf 1959, Miller 1961, Sinha and Jones 1967, Halliday 1969, Reay 1972a, b, Beaumariage 1973, Dunne 1976, Claridge and Gardner 1977, Gibson 1978). Reviewing published data on otolith zone deposition, Jones and Hynes (1950) concluded that the time of hyaline ring formation was species specific but could be in almost any month of the year. However, in the majority of temperate fish species it has been demonstrated that the opaque zones are formed during the summer months, the period of maximum growth, whilst the hyaline zones are deposited during the winter months, the period of minimum growth. One opaque and one hyaline zone constitute a year's otolith growth and hence, by counting the number of hyaline rings the age may be determined.

Periodic examination of material at the otolith edge in *A. presbyter* (Fig. 5.2) has enabled the timing of hyaline zone formation to be verified, as being within the period from late September to early January. Figure 5.3 also indicates that only one opaque and one hyaline zone are formed each year and thus establishes the validity of using these zones for ageing purposes.

Two main problems were associated with this technique. First, initial zone deposition did not start concurrently on all margins of the otolith and, therefore, an assessment had to be made as to which was the dominant material. Secondly, when a new zone is first formed it is very narrow and not easy to identify, especially in the formation of the hyaline zone. This perhaps indicates that the time of actual zone initiation was slightly earlier than that recorded.

5.3.2. *Atherina boyeri*

A. Otolith structure

The general morphology of the saccular otoliths in *A. boyeri* has already been described by Chaine (1958). As illustrated by the photographs in Fig. 3.4 they are essentially similar to those found in *A. presbyter*, although the anterior end is less pointed, giving the structure a more rounded appearance. Viewed by reflected light against a dark background they too show the alternating opaque and hyaline zones.

B. Deposition of material at the otolith edge

Due to low sample numbers the data from 1974-77 has been combined. It is apparent from Table 5.1 that hyaline zone formation is within the period October to February similar to that already found in *A. presbyter*. Thus again, only one opaque and one hyaline zone are formed each year which establishes the validity of using these zones for ageing purposes.

5.4. *Atherina presbyter*

5.4.1. Length composition

The range in length of *A. presbyter* caught by seine-net at Langstone was 30-138mm standard length and from the intake screens at Fawley, 43-142mm standard length. At both sites, the lower limit of this range is restricted by the collection technique, however, such bias is restricted only to months just after spawning when newly metamorphosed 0 group fish are abundant.

Length-frequency histograms for selected samples from Langstone Harbour and the monthly samples from Fawley are shown in Figure 5.3.a and b respectively. These are derived from data in Appendix B.5 and B.6.

Table 5.1. *A. boyeri*. Material at otolith edge (combined data)

	Opaque N	Hyaline N
January	0	15
February	8	1
March	4	0
April	5	0
May	5	0
June	2	0
July	3	0
August	-	-
September	1	0
October	2	1
November	0	1
December	0	12

Figure 5.3.

A.presbyter Length-frequency distribution

a) Langstone

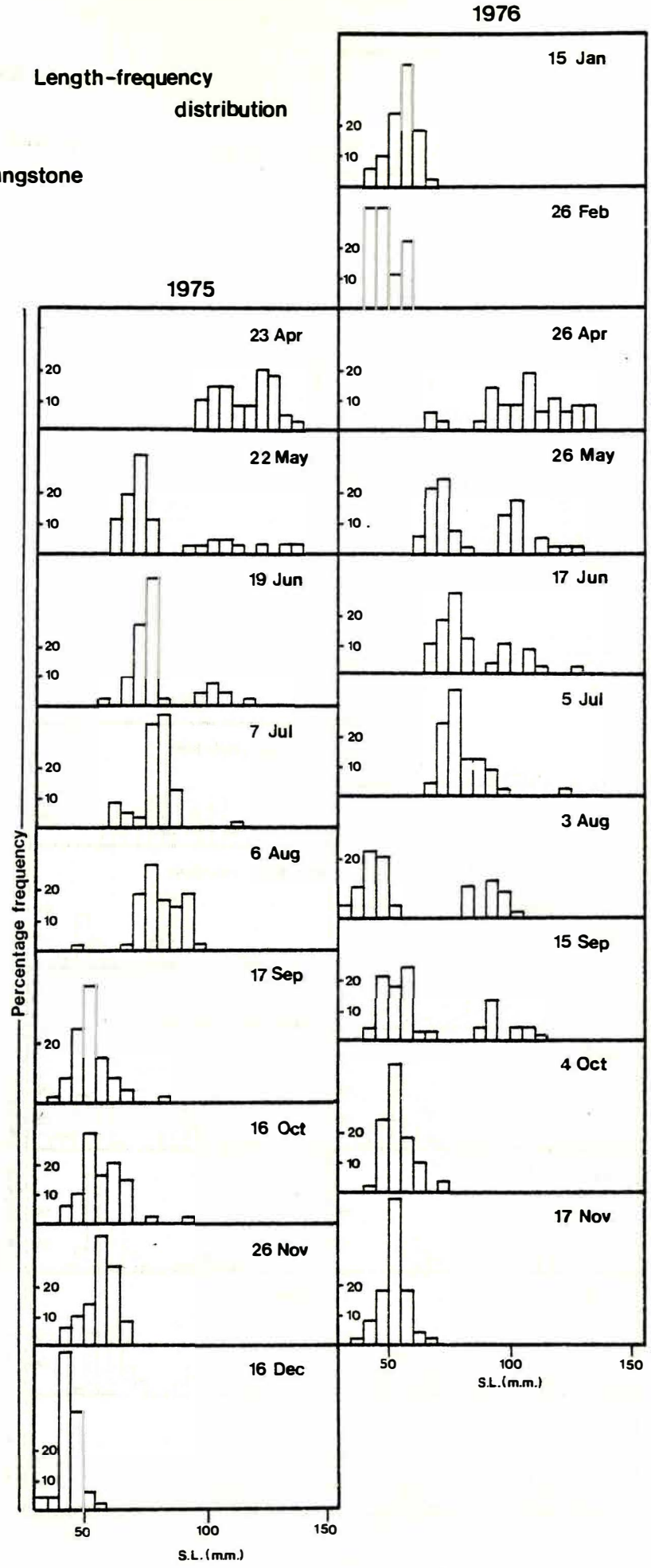
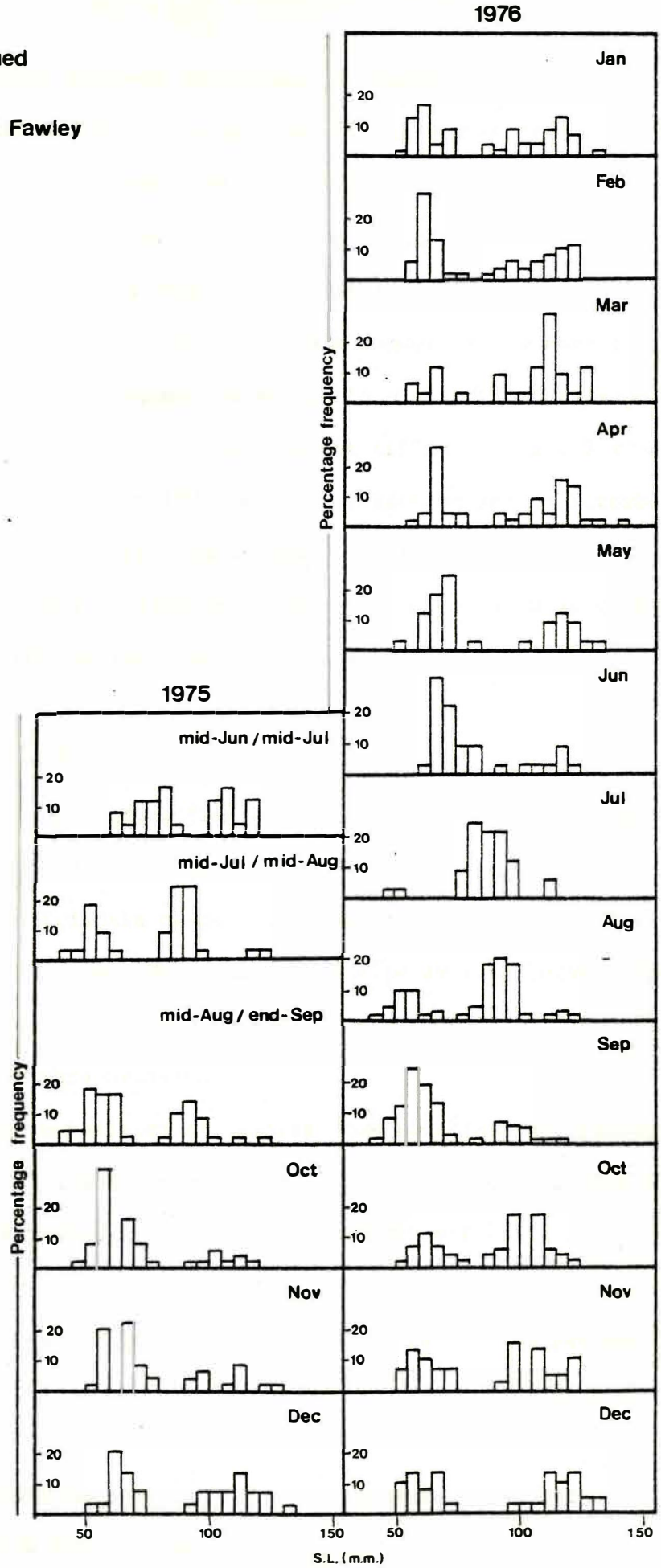


Figure 5.3. continued

b) Fawley



The conspicuous seasonal variations in length-frequency distribution of the samples is largely due to the yearly influx of 0 group fish during July, August, and September, their subsequent rapid growth, and the restriction of the II+ group at Langstone from April to September. At both sites, a year-class retains its identity within the length-frequency distribution until the late summer in its second year (as I group fish) when it become indistinct from older fish (II+ group).

Here attention is drawn to the apparent influx of small 0 group fish at Langstone in December 1975 and to a lesser extent in November 1976 a situation which was not duplicated at Fawley. The reason for this is not easy to explain although it may be due to the migration of 0 group fish from more easterly waters (see Section 4.1.3).

5.4.2. Age composition

For 0 group and I group fish early in the year, when these form distinct modal groups in length-frequency distribution, only the otoliths of a few individuals needed to be examined in order to determine the age of the whole group. The areas where size overlap between the age groups might occur received most attention. For older fish the otoliths of all fish were examined.

The age group composition of samples from Langstone and Fawley are given in Appendix B.7.a and b respectively. It will be noted that at the two sites the seasonal age composition pattern varies in the following respects:-

a) in Langstone II+ group fish are restricted to the period, April to September, whereas at Fawley they are present all year.

b) in Langstone only 0 group fish overwinter in the harbour, and I group fish are not captured from November onwards.

However, in one aspect, the patterns at the two sites are similar, in that there is initial appearance of 0 group fish in July/August which rapidly become dominant and remain so until the end of the year.

In order to investigate the relative occurrence of I-V groups in the samples, annual numbers of these fish have been extracted from Appendix B.7 and summarised in Figure 5.4 as percentage frequencies. These have been arranged under vertical year-class categories so that the progressive decrease in the relative importance of a single year-class in successive years can be seen giving an indication of year-class strength. From the data in Figure 5.4, it is tentatively suggested that the 1972 year-class at Langstone and the 1974 year-class at Fawley were relatively weak whilst the 1973 year-class at Fawley was particularly strong.

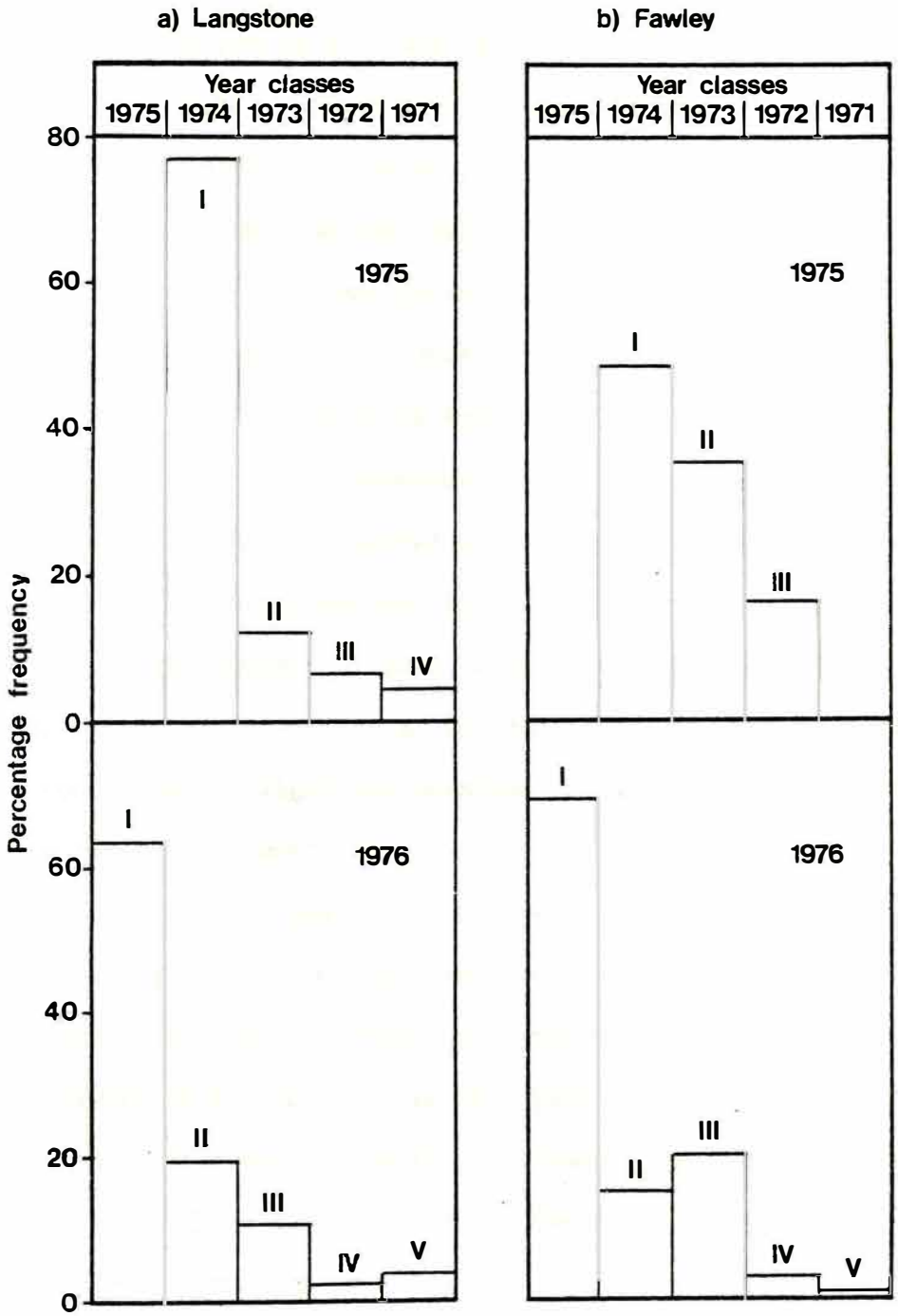
The oldest age-group encountered at both Langstone and Fawley was V group. No *A. presbyter* were found approaching the ages determined by Bracken and Kennedy (1967) from the examination of opercular bones, where a maximum of 8 or 9 annuli were found. However, the records of the British Record (Rod Caught) Committee (1979) contain captures of *A. presbyter* exceeding two ounces (57g) in weight, over twice as heavy as any captured in this study. This would seem to suggest that fish older than V group do exist. In contrast, as will be seen in Section 6.3.2 it would seem that the technique of ageing using scale annuli (Kristensen 1956) underestimates the age of older *A. presbyter*.

5.4.3. Mortality

It is possible to obtain estimates of annual mortality from age-composition data. In order to do this, and to minimise inaccuracies arising from variable year-class strength, data from the two years have

Figure 5.4.

A.presbyter Annual percentage age-group frequency for groups I to V as 1971 to 1975 year-classes



been grouped together although sites have been considered separately.

The occurrence of each age-group has been expressed as a percentage of the total (Appendix B.7) and the results plotted on semi-log. graph paper (Fig. 5.5). Counts of 0 group fish have not been included due to their restricted occurrence and the sampling bias against the smallest fish. I group fish have only been included from samples which contained older fish. This was necessary for Langstone samples as due to migration older fish are only present in the harbour from April-September. This survival curve is typical of a fish whose mortality is due to predation rather than senescence.

Mortality has been calculated as an annual percentage mortality (Table 5.2). It was expected that this would show a decrease in mortality with age, however at both sites irregularities occurred. These are most likely to be due to the variations in year-class strength outlined above and highlight the problems of amalgamating just two years for the calculation of mortality.

Predation is often implicated as the most general cause of natural mortality in fish populations (Beverton and Holt 1957). Both *Scomber scombrus* L. and *Dicentrarchus labrax* (L.) have been observed attacking shoals of *A. presbyter* in Langstone Harbour and juveniles of the species have also been found in the stomachs of older *A. presbyter* (see Section 4.4). van den Broek (1978) recorded *A. presbyter* from the stomachs of *Trisopterus luscus* (L.).

5.5. *Atherina boyeri*

5.5.1. Length composition

The range in length of *A. boyeri* retained on the intake screens at Oldbury was 45-86mm standard length. The lower limit may well be

Figure 5.5.

A. presbyter Age-group composition of samples, for conditions see text (data from Appendix B.7.).

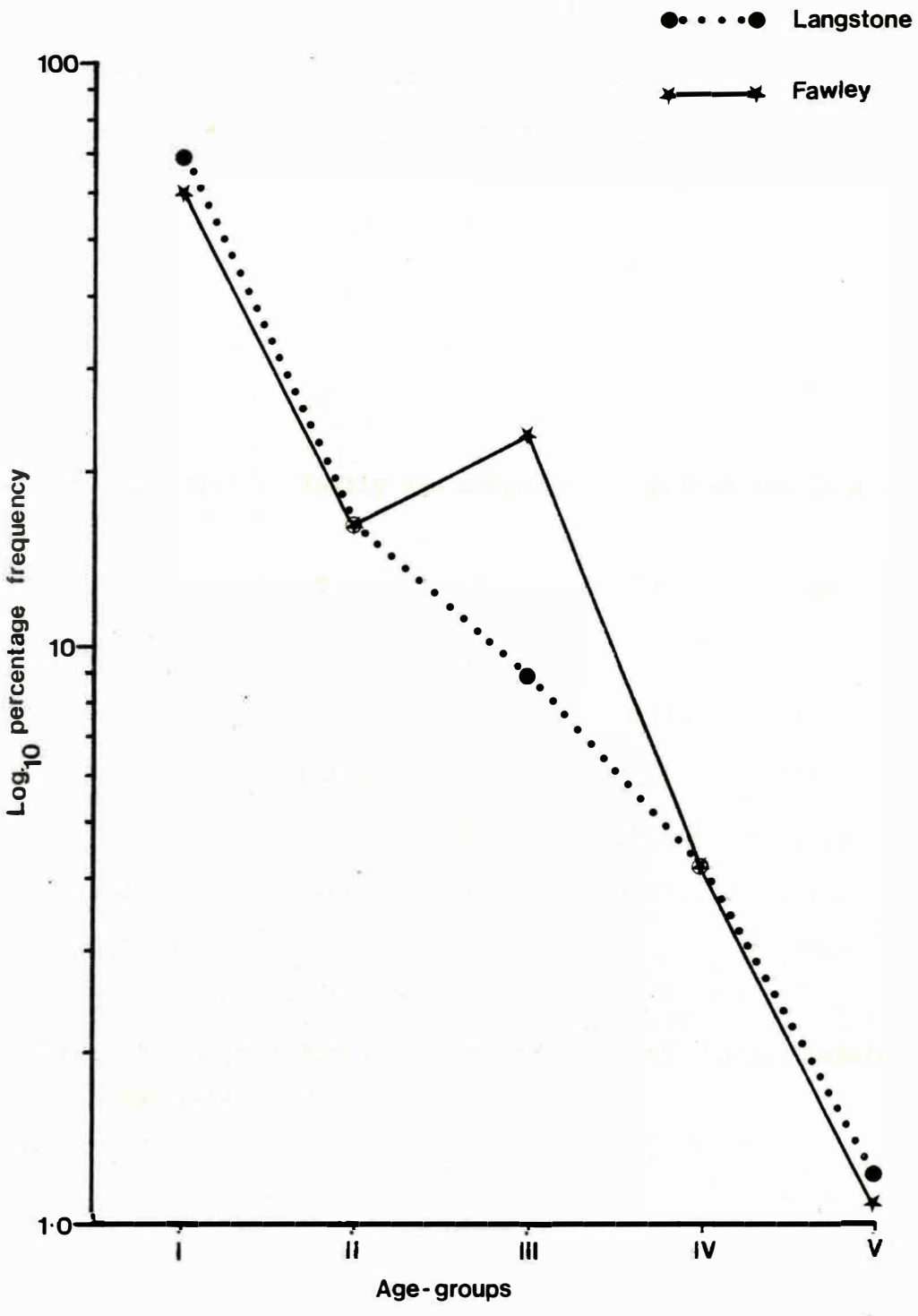


Table 5.2. *A. presbyter*. Annual percentage mortality (from Appendix B.7).

	I	II	III	IV	V
Langstone	77.0	44.4	64.0	31.2	
Fawley	72.6	-25.3	84.2	65.6	

Table 5.3. *A. boyeri*. Yearly age composition, percentage (number).

	0	I	II	III
1974		100(9)		
1975		13(3)	83(19)	4(1)
1976	16(3)	22(4)	33(6)	28(5)
1977	*	35(6)	59(10)	6(1)
Combined	4(3)	33(22)	52(35)	10(7)
% mortality				83.3%

*N.B. 1977 only contains fish caught up until March, before spawning.

restricted by the collection technique as it is very close to the lower limit recorded for *A. presbyter* from Fawley intake screens.

It was not practical to construct length-frequency histograms due to low sample numbers and therefore age in all cases had to be determined by otolith examination.

5.5.2. Age composition

Only four age-groups were encountered, 0, I, II and III. The percentage occurrence of these by age is given in Table 5.3. These present a rather confused picture. In 1974 all the fish retained were I group although there were only nine individuals over a three month period. From 1975 onwards, in each year the II group was dominant. This could possibly be explained by sample collection bias against 0 group and the smaller members of the I group. Indeed only three 0 group fish were retained throughout the study period, although the fish were obviously present as subsequent recruitment took place.

5.5.3. Mortality

The calculation of mortality requires there to be no sampling bias against the age-groups being considered (Dice 1952, Mann 1976). Such a bias is apparently inherent in the sampling of 0 and I group *A. boyeri* at Oldbury and therefore only the percentage mortality between II and III groups has been calculated (Table 5.3). This proved to be high, 83.3%.

5.6. Summary

1. The otoliths of *A. presbyter* and *A. boyeri* showed alternating rings of opaque and hyaline material, one of each being laid down in a

yearly cycle. In *A. presbyter* time of hyaline ring formation was from September to January whilst in *A. boyeri* from October to February.

2. Maximum standard length of *A. presbyter* captured was 142mm from Fawley whilst the longest *A. boyeri* had a standard length of 86mm.
3. An *A. presbyter* year-class retained its identity within the length frequency distribution until the late summer as a I group fish.
4. For both species age was determined from the saccular otoliths.
5. The oldest *A. presbyter* captured was representative of V group and the oldest *A. boyeri* of III group.
6. Only 0 group *A. presbyter* overwintered in Langstone Harbour.
7. The *A. presbyter* survival curve was typical of a species whose mortality was due to predation rather than senescence.

SECTION VI

GROWTH AND CONDITION

6.1. Introduction

The aim of this section is to investigate perhaps the most neglected aspect of the biology of the Atlantico-Mediterranean silversides, that of growth and related phenological processes namely condition, the hepatosomatic index, the intestinal-somatic index, mesenteric lipid-somatic index, and the gonadosomatic index (to be considered in more detail in reproduction, Section VII). Previously, the only data available on *A. presbyter* concerned growth in length in three subsequent years in Dutch waters (Kristensen 1956). Growth in length and weight in *A. boyeri* has not been studied although the length-weight relationship has been determined and the condition factor, hepatosomatic, and gonadosomatic index followed for the population in the Prevost lagoon, Montpellier, France (Kohler 1976).

6.2. Methods and materials

Body lengths and weights (as defined in Section 2.4) were recorded for all fish in small manageable samples and for a sub-sample in larger catches. Whenever possible, sub-samples of twenty fish of each age group (0, I and II+), ten of each sex, were subjected to further analysis. The gonad, liver, intestine and mesenteric lipid were dissected out, excess moisture removed with tissue, and then were weighed to the nearest 0.0025 gram on a single pan analytical balance. A carcass weight was then calculated by subtracting the sum total of the four body component weights from the total wet body weight. The various body component-somatic indices were then derived by expressing the

respective component weight as a percentage of the carcass weight.

In an analysis of this kind, it would have been preferable to have used dry carcass and body component weights as this would have removed the possibility of changes in water retention affecting the seasonal fluctuations recorded in these indices. Such weights have been recorded in certain samples of II+ *A. presbyter* during 1976 (Appendix C.1). However, for 0 and I group fish the weights involved were so small that the percentage error involved was too great to justify the time involved.

A procedure often followed in fisheries biology is the construction of a length-weight curve. This gives a graphic illustration of how an increase in length is accompanied by a much more rapid increase in weight. This is because length is a linear measure whilst weight is a measure of volume, and thus the weight of most fishes increases approximately as a cube of the length. However, to compare fluctuations in weight at the same length some expression of the length-weight relationship, other than a length-weight curve must be used. This relationship is usually adequately described by the formula:-

$$W = aL^b$$

where W is the weight and L the length of the fish, a, is a constant and b an exponent usually close to 3.0. The exponent b and constant a are based on regression analysis of $\log_{10}$ length on $\log_{10}$ weight data, where b is the slope and a is the intercept on the y axis. Le Cren (1951) studied the length-weight relationship with respect to age, sex and maturation in *Perca fluviatilis* L and found variations in both constant and exponent. However, as *A. presbyter* mature early and have only a narrow size range regressions were only carried out separately on males and females using five individuals of each sex of age-groups 0, I and

II+ (where available) from each month sampled. In addition to total body weight, a regression analysis was also carried out of $\log_{10}$ length on $\log_{10}$ carcass weight.

Individual variations from the mean length-weight relationship have usually been considered more interesting than the length-weight relationship itself and have frequently been studied to increase the understanding of the condition of fish. They have, therefore, been referred to as the condition factor or ponderal index. In the above equation, the intercept value is in effect the ponderal index and, therefore, the use of this in the form,

$$a \text{ (or more usually K)} = \frac{W}{L^b}$$

is a simple alternative to calculating regression equations for each sample. The higher the value of K the greater the relative weight at a given standard length.

During this investigation a mean ponderal index with 95% confidence limits was calculated for each sample of *A. presbyter* from Langstone and Fawley and *A. boyeri* from Oldbury. Age-groups and sexes were considered separately in *A. presbyter* samples but were combined for *A. boyeri*.

6.3. *Atherina presbyter*

6.3.1. Seasonal growth in body length and weight

The basic data on body length and weight are given in the form of age-grouped means with 95% confidence limits and sample numbers (Appendices C.2 and C.3). Lengths and weights are plotted separately for each age-group and localities in Figures 6.1 to 6.4, as means with 95% confidence limits. The sexes have not been separated. In addition,

Figures 6.1 to 6.4 inclusive

A. presbyter Seasonal growth in body length and weight.

year-class key:-

1971 ☆

1972 x

1973 o

1974 ■

1975 ●

1976 ★

Figure 6.1.

A.presbyter Mean body lengths for year-classes 1971-76 at Langstone.

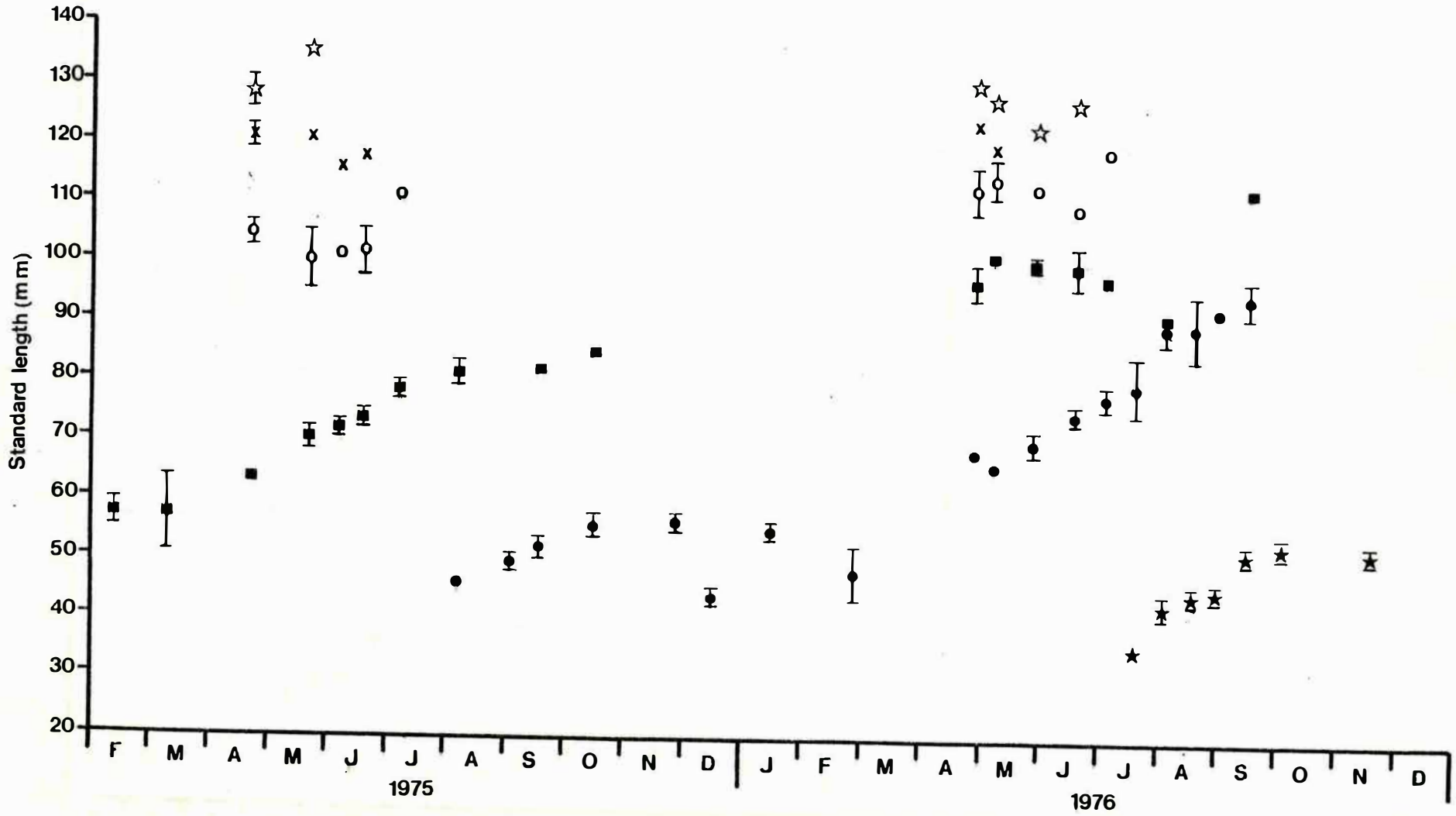


Figure 6.2.

A. presbyter Mean body weights for year-classes 1971-76 at Langstone.

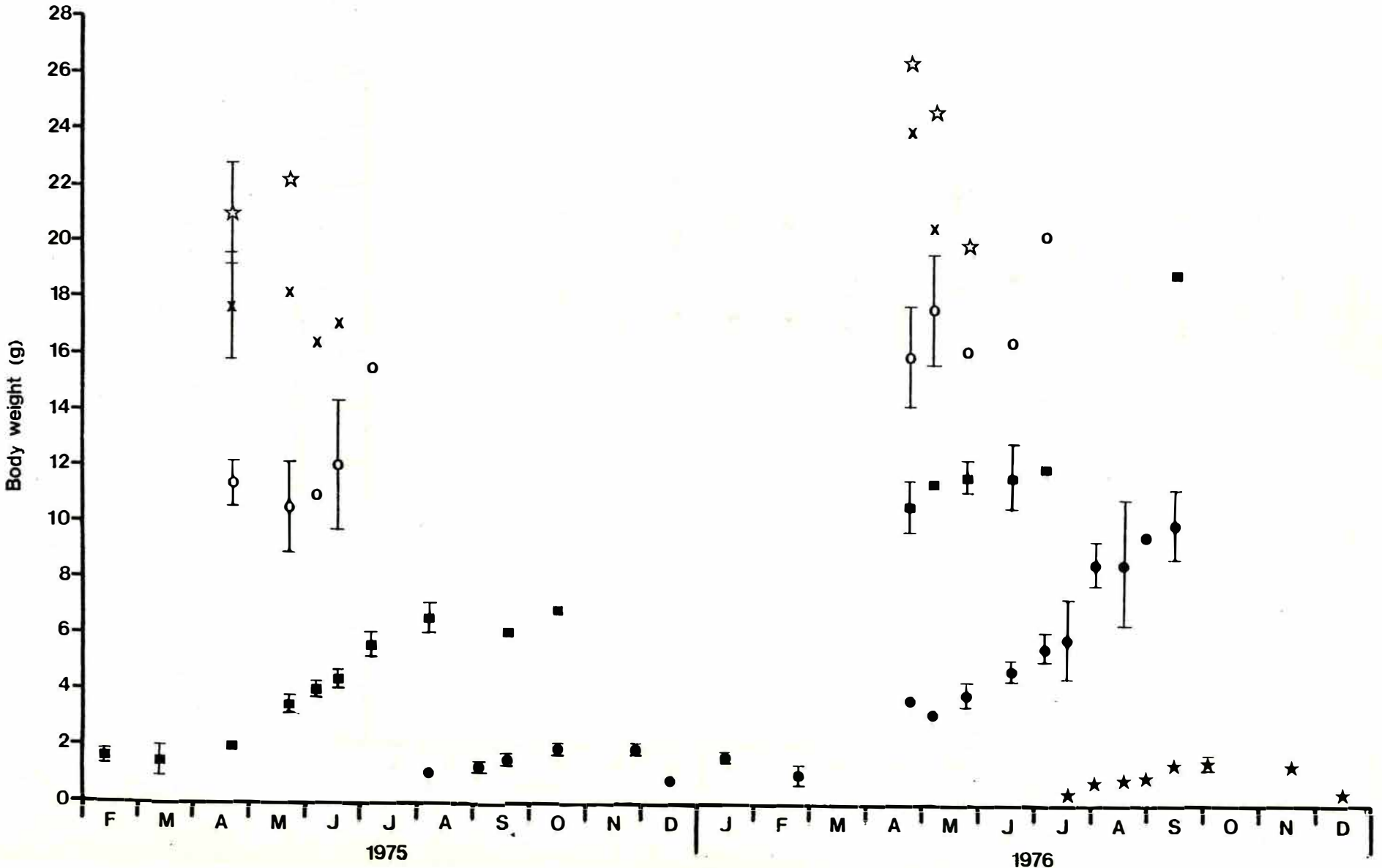


Figure 6.3.

A. presbyter Mean body lengths for year-classes 1971-76 at Fawley.

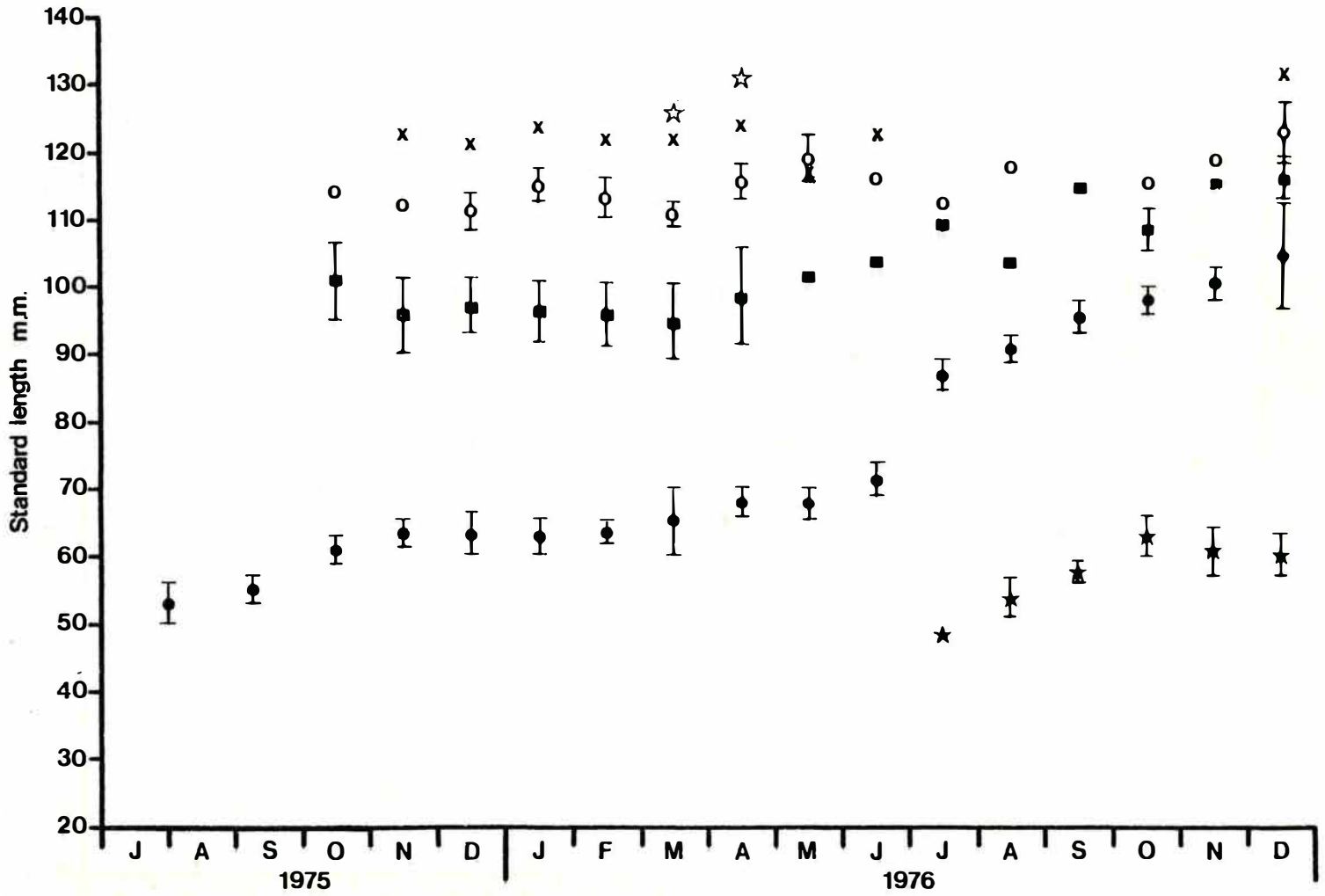
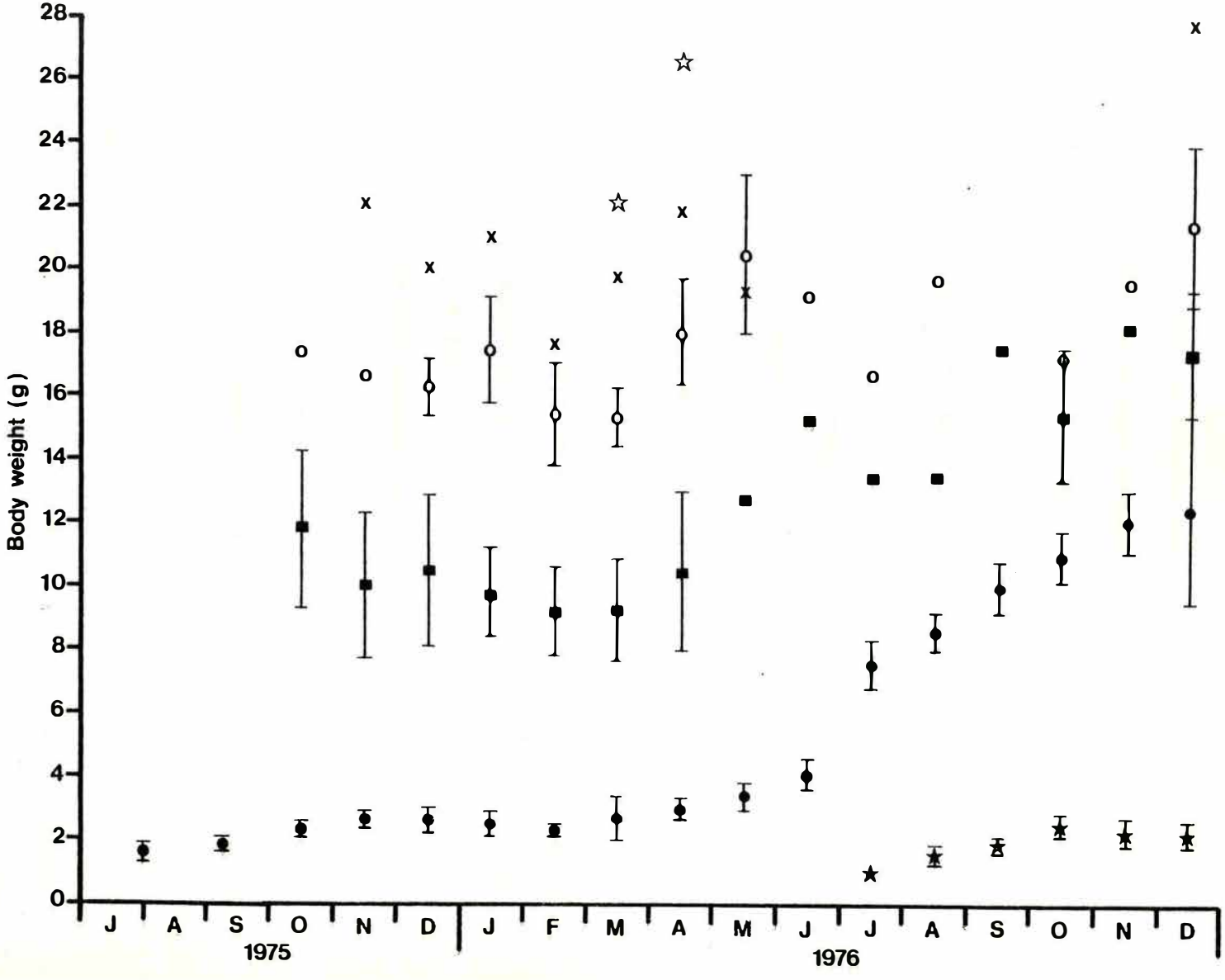


Figure 6.4.

A.presbyter Mean body weights for year-classes 1971-76 at Fawley.



to emphasise the growth pattern, instantaneous growth rates for the 1975 year-class at Fawley have been calculated (Appendix C.4) and plotted in Figure 6.5. These are in the form of average daily instantaneous growth rates calculated from the following formula:

$$G = \frac{(\log_e Y_2 - \log_e Y_1) \times 100}{t_2 - t_1}$$

where Y_2 and Y_1 are the sizes (length or weight) at times t_2 and t_1 respectively, and $t_2 - t_1$ represents the number of days between samples.

A. Langstone Harbour (Figures 6.1 and 6.2)

1971 year-class

Only twenty seven fish were captured in all and only one sample (17/23 April 1975) was large enough to apply 95% confidence limits to the means, which were a length of 128.53 $\pm$ 2.48mm and a weight of 20.98 $\pm$ 1.78g. If these are compared with the combined lengths and weights (128.30 $\pm$ 3.00mm and 24.56 $\pm$ 2.04g) of fish from this year-class caught the following year, 1976, it will be noted that although there was an insignificant increase in weight there was no increase in length.

1972 year-class

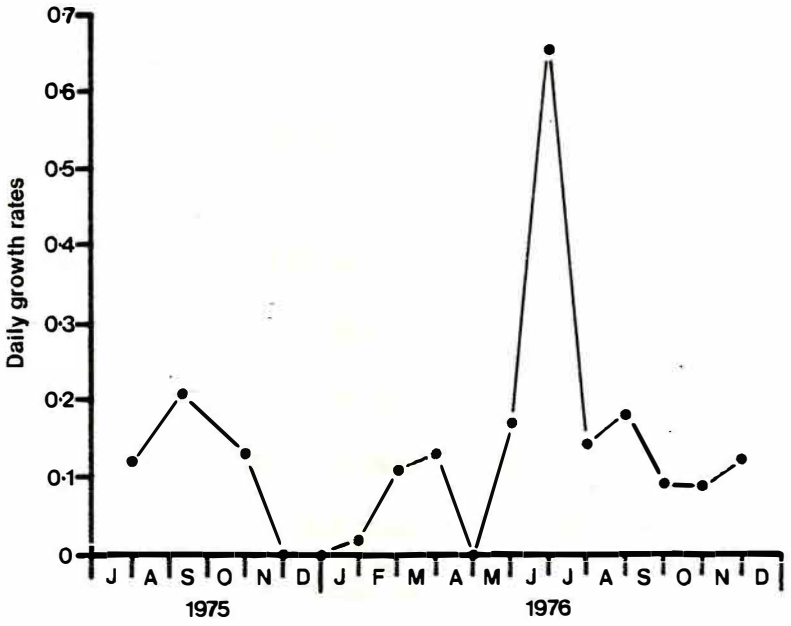
As in the previous year-class low sample numbers restrict growth analysis, however, between April 1975 (120.93 $\pm$ 2.19mm) and April-June 1976 (122.50 $\pm$ 4.49mm, combined lengths) there was an insignificant increase in length. This latter mean length was lower than that of the 1971 year-class as IV group fish, although not significantly so.

Again growth in weight was more noticeable although still insignificant, 17.72 $\pm$ 1.91g (April 1975) to 22.34 $\pm$ 3.57 (April-June

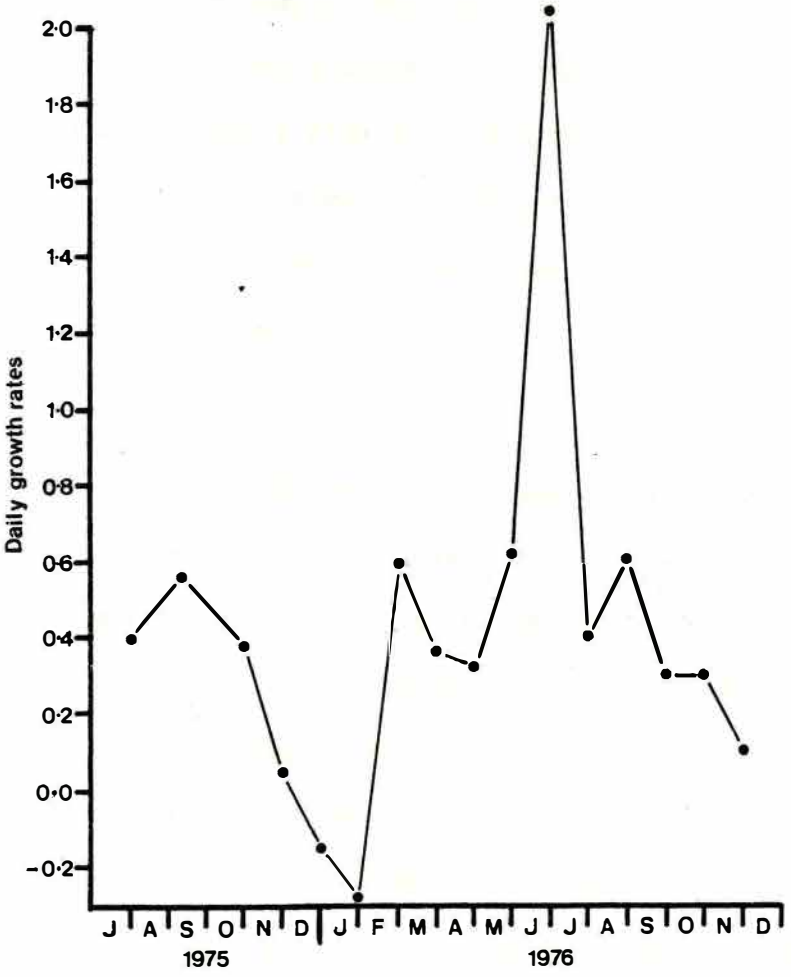
Figure 6.5.

A. presbyter Average daily instantaneous growth rates for the 1975 year-class at Fawley.

a) Body length



b) Body weight



1976, combined). Unlike length, mean body weight was higher than that of the 1971 year-class as IV group fish although not significantly so.

1973 year-class

This was better represented in the Langstone samples than the two previous year-classes, although still restricted to the April to July period. There was no significant increase in length between 17/23 April 1975 (104.52 ± 2.00mm) and 22 May 1975 (100.33 ± 5.04mm) or 19 June 1975 (101.50 ± 3.80mm) also there was no significant increase in body weight over the same period, 11.28 ± 0.76g, 10.50 ± 1.61g and 11.98 ± 2.27g respectively. By the time this year-class returned to the samples the following April as III group fish standard length and body weight had increased significantly to 113.27 ± 4.02mm and 15.95 ± 1.81g respectively. Both this sample (26 April 1976) and the following one (7 May 1976) had significantly lower body length and weight than the 1972 year-class as III group fish at this time the previous year. After May 1976 sample numbers were insufficient to determine whether further growth in length or weight took place before the year-class became absent from the samples.

1974 year-class

On 11 February 1975 this year-class had a mean length of 57.4 ± 2.29mm and a mean weight of 1.58 ± 0.19g. No significant increase in these two parameters were noted in the following sample (12 March 1975), however, by 22 May 1975 appreciable rises in both were noted (70.26 ± 1.79mm, 3.45 ± 0.26g respectively), significant rises when compared with the February and March values. Mean length and weight continued to increase in the two samples in June, by 19 June 1975 the values were 73.68 ± 1.43mm and 4.35 ± 0.29g respectively. By the time

of the next sample (7 July 1975) large significant increases in length to 78.55 ± 1.43mm and weight to 5.63 ± 0.35g were noted implying rapid growth in length and weight at this time. Increase in both parameters continued until this year-class were no longer a component of the samples, however, fairly rapid growth must have continued through the autumn and following early spring as by 26 April 1976 the mean length and weight were 97.47 ± 3.10mm and 10.60 ± 0.94g respectively. Mean lengths remained fairly constant over the April to July period during 1976 although mean body weight showed a gradual but insignificant increase. Over this period, the mean lengths and weights recorded were very close to and not significantly different from the 1973 year-class over the corresponding period during 1975.

1975 year-class

These first entered the seine-net catch in numbers on 3 September 1975 as 0 group fish with a mean length of 49.66 ± 1.21mm and mean weight of 1.31 ± 0.10g. The means of both parameters gradually increased until by 16 October 1975 they were 55.75 ± 2.04mm and 1.87 ± 0.17g respectively. Growth from this time appeared to cease as by 26 November 1975 the mean length was similar (56.64 ± 1.72mm) and the mean body weight was the same and also by 15 January 1976 the mean length was very close (55.12 ± 1.66mm) although the mean body weight had dropped a little. The samples captured on 16 December 1975 and 26 February 1976 had means much lower than these. A theory concerning the influx of these small fish was proposed in Section IV.

This year-class did not appear in numbers again until 26 May 1976 by which time the mean length and weight were 70.00 ± 1.91mm and 3.93 ± 0.39g respectively. This represents a large, significant rise in both compared with the sample in January and suggests fairly rapid growth

during the early spring period. The means of both parameters increased fairly rapidly from May and by 19 July 1976 the mean length was 80.00 ± 4.97mm and mean weight 5.89 ± 1.43g. By the time of the following sample (3 August 1976) a large, significant increase in both to 89.70 ± 2.44mm and 8.60 ± 0.76g respectively was recorded. After this period, growth appeared to slow down although by 15 September 1976 mean length had increased to 94.85 ± 3.06mm and mean weight to 10.04 ± 1.16g.

During 1976 the mean lengths and weights recorded were very close to and not significantly different from those of the 1974 year-class during 1975 recorded at similar times, with the exception of 6 August 1975 and 3 September 1975. At this time, mean lengths and weights were significantly higher although this may have been due to the warmer water temperatures experienced during June and July 1976 having promoted increased growth.

1976 year-class

These first entered the samples in numbers on 19 July 1976 as 0 group fish, six weeks earlier than the 1975 year-class the previous year. At this time, they had a mean length of 35.76 ± 0.65mm and mean weight of 0.46 ± 0.03g. Both continued to increase gradually through August and September 1976 until on 4 November 1976 they were 53.30 ± 1.74mm and 1.47 ± 0.18g respectively. Growth thereafter appeared to cease as on 17 November 1976 the means of length and weight were slightly although insignificantly less.

Although this year-class had entered the catches earlier than the 1975 year-class the previous year, mean lengths and weights at corresponding times were close and not significantly different, with the exception of the samples on 26 November 1975 and 17 November 1976, when

the latter was lower.

B. Fawley (Figures 6.3 and 6.4)

1971 year-class

Only five individuals ascribed to this year-class were retained thus making any observations on growth impossible. However, lengths recorded were close to those recorded for the same year-class at Langstone.

1972 year-class

Again low numbers restricted any analysis of growth. Fish caught between November 1975 and June 1976 had a fairly constant length of just over 120mm, however, weight fluctuated more noticeably, the lowest mean recorded was 17.66g in February 1976. One fish caught at the end of 1976, during December was 132mm long, similar to 1971 year-class fish caught earlier in 1976, although heavier.

1973 year-class

These were first retained in numbers during December 1975 when their mean length was 111.57 $\pm$ 2.92mm and mean weight 16.30 $\pm$ 0.94g. Little variation, certainly not significant, was recorded until after March 1976 when both mean length and weight began to rise. By May 1976 these were 119.45 $\pm$ 3.58mm and 20.55 $\pm$ 2.46g, significantly higher than the corresponding March 1976 means, and very close to those observed in the same year-class at the same time at Langstone. Little further growth in length and weight appeared to take place in 1976 as by December only small insignificant rises in both means were noted.

1974 year-class

In October 1976, as I group fish, this year-class had a mean length

of 101.14 ± 5.79mm and a mean weight of 11.84 ± 2.46g. From this month until March 1976 there appeared to be no growth in either parameter as both mean length and weight remained fairly constant with no significant differences between samples. The means began to increase in April 1976 although not significantly. At thistime mean length and weight (98.83 ± 7.43mm, 10.52 ± 2.54g) were not significantly different from the same year-class means at Langstone at the same time.

Unfortunately, this year-class was not retained in numbers again until October 1976 by which time length and weight had increased to 108.88 ± 3.30mm and 15.51 ± 2.05g, the latter significantly. By December 1976 these had further increased to 116.86 ± 3.18mm and 17.51 ± 2.10g, values not significantly different from the 1973 year-class in December 1975.

1975 year-class

This gave the most complete picture of growth of any year-class sampled at the two sites as it was present in numbers in all months sampled. Because of this it was possible to calculate daily instantaneous growth rates (d.i.g.r.) using the equation given earlier, throughout the sampling period and these are plotted in Figure 6.5.

These fish were first retained as 0 group fish within the period mid-July to mid-August and had a mean length of 53.25 ± 3.13mm and weight of 1.57 ± 0.26g. Growth, in terms of d.i.g.r., was fairly high in both parameters, from this time onwards, reaching a maximum between September and October of 0.21 in body length and 0.57 in body weight but then it fell away as from November onwards growth in length ceased, the mean becoming fairly constant whilst body weight actually started to decrease. By December 1975 the mean length was 63.57 ± 2.93 whilst mean body weight was 2.64 ± 0.39g, significantly higher than the same year-

class caught at Langstone over the same period. However, the sampling technique at Fawley is biased against the retention of small specimens which could effectively increase both means recorded.

Growth in length and weight began again in March 1976 and continued into April 1976. By this time mean length was 68.05 $\pm$ 2.26mm and mean weight 3.07 $\pm$ 0.35g. In May 1976 growth in length ceased although growth in body weight continued. As will be seen later (Section VII), this was the period of large increases in gonad weight which presumably utilised most of the energy available at this time. Increased mean lengths and weights were recorded in June, 71.63 $\pm$ 2.36mm and 4.10 $\pm$ 0.49g respectively. These were not significantly different from the same year-class at Langstone at the same time. From Figure 6.5 it will be noted that by far the largest d.i.g.r. occurred during July 1976 when mean length and body weight rose very significantly to 87.21 $\pm$ 2.22mm and 7.58 $\pm$ 0.74g respectively. In fact, growth in body length (37%) and weight (35%) during July 1976 was just over one third of the total growth recorded between January and December 1976 within this year-class. A steady increase in mean length and weight were evident from August 1976 onwards until by December 1976 they were 104.80 $\pm$ 8.11mm and 12.51 $\pm$ 3.07g respectively, not significantly different from the 1974 year-class in December 1975.

1976 year-class

These fish were first retained during August 1976 as 0 group fish with a mean length of 54.16 $\pm$ 2.97mm and a mean weight of 1.64 $\pm$ 0.29g. By October 1976 these had risen significantly to 63.33 $\pm$ 3.14mm and 2.54 $\pm$ 0.43g. Growth thereafter appeared to cease as both means remained fairly constant for the rest of 1976.

6.3.2. Annual growth in body length and weight with respect to age

As 1+ age-groups at Langstone were so restricted in their time of occurrence in samples, the annual growth in body weight could not be determined and body length with respect to age could not be calculated without resorting to estimation techniques using the von Bertalanffy formula (Ricker 1958) or back-calculation from otoliths (Reay 1972a, b). This analysis was therefore confined to the *A. presbyter* at Fawley and the 0 group at Langstone. No comparison of annual growth between year-classes was attempted and, therefore, length and weight data from these year-classes were combined (Appendix C.5).

Earlier in this section growth in length and weight was considered to have ceased by December and not to have begun again until the following March. Thus, annual growth in length and weight with respect to age (or length and weight at the end of each growing season) was determined by combining length and weight data from the months of December, January and February. Only one late IV/early V group fish was retained at Fawley during these months, insufficient for analysis. An annual growth-rate was also calculated as an instantaneous annual percentage growth-rate derived from the formula:

$$G = \frac{(\log_e Y_2 - \log_e Y_1) \times 100}{t_2 - t_1}$$

where Y_2 and Y_1 are the lengths or weights at t_2 and t_1 respectively and $t_2 - t_1 = 1$ (year).

A. Length

Figure 6.6 plots the range of *A. presbyter* body lengths recorded within a particular age-group during the year. The two sites differed only on a few points. At Fawley the lower end of the range in both 0

Figure 6.6.
A. presbyter Range of body lengths found within each age-group.

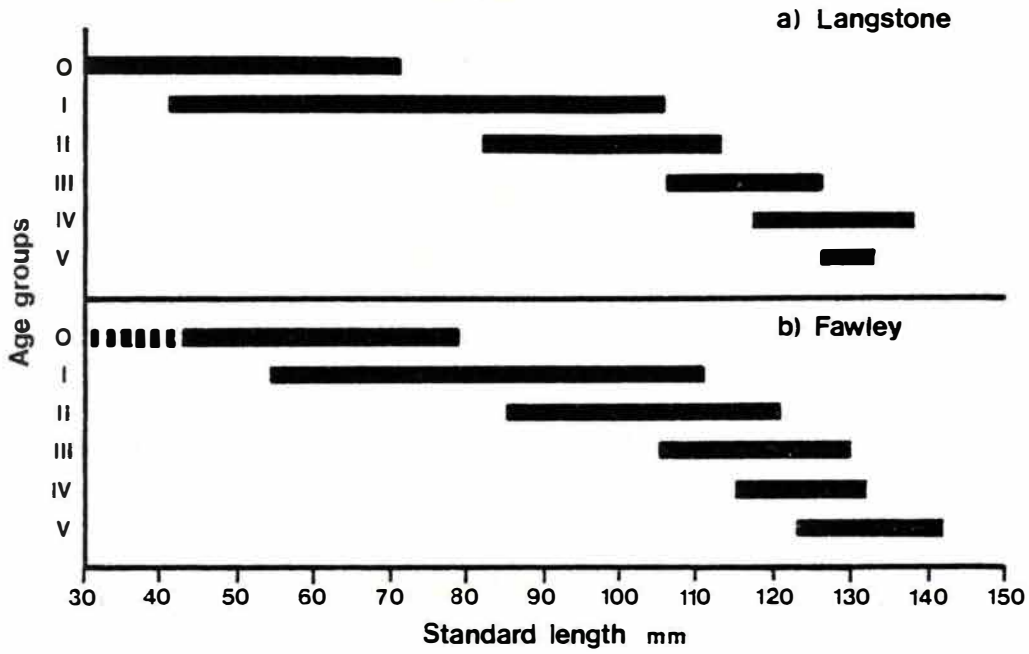
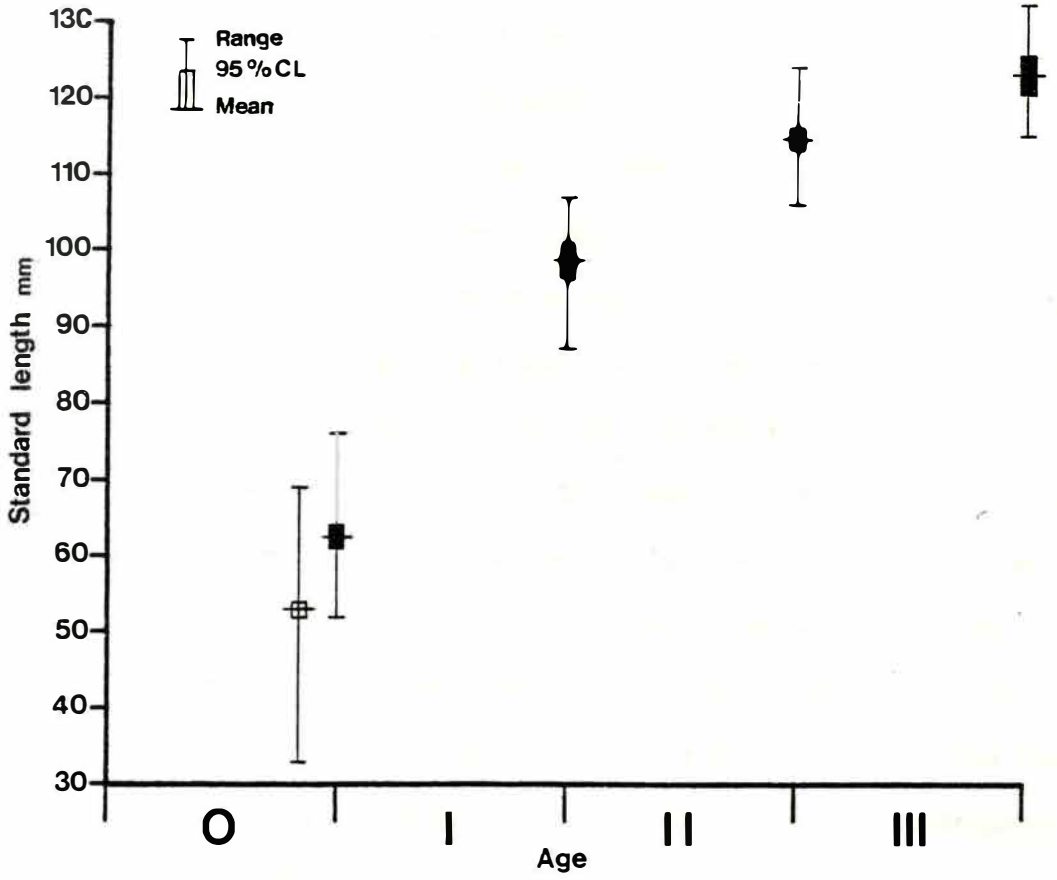


Figure 6.7.
A. presbyter Annual growth in body length with respect to age.



and I groups when compared with Langstone was probably truncated due to the bias of the sampling technique against small fish. The upper limits of age-groups I, II, III and V at Fawley were higher than those observed at Langstone. However, these age-groups were present throughout the year in Fawley samples, whereas at Langstone they were only well represented in late spring and early summer samples. Only two aspects are not easy to explain, the discrepancies between the two upper 0 group limits and the two upper IV group limits.

The length data for each age-group at the end of the growing season is given in Appendix C.5.a and the mean, 95% confidence limits and range are plotted in Figure 6.7. Annual growth rate is also given in Appendix C.5.a.

At the end of the growing season as 0 group, the fish at Fawley had a mean length of 62.65 $\pm$ 1.22mm, significantly higher than the corresponding length recorded at Langstone, 52.70 $\pm$ 1.12mm, although the ranges overlapped. This was probably due once again to a combination of the sampling bias at Fawley against small fish and the influx of small 0 group fish at Langstone during December 1975.

By the end of the I group growing season at Fawley, mean length rose to 98.59 $\pm$ 2.30mm, a very significant rise over the year where even the ranges did not overlap. During the following year, as II group, the growth rate slowed, although again there was a significant rise, and by the end of the growing season the mean length was 114.35 $\pm$ 1.45mm. However, the range of lengths recorded overlapped with those of the previous age-group. A further decrease in body length growth rate was recorded during the III group growing season although again the mean increased significantly, to 122.89 $\pm$ 2.43mm, but with an increased overlap of length ranges.

B. Weight

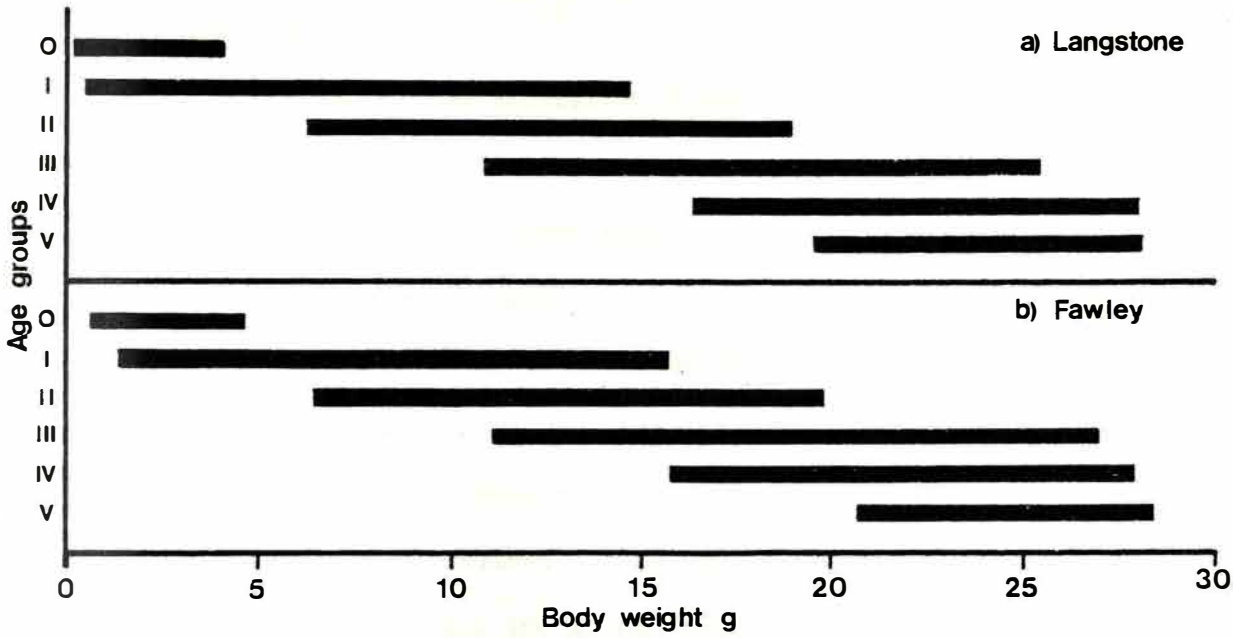
Figure 6.8 plots the range of *A. presbyter* body weights recorded within a particular age-group. The same differences between sites were recorded as were outlined for body length and probably for the same reasons.

The body weight for each age-group at the end of the growing season is given in Appendix C.5.b and is plotted in Figure 6.9. Annual growth rate is also given in Appendix C.5.b. At the end of the 0 group season the fish at Fawley averaged 2.41 $\pm$ 0.16g, which as for length, was significantly higher than the corresponding weight recorded at Langstone (1.45 $\pm$ 0.09g), although the ranges overlapped. By the end of the following growing season mean body weight had risen very significantly to 10.17 $\pm$ 0.09g, an instantaneous annual percentage growth rate of 143.91. During the following year, as II group, the growth rate, of 49.08, and the weight range recorded, overlapped with the previous age-group. However, mean weight had risen significantly to 16.61 $\pm$ 0.80g. The growth rate was further reduced during the III group growing season although mean weight again increased significantly to 20.39 $\pm$ 1.47g.

Kristensen (1956) gave some data on the growth in length, but not weight, of *A. presbyter* in three subsequent years in Dutch waters. The results were of insufficient detail to give a seasonal analysis of growth but did show annual growth for age-groups 0 and I. By their first winter fish were found to range between 75 and 95mm in length. Although not stated, this was presumably total length and from the relationship determined in Section 2.4 this would be equivalent to a range of 64 to 84mm standard length. This is fairly close to the range found at Fawley although both upper and lower limits of the range were

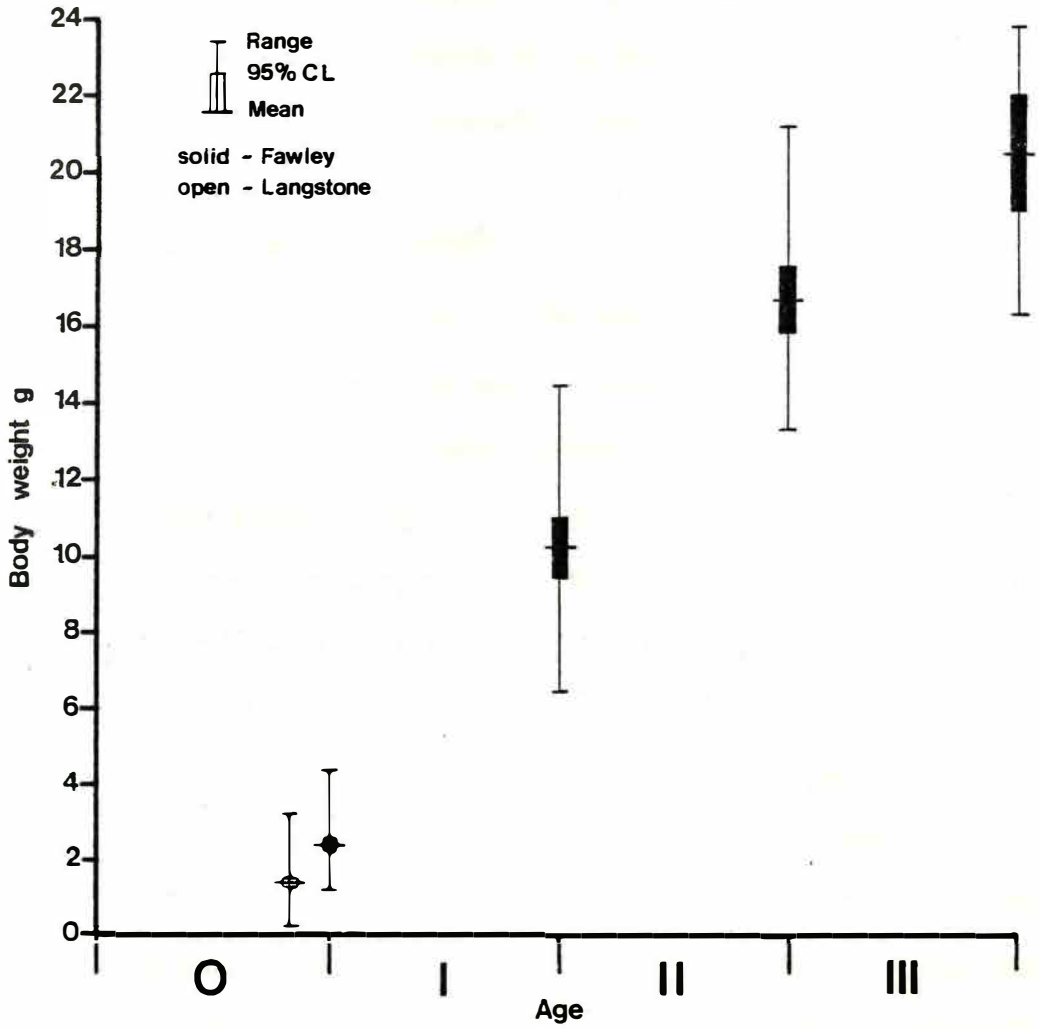
Figure 6.8.

A. presbyter Range of body weights found within each age-group.



Fiqure 6.9.

A. presbyter Annual growth in body weight with respect to age.



slightly elevated.

By their second winter Kristensen found *A. presbyter* to range between about 115 and 145mm total length (99 to 125mm SL). This is not in agreement with the present study where such a range almost exactly corresponds to the combined range of *A. presbyter* during their second and third winters. Kristensen used scales for ageing *A. presbyter* which therefore would appear to give results which are not consistent with ageing from otoliths. However, the distribution of lengths, recorded as I group by Kristensen during April, May and June appear from the results to represent two groups with about 20mm separating the upper and lower limits of the ranges of these groups. Thus, the use of scales for the age-determination of *A. presbyter* would seem to be a technique of dubious value which gives ages inconsistent with otolith studies or length-frequency distributions.

6.3.3. Length-weight relationship

The results of the regression analyses are given in Table 6.1. Length and weight, not unexpectedly, showed a highly significant correlation ($P < 0.001$) with one another. In all cases the slope, or exponent b, was greater than 3.0 which implied allometric growth.

There was no significant difference between male and female exponents at each site, although there was a significant difference between females at Langstone and those at Fawley for body weight, and females at Langstone and both males and females at Fawley for carcass weight ($P < 0.05$). However, this was not entirely unexpected as late I group and II+ groups were absent from Langstone during autumn and winter, thus making the result of the regression analysis more seasonally biased at this site. In addition, the Langstone sample contained

Table 6.1. *A. presbyter* Length-weight relationship

Site	Weight	Sex	N	Range S.L. mm	Range Weight g	$W = aL^b$ a($\times 10^{-6}$)	$W = aL^b$ b ± 95% C.L.	Correlation Coefficient r
Langstone	Body	♂♂	131	33-131	0.27-26.61	5.0645	3.1717 ± 0.0438	0.9969
		♀♀	173	36-137	0.38-28.12	5.7862	3.1401 ± 0.0426	0.9960
	Carcass	♂♂	131	33-131	0.24-23.66	6.0541	3.1051 ± 0.0458	0.9964
		♀♀	173	36-137	0.32-22.63	8.7432	3.0144 ± 0.0430	0.9956
Fawley	Body	♂♂	113	49-133	1.00-25.10	3.9823	3.2207 ± 0.0564	0.9957
		♀♀	131	43-132	0.78-26.91	3.4023	3.2578 ± 0.0560	0.9952
	Carcass	♂♂	113	49-133	0.95-21.95	4.2655	3.1854 ± 0.0510	0.9964
		♀♀	131	43-132	0.73-23.21	4.5573	3.1689 ± 0.0494	0.9960

smaller 0 group fish.

The relationships between standard length and body weight in *A. presbyter* at the two sites are graphically displayed in Figures 6.10 and 6.11. Sexes have been combined due to lack of a significant difference between them. Apart from the difference in size range the two graphs are very similar.

If sexes and sites are combined, the length-weight relationship of *A. presbyter* may be expressed as $W = 4.6718 \times 10^{-6} SL^{3.1924}$ for total wet body weight.

6.3.4. Ponderal index

This was calculated from body weight (g) and standard length (mm) data using the formula:

$$\text{Ponderal index (K)} = \frac{W \times 10^6}{L^{3.2}}$$

The exponent of 3.2 was used as this was the mean value, to one decimal place, of the regression analyses carried out of $\log_{10}$ standard length on $\log_{10}$ body weight (see Section 6.3.3).

For *A. presbyter* the mean ponderal index was calculated separately for males and females and for age-groups 0, I and II+ within each sample. These results are given in Appendix C.7. The only significant differences within samples were as follows: at Langstone between I group females and II+ females (6 June 1975) and between 0 group males and I group males and females (15 September 1976); and at Fawley 0 group males and females were significantly different from I group males, and 0 group males from I group females (September 1976), as were 0 group males and I group females (November 1976). Therefore, sexes and age-groups have been combined to give sample means with 95% confidence

Figure 6.10.

A.presbyter Length-weight relationship of fish from Langstone (see Appendix C.6.).

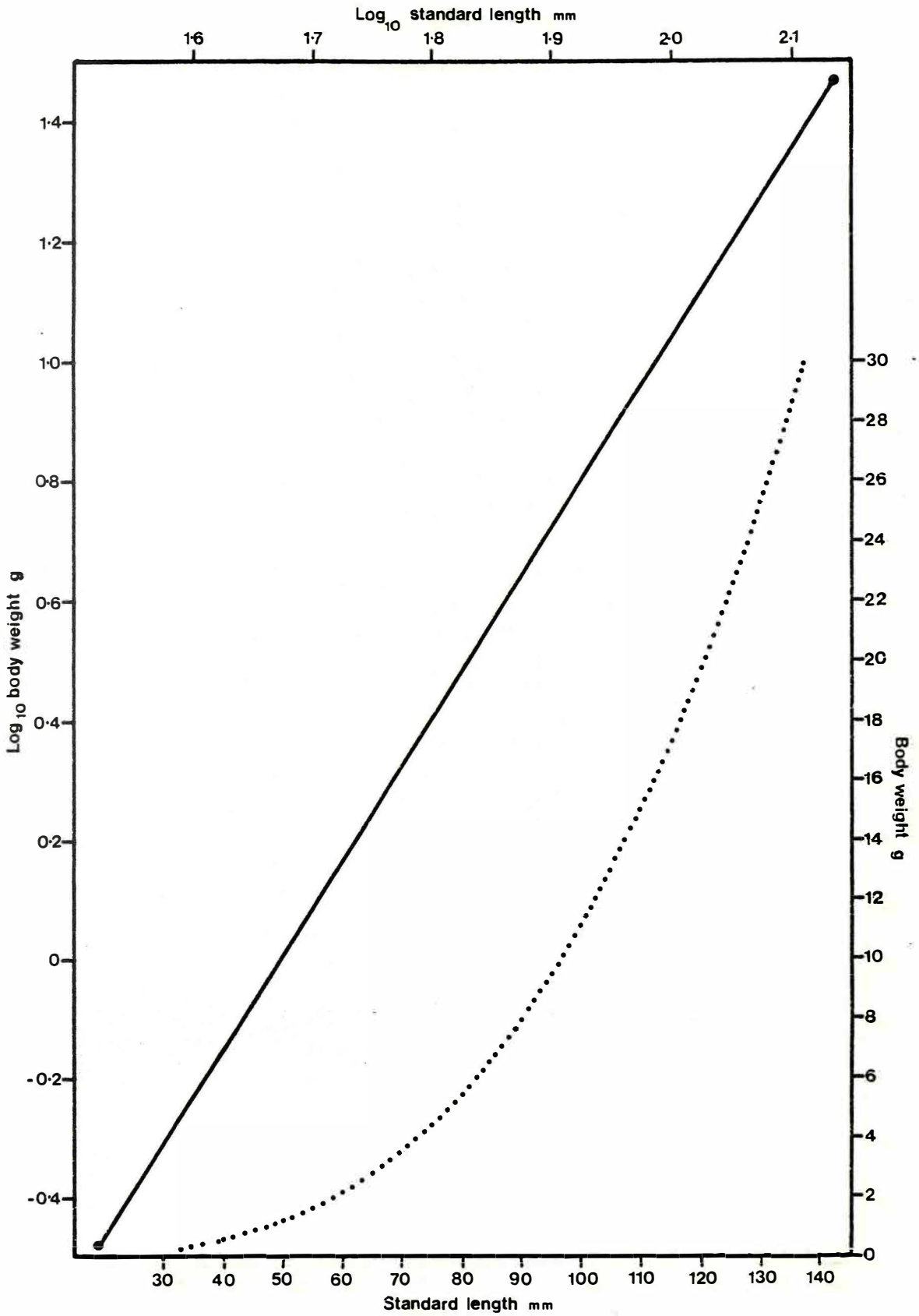
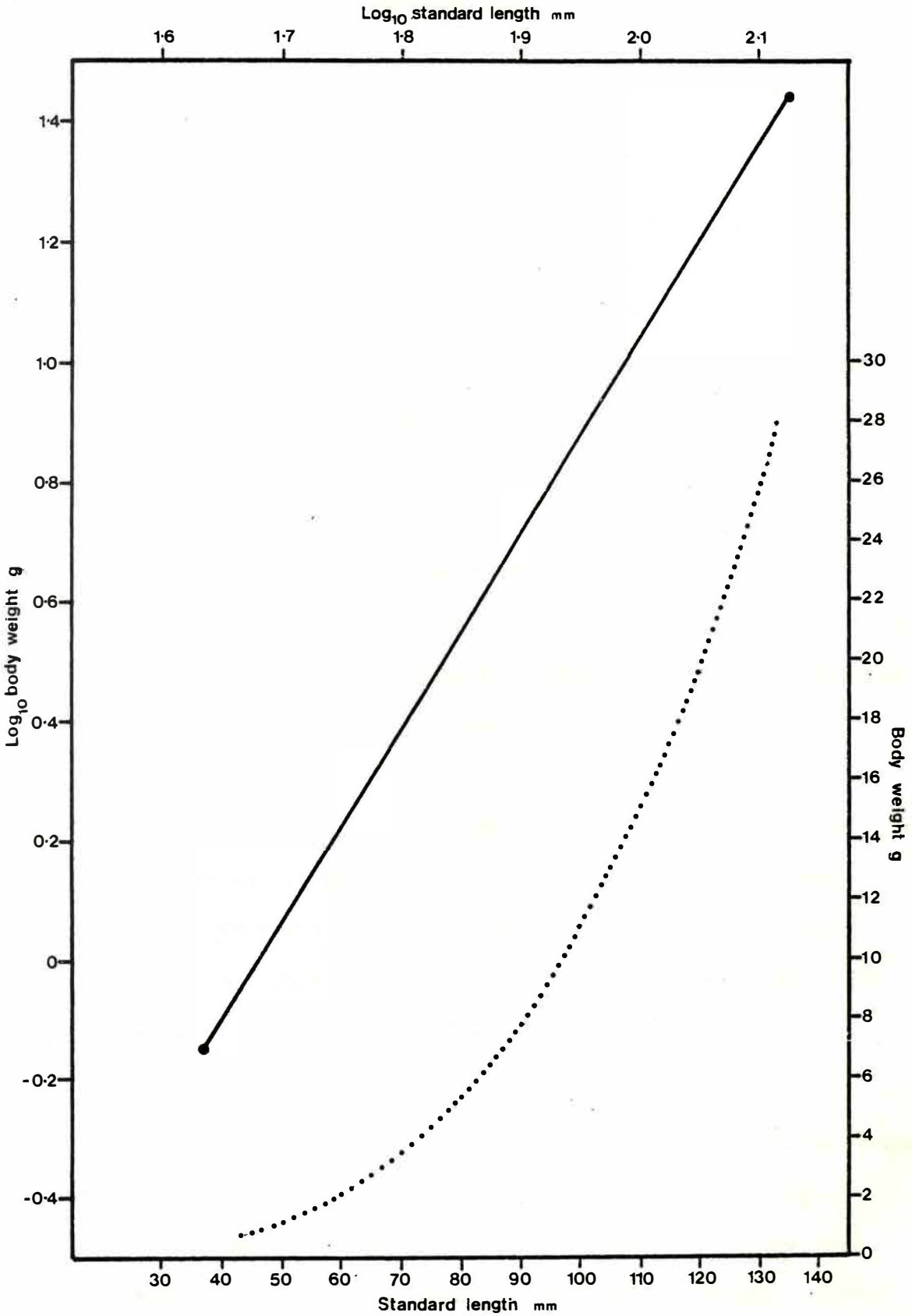


Figure 6.11.

A. presbyter Length-weight relationship of fish from Fawley (see Appendix C.6.).



limits (Appendix C.8), which have been plotted in Figure 6.12, together with mean monthly water temperatures.

a) Langstone

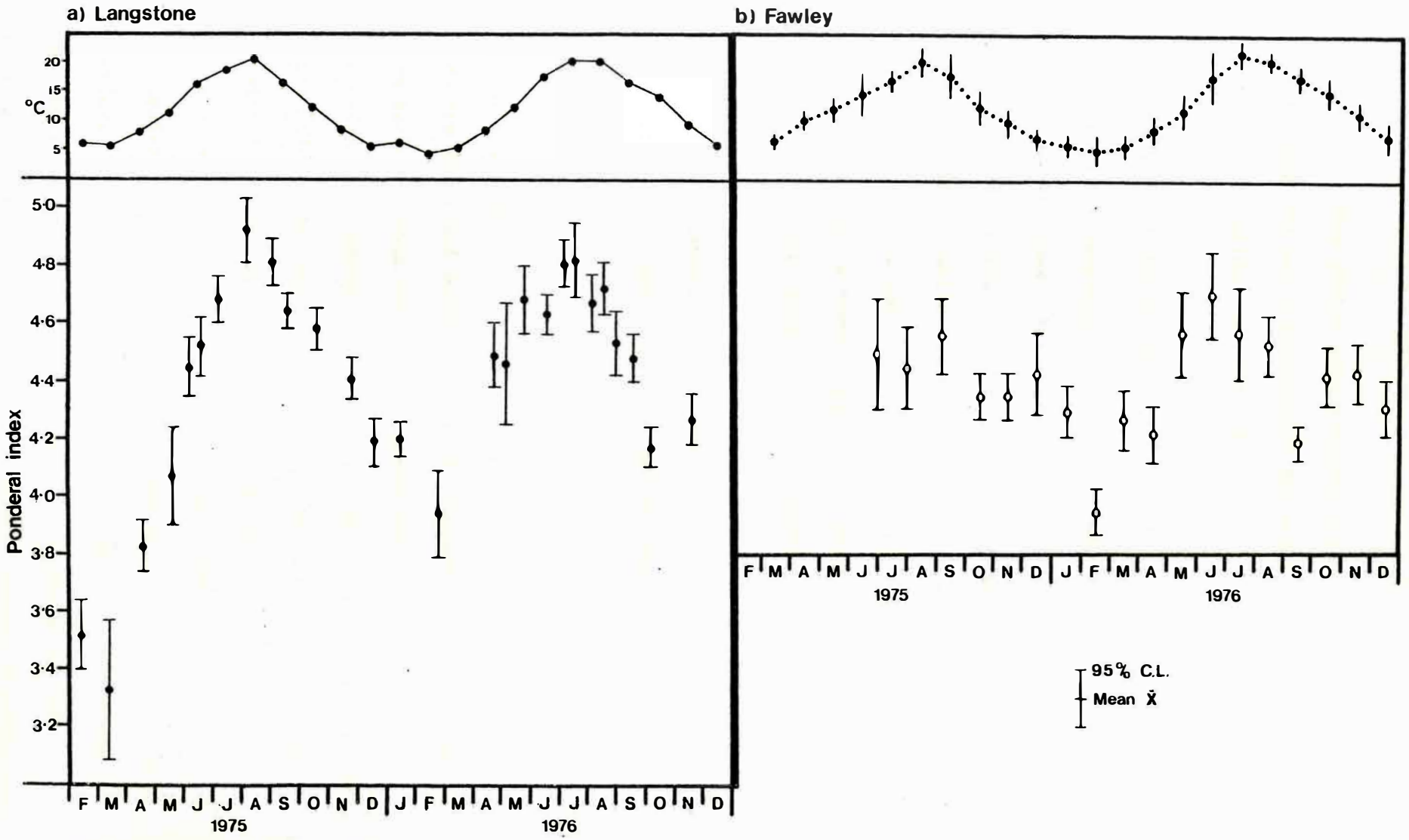
The mean ponderal index showed clear seasonal fluctuations, with the highest relative body weight occurring in the months of July and August when mean water temperature was at its highest. Mean ponderal indices at this time were between 4.60 and 4.95 and there were no significant differences between values in 1975 and 1976. From August onwards, during both years, there was a gradual decrease in relative body weight through the autumn and winter. Lowest ponderal indices (and hence relative body weight) were recorded during February and March when mean water temperature was at its lowest. The mean ponderal indices recorded during February and March 1975 were significantly lower than that recorded in February 1976. No definite reason for this can be given as very little difference in water temperature at the time was recorded. However, the late summer and early autumn water temperatures during 1974, the major period for the build up of lipid reserves (see Section 6.3.5), were substantially lower than over the corresponding period during 1975 and 1976 (see Section 2.1.1), and perhaps resulted in reduced food supplies at that time. From March onwards, in 1975 and 1976, relative body weight increased steadily to the peak values recorded during July and August.

b) Fawley

The seasonal pattern here was not as clear, and the seasonal range in mean ponderal indices recorded not as great, as that recorded at Langstone. This may be because these were monthly means rather than discrete sample means. However, maximum relative body weight occurred at about the same time (June to August) as did the minimum relative

Figure 6.12.

A. presbyter Mean ponderal index of each sample and mean monthly water temperature at each site.



weight (February). This latter mean ponderal index showed close agreement with, and was not significantly different from, the Langstone mean index during the same month.

6.3.5. Fluctuations in the weight of body cavity components

There is a considerable number of variables that can affect the value of the ponderal index. Included among these are long term factors such as food supply, the degree of parasitization, and abiotic environmental parameters which may affect condition as well as growth rate and average size attained. Probably more important in the marine environment are the shorter term, seasonal fluctuations in the ponderal index often correlated with such cycles as reproduction, feeding rate and lipid storage.

Certain of these phenological parameters have been followed, namely cycles in liver weight, intestine weight, mesenteric lipid weight and gonad weight.

i. Mesenteric lipid weight

Lipids are the chief energy source in teleosts (Shul'man 1960, 1974) and as such have been shown to be accumulated as reserves in temperate species for overwintering or during spawning when either food is in short supply or feeding is curtailed. They are also important during the winter insulating the fish from low water temperatures. Lipids may be stored at many sites, but in *A. presbyter* the most obvious and easiest deposits to measure are those accumulated in the gut mesenteries. Presumably lipids are also accumulated within the soma and in the liver as in many other species. Although in this investigation no attempt has been made to analyse seasonal fluctuations

in total lipid reserves, it was felt that this pattern would be reflected by the mesenteric reserves. This meant that the effect of total lipid reserves on the ponderal index could not be ascertained directly, but, of course, it would be greater than the effect of the mesenteric reserves alone.

The mesenteric lipid reserve was followed as a mesenteric lipid-somatic index:-

$$\text{Mesenteric lipid-somatic index} = \frac{\text{Mesenteric lipid weight (g)} \times 100}{\text{Carcass weight (g)}}$$

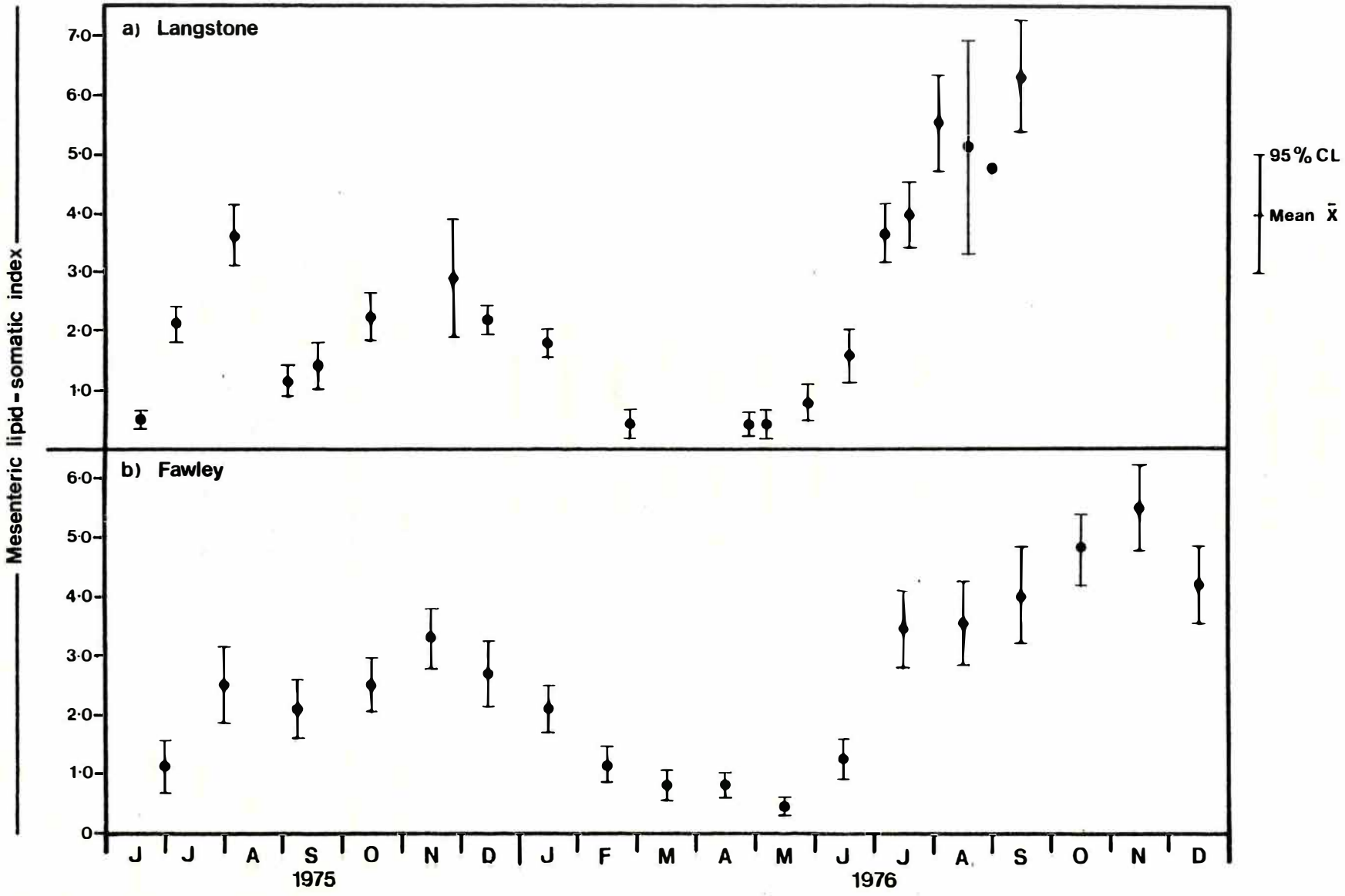
It was calculated separately for males and females and age-groups 0, I and II+. The results are given in Appendix C.7 as means with 95% confidence limits and sample numbers. From the results, the only significant differences were as follows: at Langstone between male and female I group (7 July 1975), and between female I group and female II+ group (26 May, 17 June 1976); at Fawley between male and female 0 and I groups (mid August to end September 1975), male and female I groups and male II+ group (January, February 1976), and between female I group and female II+ group (June 1976). Therefore, sexes and age-groups were combined although sites were still considered separately. These results are given in Appendix C.9 and plotted in Figure 6.13.

a) Langstone

During 1975 the mesenteric lipid weight was not recorded until 19 June, when the mesenteric lipid-somatic index was 0.52 ± 0.17. By the following sample, 7 July, the mean index had increased significantly, to 2.11 ± 0.29, and then again, to 3.59 ± 0.48, by 6 August. The two samples captured in September had a much lower mean index probably entirely due to the sample containing only 0 group fish. (In the following year which contained only I+ fish the index continued to rise

Figure 6.13.

A.presbyter Mean mesenteric lipid-somatic indices.



in September). The mean index of these 0 group fish increased fairly rapidly from 1.15 ± 0.23 on 3 September to a peak of 2.84 ± 1.06 on 26 November. Active lipid accumulation then apparently ceased and the reserves began to be utilised as the mean index started to decrease slowly at first but then significantly between 15 January 1976 (1.82 ± 0.26) and 26 February 1976 (0.46 ± 0.23). The mean index remained at this low level until early May 1976, when it was 0.45 ± 0.23 (7 May). At this time mesenteric lipid accumulation began again, slowly at first but very significantly between 17 June (1.62 ± 0.43) and 5 July 1976 (3.69 ± 0.52). The mean index of these I+ fish continued to increase until the last sample, when it was 6.33 ± 0.93 (15 September 1976). Mean indices recorded during June, July and August 1976 were significantly higher than those of the corresponding months in 1975 perhaps a reflection of the high water temperatures experienced during the early summer of 1976 increasing the food available. (It will be noted later in this section that intestinal-somatic indices were also correspondingly higher).

b) Fawley

The *A. presbyter* at Fawley showed a very similar pattern to that already outlined for Langstone fish, with corresponding mean indices rarely showing significant differences.

During the period from mid-June to mid-July 1975 the index was 1.10 ± 0.45, which increased to 2.48 ± 0.67 during mid-July to mid-August. The effect of the influx of 0 group fish during the period of mid-August to the end of September reduced the mean to 2.08 ± 0.50. However, the older fish present acted as a buffer, in contrast to the results from Langstone where a far greater reduction was recorded. During October the mean index gradually increased reaching a peak in

November 1975, of 3.32 $\pm$ 0.51, similar to, and not significantly different from that observed at Langstone during the same month. Active lipid accumulation appeared to cease at this time, as it did at Langstone, with a switch to lipid utilisation. The mean index decreased gradually during December and January and then significantly, to 1.17 $\pm$ 0.29, during February 1976. Further reductions were recorded during March and April to a minimum mean index, of 0.46 $\pm$ 0.13, during May. Active accumulation of mesenteric lipid reserves then recommenced as, during June 1976, the mean index increased significantly, to 1.23 $\pm$ 0.37, and then very significantly, to 3.47 $\pm$ 0.63, during July. After this there was only a very small increase, to 3.57 $\pm$ 0.69, during August but this was followed by more rapid accumulation during September and October to a peak index, of 5.50 $\pm$ 0.74, during November. Again accumulation then apparently ceased and lipid utilisation began as the mean index decreased, to 4.20 $\pm$ 0.63, during December 1976. The mean indices recorded during September and October 1976 were significantly higher than those recorded at the same time in 1975 probably due entirely to the omission of 0 group fish from the 1976 samples.

Thus, mean mesenteric lipid-somatic indices varied between 0.44 and 6.33, a fluctuation of almost six percent of the carcass weight. If a mean fluctuation of five or more percent of the carcass weight is considered to have a significant effect on the mean ponderal index, then the mesenteric lipid content could be significant in this respect. However, the six percent is only a mean percentage variation. The mesenteric lipid-somatic index in individual fish ranged from zero to 10.65, therefore, the effect of mesenteric lipid weight on individual

ponderal indices may be even more important.

As already outlined, the gut mesenteries are not the only site of lipid storage. As will be seen shortly the relative liver weight also fluctuated. Much of this variation was probably due to the variation in lipid content. Therefore, if this is considered together with mesenteric lipid and somatic lipid, it will be seen that the state of lipid accumulation within *A. presbyter* can have an important effect on the ponderal index.

ii. Liver weight

This was followed as the hepatosomatic index, calculated as:

$$\text{Hepatosomatic index} = \frac{\text{Liver weight (g)} \times 100}{\text{Carcass weight (g)}}$$

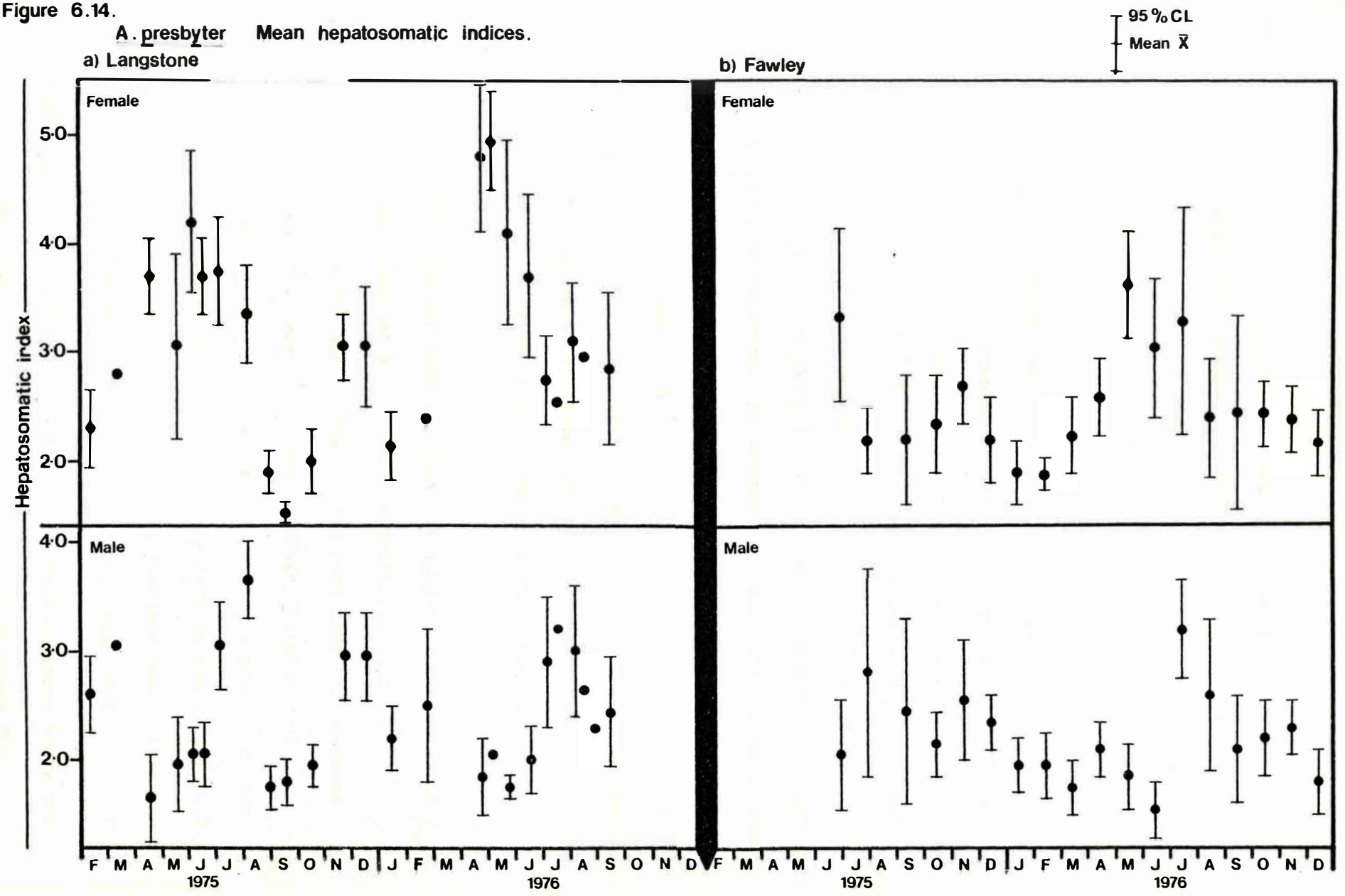
It was calculated separately for males and females and age-groups 0, I and II+ and the results are given in Appendix C.7 as means with 95% confidence limits and sample numbers. From these results it was apparent that there were important sexual differences in the hepatosomatic cycle but that generally age-groups within the sexes were not significantly different from one another with the following exceptions: at Langstone between female I and II+ groups (19 June, 1975, 26 May 1976 and 17 June 1976); and at Fawley between female 0 and I groups (mid August to end September 1975), male I and II+ groups (January 1976) and female I and II+ groups (April, May 1976). Therefore age-groups were combined but sexes were considered separately (Appendix C.10). The results are plotted in Figure 6.14.

a) Langstone

Female cycle On 11 February 1975 the female hepatosomatic mean index was 2.28 $\pm$ 0.35. This had risen significantly, to 3.69 $\pm$ 0.36,

Figure 6.14.

A. presbyter Mean hepatosomatic indices.



by 17/23 April 1975. No significant change in mean index was recorded during the following three months, the highest mean index, of 4.20 ± 0.63, occurred on 6 June. During August the mean index had decreased and by September 1975 the mean index had fallen to 1.87 ± 0.18 and 1.52 ± 0.09 on the 3 and 17 September respectively. This was probably because the sample consisted entirely of 0 group fish as in the following year during September the I+ mean index was significantly higher. During October the mean index began to increase until by 26 November 1975 it was 3.04 ± 0.28. This autumn increase of the mean probably resulted from the accumulation of lipids, as in temperate fish species the liver is often an important site for the accumulation of overwintering food reserves. By November further lipid accumulation had presumably ceased because the mean index of the next sample, 16 December 1975, was the same (3.04 ± 0.54). These lipid reserves were apparently subsequently utilised (as were mesenteric reserves) because by 15 January 1976 the mean hepatosomatic index had fallen, to 2.16 ± 0.32, close to that recorded in early February the previous year.

A. presbyter were not recorded again in numbers until 26 April 1976 by which time there had been a large significant increase to 4.78 ± 0.68, significantly higher than at the same time the previous year. By 7 May there had been a further although insignificant increase which was followed in subsequent samples by a gradual steady decrease in the mean index until by the 5 July 1976 it was 2.73 ± 0.37, significantly lower than at the same time the previous year. From then it remained fairly constant during August and September 1976.

Male cycle On 11 February 1975 the mean hepatosomatic index was 2.59 ± 0.35, higher than the corresponding female mean index but not

significantly so. By 17/23 April 1975 the mean had dropped significantly to 1.66 $\pm$ 0.41, significantly lower than females caught on the same day. However, in subsequent samples the mean index gradually began to increase, although not significantly, until by 19 June 1975 it was 2.07 $\pm$ 0.29. Throughout this period, with one exception (22 May), the male mean index remained significantly below that of the female. By the next sample, 7 July 1975, a large significant increase in mean index to 3.05 $\pm$ 0.38 was recorded. This was still less than the corresponding female mean index at that time but no longer significantly so. However, by 6 August 1975, it was slightly higher at 3.63 $\pm$ 0.34. During September 1975 the same large significant drop in the mean hepatosomatic index was recorded, as for females. This has already been attributed to the sample containing only small 0 group fish. Through September and October the mean index rose gradually until by 26 November 1975 it was 2.96 $\pm$ 0.38, very close to that of the female. Again accumulation of lipid reserves must have been completed by this time as the mean index on 16 December 1975 was exactly the same. After this peak the mean index began to decrease, presumably as lipid reserves were utilised, and by 15 January it was 2.19 $\pm$ 0.29, close to that of the female and not significantly different from that recorded during early February the previous year. During 1976 the male hepatosomatic index was at its lowest during April and May, with means recorded of 1.84 $\pm$ 0.36 (26 April) and 1.74 $\pm$ 0.08 (26 May), significantly lower than the corresponding female mean indices. As in the previous year the mean increased during June to reach a peak in July and early August of around 3.00, close to and r significantly different from female mean indices at this time. By 15 September the mean hepatosomatic index had decreased insignific

to 2.47 $\pm$ 0.48. This sample was composed of only I+ fish unlike the sample on the 17 September 1975 which contained only 0 group, however, although the former mean index was higher it was not significantly so.

b) Fawley

Female cycle In 1975 during the period mid-June to mid-July the mean hepatosomatic index was 3.35 $\pm$ 0.82 not significantly different from Langstone female mean indices at that time. The mean decreased significantly, to 2.18 $\pm$ 0.30, during late July and early August but then remained constant through late August and September. During October the mean index began to increase again and, as it did in the Langstone fish, reached a peak during November (2.72 $\pm$ 0.36). Presumably at this time active lipid accumulation had ceased and a switch-over to utilisation of these reserves occurred as the mean index began to decrease reaching minimum values during January and February 1976 of 1.89 $\pm$ 0.28 and 1.89 $\pm$ 0.15 respectively, similar to those observed at Langstone. This was followed by a fairly rapid increase in mean index during March and April reaching a peak of 3.67 $\pm$ 0.50 during May 1976, significantly lower than was observed in Langstone females at this time. Subsequent samples showed a gradual decrease in the mean index until by August 1976 it was 2.42 $\pm$ 0.56. During the rest of 1976 the mean index remained constant with no sign of the November peak seen the previous year although there were no significant differences in actual mean values.

Male cycle In 1975 during the period mid-June to mid-July the mean hepatosomatic index was 2.07 $\pm$ 0.48, not significantly different from Langstone male indices at that time and, although substantially lower, not quite significantly lower than the Fawley female mean index. Unlike the latter the male mean index increased during late July and

early August to 2.79 $\pm$ 0.96, slightly higher than the female mean index. During the rest of 1975, there was no significant change in the mean index although the suggestion of a peak occurred in November. In early 1976, the mean index decreased gradually to 1.75 $\pm$ 0.23 in March. Over this period the mean indices were similar to those recorded for females and also to those of males and females in Langstone. After a brief insignificant rise during April the male mean index continued to decrease reaching its minimum mean value, during June, of 1.57 $\pm$ 0.24. During July, a large significant increase in the mean index, to 3.21 $\pm$ 0.44, took place, an occurrence already described during both 1975 and 1976 for Langstone male indices. Through August, the mean index decreased until by September it was 2.12 $\pm$ 0.48. It then remained fairly constant with only a slight increase, reaching 2.31 $\pm$ 0.26 in November. Finally, there was a decrease, to 1.82 $\pm$ 0.27, by December.

From these results it will be noted that mean hepatosomatic indices in *A. presbyter* varied between 1.52 and 4.94, a fluctuation of almost three and a half percent of the carcass weight which can be considered to have an insignificant effect on the mean ponderal index. However, once again the three and a half percent was only a mean percentage variation. The hepatosomatic index in individual fish ranged from 0.95 to 6.32, only just over five per cent variation. Therefore, even the effect of liver weight on individual ponderal indices is rarely significant particularly in male fish.

iii. Intestine weight

The intestine weight here refers to the weight of the whole

alimentary tract. It was followed as an intestinal-somatic index calculated as:

$$\text{Intestinal-somatic index} = \frac{\text{Intestine weight (g)} \times 100}{\text{Carcass weight (g)}}$$

Its use, not only enabled gross fluctuations in index and its subsequent effect on condition to be investigated, but in some cases it illustrated seasonal changes in feeding activity. The index was calculated separately for males and females and for age-groups 0, I and II+. The results are given in Appendix C.7 as means with 95% confidence limits and sample numbers. From the results it was apparent that there were no significant differences in this index with respect to sex and age, with only two exceptions both at Langstone; between II+ group males and females (17/23 April 1975) and between I group males and females (15 September 1976). Therefore, sexes and age groups were combined although sites were still considered separately. These results are given in Appendix C.11 and plotted in Figure 6.15.

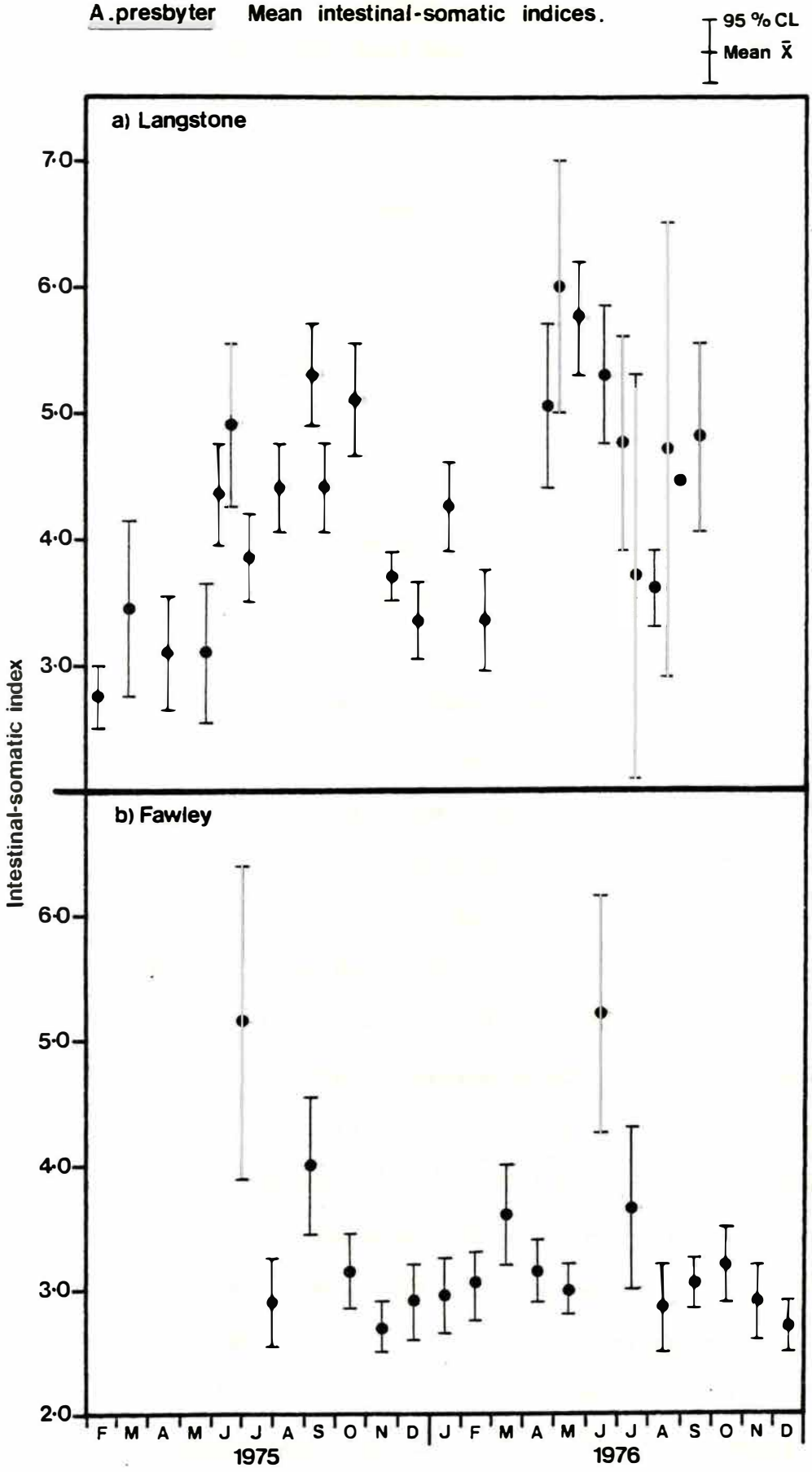
a) Langstone

Intestinal-somatic indices were very variable which gave rise to the large range of 95% confidence limits calculated. The sampling method at Langstone was not really suitable for monitoring seasonal fluctuations in feeding activity as it represented the situation at the precise time at which the fish were caught (always low tide) rather than the average level of feeding activity over a given period. However, certain seasonal trends were evident.

In 1975 and 1976 during January, February and March the intestinal-somatic index remained low, below 4.0 with the exception of 15 January 1976 (4.24 ± 0.35). In April and May 1975 the index

Figure 6.15.

A.presbyter Mean intestinal-somatic indices.



remained low but in April the mean index increased and generally remained over 4.0, with a few exceptions, throughout the summer and autumn up to and including October, after which it again fell below 4.0. Mean indices during the summer of 1976 were slightly higher than were recorded during 1975, although not significantly with the exception of the April and May indices. This was probably due to the high early summer water temperatures in 1976 resulting in an increased rate of metabolism and leading to an increased food supply.

b) Fawley

The sampling method at Fawley enabled an average monthly index to be calculated and, therefore, gave a better idea of seasonal fluctuations in feeding activity. As such, Fawley samples are not directly comparable with those from Langstone.

In 1975, during the period mid-June to mid-July 1975, the mean index was high, 5.17 ± 1.25. For some reason the mean index fell significantly, to 2.82 ± 0.33 from mid-July to mid-August, a situation which was not repeated the following year. From mid-August to the end of September, the mean index was 3.98 ± 0.53 decreasing significantly, to 3.14 ± 0.29, by the October sample and reaching a minimum in November, of 2.69 ± 0.20. Over subsequent months the index remained fairly low although there was a gradual increase in the mean index which reached a peak in March 1976, of 3.59 ± 0.42, before decreasing again, to 3.01 ± 0.19, for the sample in May 1976. There was a highly significant rise in the index by the following month, to 5.19 ± 0.96, which suggests a sudden increase in feeding activity at this time. In July 1976, the mean index had fallen insignificantly, to 3.65 ± 0.65, with a further insignificant reduction, to 2.86 ± 0.37, recorded in August. The mean index then remained fairly constant with only a slight

suggestion of a peak in October, of 3.22 $\pm$ 0.31, before decreasing again, to 2.68 $\pm$ 0.21, by the sample for December 1976.

Thus, mean intestinal-somatic indices varied between 2.5 and 6.0 a fluctuation of only three and a half percent and therefore can be considered to have little effect on the mean ponderal index. However, this was only the mean percentage variation. The intestinal-somatic index in individual fish ranged from 1.5 to just over 10.0 giving an individual variation of nearly nine percent. Therefore, the effect of intestine weight on individual ponderal indices may be much more important.

iv. Gonad weight

This was followed as the gonadosomatic index, calculated as:

$$\text{Gonadosomatic index} = \frac{\text{Gonad weight (g)}}{\text{Carcass weight (g)}} \times 100$$

It was calculated separately for males and females and age-groups 0, I and II+ and the results are given in Appendix C.7 as means with 95% confidence limits and sample numbers. These results are analysed in detail in Section VII.

Mean gonadosomatic indices at Langstone and Fawley varied between zero and 18.16 a fluctuation of over eighteen percent of the carcass weight, the extent dependent on age and sex. Therefore, variation in mean gonad weight can be considered to have a significant effect on the mean ponderal index. However, once again this was only the mean percentage variation. The gonadosomatic index in individual fish varied from nil to almost thirty two percent of the carcass weight, and thus the effect of the gonad weight on the individual ponderal index may be even more important.

6.3.6. Summary

1. The growing season extended from March until October or November, inclusive. For I group fish maximum growth rates (as daily instantaneous growth rates) for body length (0.66%) and weight (2.05%) were recorded during July.

2. An analysis of annual growth showed that *A. presbyter* at Fawley had a mean length of 62.7mm (52.7mm at Langstone) and a mean weight of 2.4g (1.5g at Langstone) by their first winter. These increased to 98.6mm and 10.2g by their second; to 114.4mm and 16.6g by their third; and to 122.9mm and 20.4g by their fourth winter.

3. The length-weight relationship of *A. presbyter* was calculated as $W = 4.6718 \times 10^{-6} SL^{3.1924}$ with no significant difference ($P < 0.05$) between the sexes.

4. Condition was determined using the formula $K = W \times 10^{6}/SL^{3.2}$. It showed an annual cycle with *A. presbyter* at their peak condition during June, July and August and at their poorest condition during February and March. These were the times when mean monthly seawater temperatures were at their highest and lowest respectively.

5. Seasonal fluctuations in the wet weights of mesenteric lipid deposit, liver, intestine and gonad were followed by expressing each as a percentage of carcass weight.

6. Mesenteric lipid reserves were at their maximum during November and at their minimum during the period February to May inclusive. Seasonal variations in these reserves were considered to have a significant effect on both mean and individual condition.

7. There were important seasonal differences in the liver weight cycle.

In females the liver was at its minimum weight during January and February and at its maximum weight during May whilst in males it was at a minimum during April, May and June but at its maximum during July and August. However, these seasonal variations in weight were small and were considered to have an insignificant effect on both mean and individual condition.

8. The intestine weight showed no clear seasonal pattern but there was a tendency to be at a maximum from June to October inclusive. Although intestine weight was considered to have an insignificant effect on mean condition, its effect on individual condition may be important.

9. Gonad weight was considered in more detail in Section 7.3 where it was found to be at a maximum from April to June inclusive and at a minimum from July to October inclusive. It was considered to have a significant effect on both mean and individual condition.

10. From a comparison of 'wet' and 'dried' weights (Appendix C.1) it was concluded that for the mesenteric lipid, liver and gonad variations in 'wet' weight reflected changes in actual organic matter. However, for the intestine this was not necessarily the case as there seemed to be a variation in the amount of associated fluid.

6.4. *Atherina boyeri*

6.4.1. Growth in length and weight

Due to low sample numbers no analysis of seasonal growth in either of these parameters was possible. However, annual growth in body length and weight with respect to age could be calculated. As in *A. presbyter*, this was determined by combining length and weight data

from the months of December, January and February during all years sampled. Annual growth rate was also calculated as an instantaneous annual percentage growth rate (see Section 6.3.2).

A. Length

Table 6.2 records the distribution of body lengths found within a particular age-group during the year. It will be noted that the 0 group are poorly represented. This was probably due to the bias of the sampling technique against small fish. (A problem also experienced with 0 and early I group *A. presbyter* at Fawley).

The length data for each age-group at the end of each year is given in Appendix C.12.a and the mean, 95% confidence limits and range are plotted in Figure 6.16.a. Also given in Appendix C.12 are instantaneous annual percentage growth rates.

At the end of the growing season as 0 group fish the *A. boyeri* at Oldbury had a mean body length of 55.63 $\pm$ 4.73mm. This increased significantly, to 70.77 $\pm$ 2.24mm, by the end of the I group growing season, an instantaneous annual percentage growth rate of 24.07. During the following year as II group the mean body length increased to 80.25mm, an annual growth rate of 12.57. However, this was based on data from only four individuals, hence the lack of 95% confidence limits.

B. Weight

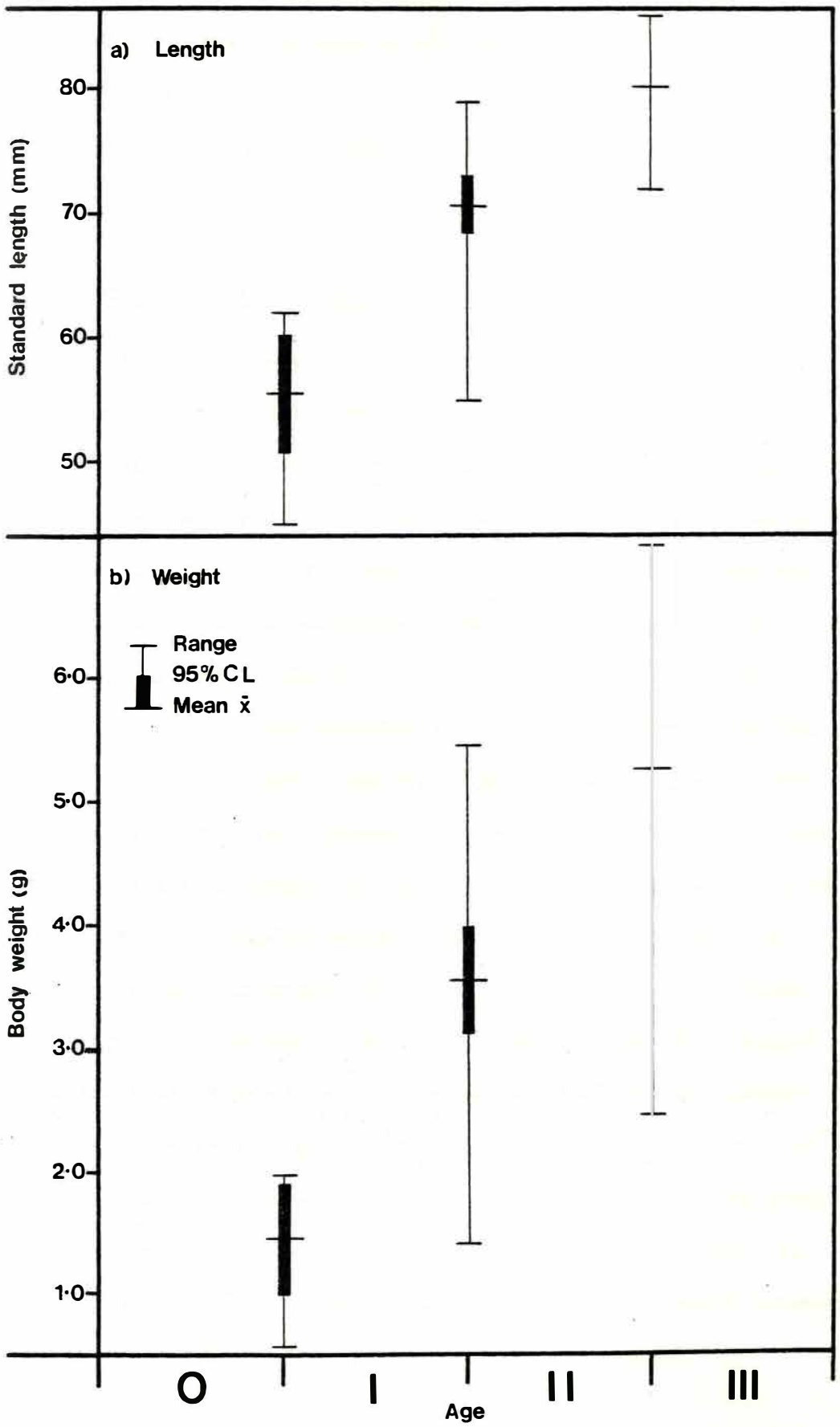
The weight data for each age-group at the end of each year is given in Appendix C.12.b and the mean, 95% confidence limits and range are plotted in Figure 6.16.b. Also given in Appendix C.12.b are instantaneous annual percentage growth rates. By their first winter the mean body weight of *A. boyeri* at Oldbury was 1.44 $\pm$ 0.47g. This increased significantly, to 3.56 $\pm$ 0.42g, by the end of the I group

Table 6.2. *A. boyeri* Distribution of body lengths found within each age-group, sexes, age-groups and years combined.

	Standard Length (mm)																				
	45–46	47–48	49–50	51–52	53–54	55–56	57–58	59–60	61–62	63–64	65–66	67–68	69–70	71–72	73–74	75–76	77–78	79–80	81–82	83–84	85–86
0					1		2														
I	1		1	1	1	1	3		2		2	1	2	4	1	1					
II						1	1				2	1	5	4	4	5	3	3	1		
III														2			1	1	1		2

Figure 6.16.

A.boyeri Annual growth with respect to age.



growing season, an instantaneous annual percentage growth rate of 90.51. Again only four individuals were captured during December, January and February as late II or early III group fish. These had a mean body weight of 5.25g, a growth rate during their year as II group fish of 38.85.

6.4.2. Length-weight relationship

The results of the regression analyses carried out of $\log_{10}$ standard length on $\log_{10}$ total body weight and $\log_{10}$ carcass weight are given in Table 6.3. Length and weight showed a highly significant correlation with one another ($P < 0.001$) and in all cases the slope or exponent b was greater than 3.0, which, as in *A. presbyter*, implied allometric growth. The relationship between standard length and total body weight is plotted in Figure 6.17. There was no significant difference ($P < 0.05$) in the exponent with respect to sex for either total body or carcass weight. However, female exponents were higher than the corresponding male exponents and may have proved significantly higher if only a larger sample had been available. Both exponents of female *A. boyeri* were significantly higher than the corresponding exponents of female *A. presbyter* at Langstone. Further differences would probably also have been evident if larger numbers of *A. boyeri* had been available for analysis. If sexes are combined the length-weight relationship of *A. boyeri* may be expressed as $W = 2.4866 \times 10^{-6} SL^{3.3603}$ for total wet body weight. Kohler (1976) recorded the length-weight relationship of *A. boyeri* in the Prevost lagoon, Montpellier, France as $W = 0.48 \times L^{3.2}$. However, this was the relationship between total weight and total length rather than standard length.

Table 6.3. *A. boyeri* Length-weight relationship of fish from Oldbury

Weight	Sex	N	Range S.L.mm	Range Weight g	$W = aL^b$ a	$W = aL^b$ b ± 95% C.L.	Correlation Coefficient r
Body	♂♂	30	50-81	1.10-5.61	4.0129×10^{-6}	3.1955 ± 0.5290	0.9192
	♀♀	30	45-86	0.57-7.05	9.6020×10^{-7}	3.5250 ± 0.3063	0.9756
Carcass	♂♂	30	50-81	0.98-5.26	3.1528×10^{-6}	3.2357 ± 0.5060	0.9270
	♀♀	30	45-86	0.54-6.29	9.6825×10^{-7}	3.4991 ± 0.3098	0.9747

Figure 6.17. *A. boyeri* Length-weight relationship (data from Appendix C.13.a.)

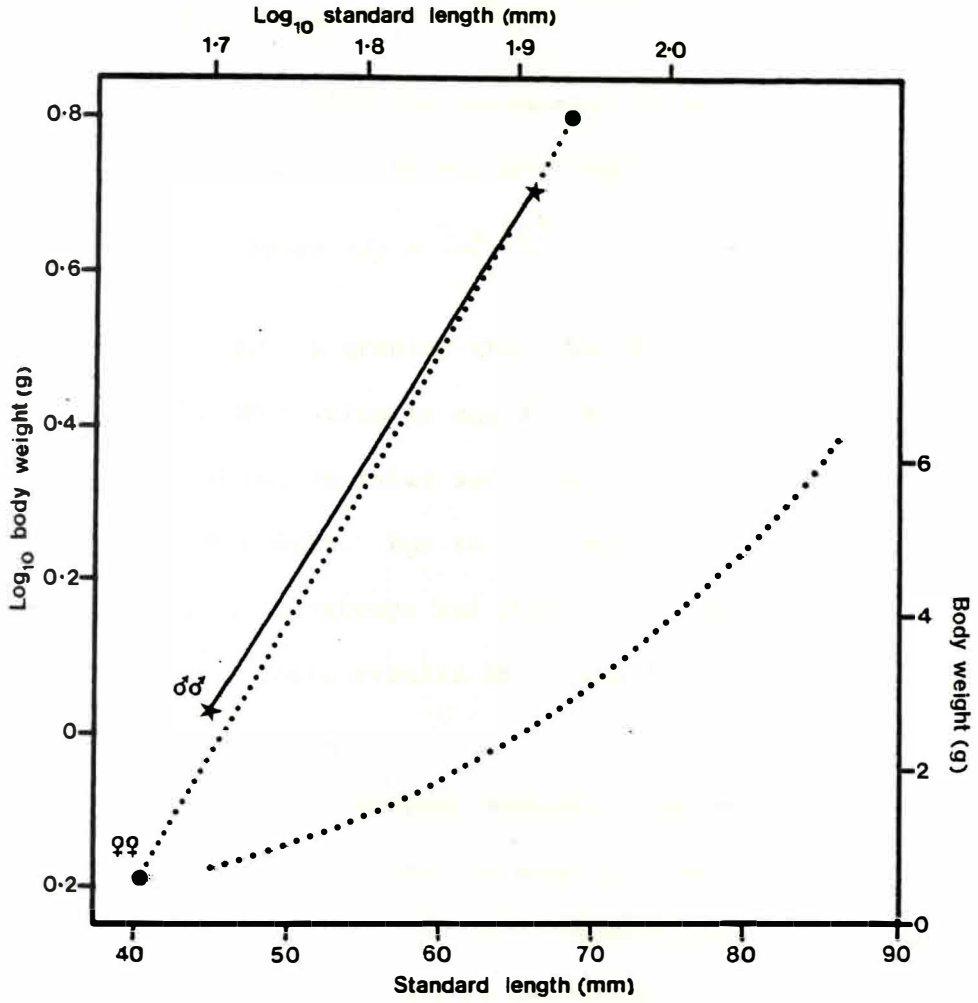
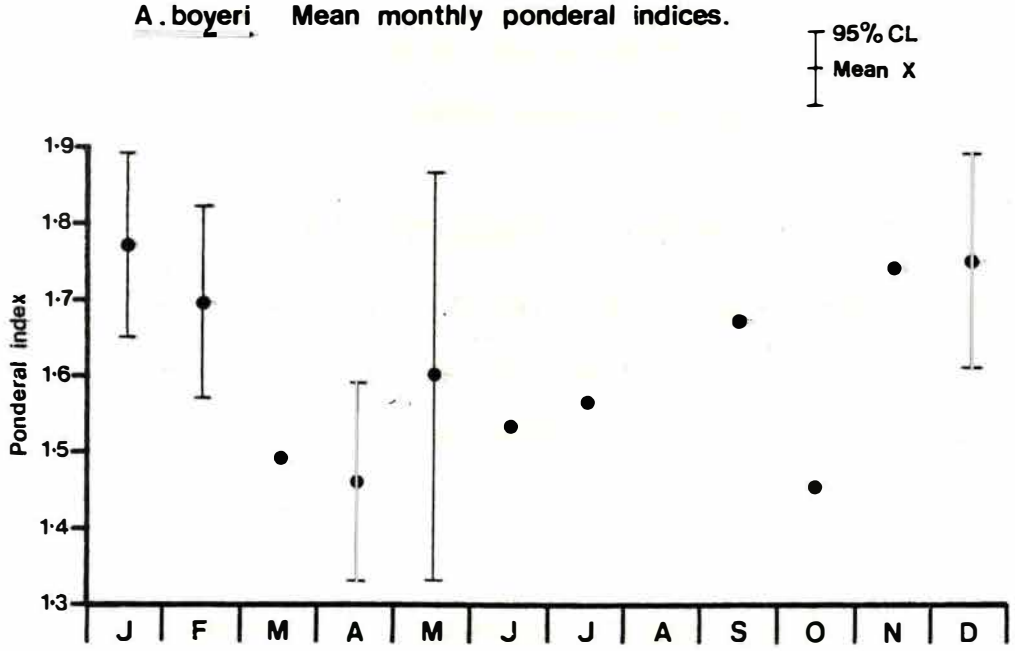


Figure 6.18. *A. boyeri* Mean monthly ponderal indices.



6.4.3. Ponderal index

In *A. boyeri* this was calculated from body weight (g) and standard length (mm) data using the formula:

$$\text{Ponderal index (K)} = \frac{W \times 10^6}{L^{3.4}}$$

The exponent of 3.4 is greater than that for *A. presbyter*, and was used as this was the mean value to one decimal place of the regression analyses carried out on males and females of $\log_{10}$ standard length on $\log_{10}$ total body weight. Due to low sample numbers the ponderal indices of sexes, age-groups and years were combined to give mean monthly indices. These results are given in Appendix C.13.b and plotted in Figure 6.18.

No clear seasonal pattern emerged from these results. However, the highest mean ponderal indices were recorded during December and January, 1.75 $\pm$ 0.14 and 1.77 $\pm$ 0.12 respectively. The mean index then decreased and during April was at its lowest (1.46 $\pm$ 0.13) before increasing again to 1.60 $\pm$ 0.26 in May. Few *A. boyeri* were impinged on the screens during the summer and autumn months, but those that were investigated showed a gradually increasing ponderal index.

6.4.4. Fluctuations in the weight of body cavity components

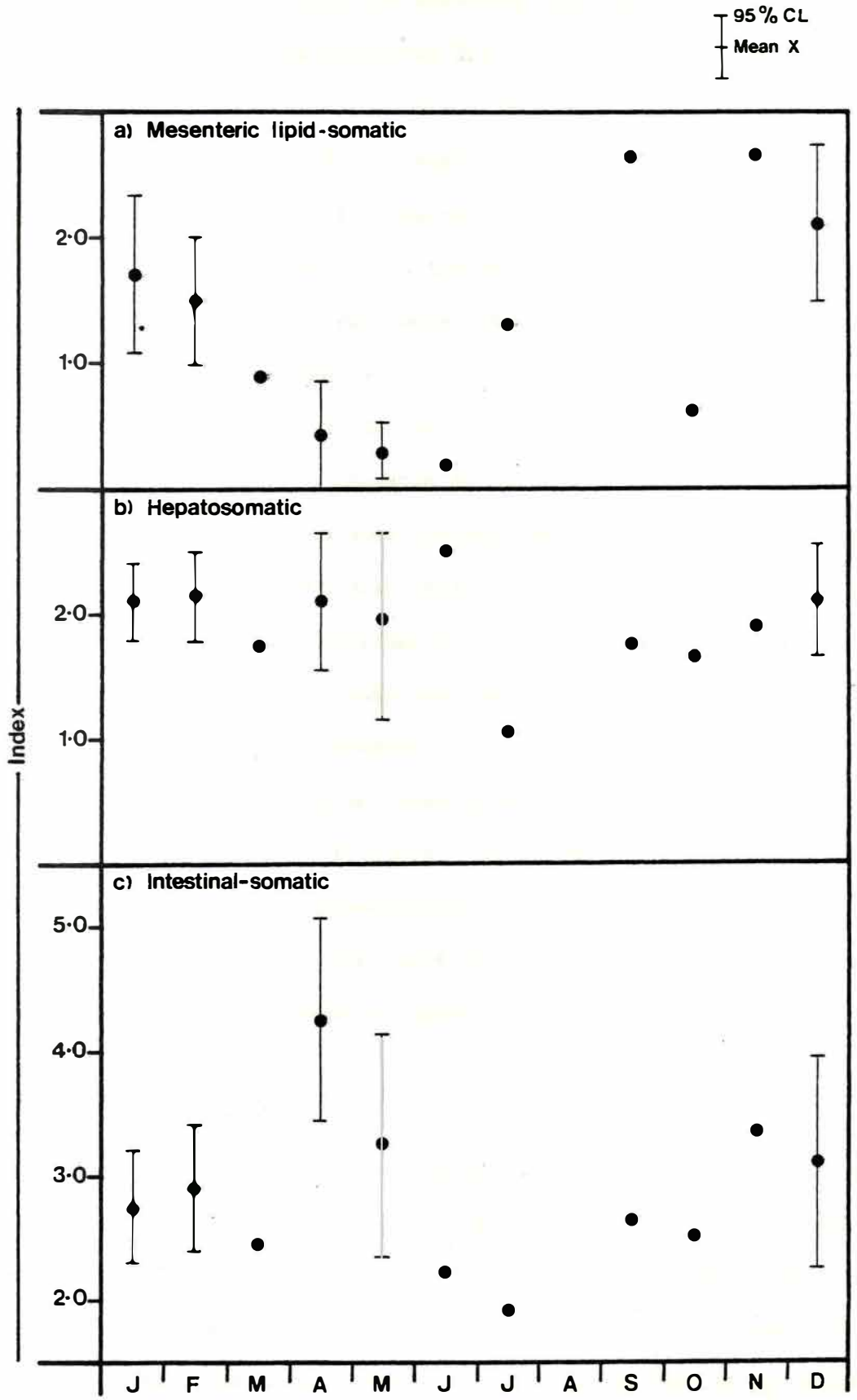
These were followed in the same way as already outlined for *A. presbyter*, however, due to low numbers, age-groups and years were combined to give monthly means with 95% confidence limits when numbers were sufficient (Appendix C.14). These are plotted in Figure 6.19.

i. Mesenteric lipid weight (Figure 6.19.a)

During January, the *A. boyeri* at Oldbury had a mean index of

Figure 6.19.

A.boyeri Mean monthly body component indices.



1.69 ± 0.62, not significantly different from the corresponding means of *A. presbyter* at both Langstone and Fawley. By February, the mean had decreased insignificantly to 1.51 ± 0.50. This decrease continued until May (0.31 ± 0.22) and probably into June (0.18, two fish). During July, mesenteric lipid accumulation apparently began again as the mean index increased. With the exception of October, all remaining indices in the year were over 2.0, however, only in December (2.09 ± 0.62) were enough fish retained to apply confidence limits.

Thus, the pattern of mesenteric lipid accumulation and utilisation in *A. boyeri* appeared to be very similar to that of *A. presbyter* with minimum mean indices recorded in late spring and early summer, and maximum mean indices in late autumn and early winter. However, the mean and individual variation in indices were less than recorded in *A. presbyter*, only two and a half and four and a half percent respectively. Therefore, the state of mesenteric lipid reserves in *A. boyeri* can be considered to have an insignificant effect on the ponderal index. Of course, the gut mesenteries are probably not the only site of lipid accumulation, the soma and liver may also be important sites. Hence, the state of total lipid reserves may well have an effect on the ponderal index.

ii. Liver weight (Figure 6.19.b)

Very little variation in the hepatosomatic index was recorded. For all months during which sufficient fish were retained to apply confidence limits the mean index was close to 2.0. In addition to the small mean variation, the individual variation was only just over three percent. Thus, variation in liver weight can be considered to have an insignificant effect on the ponderal index. Kohler (1976) followed a

hepatosomatic index for the *A. boyeri* in the Prevost Lagoon, Montpellier, France. However, the index used expressed the liver weight as a percentage of total body weight rather than a carcass weight. Females invariably had a higher mean index than males and like the *A. boyeri* at Oldbury the variation in the monthly mean index was small, about two and a half percent.

iii. Intestine weight (Figure 6.19.c)

During January the mean index was 2.77 ± 0.44 which increased insignificantly to 2.91 ± 0.50 during February. By April this had further increased to 4.25 ± 0.82, significantly with respect to the February mean. The mean index during May was slightly less (3.23 ± 0.90). Lowest mean indices were recorded during June and July. However, these were based on only two fish in each month. The only other month during which fish were retained in any numbers was December which had a mean index of 3.10 ± 0.84.

Variation in the mean intestinal-somatic index was again less than in *A. presbyter* only just under two and a half percent, as was the individual variation of four and a half percent. Thus, variations in the weight of the intestine can be considered to have an insignificant effect on the ponderal index. No observations on seasonal fluctuations in feeding activity were possible due to the low sample numbers.

iv. Gonad weight

The seasonal fluctuation in gonadosomatic index is considered in more detail in Section 7.5. As males and females were considered separately, numbers were insufficient to determine variation in the mean gonadosomatic index. However, individual variation in gonad weight

was almost thirteen percent in males and thirty six percent in females, as a percentage of carcass weight. Thus, the effect of the gonad weight on the individual ponderal index may be very significant.

6.4.5. Summary

1. Due to low sample numbers no analysis of seasonal growth was possible. However, an analysis of annual growth showed that *A. boyeri* at Oldbury had a mean length of 55.6mm and a mean weight of 1.4g by their first winter. These increased to 70.8mm and 3.6g by their second, and to 80.3mm and 5.3g by their third winter.

2. The length-weight relationship of *A. boyeri* was calculated as $W = 2.4866 \times 10^{-6} SL^{3.3603}$ with no significant difference ($P < 0.05$) between the sexes.

3. Condition was determined using the formula $K = W \times 10^{6}/SL^{3.4}$. It showed no clear seasonal cycle, although *A. boyeri* appeared to be at their peak condition during December and January and at their poorest condition during April.

4. Seasonal fluctuations in the wet weights of mesenteric lipid deposit, liver, intestine and gonad were followed by expressing each as a percentage of a carcass weight.

5. Mesenteric lipid reserves were highest from September to December inclusive and lowest from April to June inclusive. Seasonal variations in these reserves were considered to have an insignificant effect on both mean and individual condition.

6. Very little seasonal variation in liver weight was recorded and, as such, it was considered to have an insignificant effect on mean or individual condition.

7. The intestine weight showed no clear seasonal pattern although the highest weights were recorded in April and the lowest in June and July. It was considered to have an insignificant effect on both mean and individual condition.

8. Gonad weight was considered in more detail in Section 7.5 where it was found to be at a maximum from May to July inclusive and at a minimum from September to March. It was considered to have a considerable effect on individual condition.

SECTION VII

REPRODUCTION

7.1. Introduction

Nelson (1976) suggests that the Atherinidae comprises about 29 genera with about 156 species. The breeding habits of only 7 genera seem to be represented so far in the literature. Within these there appear several shared characteristics which can perhaps be applied to Atherinidae generally. The breeding season is during the spring or summer and is usually spread over several months with each female often spawning several times, occasionally with specific periodicity. The eggs are relatively large and demersal secured by attachment filaments (with the exception of those of *Leuresthes tenuis*). Clark (1925) grouped atherinid eggs into four categories depending upon the presence or absence, and on the form and number, of these filaments. Larvae hatch at an advanced stage, are planktonic and grow rapidly. Maturity is usually achieved within the first year.

The spawning season of *A. presbyter* has been described as falling within the period April to August (Yarrell 1836, Couch 1868, Day 1880-84, Fabre-Domergue and Béatrix 1897, Jenkins 1936, Duncker and Ladiges 1960, Ladiges and Vogt 1964, Schrieken 1964, Bracken and Kennedy 1967, Wheeler 1969, Muus and Dahlstrom 1974, Maitland 1977).

The spawning habits of *A. boyeri* at British localities have not been recorded, although breeding is known to have occurred at Queen's Dock, Swansea and may well also have been achieved at Cavendish Dock (Wheeler 1969). Breeding of the *A. boyeri* population at Oldbury has previously been reported (Palmer *et al* 1979).

Elsewhere in its range the spawning habits of *A. boyeri* have been observed and documented and gonad development described (Arru 1968).

The spawning season has been described variously within the period January to August (Marion 1891, Jorné-Safriel and Shaw 1966, El-Zarka 1968, Boscolo 1970, Kohler 1976, Maitland 1977). However, these references cover a large geographical area with large water temperature and salinity differences, at a particular locality the actual spawning period is more discrete. An interesting aspect of reproduction in *A. boyeri* is that spawning occurs in a wide range of salinities. Kiener and Spillmann (1969) discuss this point at some length and quote examples of breeding in salinities from 2°/oo to 42°/oo.

In order to determine the breeding season and to follow the sexual cycle in *A. presbyter* and *A. boyeri*, certain techniques have been employed which are frequently used in fisheries biology; sex ratio, gonadosomatic index, testis and oocyte maturation stages, oocyte size-frequency distribution and fecundity.

The gonadosomatic index normally involves expressing the gonad weight as a percentage of the total body weight (Le Cren 1951, Halliday 1969, Healey 1971, Kennedy and Fitzmaurice 1972, Reay 1972, Aceituno and Vanicek 1976, Mann 1976, Claridge and Gardner 1977, Badsha and Sainsbury 1978, Htun-Han 1978a, Wooton *et al* 1978) or body weight minus gonad weight (Gibson and Ezzi 1978). However, the gonad is not the only body component which undergoes seasonal variation. The liver, lipid content and gut weight are all known to vary. In an attempt to reduce these variables, the gonad weight has been expressed as a percentage of the gutted weight plus gonads (de Veen 1976) or simply the gutted weight (Hickling 1970, Jones 1974). The latter ratio has been used in this study. Unfortunately, this does preclude direct comparison with the gonadosomatic indices for *A. boyeri*, given by Kohler (1976), as here total body weight was used.

Hickling (1945, 1970) plotted actual gonad weights while Okera (1974) measured the length and width of gonads. Several authors describe various maturation stages in the gonads either in gross terms (Qasim 1957, Miller 1961, Otsu and Hansen 1962, Halliday 1969, Jones 1974) or by histological preparation (Matthews 1938, James 1946, Gokhale 1957, Bowers and Holliday 1961, Beaumariage 1973, Jones 1974, Htun-Han 1978b, 1978c).

Beaumariage (1973) and Mann (1976) plotted the seasonal changes in mean oocyte diameter. Such measurements may also be used to plot the oocyte size-frequency distribution of an ovary (Clark 1925, 1929, Miller 1961, Halliday 1969, Jones 1974, Fox 1978, Gibson and Ezzi 1978). This is a useful technique as it not only establishes the spawning period but indicates the mode of egg maturation and eventual release (Hickling and Rutenberg 1936). Thus it may be used to determine whether specific spawning periodicity exists.

Estimation of the number of eggs produced by a mature female within the spawning season is termed fecundity. Cushing (1975) considered fecundity to be a function of weight. Miller (1961) and Gibson and Ezzi (1978) demonstrated a relationship between fecundity and standard length, while Jones (1974) found fecundity to be proportional to the body weight and close to the cube of the length. Because of this fecundity values are often given as the number of eggs per gram weight of fish.

Holt (1899) described atherine ova as "of large size and furnished with long attachment filaments arising from all parts of the zona" in which "the yolk appears to be translucent and practically homogeneous" with "a number of small oil-globules". It is not at all clear whether he was referring specifically to *A. presbyter* or atherines in general.

The only other descriptions of *A. presbyter* ova refer to egg diameter and the presence of filaments by which the eggs are attached to marine algae, *Zostera* or other suitable substrates (Kennedy 1954, Miller 1962, Bracken and Kennedy 1967, Wheeler 1969). No account of the embryology or time to hatching appears to exist.

According to Russell (1976), the newly hatched postlarva had not been described. However, postlarvae at various lengths above 6.3mm have been described and figured in some detail (Holt 1899, Ehrenbaum 1905-9, Kennedy and Fitzmaurice 1969, Fives 1970, Russell 1976).

Postlarvae or juveniles have been recorded from various stations around the British Isles which would seem to indicate spawning in the close vicinity; at Penzance and Falmouth (Holt 1899); in brackish water lochs of North Uist in the Outer Hebrides (Nicol 1936); Castletown Bay, Isle of Man (Miller 1962); St. Helen's Harbour, Co. Wexford, Ireland (Kennedy and Fitzmaurice 1969); Kilkieran Bay, Ireland (Fives 1970). In addition, although not geographically part of the British Isles, a record for Guernsey, in the Channel Islands, is of interest as the present study includes collections of postlarvae from Jersey. Wheeler (1970) recorded postlarval *A. presbyter* from shore pools at Fort Saumarez and Fort Houmet.

From many of these references observations were made about the compact shoals in which the postlarvae occurred. Although the schooling behaviour of *A. presbyter* does not seem to have been investigated Jorné-Safriel and Shaw (1966) showed that in *A. boyeri* (as *A. mochon*) schooling developed gradually rather than immediately after hatching. A similar situation had already been demonstrated in *Menidia* (Shaw 1960, 1961).

No description of the egg or postlarvae of *A. boyeri* appears to

exist, although size at hatching and subsequent growth, over a four week period, has been reported for laboratory reared *A. boyeri* (Jorné-Safriel and Shaw 1966).

The conception of this study was to elucidate the breeding season and sexual cycle of *A. presbyter*, by the use of the techniques outlined above, and then, by stripping ripe spawning adults, to follow egg and postlarval development under laboratory conditions. Fortunately, the discovery of the *A. boyeri* population at Oldbury has enabled a useful comparison to be made between the species. However, the low numbers available, all of which have been preserved, has meant that only the sex ratio, gonadosomatic index and oocyte size-frequency distribution could be followed for this species.

7.2. Methods and materials

7.2.1. Sex Ratio

Ratios were calculated separately for age-groups 0, I and II+ for both Langstone and Fawley. These were then compared to the expected 1 : 1 ratio by means of the "chi-squared (χ^2) distribution and the construction of a two by two contingency table. For example:-

	♂♂	♀♀	Total
Observed	a	b	(a+b)
Expected	c	d	(c+d)
	a+c	b+d	N

then

$$\chi^2 = \frac{N\,(ad-bc)^2}{(a+b)\,(a+c)\,(b+d)\,(c+d)}$$

7.2.2. Gonadosomatic index

The gonad was removed, weighed to the nearest 0.0025g on a top-

pan analytical balance and this weight expressed as a percentage of the carcass weight (see also Section 6.2).

$$\text{Gonadosomatic index} = \frac{\text{Gonad Weight g} \times 100}{\text{Carcass Weight g}}$$

The sexes and age-groups (0, I, II+) were treated separately. Means ($\bar{x}$) were calculated and 95% CL applied if the sample numbered five or more individuals.

7.2.3. Oocyte size-frequency distribution

The whole ovary or a portion of it, depending on the size, was placed in Gilson's fluid (Bagenal 1968) to facilitate the separation of oocytes. Oocyte diameter was measured by means of an eye-piece micrometer in a binocular microscope at a magnification which gave a value of 0.7mm for each 1.0 micrometer unit (epu). Each diameter was determined by placing the micrometer in a horizontal position across the field of the microscope and then reading the diameter of the oocyte along whichever axis lay parallel with the micrometer. As the oocytes, due to distortion during preservation, were almost never spherical in shape, this method resulted in measurements of all axes between the longest and shortest diameter. However, Clark (1925) suggested that this had a negligible effect on the frequency curve obtained.

A minimum of 200 oocytes with a diameter greater than 0.2 epu (0.14mm) were measured in each fish investigated. At least three *A. presbyter* of age groups I and II+ were examined, when available, in each sample taken in 1976 from both Langstone and Fawley.

The numbers of *A. boyeri* available were never great, therefore, each female retained was examined in this context.

7.2.4. Fecundity per spawning

This was determined in twenty five *A. presbyter* of varying ages from Langstone and in two *A. boyeri* from Oldbury. Only fish containing a discrete group of ripe oocytes were examined.

The ovary was opened under Gilson's fluid and the ripe oocytes removed and counted. This value was also expressed as number per gram weight of fish. Both were then subjected to regression analysis against fish SL and weight.

7.2.5. Egg and postlarval development

After several earlier attempts artificial and natural fertilisation were both achieved in June 1978. Artificially fertilised ova failed to develop beyond the germinal disc stage.

The naturally shed and fertilised ova were obtained from I and II+ *A. presbyter* kept in tanks (61 x 61 x 29cm) supplied with fresh running seawater. These were subsequently placed in petri dishes containing filtered seawater with added crystamycin and subjected to three differing temperature regimes $10^{\circ} \pm 1^{\circ}C$, $15^{\circ} \pm 1^{\circ}C$, and $20^{\circ}C \pm 1^{\circ}C$ and 16 hours of light and 8 hours of darkness. The water in the dishes was changed every 48 hours.

Even with the added crystamycin, algal and fungal growths thrived on the surface of the developing egg and amongst the attachment filaments. Although this did not seem to affect the embryo development it made observation and photography difficult. However, by a fortunate accident it was discovered that small mysids would graze the ovum surface, remove the attachment filaments and epizoic growth, and hence make observation of embryo development possible, without apparently affecting the embryo.

The description of larval development was based on specimens obtained by dipnet from Langstone Harbour in June, July and August 1978. Measurements refer to the total length of specimens immobilised in cooled seawater, this made drawing of the specimens possible without the shrinkage caused by death, anaesthetics and preservatives.

7.3. *Atherina presbyter* - Spawning and sexual cycle

7.3.1. Sex ratio (Table 7.1)

Initially males predominate as 0 group fish although not significantly ($P < 0.05$). However, by the time the fish become II+ females predominate, significantly so in Langstone Harbour ($P < 0.05$).

Such a trend is not unusual in fish, in many species the longevity of males is less than in females (Woodhead in press). Gibson and Ezzi (1978) demonstrated an increasing female to male ratio with age in a Scottish population of *Lesueurigobius friesii* (Malm). The reasons for this are not always clear although reproductive stress is often implicated.

Table 7.1. *A. presbyter*. Sex ratio with respect to age.

	Langstone			Fawley		
	0	I	II+	0	I	II+
N	289:281	241:229	38:103	160:143	137:151	88:113
♂ ♀ ratio	1:0.97	1:0.95	1:2.71	1:0.89	1:1.10	1:1.28
χ^2	0.0056	0.1532	15.8229	0.7227	0.5216	2.9359

For the ratio of males:females to be significantly different from 1:1 at $P < 0.05$ and 1 degree of freedom χ^2 must exceed 3.84.

7.3.2. Testis cycle

A. Testis-somatic index (Appendix C.7)

a) Langstone Harbour (Fig. 7.1)

0 group. During 1975 these fish first entered the seine-net catches in September. The testis was recognisable at this time as a small thin transparent tube, with a zero testis-somatic index. It remained as such until the November sample (0.08 ± 0.03). The index again dropped to zero in the December sample although this probably resulted from the corresponding drop in average fish size of this sample (see Section 6.3.1).

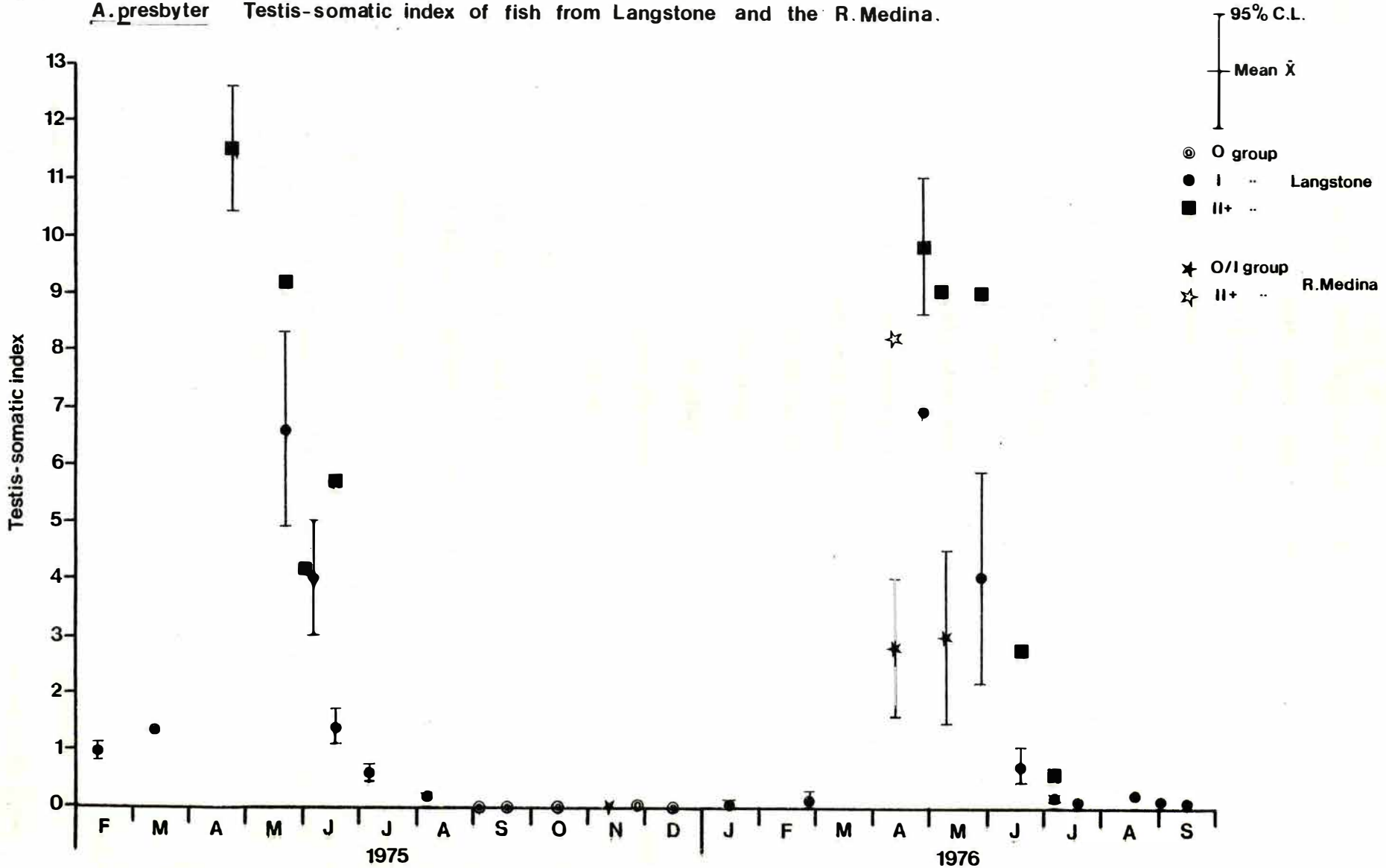
I group. From January onwards the index began to rise. However, the February index during 1975 (0.95 ± 0.17) was significantly higher than that found in 1976 (0.16 ± 0.18). This may be due to the warmer winter water temperatures experienced in Langstone Harbour in 1975 compared with 1976 (Table 2.2).

I group males for some reason are rarely encountered until the end of May or early June. In 1975 an average index of 1.29 was noted for four fish in mid-March. During 1976 three fish caught at the end of April had an average index of 6.97 whilst in early May the average for two fish was 5.92.

The average index by the end of May was 6.63 ± 1.72 in 1975 and 4.05 ± 1.82 in 1976; overlap of the 95% CL indicates that these two values were not significantly different. However, it may be that the warmer spring water temperature experienced in 1976 (Table 2.2) initiated earlier spawning. Thereafter, the index fell fairly rapidly, although more so in 1976 than in 1975, until the spent condition was reached in July. The index recorded on 7 July 1975 was significantly higher than that recorded on 5 July 1976. This supports the assumption that the

Figure 7.1.

A. presbyter Testis-somatic index of fish from Langstone and the R. Medina.



spawning of I group males both started and finished later in 1975 compared with 1976. Once the spent condition was reached the average index then remained below 0.3 until the age-group disappeared from the seine-net catches in September.

At no time during late-April and May were low insignificant male indices found. This suggests that all males reached maturity in their first year regardless of size. The greatest testis-somatic index found in 1975 was 9.09 and in 1976 was 11.39. A spawning period of late-April, through May, June and possibly into early July was inferred.

II+ group. These only occurred in the seine-net catches from late-April to early July and were never abundant. In late-April the average indices were 11.53 $\pm$ 1.09 in 1975 and 9.89 $\pm$ 1.23 in 1976. From this time the index appeared to drop steadily although this is an interpretation based on very low sample numbers. This continued until the fish either disappeared from the catches, as happened in 1975, or the spent condition was reached (0.59 on 5 July 1976).

Although comparatively few II+ males seem to be present in Langstone Harbour the evidence suggests that they do participate in spawning and over a similar period to I group males. Again there was a suggestion that spawning was initiated earlier and finished earlier in 1976 compared with 1975.

The highest testis-somatic index found in 1975 was 12.77 whilst in 1976 it was 12.56, only slightly higher than was observed in I group males.

b) River Medina (Fig. 7.1)

0 group. The fish taken in the one sample on 12 November 1975 had the same small thin transparent testis with zero index as fish from

Langstone.

I group. Only two samples were captured, on the 12 April 1976 and 10 May 1976. These had mean testis-somatic indices of 2.78 $\pm$ 1.17 and 3.04 $\pm$ 1.50 respectively. Although lower than the Langstone male I group indices at this time they are not significantly so if 95% CL are applied to the small sample means of the Langstone indices. Again the inference is that all males mature within their first year.

II+ group. Only four fish were captured all on the 12 April 1976. The testis-somatic index averaged 8.24 which was greater than the I group males caught on the same date and comparable with Langstone males captured later in the month.

c) Fawley (Fig. 7.2)

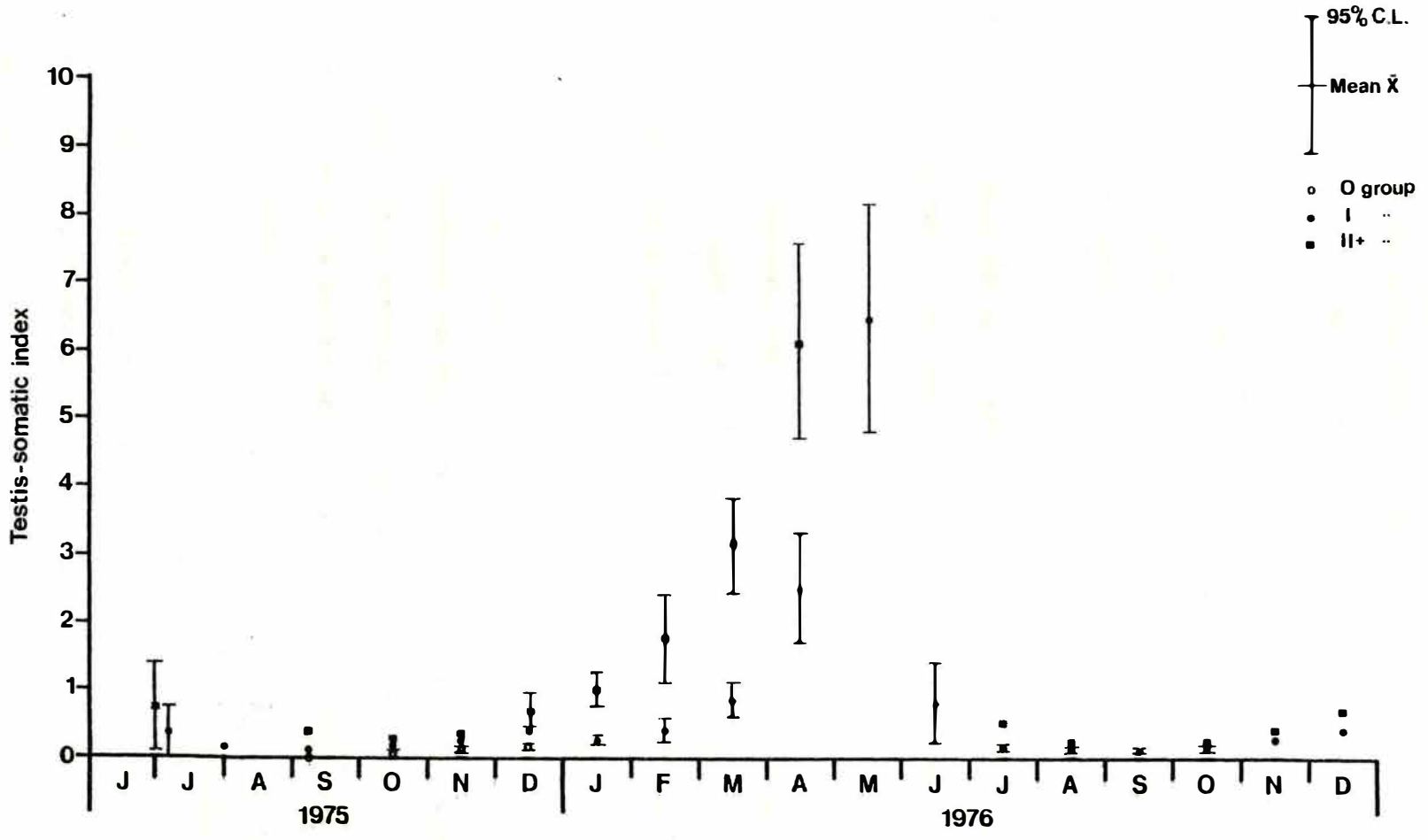
0 group. In 1975 these were retained from mid-August onwards at which time they had a zero testis-somatic index. However, this gradually increased through the autumn until a mean index of 0.13 $\pm$ 0.06 was reached by December.

I group. The index continued to increase through the winter and spring until a mean peak of 6.51 $\pm$ 1.69 was reached in May 1976. This peak had a similar peak to that already observed for Langstone fish. The maximum index found, 10.23, was also similar. From May the index then fell rapidly through June until the spent condition was reached in July 1976. The index remained at this low level (< 0.20) until it began to rise again in November. Again the evidence suggests that spawning continued a little later in 1976 compared with 1976 and that all males reach maturity within their first year.

II+ group. In January 1976 this group had a mean testis-somatic index of 1.01 $\pm$ 0.24. This index gradually increased to 6.12 $\pm$ 1.42 by

Figure 7.2.

A. presbyter Testis-somatic index of fish from Fawley.



April 1976. Throughout this period the index was significantly higher than for I group fish captured at the same time. The peak index was probably not represented as the males were then absent from the sample until July 1976 when a spent fish was retained. However, five fish were retained in the period mid-June to mid-July 1975 and these had a mean index of 0.75 $\pm$ 0.65 and evidently were in the final stages of spawning.

During both 1975 and 1976 the testis-somatic index remained at a low level through the autumn until, like the I group, it began to rise again during November.

Thus, Fawley II+ males do participate in spawning but as in Langstone Harbour, they appear to be fewer in number than I group males.

d) Lowestoft

One male only was examined, caught on 23 August 1977, it was a II group fish with a testis-somatic index of 0.39. This is slightly higher than has been observed at other localities for this time of the year.

B. Testis development classification

The testis of *A. presbyter* and has been described as an off-white, lobed organ (Couch 1868). This arbitrary classification attempts to equate observations on the gross morphology of the testis with testis-somatic index values as follows:-

Stage		Testis-somatic index
I	Immature. Testis is small, transparent and thread-like not lobed; observed only in 0 group males; length up to $\frac{1}{4}$ of the body cavity (b.c.).	< 0.05

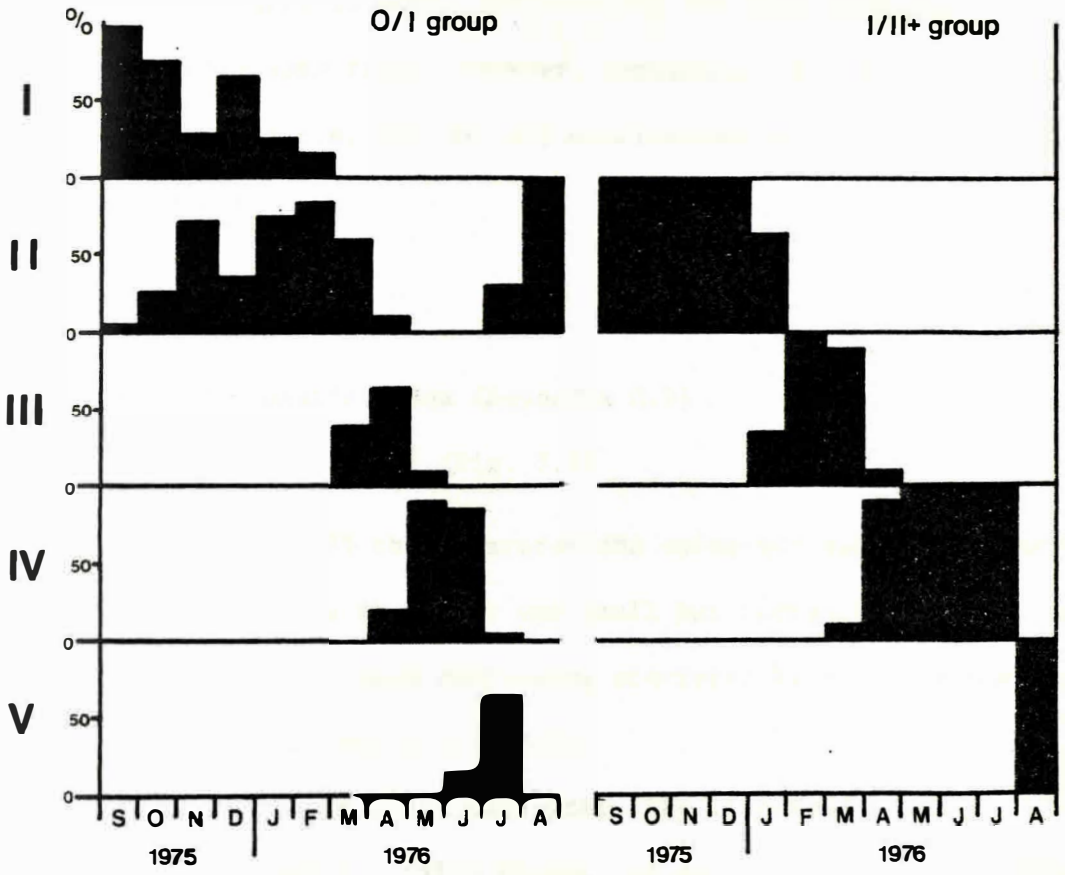
Stage		Testis-somatic index
II	Maturing virgin and recovering spent. Testis is opaque and off-white; wall becoming lobed; length 1/4 to 1/3 b.c., ducts not evident as a contrasting white.	0.05 - 1.00
III	Ripening. Testis remains opaque and off-white although lobes more evident; length 1/3 to ½ b.c., later stages difficult to distinguish from IV.	1.00 - 4.00
IV	Ripe. Milt extruded under slight pressure; still opaque and off-white but ducts containing milt of a contrasting white; length more than ½ b.c. initially but reduced dramatically over spawning period.	> 0.30
V	Spent. Testis pink due to vascularization; ducts a contrasting white which distinguishes from Stage II; length less than ¼ b.c.	0.05 - 0.30

The seasonal occurrence of these developmental stages from September 1975 - September 1976 for Langstone and Fawley males combined are given in Fig. 7.3, for the 0/I group and I/II+ groups separately. These are derived from the data given in Appendix D.1.

From the results presented it is apparent that II+ males were ripe earlier and carried on spawning slightly later than I group males during 1976. I group males were ripe from April to July 1976 although only a small percentage was ripe in April and July. The first ripe II+ males were found at the end of March 1976, although these comprised

Figure 7.3.

A.presbyter Seasonal occurrence of testis developmental stages, Langstone and Fawley data combined.



only ten percent of the fish in the month as a whole. Ninety percent of the II+ males examined in April 1976 and all the fish examined in May, June and July 1976 were ripe. However, throughout this period II+ males were particularly scarce, and so, any conclusions are based on extremely low sample numbers.

7.3.3. Ovary cycle

A. Ovary-somatic index (Appendix C.7)

a) Langstone Harbour (Fig. 7.4)

0 group. In 1975 these entered the seine-net samples in early September. At this time the ovary was small but recognisable as a sac with a transparent peritoneum containing scattered black melanophores. The ovary-somatic index was 0.11 ± 0.05.

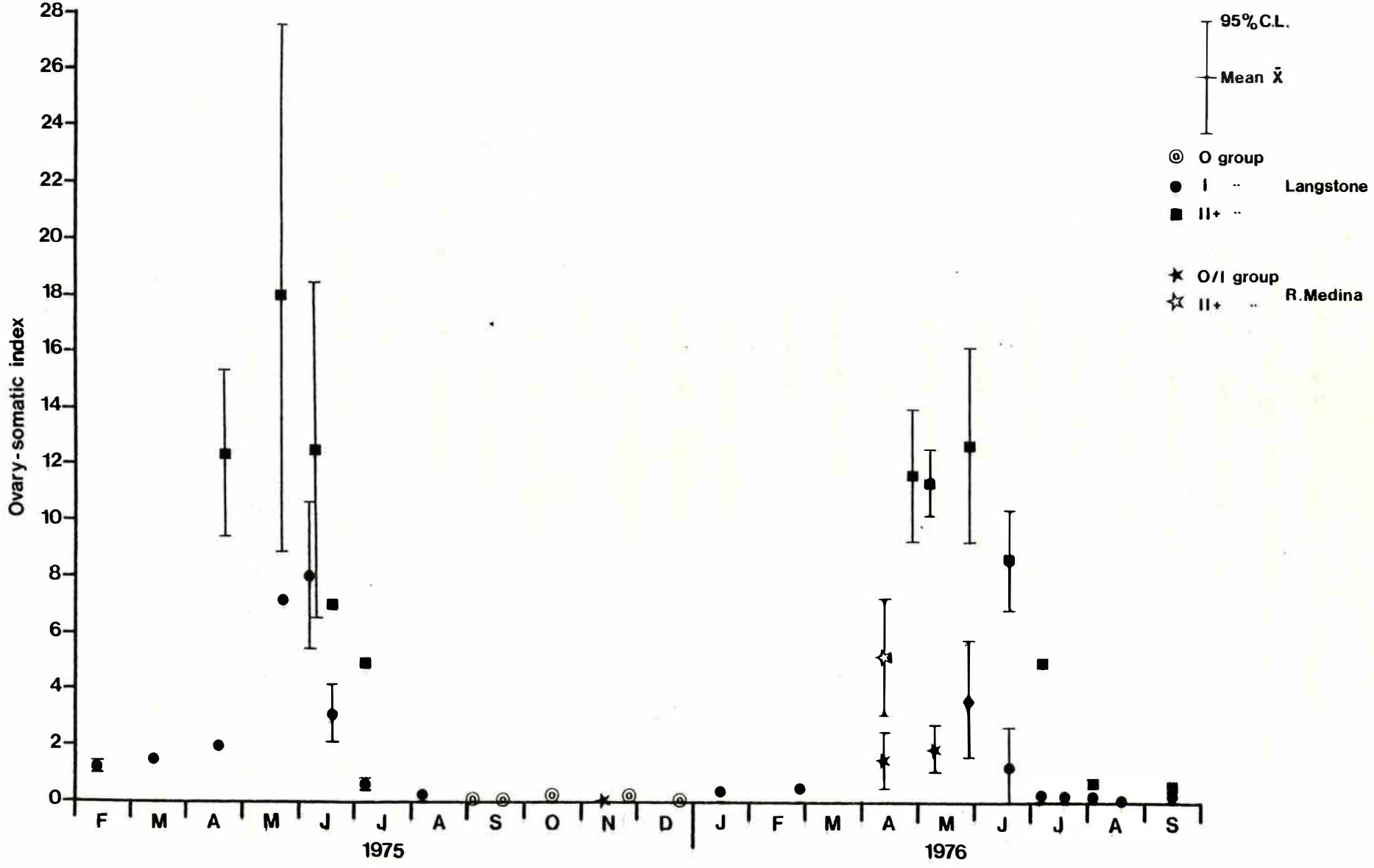
During the autumn this index gradually increased and the peritoneum darkened until totally black. An exception was the December sample when a drop in the index was noted. This was also noted for males at this time and has already been ascribed to the corresponding drop in the average fish size of this sample.

I group. In January 1976 a mean index of 0.38 ± 0.09 was noted and by late February this had risen to 0.51. However, in February 1975 a mean index of 1.20 ± 0.19 had been found. A similar rise for 1975 compared with 1976 has already been described in males and attributed to the warmer winter water temperatures experienced in 1974/75.

In 1976 I group females were absent from the samples from late February to late May. However, in 1975 fish were present in these months although low in number. These showed a steady increase until a peak of 8.00 ± 2.58 was found in early June, followed by a rapid fall to the spent condition in July.

Figure 7.4.

A. presbyter Ovary-somatic index of fish from Langstone and the R. Medina.



By late May 1976 spawning was obviously well advanced and the mean index was already lower than had been observed in early June 1975, although not significantly so. Sample means noted for the second week of June in both years were not significantly different although in 1976 some fish were already in the spent condition. A similar situation was observed in both years for I group Langstone males and supports the view that spawning started and finished earlier in 1976 compared with 1975.

In 1976 the low ovary-somatic index, indicative of the spent condition, remained until the fish became absent from the samples in the autumn.

The maximum index observed was 23.11 on 6 June 1975, twice any male I group maximum index observed.

II+ group. As with the males, captures were mainly restricted to late April to July, although two fish were caught later in the year, one in early August and the other in mid-September 1976, both had low indices (0.71 and 0.49 respectively).

In late April when the fish first entered catches the ovaries were already well advanced with mean indices of 12.28 ± 3.05 and 11.73 ± 2.39 for 1975 and 1976 respectively. These continued to rise until peaks of 18.16 ± 9.39 and 12.84 ± 3.46 were reached respectively. Maximum indices were also observed at this time of 31.29 in 1975 and 24.19 in 1976.

The index reduced more gradually than was observed for males and I group females, and was still close to 5.0 in early July during both years. This suggests that II+ females are normally capable of spawning well into July.

b) River Medina (Fig. 7.4)

0 group. The fish taken in the one sample on 12 November 1975 had an ovary-somatic index of 0.16 $\pm$ 0.10 not significantly different from Langstone 0 group females at this time.

I group. Only two samples were captured, 12 April 1976 and 10 May 1976. These had mean indices of 1.54 $\pm$ 1.03 and 1.94 $\pm$ 0.76 respectively. This implies that the ovaries were still actively developing and the spawning condition had not yet been reached. These figures were lower than the corresponding I group male indices, although not significantly so.

II+ group. Only five fish were captured all on the 12 April 1976. These had a mean index of 5.18 $\pm$ 2.09, lower than the corresponding II+ males but significantly higher than I group females.

c) Fawley (Fig. 7.5)

0 group. In 1975 these were retained from mid-August onwards at which time they had an ovary-somatic index of 0.10 $\pm$ 0.07 and the ovaries had the same appearance as those from Langstone fish. The index gradually rose to 0.51 by December.

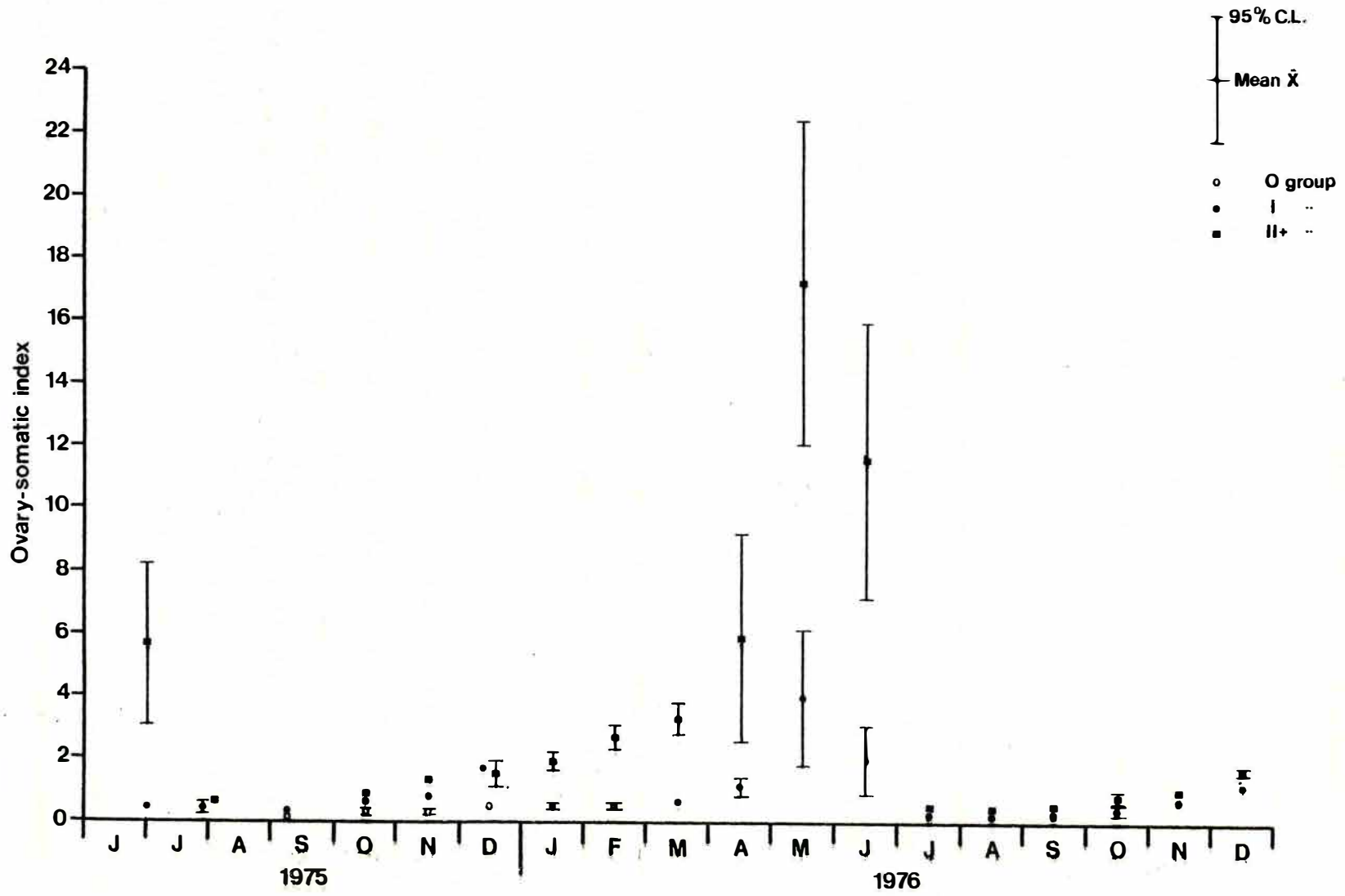
I group. By April 1976 the index had risen to 1.14 $\pm$ 0.27, significantly lower than males at this time. However, from this time development was more rapid and a mean peak of 4.03 $\pm$ 2.16 was reached in the following month, still lower than corresponding males, although not significantly so. The maximum index observed at this time was 8.57.

By July, in both 1975 and 1976, the spent condition had been reached and the index did not begin to rise again until October.

II+ group. In January 1976 the mean index was 1.88 $\pm$ 0.28,

Figure 7.5.

A.presbyter Ovary-somatic index of fish from Fawley.



significantly higher than the corresponding male mean index, and remained so until March (3.30 $\pm$ 0.48). Also at this time the mean index began to rise more rapidly through April (5.93 $\pm$ 3.32) reaching a peak in May (17.26 $\pm$ 5.19). The maximum ovary-somatic index, observed at this time, was 30.88, very close to the maximum II+ female index at Langstone (31.29) and over twice the maximum II+ male index observed (12.77, Langstone).

After May 1976 the index decreased through June (11.58 $\pm$ 4.43) to the spent condition in July. However, the latter observation was based on only one specimen. The 1975 data suggest that spawning extends into early July, a situation already demonstrated for Langstone in both 1975 and 1976.

d) Lowestoft

Five fish only were examined, three in late August and two in early September. These all had an ovary-somatic index of 1.00 or below.

B. Oocyte size-frequency distribution

The ovary of *A. presbyter* is unpaired and, when mature, is surrounded by a black peritoneum. This black colouration is caused by a thick layer of melanophores in the wall of the ovary (Denton and Nicol 1966). The external morphology of the ovary, unlike that of the testis, proved difficult to classify other than by size. However, oocytes could be classified into arbitrary stages of maturation as follows:-

Immature. Present as many tiny translucent cells of 0.4 epu (0.28mm) diameter or less, they become opaque and cream coloured as they increase in size. Oocytes of this type are found at all times even in spent, recovering spent and virgin ovaries.

Early ripening. Opaque and cream coloured oocytes, 0.4 epu (0.28mm) to 1.0 epu (0.7mm) in diameter.

Late ripening. The oocytes are now translucent and yellow; oil globules develop and filaments become apparent, although still tightly wrapped around the oocytes in a zig-zag pattern; 1.0 epu (0.7mm) to 1.5 epu (1.05mm) in diameter.

Ripe. The diameter of the ripe oocytes is 1.5 epu (1.05mm) to 2.6 epu (1.82mm). They are still translucent and yellow with a variable number of oil globules. At this stage, the oocytes burst from their follicles and become segregated in the lumen of the ovary. The distal ends of the filaments are freed and become entangled with those of other oocytes at this stage, holding the mature oocytes together in a mass.

It should be noted that measurements quoted here refer to oocyte diameters in Gilson's fluid and do not necessarily correspond with actual diameters. Indeed, the normal size range of ripe oocytes has been measured as 1.6 to 1.8mm (see 7.4.1).

The most mature oocyte size-freqency distribution in each sample examined, during 1976, has been plotted with respect to date. Age-groups I and II+ have been considered separately, as have Langstone and Fawley samples.

a) Langstone Harbour

I group (Fig. 7.6). In 1976 these were absent from the samples from late February until their reappearance in late May. The most mature fish investigated at this time had mean oocyte diameters of 0.84 epu (0.59mm) and contained ripe oocytes. All three fish examined from this date (26 May 1976) had varying oocyte size-frequency distributions.

Figures 7.6 to 7.9 inclusive

A. presbyter Selected oocyte size-frequency distributions. (Thickness denotes percentage frequency, each 1mm = 5%).

Figure 7.6.

I group fish from Langstone

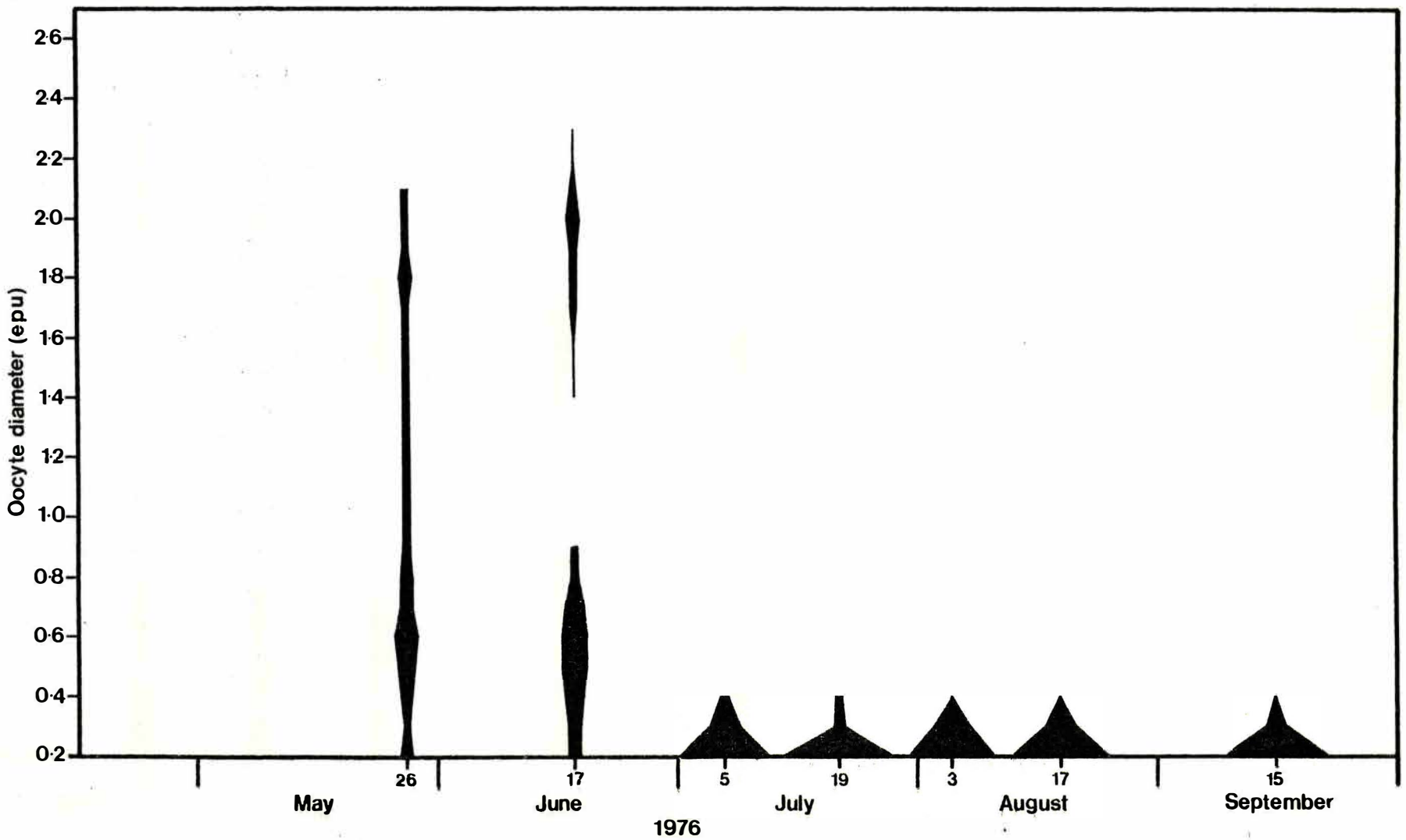


Figure 7.7.

II+ group fish from Langstone.

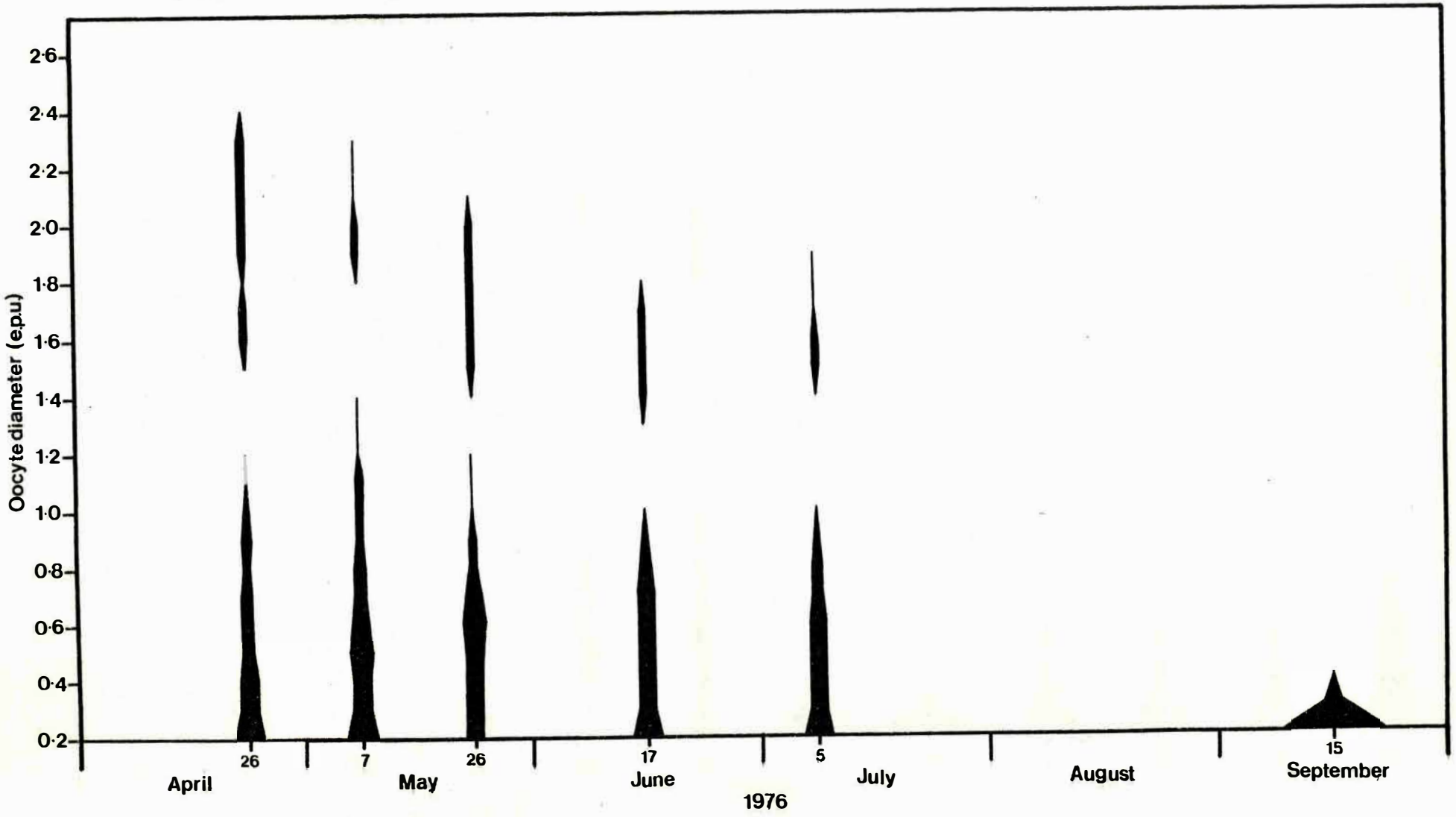


Figure 7.8.
I group fish from Fawley.

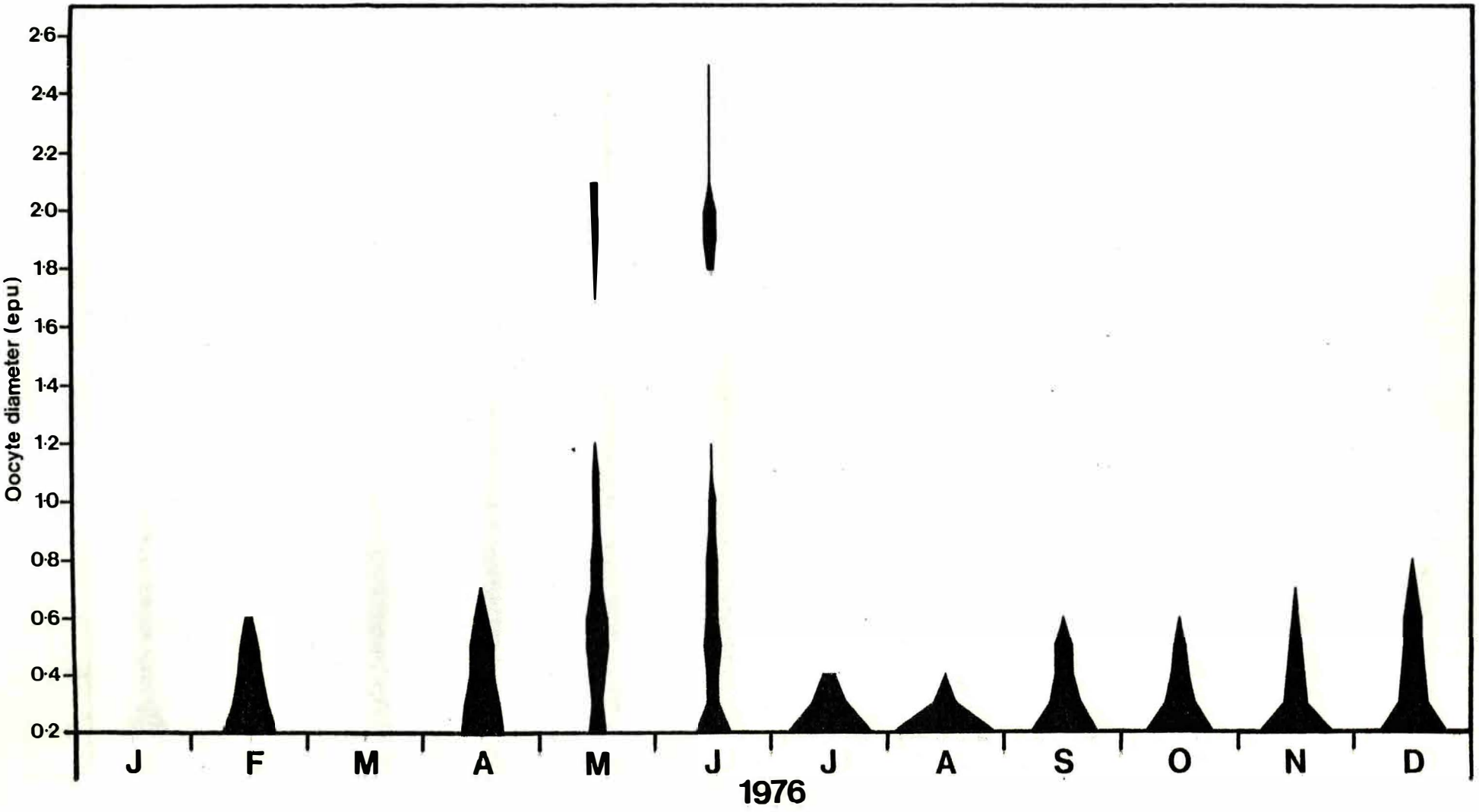
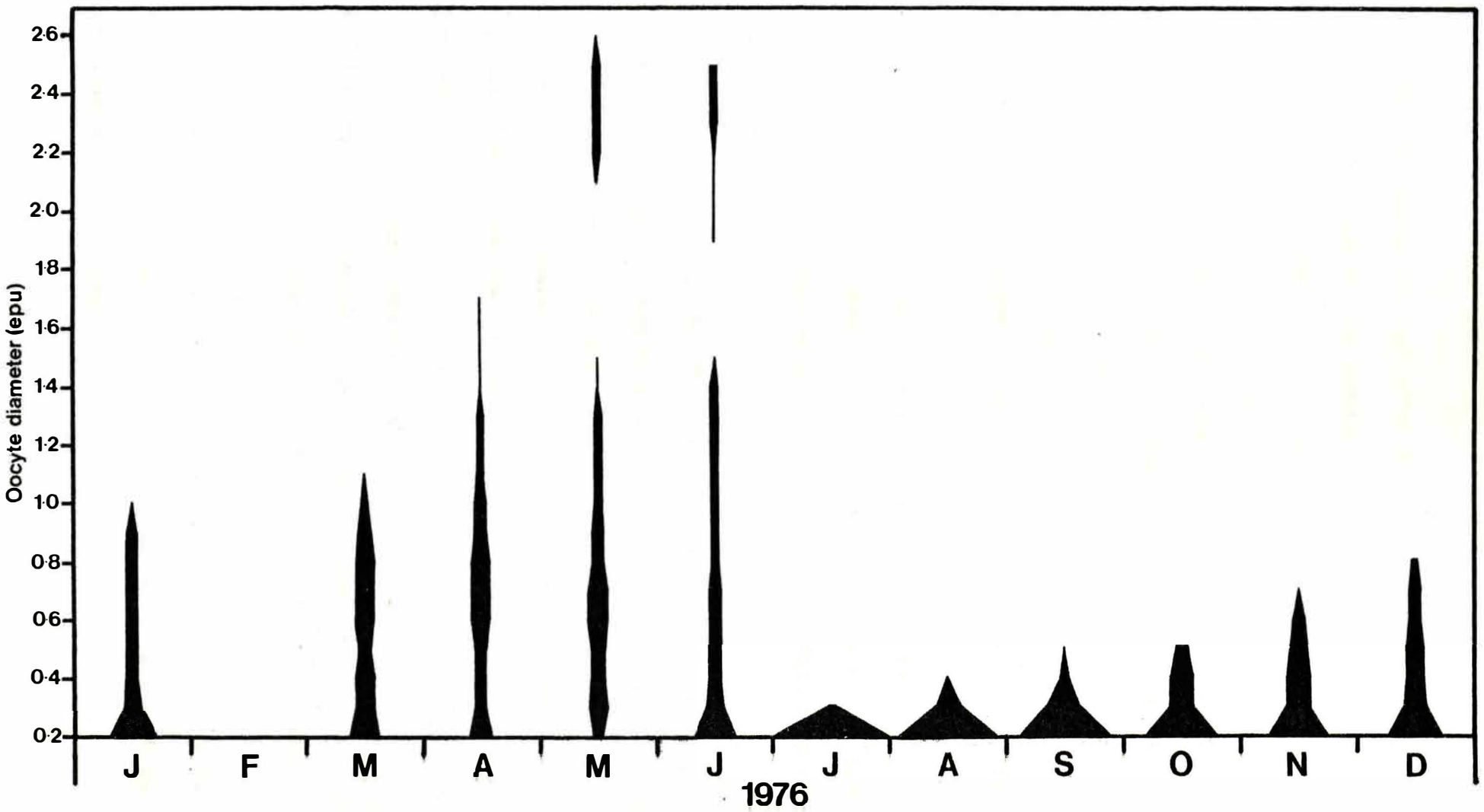


Figure 7.9.

II+ group fish from Fawley.



In the next sample (17 June 1976) the most mature female contained a discrete group of ripe oocytes ($\bar{x}$ = 1.92 epu or 1.34mm) and was presumably close to spawning. All fish examined on this date contained late ripening and ripe oocytes, although each fish was at a slightly different maturation stage. However, on average there tended to be fewer immature (up to 0.2 epu or 0.14mm diameter) oocytes present and these did not form a distinct peak as they had in the previous month. This suggests that the end of spawning was approaching and that differentiation of oocytes below 0.2 epu (0.14mm) had slowed or ceased altogether.

All fish captured in July 1976 were spent, containing only immature oocytes, 0.4 epu (0.28mm) in diameter or less. The oocyte size-frequency distribution remained as such until the I group fish left the harbour in mid-September.

II+ group (Fig. 7.7). In 1976 these were first captured in the harbour at the end of April. One of the five fish examined at this time (26 April 1976) contained a discrete group of ripe oocytes, and thus, appeared to be close to spawning. The others all contained immature, early and late ripening oocytes but each was at a slightly different maturation stage.

All four subsequent samples 7 and 26 May, 17 June and 5 July contained fish with ripe oocytes. Again it must be emphasised that within each sample fish did not have a uniform oocyte size-frequency distribution.

This group was not represented in the samples again until mid-September 1976. At this time only immature oocytes were present which had a mean diameter of 0.21 epu (0.15mm).

b) Fawley

I group (Fig. 7.8). During 1976 only fish in January and March were not examined. In February the mean oocyte diameter was 0.30 epu (0.21mm) and contained a few early ripening oocytes up to 0.6 epu (0.42mm). By April the mean had risen to 0.34 epu (0.24mm) and early ripening oocytes up to 0.7 epu (0.49mm) were present in the most mature female examined.

Variable distributions were found in May 1976. The most mature oocyte distribution contained a discrete group of ripe oocytes with a mean diameter of 1.97 epu (1.38mm). However, one individual with only immature and early maturing oocytes, comparable with April fish, was examined but this was probably a product of the extended collection technique.

Of the six fish examined in June half were spent but the other three contained late ripening or ripe oocytes. By July, however, all four fish examined were spent with mean oocyte diameters ranging from 0.20 epu (0.14mm) to 0.24 epu (0.17mm) and contained only immature oocytes. A similar distribution was found in August.

In September the mean oocyte diameter began to rise again and the ovaries contained a few early ripening oocytes up to 0.6 epu (0.42mm). This gradual development continued and by December the most mature individual had a mean oocyte diameter of 0.33 epu (0.25mm) and contained early ripening oocytes up to 0.8 epu (0.56mm).

II+ group (Fig. 7.9). During 1976 the only month in which this group was not available for examination was February. The most advanced fish in January contained immature and early ripening oocytes with a mean diameter of 0.43 epu (0.30mm). By March a few late ripening oocytes were also present and the mean oocyte diameter had increased to 0.51 epu

(0.36mm).

The most mature fish captured in April contained a few ripe oocytes but these had not yet become a discrete group. In May, however, four of the five fish examined did contain a discrete group of ripe oocytes and were therefore considered about to spawn. The two June fish examined had a similar distribution.

Only one II+ female was retained in July and this was in the spent condition containing only immature oocytes with a mean diameter of 0.20 epu (0.14mm). The one fish retained in August also contained only immature oocytes but in September early ripening oocytes once again became evident and the mean oocyte diameter had begun to increase. Development was seen to progress gradually through the autumn until a fish retained in December had a mean oocyte diameter of 0.36 epu (0.25mm) and contained early ripening oocytes up to 0.8 epu (0.56mm). This was very similar to the distribution already observed in I group Fawley females at this time of the year.

c) Seasonal cycle of the maturing oocyte

It is proposed here to describe the suggested mode of oocyte maturation with the aid of selected oocyte size-frequency distributions, from both Langstone and Fawley.

August-December

Virgin 0 group females contain only immature oocytes. The I and II+ groups, although initially containing only immature oocytes, gradually over this period produce an increasing percentage of early ripening oocytes (Figs. 7.8 and 7.9).

January-March

The 0 group, now I group females, start to produce early ripening

oocytes which gradually increase in size and importance (Fig. 7.8).

In the II+ group (also incorporating the I group of the previous period) the early ripening oocytes continue to increase in importance until by March the first late ripening oocytes are produced (Fig. 7.9). At this time a secondary peak in the oocyte size frequency distribution first becomes apparent at 0.7 epu (0.49mm).

April-August

In April I group fish still contain only immature and early ripening oocytes and it is not until May that a peak at 0.7 epu (0.49mm) develops, similar to that already observed in II+ ovaries by late March. Hereafter, I group ovaries show the same sequence of maturation as II+ ovaries, although over a more restricted time period.

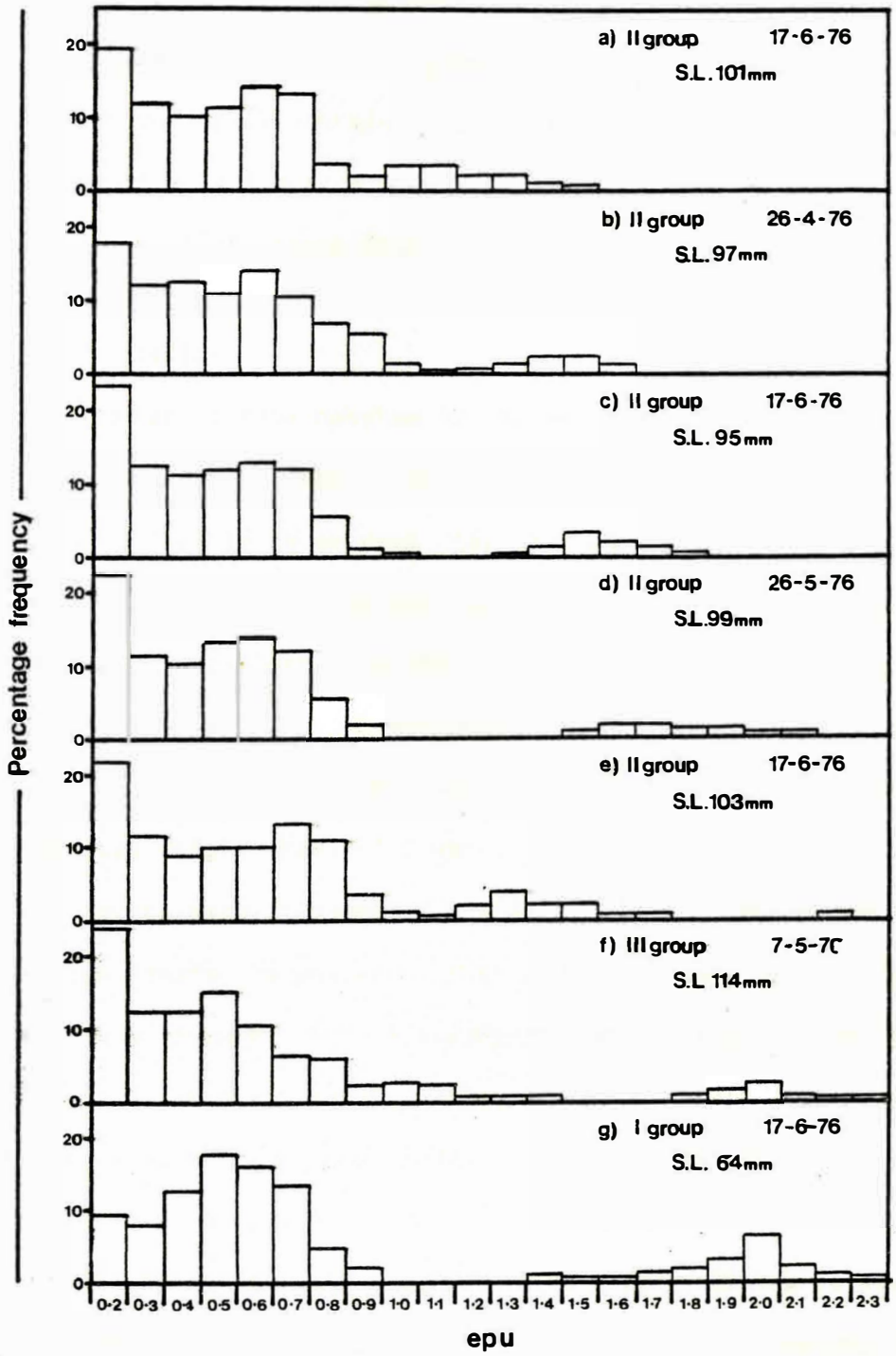
The peak at 0.7 epu is maintained whilst the late ripening oocytes increase in size and importance themselves forming the suggestion of a peak (Fig. 7.10). This peak is further emphasised as they gradually become ripe (Fig. 7.10.b). Eventually these late ripening and ripe oocytes become a discrete group (Fig. 7.10.c), and when all are ripe (Fig. 7.10.d), they are released from the lumen of the ovary. Occasionally the odd ripe oocyte is not released (Fig. 7.10.e) but whether this is resorbed or remains to be expelled with a subsequent egg release is not clear.

Whilst the ripe oocytes are still in the ovary the next batch of late ripening oocytes begins to differentiate (Fig. 7.10.f) and will form the basis of a subsequent egg release.

Throughout the early stages of spawning three peaks of oocyte size are normally evident; at diameters of 0.2 epu (0.14mm) and below, 0.5 to 0.7 epu (0.35 to 0.49mm), and more than 1.0 epu (> 0.70mm). However, as the spawning season reaches its close the peak at 0.2 epu

Figure 7.10.

A presbyter Selected oocyte size-frequency distributions of fish from Langstone.



(0.14mm) becomes reduced and finally disappears (Fig. 7.10.g). This is probably the result of the abandonment of differentiation in oocytes of less than 0.2 epu (0.14mm) in diameter and their subsequent maturation.

Spent individuals contain only immature oocytes up to 0.4 epu (0.28mm). No oocyte size-frequency distributions have been found to contain only immature and ripe oocytes. This suggests that once spawning ceases the ovaries still contain early ripening oocytes which are then resorbed leaving only immature oocytes. Indeed spent ovaries were found to contain substantial tissue debris in addition to the immature oocytes.

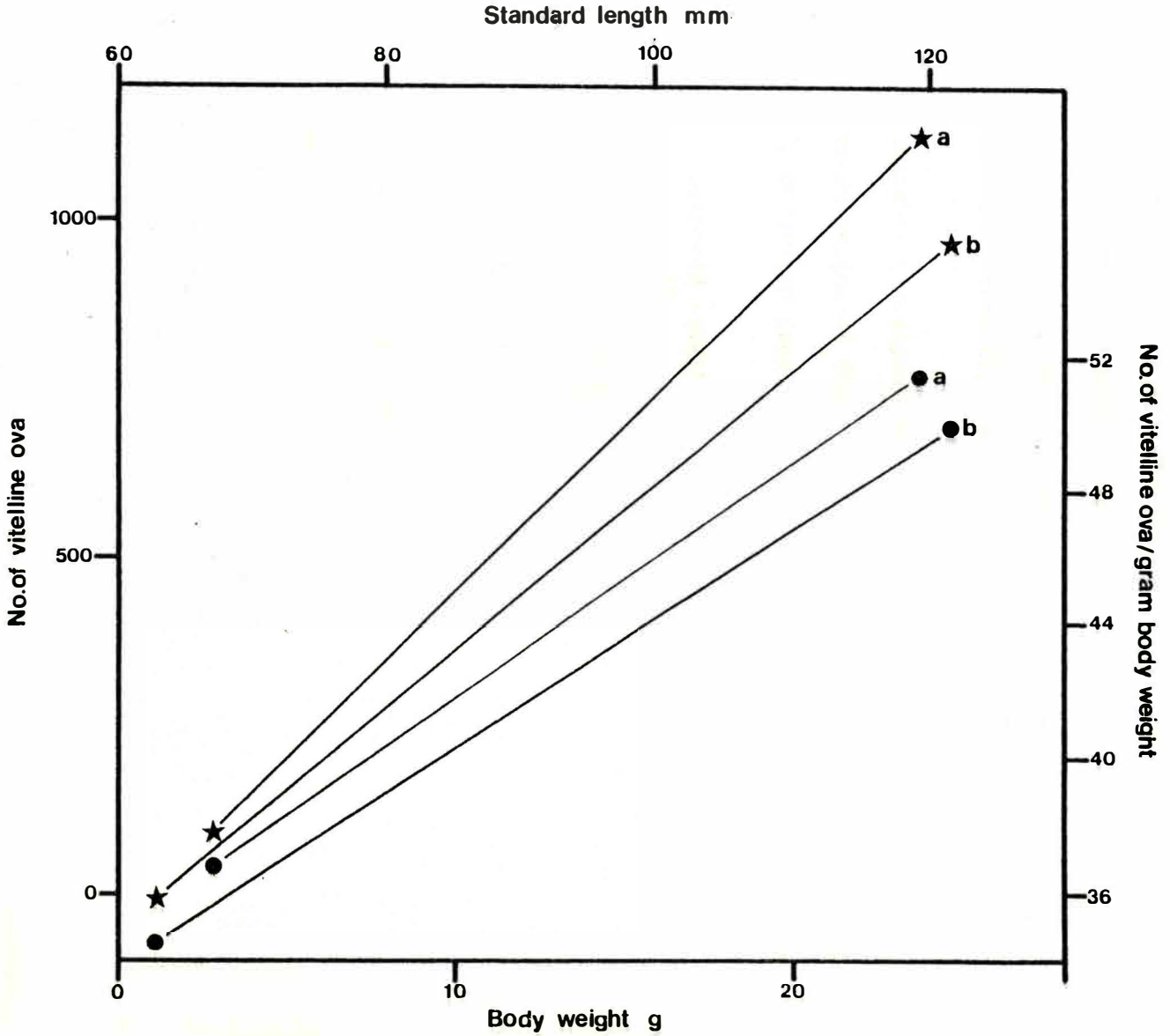
C. Fecundity

The number of ripe oocytes due to be released during a particular spawning act varies with size of the female. From the regression analyses (Table 7.2) it is evident that the number of ova produced is correlated very closely with SL and the weight of the fish. This relationship has been plotted in Fig. 7.11. The number of ova shed per gram weight of fish in *A. presbyter* ranged from 21.11/g to 57.08/g with a mean value of 43.75/g although this ratio too seems to be correlated with SL and fish weight (Table 7.2 and Fig. 7.11).

The oocyte size-frequency distribution investigation has shown that once ripe oocytes become a discrete group they are not supplemented in number by the ripening of less mature oocytes. Thus, because the number of ripe oocytes is closely correlated with SL and fish weight, the suggestion is that all the ripe oocytes are shed at one time and not gradually over a given period.

This investigation has determined the number of ova released at a particular spawning act but fecundity is often considered as the total number of eggs produced over the spawning period. The oocyte size-frequency distribution investigation has shown that at all times there

Figure 7.11. *A. presbyter* The relationship of fish weight (a) and length (b) to fecundity of a single spawning (★) and the number of vitelline ova / gram weight of fish (●).



were large numbers of oocytes present of less than 0.2 epu (0.14mm) in varying stages of development, even in spent ovaries. These appeared to be differentiated during the spawning season but to what extent could not be determined. Thus, the number of spawning acts undertaken by a female during the spawning season can only be determined by keeping each female separately under laboratory conditions. Unfortunately, this has not been achieved for a variety of reasons, although even if it had, findings would not necessarily correlate with the natural environment.

Table 7.2. Regression analyses of SL and fish weight on ova no. and no./g weight of fish for a single spawning release in *A. presbyter* (see Appendix D3).

	Standard length to		Total Fish weight to		r at
	No. ova	No/g of fish	No. ova	No/g of fish	$p < 0.05$
r	0.9623	0.5553	0.9726	0.5007	$\pm$ 0.381
slope	16.2543	0.2552	49.2141	0.6896	
intercept	-1,028.7994	18.5008	-38.9708	35.0942	

	SL	No.	No/g	T.Wt	No.	No/g
For graph	63	-4.78	34.58	2.70	93.91	36.96
	123	970.48	49.90	23.73	1128.88	51.46

7.3.4. Summary

1. Sex ratio 1:1 initially but females predominate from II group onwards.
2. The breeding season extended from late April through to early July, although the actual spawning period may be influenced by water temperature.

3. All males and females are capable of reaching maturity in their first year regardless of size.

4. The morphology of male testes can be classified into five developmental stages.

5. I group males with ripe testes were found from late April until early July and II+ group males from late March until mid July.

6. The maximum testis-somatic index observed in I and II+ group males was 11.39 and 12.56 respectively.

7. The maximum ovary-somatic index observed in I and II+ group females was 23.11 and 31.29 respectively.

8. Oocytes can be classified into four arbitrary stages of maturation.

9. I group ovaries containing ripe oocytes were found during May and June and II+ group ovaries from late April until early July.

10. Examination of the oocyte size-frequency distribution showed that each female spawns several times during the season.

11. Ovaries examined on the same day not necessarily at the same maturation stage suggesting that spawning does not have specific periodicity.

12. Total fecundity during the breeding season could not be determined but the number of ova released at a spawning averaged 43.75/gram weight of fish, although both this ratio and the total number of eggs released were correlated with the length and weight of the fish.

7.4. *Atherina presbyter* - Egg and larval development

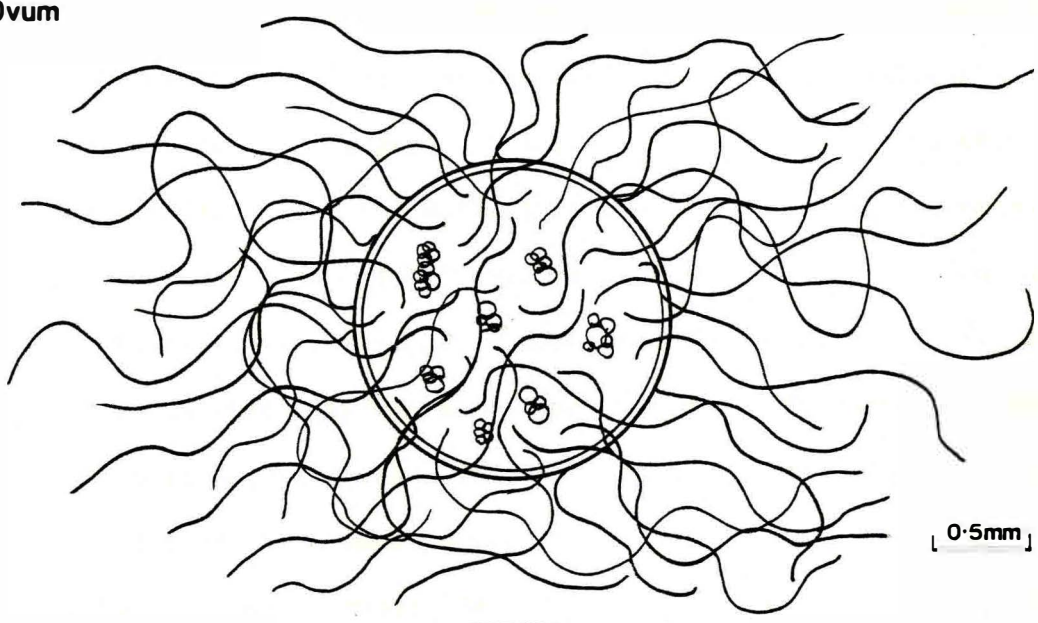
7.4.1. The ovum (Fig. 7.12.a)

The eggs of *A. presbyter* are spherical from 1.6 to 1.8mm in

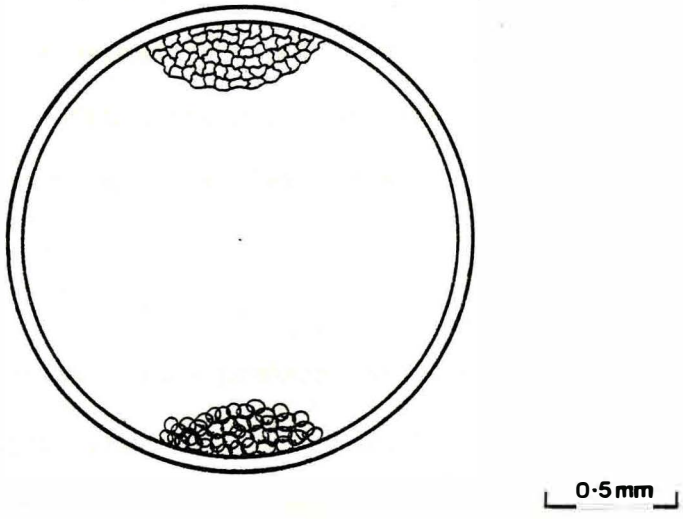
Figure 7.12.

A. presbyter The ovum and embryonic developmement.

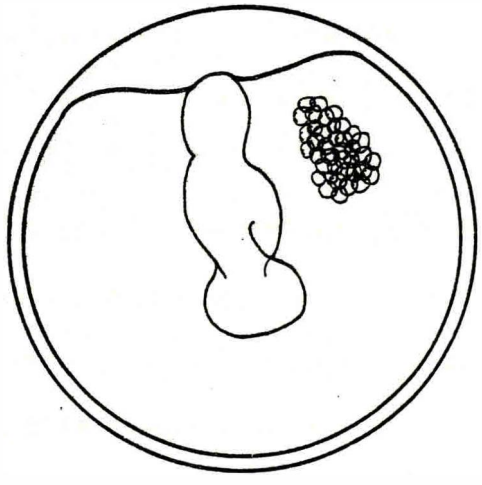
a) Ovum



b) 1 day at 20°C



c) 3 days at 20°C



diameter and remain as such until hatched. This is slightly smaller than the diameters given by Kennedy (1954) and Wheeler (1969) which were from 1.85 to 1.90 and from 1.85 to 1.95 respectively. They are slightly heavier than seawater and appear a translucent yellow colour to the unaided eye. Arising from the surface of the egg are long filaments. The origins of these are randomly distributed over the ovum surface and are not restricted to one pole as in some atherinids (Clark 1925). These filaments are remarkably strong and often entangle with those of other ova forming loose aggregations. They also adhere to most surfaces and thus provide for an attachment to algae, *Zostera* or other suitable substrates (Bracken and Kennedy 1967, Miller 1962, Wheeler 1969). Under magnification, there is a perceptible space between the egg membrane and the vitelline membrane. Within the vitelline area are a variable number of oil globules apparently randomly distributed.

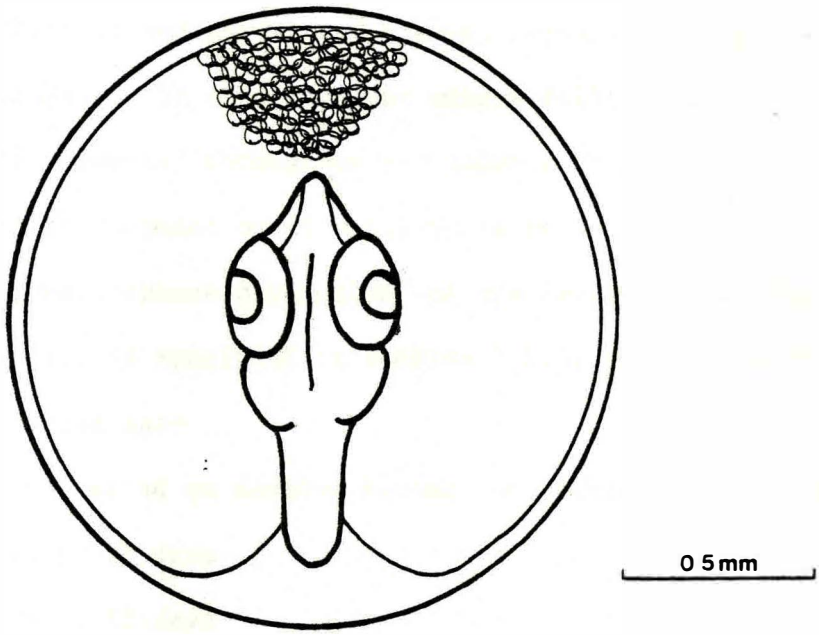
7.4.2. Embryology

After fertilisation the protoplasm becomes concentrated at one pole forming the germinal disc. At this stage the oil globules, previously randomly distributed, come together at the opposite pole on the periphery of the vitelline area. Cleavage is then regular until after 1 or 2 days (20°C) the blastoderm on the yolk contains many cells (Fig. 7.12.b).

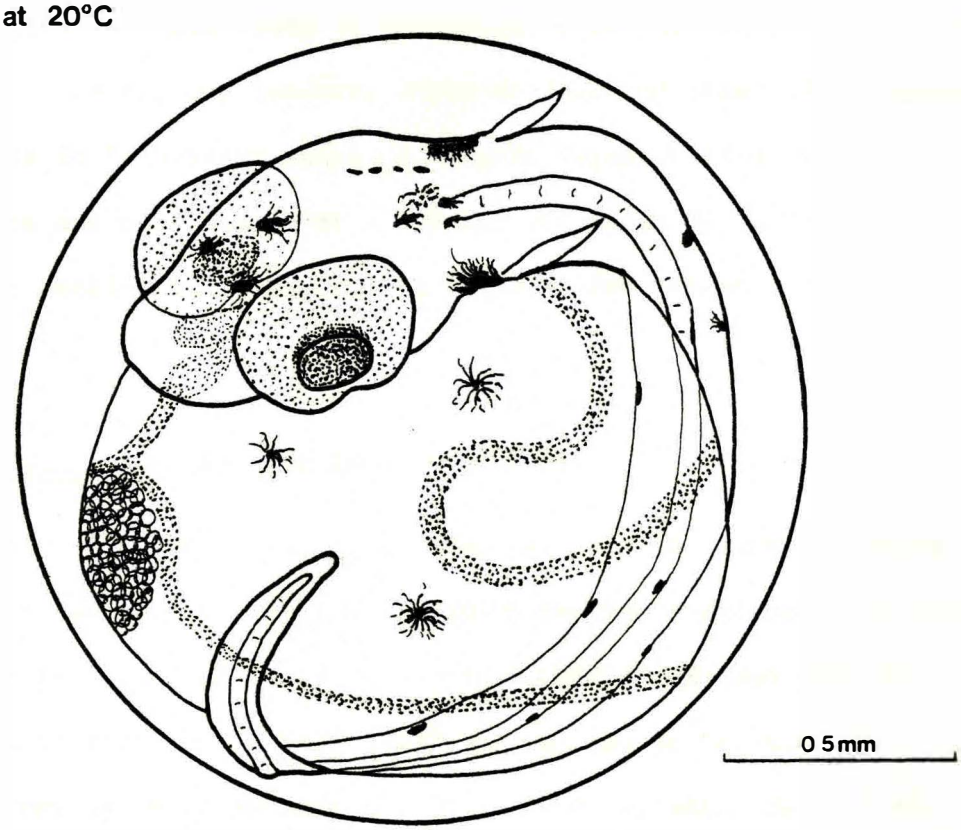
At 3 days (20°C) the embryo outline becomes visible (Fig. 7.12.c). It is curved around the periphery of the vitelline area and as growth proceeds the anterior end of the embryo approaches the oil globules at the opposite pole. At this stage (4 days at 20°C) the head is clearly visible (Fig. 7.12.d) particularly the large eyes. Shortly afterwards (6 days at 20°C) the heart begins to pulsate and large blood vessels may be seen transversing the vitelline area (Fig. 7.12.e). These connect

Figure 7.12. continued.

d) 4 days at 20°C



e) 6 days at 20°C



with the embryo by the duct of Cuvier. The blood at first contains relatively few corpuscles, which flow slowly, but their number and speed increase with the development of the embryo. At this stage melanophores appear on the periphery of the vitelline area and in the embryo. Head, peritoneal, mediolateral and dorsal and ventral contour melanophores are all distinguishable. By this time the embryo fully encircles the vitelline area, is segmented throughout and capable of considerable movement. Further development until hatching is only recognisable in terms of increased melanophore production and eye development. Under the laboratory conditions specified in Section 7.2.5, the period of incubation was recorded as:-

10°C - ova failed to develop beyond the germinal disc stage

15°C - 26 to 27 days

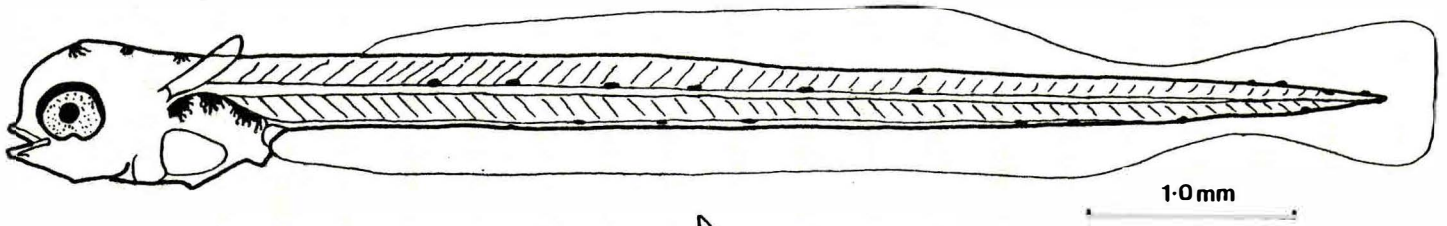
20°C - 13 to 15 days

No previous data seems to be available on the length of time to hatching in *A. presbyter*, however, Jorné-Safriel and Shaw (1966) recorded that hatching in laboratory reared *A. boyeri* began 10 days after fertilisation and continued over a two day period at 22 to 23°C. This was slightly earlier than observed in *A. presbyter* but at a higher temperature.

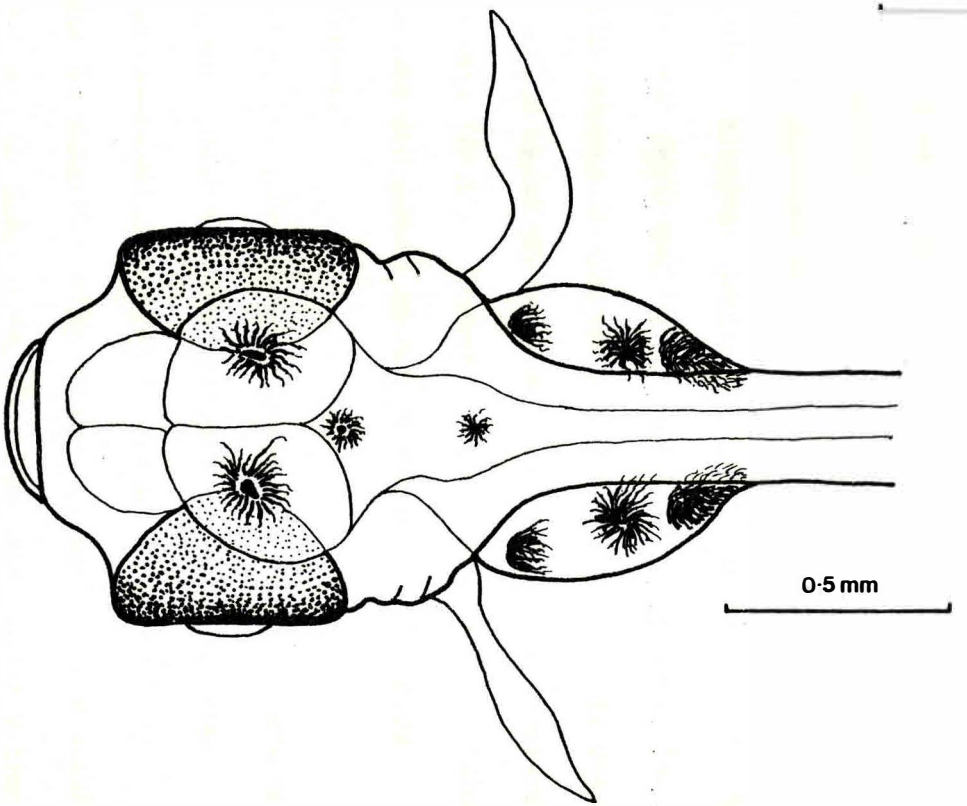
7.4.3. The newly hatched postlarva (Fig. 7.13)

At hatching (20°C) the postlarvae were 6.5 to 7.2mm in length. This compares favourably with the length of the newly hatched postlarvae given as 6.8 to 7.5mm and c. 7mm given by Miller (1962) and Wheeler (1969) respectively. It is also close to the size at hatching of *A. boyeri* given by Jorné-Safriel and Shaw (1966) as 6mm. No yolk sac was apparent or has been noted by previous workers and therefore

Figure 7.13. A. presbyter A newly hatched postlarva, total length 7·0 mm, drawn on 21 June 1978.



a) Postlarva



b) Head

A. presbyter hatch as postlarvae rather than as larvae.

The body was slender with a very long tail and the anus well forward. Pectoral fins were well developed, although other fins were not distinguishable within the primordial fin. Eyes were large; iris silver, sclera, when viewed dorsally, black green and yellow. Pigmentation was very characteristic with two large melanophores over the anterior end of the eye as described by Russell (1976) in specimens up to 11mm in length. However, in other pigmentation patterns the postlarvae were similar to the postlarvae 6.3mm long described and figured by Russell (1976), although numbers of melanophores varied. The peritoneal pigment was well developed in the postlarvae figured, there were six elongated melanophores in the mediolateral line (Russell noted ten); eight ventral contour melanophores (two) and four dorsal contour melanophores near the tail (four). However, even in postlarvae hatched from the same batch of ova the number of melanophores within these lines were rarely constant.

According to Russell (1976) newly hatched *A. presbyter* have not previously been described. However, the postlarva 6.5mm long from Kilkieran Bay, Ireland described and drawn by Fives (1970) and the postlarva 6.3mm figured by Russell (1976) closely resemble those hatched under laboratory conditions in this study, and thus, are probably the first descriptions of the newly hatched larva.

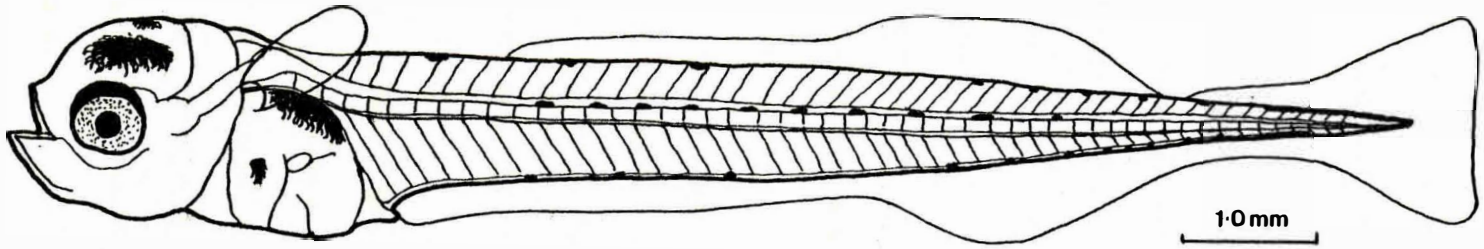
7.4.4. Subsequent postlarval development

This is most easily described in terms of the appearance of melanophores and fin differentiation.

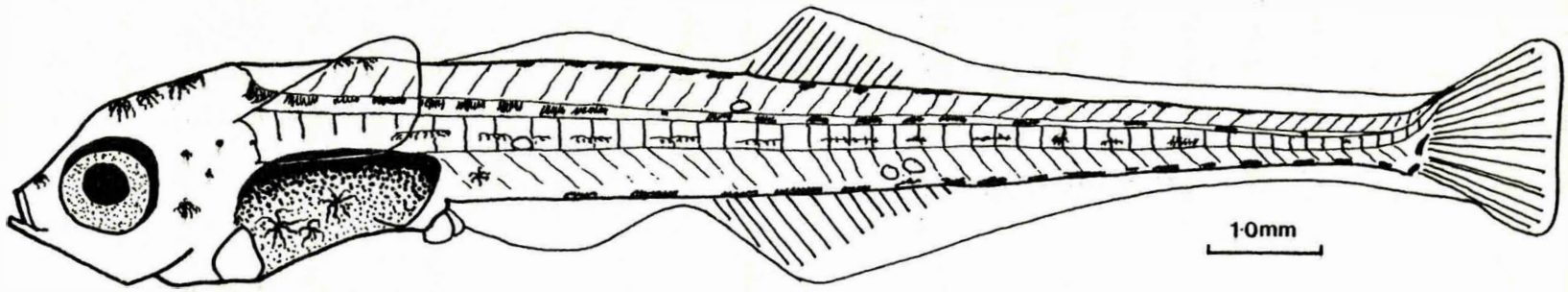
A postlarva 10.7mm long (Fig. 7.14.a) showed a similar pigmentation pattern to the newly hatched postlarva although the number

Figure 7.14.

A.presbyter Postlarval development.



a) A specimen, 10·7 mm total length, captured on 6 June 1978



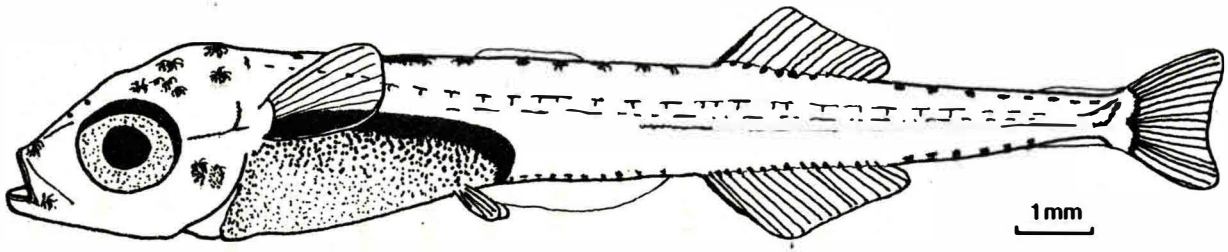
b) A specimen, 13·4 mm total length, captured on 23 June 1978

of dorsal and ventral contour and mediolateral melanophores were greater in number. The second dorsal and anal fins had started to differentiate from the primordial fin although no evidence of rays could be seen. In contrast, Russell (1976) noted the first traces of the interspinous areas in these fins in a postlarva 8.25mm long, Ehrenbaum (1905-1909) in a postlarva 11.0mm long, and Holt (1899) in a postlarva 9.0mm and 11.5mm. It is not clear whether these measurements were of fresh specimens or preserved specimens in which shrinkage was likely to have occurred. In a live specimen of 11.5mm Kennedy and Fitzmaurice (1969) figured interspinous areas in the anal and caudal fins.

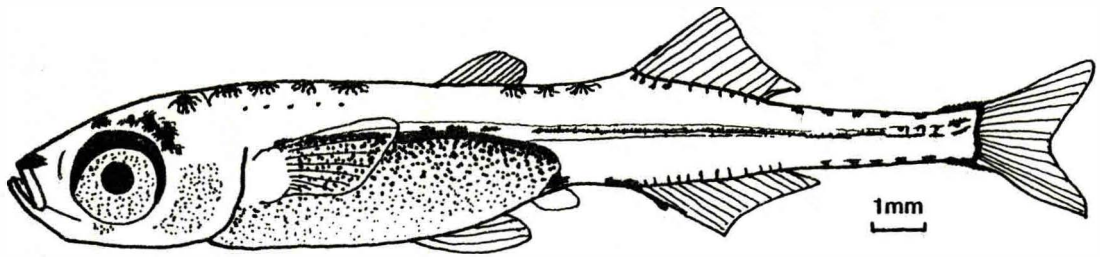
In a postlarva 13.4mm long (Fig. 7.14.b) rays were evident in the second dorsal and anal fins and also in the caudal fin. Pelvic fins were also apparent on each side of the anus. Pigmentation had increased at this stage. A row of internal notochordal melanophores were present, as noted in the postlarva 11.0mm long figured and described by Russell. Two large melanophores were present above the mouth and one large and three small ones on the operculum. The peritoneal pigment had expanded to surround the body cavity completely giving it a silvery appearance. This postlarva closely resembles the postlarva 14.0mm long figured by Ehrenbaum (1905-1909).

In a postlarva 15.4mm long (Fig. 7.14.c) the second dorsal, anal and caudal fins were discrete, the primordial fin being much reduced. At this stage, the head and body cavity occupy a greater percentage of body length than previously. This trend continues as the postlarva develops further, as may be seen in a postlarva 19.0mm long (Fig. 7.14.d). By this stage the larva has assumed most of the adult characteristics. All fins are now complete and fully rayed although a relic of the primordial fin still remains between the anus and anal fin, a

Figure 7.14.continued.



c) A specimen, 15·4 mm total length, captured on 29 June 1978



d) A specimen, 19·0 mm total length, captured on 15 August 1978

characteristic also noted by Ehrenbaum (1905-1909) in a postlarva 18.0mm long. Pigmentation, however, is still incomplete as the characteristic intense silvery strip along the midline of each flank is not present. This eventually becomes evident in fish of about 23.0mm length by which time morphological postlarval development is complete.

7.4.3. Postlarval distribution

During the study period *A. presbyter* postlarvae have been collected or observed at the following locations:-

Langstone Harbour, June, July and August in each year 1975-1978;

Chapman's Pool, Dorset, 9 August 1976;

Gorey Harbour and St. Aubins, Jersey, 14 July 1976;

L'Etaq, Petit Port, St. Brelades and Portelet, Jersey, 11-20 July 1978;

and Maitresse Ile, Les Minquiers, 21 July 1978.

Lengths are not recorded here as they would bear little relationship to lengths given in the developmental stages described above as preservation caused shrinkage and distortion. Localities where *A. presbyter* postlarvae have previously been recorded in the British Isles were listed in Section 7.1. These were confined to the south-west peninsula, the west coast of Britain, Ireland and Guernsey. It was suggested that these records indicate that *A. presbyter* spawn close to these sites. Therefore, the present study has confirmed that successful spawning also takes place in the coastal waters of the central English Channel.

7.5. *Atherina boyeri* - Spawning and the sexual cycle

In all, thirty females and thirty two males were examined. These were captured over a period of thirty months from October 1974 to

March 1977. Although the number of specimens available for examination was more limited than for *A. presbyter*, certain useful observations can still be made.

7.5.1. Sex ratio

Numbers were insufficient to investigate by age-group as for *A. presbyter*. However, the overall sex ratio of males:females was 1:0.9375 (χ^2 = 0.0323, therefore not significantly different from 1:1 at $P < 0.05$), very close to the ratios found in previous studies. Kohler (1976) found that in the *A. boyeri* population of the Prevost lagoon, Montpellier, France that males dominated up to a total length of 70.0mm but that females were the more numerous of larger fish. However, the overall male:female ratio was 1:0.9058. Boscolo (1970) found a similar situation for the species in the Adriatic, with males again dominating up to a fork length of 70.0mm and an overall male:female ratio of 1:0.9885.

7.5.2. Testis cycle

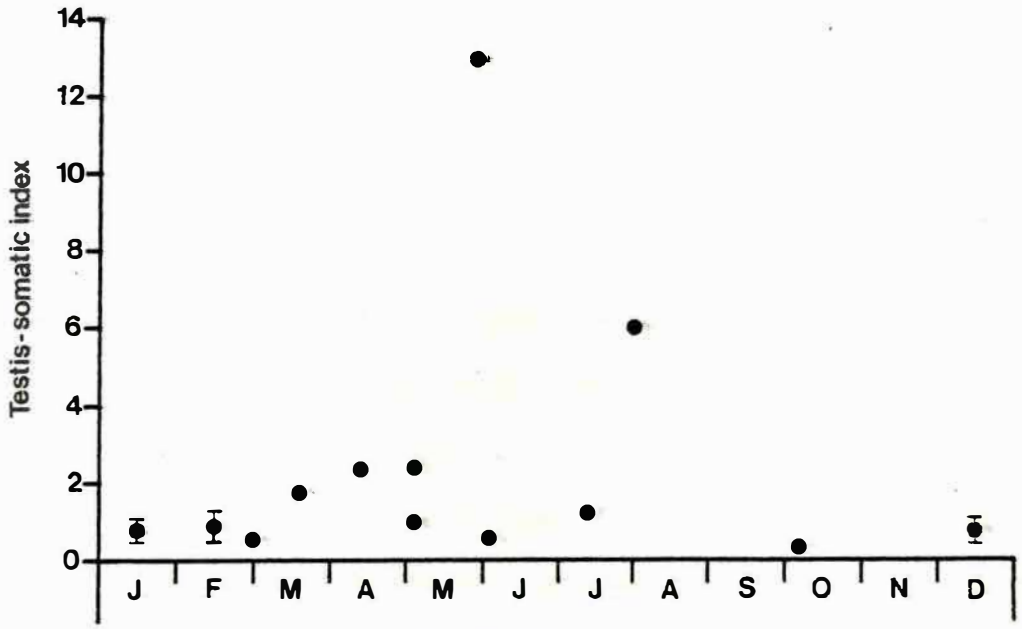
The same testis development classification already outlined for *A. presbyter* was found to be equally applicable to *A. boyeri*. Numbers were insufficient to show graphically the seasonal occurrence of these developmental stages. However, the testis cycle has been followed by use of the testis-somatic index (Fig. 7.15.a). Due to low numbers age groups have not been separated.

Low indices were found throughout the autumn and winter, often well below 1.0. The ratio began to rise during March, April and May although even during these only once was it found to exceed 2.0. In only two instances were males retained in which spawning could be

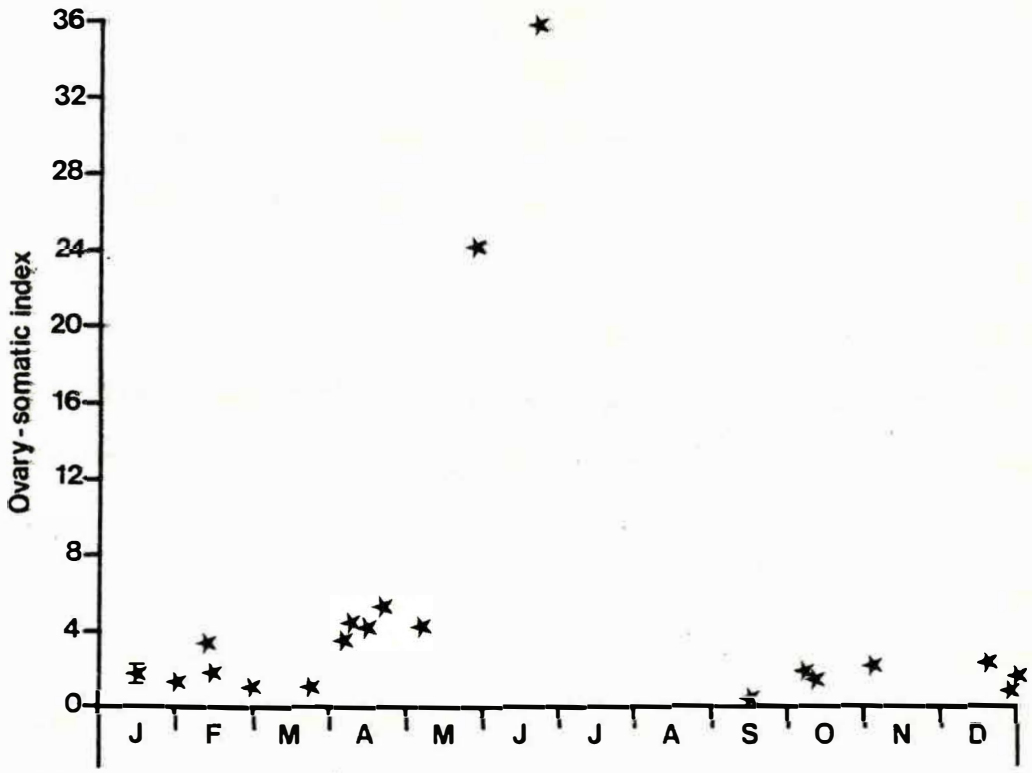
Figure 7.15.

A. boyeri Gonadosomatic indices (data from Appendices D.4. & D.5.)

a) Males



b) Females



considered to be in progress, both were caught in 1975. The first was captured on the 27 May and was a II group male with an index of 12.98. This was followed on 29 July by a I group male with an index of 6.09. The latter was an important capture as it suggests that male *A. boyeri* are able to reach maturity within their first year.

7.5.3. Ovary cycle

A. Ovary-somatic index (Fig. 7.15.b)

The lowest index was observed in September 1975 (0.44). Autumn and winter indices were generally higher than was observed in males, although not exceeding 3.0 until after January. This does not necessarily mean that the index remains static over this period. The winter of 1974/75 showed a steady increase in the ratio between October and February. However, in subsequent winters this trend was not clear although these did contain mixed age-groups.

Again only two individuals were captured in which spawning could be considered to be occurring or about to occur. In late May 1975 a II group female with an index of 23.89 was retained (on the same day a male with mature testis was also retained). During the following year a I group female with an index of 35.66 was retained in late June. The latter establishes that, like males, female *A. boyeri* at Oldbury are able to reach maturity during their first year. It also suggests that the maximum ovary-somatic index far exceeds the maximum testis-somatic index, a situation already demonstrated in *A. presbyter*.

Direct comparison of the gonadosomatic indices found in this study with those given by Kohler (1976) is not possible as she derived indices using total body weight rather than a carcass weight. However, maximum gonadosomatic indices in Prevost lagoon occurred during April

and May, whereas at Oldbury this was later, late May to July.

B. Oocyte size-frequency distribution

The oocytes were classified into the same arbitrary stages of maturation as *A. presbyter*, no differences were noted even in size. The most mature oocyte size-frequency distribution in each sample examined has been plotted with respect to date, although years have been combined (Fig. 7.16).

0/I group. Few of these were retained at Oldbury. During the winter of 1976/77 the ovaries examined contained only immature and a few early ripening oocytes.

The I group fish with the high ovary-somatic index of 35.66 caught in late June 1976 contained a discrete group of ripe oocytes. Looked at in more detail (Fig. 7.17.a), two further peaks are evident in the oocyte size-frequency distribution at 0.2 epu (0.14mm) and 0.5 to 0.6 epu (0.35–0.42mm), thus displaying a close similarity with the oocyte size-frequency distribution found in spawning *A. presbyter*. A single oocyte 2.6 epu (1.82mm) in diameter was found, possibly as a relic of the previous spawning.

I/II group. During the winter of 1974/75 the ovaries examined contained immature and early ripening oocytes with a single peak at 0.2 epu (0.14mm). In April 1975 the distribution altered and a second peak became apparent at 0.5 to 0.6 epu (0.35 to 0.42mm). In early May this secondary peak was maintained and the first late ripening oocytes produced. A fish captured in late May contained a discrete group of ripe oocytes, 1.6 to 2.6 epu (1.12 to 1.82mm). In this distribution (Fig. 7.17.b) there was no peak at 0.2 epu (0.14mm). For *A. presbyter* it was envisaged that the disappearance of this peak signalled that the

Figure 7.16. A boyeri Selected oocyte size-frequency distributions (data from Appendix D.6.).

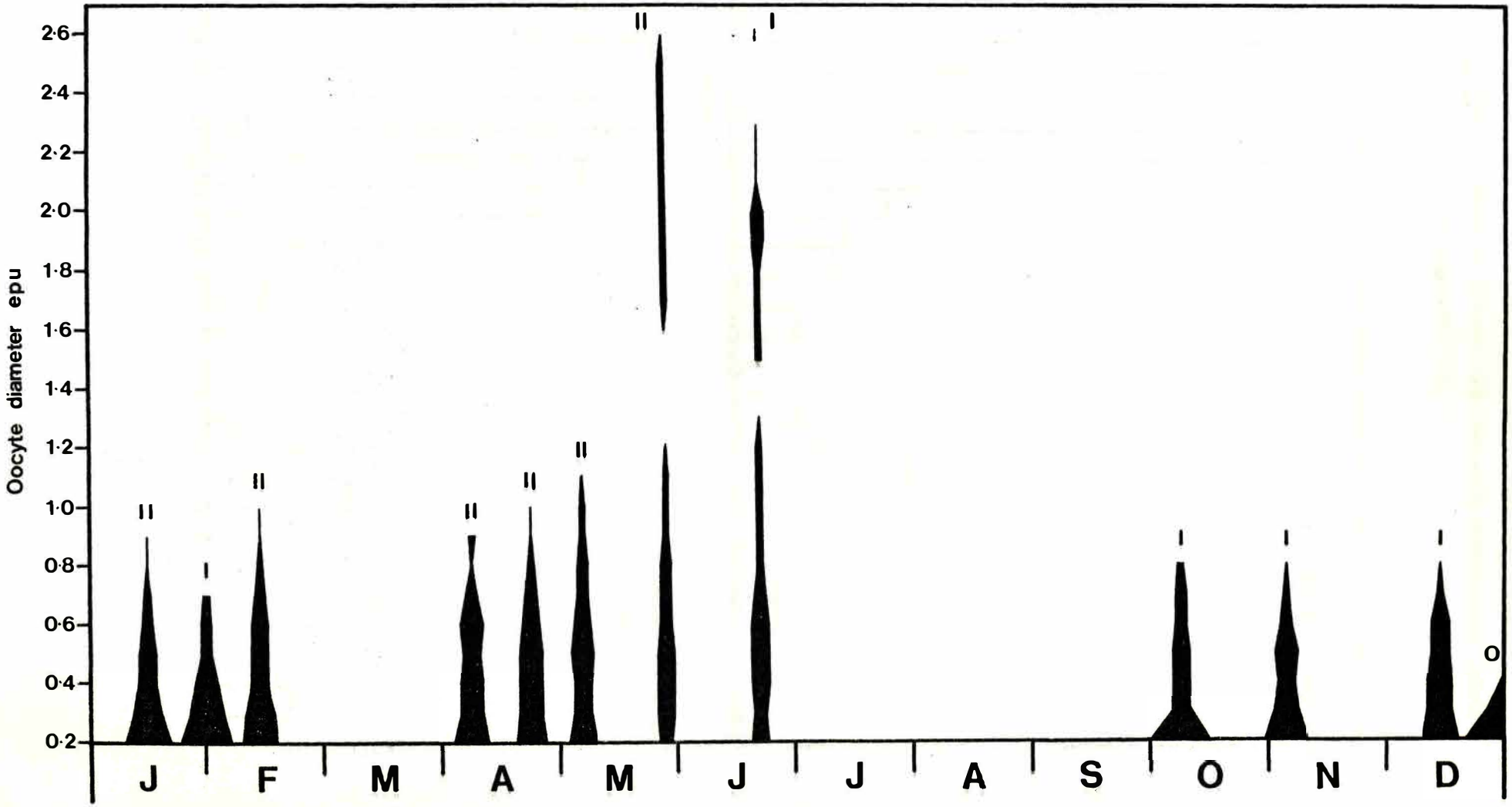
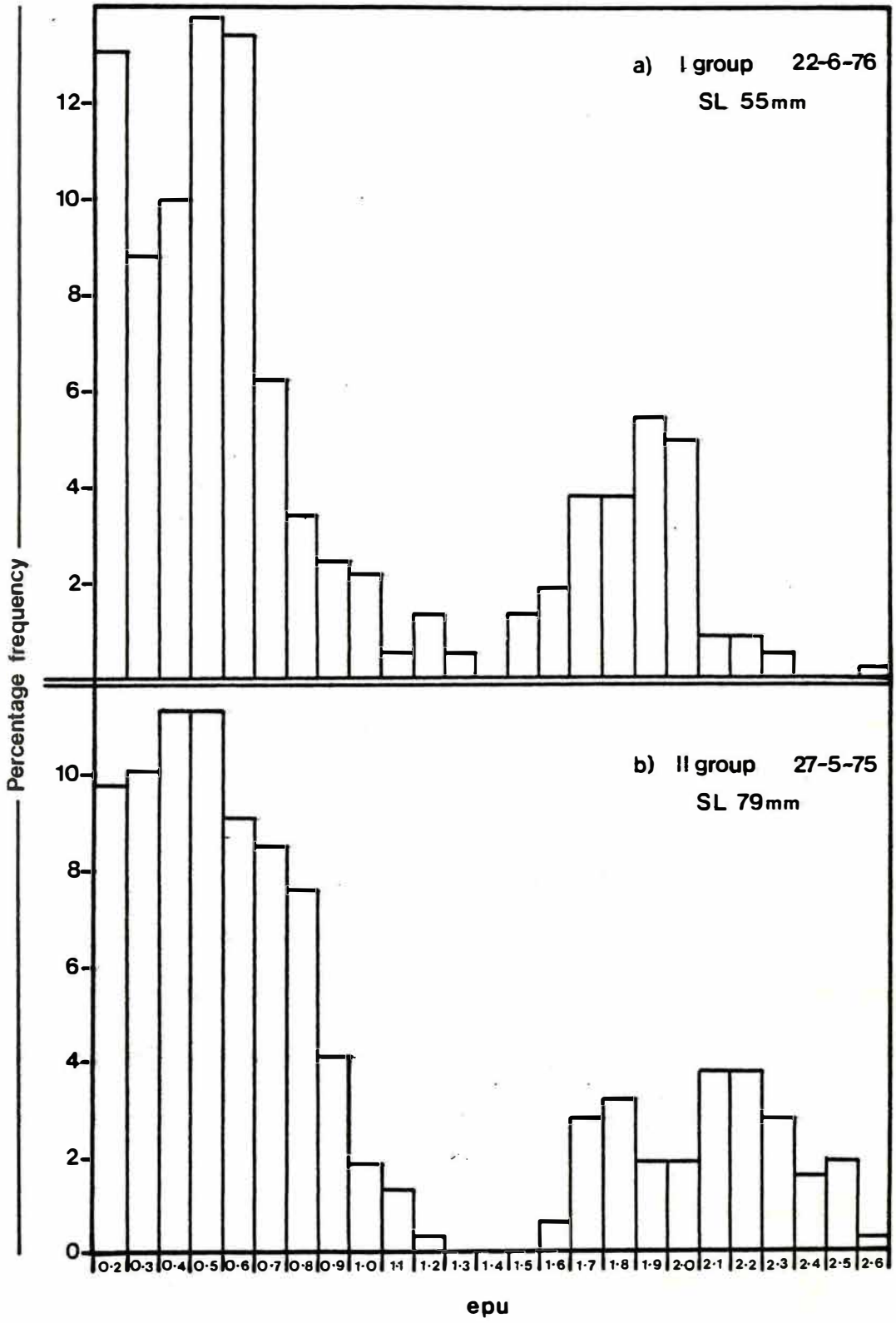


Figure 7.17.

A. boyeri Selected oocyte size-frequency distributions (data from Appendix D.6.)



end of spawning was close and was due to differentiation in oocytes less than 0.2 epu having ceased.

C. Fecundity

The same problems were experienced as in the determination of total fecundity during the spawning season in *A. presbyter*. Only the number of oocytes to be released in a particular spawning act could be calculated.

Only two females containing mature oocytes were captured. The results from these are given below:-

Date	S.L.	Age	Fish Weight g	Ovary Weight g	No. of Mature oocytes	No./g of fish
22.6.76	55	I	1.47	0.37	212	144.22
27.5.75	79	II	4.85	0.89	502	103.51
						$\bar{x}$ = 123.87

From these limited results it appears that the relative number of ova produced during a spawning act in *A. boyeri* at Oldbury is three times greater than that of *A. presbyter* in Langstone Harbour. Because the eggs of *A. boyeri* and *A. presbyter* are the same size, it results in female *A. boyeri* having a greater distended appearance at this time.

The significance of the spawning of *A. boyeri* in British waters was discussed in Section 4.2.2.

7.5.4. Summary

1. The overall sex ratio is not significantly different from 1:1.
2. The breeding season extended from late May through to July.
3. Males and females are capable of reaching maturity in their first year.

4. Only two males were found with ripe testes, one in late May and the other in late July.

5. The maximum testis-somatic index recorded was 12.98.

6. Only two females were found with ripe ovaries, one in late May and the other in late June.

7. The maximum ovary-somatic index recorded was 35.66.

8. Oocytes could be classified into the same four arbitrary stages of maturation as were observed in *A. presbyter*.

9. The fecundity of an ova release averaged 123.87/gram weight of fish.

SECTION VIII

DISCUSSION AND CONCLUSIONS

The aim of this study has been to investigate aspects of the general biology of the two atherinid fishes recorded in British waters. Details of the biology have been discussed in the relevant sections of this thesis, how these interrelate and how the two species compare will be dealt with here. However, in addition, the study must also be considered in the wider context of the adaptation of a fish to its environment and the evolution of life-history. Further evidence is then produced on which to base ideas and theories concerning the topic of evolution of the life-histories of fish.

Before the life-history tactics of any fish species may be investigated it is essential to establish the identity of the species, by systematic analysis. A biometric study of the atherinids from seven sites around Britain found that two species were represented. Of these, the common sandsmelt, *Atherina presbyter* Cuvier, was the most numerous and widespread, occurring at all but one of these sites, and, in addition, at Jersey in the Channel Islands. The less common Boyer's sandsmelt, *A. boyeri* Risso, was found only at one site, impinged on the intake screens of the power station at Oldbury-upon-Severn. This was a notable find as it has previously been recorded from only three other British localities.

The specific identification was undertaken using a key compiled from information given by Kiener and Spillmann (1969) in their systematic revision of the Atlantico-Mediterranean silversides. This key appeared to work reasonably well for both species, and only two aspects of it gave cause for concern. The use of the 'shape index' to

separate the two sub-genera *Atherina* and *Hepsetia* appeared to be of little value. Also, the upper limit in ranges of both vertebral and lateral scale counts for *A. presbyter* requires to be raised to encompass the fish from the more northerly latitudes covered by this present study. In the light of these discoveries, a modified species key has been suggested. However, during this programme of research no evidence to contradict the taxonomic scheme for the Atlantico-Mediterranean silversides, as proposed by Kiener and Spillmann (1969), has been found. Indeed, it should support the reliability of this key since, previously, little British data was available, particularly for *A. presbyter*.

As well as establishing the specific identities of each population under investigation, this biometric study highlighted the problems involved in the application of morphometrics to specific determination in the sub-genus *Hepsetia*. It appears that such morphometric ratios are often correlated with standard length, and, therefore, need to be used with great care in the separation of species and sub-species.

Having established the specific identities of the atherinid populations under investigation it was then possible to consider their life-histories. The ultimate and sole aim of any fish must be to reproduce. As a consequence, the resulting body form and function of a species must be seen as the most efficient vehicle that has yet been evolved to achieve this for a given species. Since, form, function, and mode of life are inseparably related, any consideration of the evolution of the life-history of a species is only possible if it is based upon a knowledge of the body structure, function, and reproductive methods of that species. Any consideration of body form

should not only be based upon a study of gross morphology but should also include an investigation of the factors and processes which determine the morphology or make changes in it, such as age and growth.

Although the egg and larval development of *A. presbyter* was described and figured in some detail, this was, unfortunately, not possible for *A. boyeri*. However, the morphology of adult *A. presbyter* and *A. boyeri*, as one might anticipate in closely related species, is essentially similar, but of course there are important differences. The biometric study established differences in the numbers of vertebrae, lateral scales, dorsal and anal fin rays, and in all morphometric ratios investigated other than those concerning the origins of the dorsal fins and the dorsal interspace. There are also important differences in the pigmentation, in the number of teeth on the ectopterygoids, and in the size attained. In neither species is there any biometric or other external sexual dimorphism.

Age, in both *A. presbyter* and *A. boyeri*, was determined by counting the growth zones in the otoliths and from studying length-frequency distributions. Neither scales nor opercular bones were considered to be of particular use for reliable age determination. By following the deposition of material at the otolith edge, it was found that one opaque and one hyaline zone was laid down each year. There is apparently a slight difference in the timing of the hyaline zone formation between the two species, although in both it is deposited during autumn and early winter. *A. presbyter* seems to be a longer lived species and representatives of V group (six years old) were recorded, although older fish probably exist. For *A. boyeri* the oldest fish recorded were III group (four years old).

Both species are small fish. Kiener and Spillmann (1969) gave the

maximum length attained by *A. presbyter* as 200mm and by *A. boyeri* as 130mm total length. The longest *A. presbyter* recorded during this investigation was 142mm standard length (164mm total length) and the heaviest 28g, while the longest *A. boyeri* was 86mm standard length and the heaviest 7g.

Although the age and size attained are species specific features (Nikolsky 1963), within the limits of these parameters there may be variation among the different forms, in both the maximum and average size, and the age of individuals in the population, in relation to the environmental conditions. *A. boyeri,* in particular, exhibits considerable variability owing to the diversity of ecological conditions in which it is found. This is not only reflected in the meristics and morphometrics but also in the size attained. The maximum length, given by Kiener and Spillmann (1969) for *A. boyeri,* includes fish from the Caspian and Aral Seas which do grow to this size (Kiener and Spillmann 1972), although, at other localities, this size is rarely approached.

Nikolsky (1963) considered that the growth process is also specific for each fish species. Growth is a rather vague term to describe the integrated results of very complex processes. Weatherly (1972) considered growth in an individual to be change in size (length, weight, volume) with time. In contrast, Iles (1974) defined growth as increase in length only, as increases in weight are obscured by seasonal changes in condition. However, during this investigation the more comprehensive definition of growth has been applied, where changes in both length and weight are considered.

By the construction and comparison of growth curves depicting growth in length or weight with time, it appears that both species grow most rapidly during their first year, before the onset of maturity, and

are of similar size. This is found in most other species and is an important adaptation giving decreased mortality through predation. It also ensures that the maximum possible fecundity is achieved during the first (and perhaps only) spawning, as fecundity, in *A. presbyter* at least, is correlated with the size of the fish. In subsequent years annual growth rate decreases, although, less so in *A. presbyter* than in *A. boyeri*.

Most fishes, in contrast to the majority of other vertebrates, do not cease growth after they have reached sexual maturity. It has been proposed that this is because fish live in a fluid medium which imposes less mechanical constraints (Lagler *et al*, 1962). However, it is perhaps naive to compare growth in fish, which are more overt poikilotherms, with growth in other vertebrates, the majority of which are either homoiotherms or behavioural thermoregulators.

A characteristic feature of growth in fish, particularly temperate species, is its seasonality. This has been demonstrated in a number of species (Iles 1974). In certain seasons of the year the fish grows rapidly, in others more slowly or not at all. These fluctuations in growth may often be linked to temperature, since this affects metabolism, food consumption and food availability, or to the reproductive state.

No comparison of seasonal growth in the two species is possible owing to the low sample numbers of *A. boyeri*. However, the growing season of *A. presbyter* extended from March until October or November inclusive. For the 1975 year-class at Fawley, growth was at a maximum during July 1976 when the seawater temperature was also at its maximum and spawning had finished. Minimal or no growth occurred between December and February inclusive. This is typical of a warm temperate species which is unable to maintain growth in low water temperatures.

A reduction in somatic growth for this year-class also occurred during April, which corresponded to the time of the large build up in gonadal tissue prior to spawning. Clark (1925) recorded a similar cessation of growth over the maturation and spawning period in *Leuresthes tenuis*. At this time of the year most of the energy of *A. presbyter* is channelled into reproductive effort in order to achieve the maximum possible fecundity. However, the remainder is required for body maintenance to ensure survival for spawning the following year (Iles 1974). This is in contrast to a fish exhibiting semelparity, in which further somatic growth or general body maintenance is unnecessary and wasteful, at a time when maximum fecundity is required.

The optimum temperature for rapid growth in a fish is that at which the appetite is high and maintenance requirements are low. Above this optimum, growth decreases because, although appetite is high, so are maintenance requirements because activity is increased. Below the optimum, growth also decreases this time because, even though maintenance requirements are low, there is a decrease in appetite. As outlined above, maximum growth in *A. presbyter* was observed when the seawater temperature was at a maximum. Thus, it is possible that maximum growth is not achieved in British waters. Slow growth increases predation pressure and for a species to survive it is essential that growth is sufficient for the fish to reach a minimum size for maturity and also a minimum fecundity level. The reason why *A. presbyter* reaches the northern limit of its range in British waters is probably due to a combination of these and other factors.

The technique adopted for recording seasonal growth, by comparison of mean lengths within year-classes, is far from perfect, as variations in mean length and weight of age-groups in successive samples may be

due to a variety of factors other than growth. Many workers have determined annual growth in length by back-calculation from marks in scales and, more rarely, otoliths. However, Pannella (1971, 1974) has suggested that daily marks may be formed in the otoliths of some temperate species and even some tropical species. This has since been confirmed by Brothers *et al* (1976). By back-calculating body length from such daily marks, if present, a more precise picture of seasonal growth in *A. presbyter* might be possible.

In any consideration of body form and growth, the relationship of body length to weight must be of importance. Again within certain limits, this is species specific and in some cases even sex specific within a species. Often the relationship may alter during the fishes life, as it grows (Keys 1928). The formulae expressing this relationship and the length-weight curves derived from them were similar for both *A. presbyter* and *A. boyeri*. No significant sexual differences were recorded and growth could be described as allometric, that is, where weight increases by slightly more than the cube of the length.

However, even for individuals of the same species sampled from one population on a single date, there may be considerable variation in the length-weight relationship. In addition, populations of a species may often display considerable changes in the average length-weight relationship. These reflect normal seasonal fluctuations in bodily functions, for instance, in metabolic balance, fullness of the alimentary canal, and reproductive stage (Weatherly 1972). Such differences in the individual or mean length-weight relationship from the expected relationship have been termed variations in condition, and calculated as the condition factor, condition coefficient, ponderal index or simply K (or k) factor. The heavier the weight of an

individual fish (or the mean weight of a population) at a particular length, the better the condition of the individual (or population) is said to be.

In *A. presbyter*, condition showed an annual cycle with fish at their peak condition during June, July and August and at the poorest condition during February and March. There seemed to be a correlation between condition and water temperature, the higher the water temperature the better the condition. In *A. boyeri*, the seasonal cycle was not so clear, probably due to the low sample numbers. However, in contrast to *A. presbyter*, this species appeared to be in peak condition during December and January and in poorest condition during April, there being here no correlation with water temperature.

Perhaps the most important indication of future metabolic potential of a fish is its coefficient of fat or lipid content. In fish, as in most animals, energy is stored mainly in the form of neutral fats or triglycerides which can be rapidly mobilised and degraded and are, therefore, a most convenient form of energy reserve (Shul'man 1974). These account for up to three quarters of the fat deposits, the remainder consisting of phospholipids, sterols, sterol esters, waxes, free fatty acids and some other compounds. As well as an energy source, fats may be of importance to fish as an insulator against low water temperature or have hydrostatic functions (Shul'man 1974).

Lipids may be stored at many sites but, in *A. presbyter* and *A. boyeri* probably the largest, most obvious, and easiest to measure are those accumulations in the gut mesenteries. For following seasonal changes in these deposits the weight of this mesenteric fat was expressed as a percentage of a carcass weight of the fish. It was considered that changes in this coefficient of fat content would reflect

changes in total fat content of the fish. Both species showed seasonal fluctuations in this coefficient. In *A. presbyter*, lipid reserves were at a maximum during November and at a minimum during the period February to May inclusive, while in *A. boyeri*, these periods were September to December inclusive and April to June inclusive, respectively. Thus, in both species, variations in the mesenteric lipid reserve were not in complete accord with variations in condition (as determined from the length-weight relationship), even though, in *A. presbyter*, fluctuations in such reserves were considered to have a significant effect on condition.

Sexual differences in fat content have been demonstrated in a number of fish species, owing to the larger amount of energy required for ovogenesis than for spermatogenesis (Shul'man 1960). Neither *A. presbyter* nor *A. boyeri* displayed such sexual differences in mesenteric lipid reserves. However, in *A. presbyter* significant sexual differences occurred in the liver weight cycle.

Maximum female liver weights were recorded in May, the early part of the spawning period, while minimum weights were recorded during January and February. Male liver weights displayed a very different cycle; at a minimum during April, May and June and at a maximum during July and August. The liver is often an important site of lipid accumulation (Lagler *et al* 1962). If such fluctuations in liver weight are due to variations in the amount of fat present rather than protein, then the lipids here exhibit a different pattern of accumulation and use than those deposited in the gut mesenteries. However, in both *A. presbyter* and *A. boyeri* the fluctuations in liver weight were considered to have a negligible effect on condition (as determined from the length-weight relationship).

As suggested previously, changes in condition may also reflect changes in the fullness of the alimentary canal and reproductive state. In both *A. presbyter* and *A. boyeri* variations in the weight of the alimentary canal showed no particular seasonal pattern and again was considered to have an insignificant effect on mean condition, although in *A. presbyter* the effect on individual condition may be of importance. However, the effect of gonad weight on condition is of much greater importance. In both species, the large increase in testis and ovary weight prior to the spawning period and then the gradual decrease in weight, through release of the reproductive products, was considered to have a significant effect on condition during the period.

Changes in condition are reflected in changes in gross body shape. In winter *A. presbyter* often appear lean, a combination of low fat reserves, small gonads and fairly empty guts. In contrast, during the breeding season, the body may have a distended appearance. This is particularly noticeable in female *A. boyeri* at this time.

Reproduction is the most important function and the ultimate goal of any animal, therefore, reproductive mechanisms will have a major influence on the life-history tactics. Stearns (1976), in his review of the subject, listed the key life-history traits as brood size, size of young, the age distribution of reproductive effort, the interaction of reproductive effort with adult mortality, and the variation in these traits among an individual's progeny. Two groupings of these life-history traits are recognised and have been referred to as r-selection and K-selection. Some of the biological traits exhibited by r- and K-selected animals, relevant to this study, are given in Table 8.1. How these features are reflected in the life-histories of British atherinids will now be discussed.

Table 8.1. Some of the correlates of r- and K-selection (from Stearns 1976).

r-selection	K-selection
small body size	large body size
rapid development	slow development
shorter life	longer life
early age at first reproduction	delayed reproduction
large brood size	small brood size
semelparity	iteroparity
no parental care	parental care
large reproductive effort	smaller reproductive effort
small, numerous offspring	a few, large offspring

In the earlier treatment of body form, it was established that *A. presbyter* and *A. boyeri* are small, relatively short-lived, fish which grow rapidly. This already suggests that the two species are r-selected and this premise is reinforced by their reproductive strategy.

The spawning of *A. presbyter* and *A. boyeri* in British waters takes place during late spring and early summer. Many eggs are produced, of identical size and appearance (preserved) in both species. These eggs are of intermediate size when compared with other demersal eggs. This is a compromise between many small young (with high mortality) and few large young (with low mortality). It was from a study featuring fish that this concept first derived (Stearns 1977). Although the eggs are attached by filaments to algae and other suitable substrates there is no nest-building or subsequent parental care.

As characterised by other members of the family, both species are multiple spawners but show no specific periodicity as in the genus *Leuresthes* (Thompson and Thompson 1919, Clark 1925, Thomson and Muench 1974). This was surmised from the examination of oocyte-size frequency distributions and seems to be an adaptation to ensure a large reproductive capacity and to prevent total reproductive failure. As multiple spawners, it has proved impossible to determine the total number of eggs produced by a female during the breeding season, although this must be high. However, *A. presbyter* on average produces about 8% of its total body weight in eggs at each spawning while for *A. boyeri* the figure is higher, about 20%. This difference between the species is also reflected in the number of eggs produced at each spawning, *A. boyeri* produces three times as many eggs per gram weight of fish as does *A. presbyter*. Of course, this does not necessarily mean that *A. boyeri* enjoys a higher total fecundity, either annual or during its

entire life. It may not spawn so many times during the season and it certainly does not live as long as *A. presbyter*. In the latter species, fecundity is correlated with body size. Thus it is important for the females to be as large as possible by their first (and possibly only) spawning to ensure maximum fecundity.

Incubation time is short. *A. presbyter* hatch after 13 days at 20°C as pelagic postlarvae, all traces of yolk sac having disappeared. These are about 7mm in length but develop rapidly, completing postlarval development within a matter of weeks, at a length of around 23mm. *A. boyeri* may take less time to hatch although the resulting postlarvae are slightly smaller. Subsequent morphological development of this species has not been described but they do grow rapidly in size (Jorné-Safriel and Shaw 1966).

Both species reach maturity within their first year of life. It is probable that they have the capability to mature earlier, perhaps by even their first autumn. However, as warm temperate species, under the temperature regime in British waters, such early reproduction would probably lead to heavy egg and postlarval mortality under the cold water conditions of the ensuing winter. Thus energy is diverted from gonad maturation to lipid storage, for overwintering, and to body growth, to ensure maximum fecundity when conditions are favourable, in the late spring and early summer following the first winter of life.

Both species exhibit iteroparity by multiple spawning. This is not a typical feature of an r-selected animal. It must have been directly selected for during evolution as further insurance (in addition to multiple spawning) against the risk of total reproductive failure in any given year, as might happen in the single reproduction of semelparity. However, as both reproductive effort and the risk of

predation each year are high, neither is a long-lived species. Evidently the mortality of males is higher after the first breeding season suggesting greater reproductive effort.

Throughout this discussion body form and function have been considered in isolation. From this it may be concluded that the life-history tactics evolved by British atherinids are a result of r-selection. The selection pressures and the extrinsic factors which exert them will now be considered.

Stearns (1976) considered r-selection to be a result of unstable and unpredictable environmental conditions. In British waters *A. presbyter* and *A. boyeri* are found in coastal waters inhabiting bays, docks and estuaries. These are very unstable areas with a fluctuating abiotic environment. Each species was found to differ in its choice of abiotic conditions and these apparently delimit the distribution of the two species, so that competition between them is rare. *A. presbyter* is less tolerant of high water temperatures, is less euryhaline but is more tolerant of exposed conditions than *A. boyeri*. It is probably the combination of these factors which results in *A. presbyter* being common in British waters while *A. boyeri* is rare, possibly only an immigrant species.

As well as abiotic, many biotic factors also exert selection pressure. Of these, food availability is perhaps one of the most fundamental. *A. presbyter* and *A. boyeri* are pelagic feeders, eating a wide range of animals. This is an important attribute and has probably been selected for as a result of the unstable nature of their habitats. However, in both species, amphipods and copepods are the most widely utilised species. This would, of course, lead to direct competition if the species were found in exactly the same habitat.

As small pelagic fish both species are exposed to heavy pressure from predation, throughout life. To reduce this pressure, British atherinids, like most other pelagic species, have adopted the protective schooling habit (Radakov 1973). This develops at a very early age in the postlarvae. It may have an additional nurtritional significance, in that it enables co-operative searching for food but also leads to intraspecific competition under impoverished conditions. As a further protection, to make them less obvious to predators, *A. presbyter* and *A. boyeri*, like most pelagic species, have evolved the principle of camouflage by obliterative countershading.

A further biotic pressure is that of parasitism. In British waters, *A. presbyter* is infected by at least two parastic species and *A. boyeri* by one. These do not seem to have any serious detrimental effect on the host, and it is this which allows the parasites to occur so frequently and in such high numbers. In a host-parasite relationship where the life-cycle of the parasite requires the death of the host, infection is less frequent. This is because, if the infection exceeds a certain level, disruption of the host reproduction follows, and both host and parasite could disappear.

Thus, it may be concluded that, both biotic and abiotic factors introduce strong elements of uncertainty in the life expectancy for atherinids. However, the separate elements of the biotic and abiotic environment cannot really be isolated. They form a united, inseparable system of relationships which determined the life-history tactics that evolved in *A. presbyter* and *A. boyeri*. Parameters characterising the adaptive features in life-history have been recorded by this investigation and presented as a further contribution to the knowledge of two little known British fish species; species which illustrate

further the way in which life processes have evolved to ensure effective reproduction.

REFERENCES

ABOUSSOUAN, A. (1964). Contribution à l'étude des oeufs et larves pélagiques des poissons téléostéens dans le Golfe de Marseille Rec. Travaux St. Marine Endoume, 32(48): 87.

ACEITUNO, M.E. & VANICEK, C.D. (1976). Life history studies of the sacramento perch, *Archoplites interruptus* (Girard), in California. Calif. Fish and Game, 62(1): 5-20.

AL-ABDUL-JABBAR, H.A.-R. (1978). Studies on the biology of the Pleuronectidae. Ph.D. Thesis, University of Wales.

ALBUQUERQUE, R.M. (1956). Peixes de Portugal e Ilhas adjacentes. Port. Acta biol. Ser. B, 5: 1164 pp.

ALEXANDER, R. McN. (1967). Mechanisms of the jaws of some atheriniform fish. J. Zool., Lond., 151: 233-255.

AL-HUSSAINI, A.H. (1947). The anatomy and histology of the alimentary tract of the plankton feeder, *Atherina forskali* Rüpp. J. Morph., 80(2): 251-286.

ALLEN, E.J. & TODD, R.A. (1900). The fauna of the Salcombe Estuary. J. mar. biol. Ass. U.K., (N.S.) 6(2): 151-217.

ALLEN, E.J. & TODD, R.A. (1902). The fauna of the Exe Estuary. J. mar. biol. Ass. U.K., (N.S.) 6(3): 295-335.

ANON. (1900). The Victoria History of the counties of England. Vol. 1. Hampshire and the Isle of Wight. Constable, London.

ARRU, A. (1968). Formazione della gonade unica e modalità del differenziamento sessuale in *Atherina mochon* Cuv. Boll. Zool., 35: 421-441.

AUSTIN, H.M., SOSNOW, A.D. & HICKEY, C.R. (1975). The effects of temperature on the development and survival of the eggs and larvae of the Atlantic silverside, *Menidia menidia*. Trans. Am. Fish. Soc., 104(4): 762-765.

BADSHA, K.S. & SAINSBURY, M. (1978). Aspects of the biology and heavy metal accumulation of *Ciliata mustela*. J. Fish Biol., 12(3): 213-220.

BAGENAL, T.B. (1968). Eggs and early life history. I. Fecundity. pp. 160-169. In: RICKER, W.E. (ed.). Methods for assessment of fish production in fresh waters. I.B.P. Handbook No. 3. Blackwell Scientific Publications, Oxford.

BĂNĂRESCU, P. (1964). Pisces. Osteichthyes. Fauna Repub. pop. rom., Bucuresti, 13: 1-962.

BAUCHOT, M.-L., BAUCHOT, R. & LUBET, P. (1959). Étude de la faune ichthyologique du bassin d'Arcachon (Gironde). Bull. Mus. 2° Ser., 29(5): 385-406.

BERG, L.S. (1949). Ryby presnykh vod SSSR i sopredel'nykh stran. Opred. profaune SSSR, 30: 927-1382.

BEAUMARIAGE, D.S. (1973). Age, growth, and reproduction of king mackerel, *Scomberomorus cavalla*, in Florida. Florida Marine Research Publications No. 1.

BEVERTON, R.J. & HOLT, S.J. (1957). On the dynamics of exploited fish populations. 533 pp. H.M.S.O., London.

BINI, G. (1965). Catalogue des noms de poissons, mollusques et crustacés d'importance commerciale en Méditerranée. 407 pp. Vito Bianco (FAO), Rome.

BLACKER, R.W. (1969). Chemical composition of the zones in cod (*Gadus morhua* L.) otoliths. J. Cons. perm. int. Explor. Mer., 33(1): 107-109.

BLACKER, R.W. (1974). Recent advances in otolith studies. pp. 67-90. In: HARDEN JONES, F.R. (ed.). Sea Fisheries Research. 510 pp. Elek Science, London.

BLANC, M. & HUREAU, J.C. (1972). Catalogue critique des types de Poissons du Muséum national d'Histoire naturelle (suite) (Mugiliformes et Polynémiformes). Bull. Mus. natn. Hist. nat., Paris, (3) 1971, Zool. (15): 673-734.

BONAPARTE, C.L. (1836). Iconografia della Fauna italica per le quattro classi degli Animali Vertebrati, 3: Pesci. Rome.

BORSIERI, C. (1904). Contribuzione alla conoscenza della specie europee del genere *Atherina*. Annali Agric., Roma, 1902: 92 pp.

BOSCOLO, L. (1970). Osservazioni sulla biologia e sulla pesca dell' *Atherina boyeri* Risso 1810 vivente nelle acque dell' alto Adriatico. Boll. Pesca Piscic. Idrobiol., 25(1): 61-79.

BOULENGER, G.A. (1907). Zoology of Egypt: Fishes of the Nile. 578 pp.

BOWERS, A.B. & HOLLIDAY, F.G.T. (1961). Histological changes in the gonad associated with the reproductive cycle of the herring, (*Clupea harengus* L.). Mar. Res. Dep. Agric. Fish. Scotl., 5: 1-16.

BOWERS, A.B. & NAYLOR, E. (1964). Occurrence of *Atherina boyeri* Risso in Britain. Nature (London) 202: 318.

BRACKEN, J. & KENNEDY, M. (1967). Notes on some Irish estuarine and inshore fishes. Irish Fisheries Investigations, Series B (Marine), 3: 1-29.

BRAY, R.A. & GIBSON, D.I. (in press). The Fellodistomidae (Digenea) of fishes from the north-east Atlantic. Bull. Br. Mus. nat. Hist. (Zool.).

BRIAN, A. (1921). A proposito di un Isopodo parassita dell' *Atherina mochon* Cuv. e Val. Monit. zool. ital., 32: 20-24.

BROTHERS, E.B., MATHEWS, C.P. & LASKER, R. (1976). Daily growth increments in otoliths from larval and adult fishes. Fishery Bulletin, 74(1): 1-8.

BRUCE, J.R., COLMAN, J.S. & JONES, N.S. (ed.) (1963). Marine fauna of the Isle of Man and its surrounding seas. 307 pp. Liverpool Marine Biology Committee, Memoir No. 36. Liverpool University Press.

BULLIMORE, B., DYRYNDA, P.E.J. & BOWDEN, N. (1977). The effects of falling temperature on the fauna of Swansea docks. pp. 135-146. In: GAMBLE, J.C. and YORKE, R.A. (ed.) Progress in Underwater Science, (New Series of the Report of the Underwater Association), 3. Pentech Press, London.

CANESTRINI, G. (1872). Pesci d'Italia. Parte II: Pesci marini. pp. 37-208. In: CORNALIA, E. (1870-74). Fauna d'Italia, Milano, 3: 1-208.

CARPELAN, L.H. (1955). Tolerance of the San Francisco topsmelt, *Atherinops affinis affinis*, to conditions in salt-producing ponds bordering San Francisco Bay. Calif. Fish and Game, 41(4): 279-284.

CARUS, J.V. (1893). Vertebrata. I. Class Pisces. pp. 498-711. In: Prodromus faunae Mediterraneae sive Descriptio Animalium Maris Mediterranei incolarum quam comparata silva rerum quatenus innotuit adiectis locis et nominibus vulgaribus ..... Stuttgart. (1889-93). 2: 854 pp.

CAZAUX, C. & LABOURG, P.-J. (1973). Contribution à l'étude de la faune marine de la region d'Arcachon. VII. Bulletin de la Société Linnéenne de Bordeaux, 3(6): 133-143.

CHAINE, J. (1958). Recherches sur les otolithes des poissons. Bull. Cent. Etud. Rech. sc. Biarritz, 2(2): 196-209.

CHESNEY, E.J. Jr. & IGLESIAS, J. (1979). Seasonal distribution, abundance and diversity of demersal fishes in the Inner Ria de Arosa, Northwest Spain. Estuarine and Coastal Marine Science, 8(3): 227-239.

CHRISTENSEN, J.M. (1964). Burning of otoliths, a technique for age determination of soles and other fish. J. Cons. perm. int. Explor. Mer., 29: 73-81.

CLARIDGE, P.N. & GARDNER, D.C. (1977). The biology of the northern rockling, *Ciliata septentrionalis*, in the Severn Estuary and Bristol Channel. J. mar. biol. Ass. U.K., 57: 839-848.

CLARIDGE, P.N. & GARDNER, D.C. (1978). Growth and movements of the twaite shad, *Alosa fallax* (Lacépède) in the Severn Estuary. J. Fish Biol., 12(3): 203-211.

CLARK, F.N. (1925). The life history of *Leuresthes tenuis*, an atherine fish with tide controlled spawning habits. State of California Fish and Game Commission, Fish Bulletin, No. 10: 51 pp.

CLARK, F.N. (1929). The life history of the California jacksmelt, *Atherinopsis californiensis*. State of California Fish and Game Commission, Fish Bulletin, No. 16: 22 pp.

COCCO, A. (1885). Indice ittiologico del mare di Messina. Naturalista sicil., 4: 238-240.

COOK, S.F. Jr. (1968). The potential role of fishery management in the reduction of chaoborid midge populations and water quality enhancement. California Vector Views, 15(7): 63-70.

COOK, S.F. Jr. & MOORE, R.L. (1970). Mississippi silversides, *Menidia audens* (Atherinidae), established in California. Trans. Am. Fish. Soc., 99(1): 70-73.

COUCH, J. (1849). Addition of a new fish to the Cornish fauna. Rep. Penzance Soc. Nat. Hist.: 284-285.

COUCH, J. (1868). A history of the fishes of the British Islands. 3: 208 pp. London.

CULLEY, M.B. & PALMER, C.J. (1978). The small and juvenile fish of Langstone Harbour together with a checklist of its fish. Journal Portsmouth and District Natural History Society, 3(1): 5-18.

CUSHING, D. (1975). Fisheries resources of the sea and their management. 87 pp. Oxford University Press.

CUVIER, G. (1829). Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. 2: 122-406. Nouvelle édition, Paris.

CUVIER, G. & VALENCIENNES, A. (1835). Histoire naturelle des poissons. 10: 482 pp. Paris-Strasbourg.

DANNEVIG, A. (1956). The influence of temperature on the formation of zones in scales and otoliths of young cod. Rep. Norw. Fish and Mar. Invest., 11(7): 16 pp.

DAWES, B. (1968). The Trematoda. University Press, Cambridge.

DAY, F. (1880-84). The fishes of Great Britain and Ireland. I. Williams and Norgate.

DELAROCHE, F.E. (1809). Suite du mémoire sur les espèces de poissons observées à Iviça. Observations sur quelques-uns des poissons indiqués dans le précédent tableau et descriptions des espèces nouvelles ou peu connues. Annls. Mus. Hist. nat., Paris, 13: 313-361.

DENTON, E.J. & NICOL, J.A.C. (1966). A survey of reflectivity in silvery teleosts. J. mar. biol. Ass. U.K., 46: 685-722.

DEPERET, C. (1883). Note sur la présence d'une espèce d'Atherine (*A. boyeri* Risso) dans les eaux du canal du Midi, à Castelnaudary. Bull. Soc. Hist. nat., Toulouse, 17: 82-84.

DICE, L.R. (1952). Natural Communities. 547 pp. University of Michigan Press.

DIEUZEIDE, R., NOVELLA, M. & ROLAND, J. (1955). Catalogue des poissons des côtes algériennes. Bull. Stn. Aquic. Pêch. Castiglione, 3(N.S.)(6): 1-384.

DOUDOROFF, P. (1945). The resistance and acclimatization of marine fishes to temperature changes. II. Experiments with *Fundulus* and *Atherinops*. Biol. Bull. mar. biol. Lab., Woods Hole, 88: 194-206.

DUKA, L.A. (1973). Feeding and food relationships between larvae and young fishes of some ecological groups from the Black Sea *Cystoseira biocenosis*. Biologiya Morya, 31: 46-70.

DUNCKER, G.W. & LADIGES, W. (1960). Die fische der Nordmark. 432 pp. Hamburg.

DUNN, J. (1972). A general survey of Langstone Harbour with particular reference to the effects of sewage. Report commissioned by Hampshire River Authority and Hampshire County Council. 79 pp. Portsmouth Polytechnic.

DUNNE, J. (1976). Littoral and benthic investigations on the west coast of Ireland - V. (Section A: Faunistic and ecological studies). A contribution to the biology of the leopard-spotted goby, *Thorogobius ephippiatus* (Lowe) (Pisces: Teleostei: Gobiidae). Proc. R. Ir. Acad., 76 (Section B, No. 8): 121-132.

ECHEVERRIA, J.S. (1926). Datos sobre el otolito sagita de los peces de España. Bolètin de la Real Sociedad Espanola de Historia Natural, 26(1): 145-160.

EHRENBAUM, (1905-1909). Eier und larven von fischen. Nordisches Plankton: Zoologischer Teil, 1.

EICHWALD, C.E. von (1831). Zoologia specialis quam expositis animalibus tum vivis ..... adidit D. Eduardus Eichwald. Pars posterior: 404 pp.

EICHWALD, C.E. von (1838). Faunae Caspii maris primitiae. Bull. Soc. Nat. Moscou, 11(1): 125-147.

EL-ZARKA, S. (1968). Rehabilitation of the fisheries of an inland saline lake in the United Arab Republic. Stud. Rev. gen. Fish. Coun. Medit., 35: 21-43.

FABRE-DOMERGUE, P. & BÉATRIX, E. (1897). Recherches biologiques applicables à la pisciculture maritime sur les oeufs et les larves des poissons de mer et sur le Turbot. Ann. Sci. Nat. Zool., (8) 4: 151-220.

FAO (1978). 1977 Yearbook of fishery statistics - catches and landings. 44: 343 pp. Rome.

FISHER, F. (1973). Observations on the spawning of the Mississippi silversides, *Menidia audens*, Hay. Calif. Fish and Game, 59(4): 315-316.

FIVES, J.M. (1970). Investigations of the plankton of the west coast of Ireland - IV. Larval and post-larval stages of fishes taken from the plankton of the west coast in surveys during the years 1958-1966. Proc. R. Ir. Acad., 70 (section B): 15-93.

FORSTER, R. (1978). Undergraduate project. University of Wales, Bangor.

FOWLER, H.W. (1936). The marine fishes of West Africa, based on the collection of the American Museum Congo Expedition, 1909-15. Bull. Am. Mus. nat. Hist., 70(1): 606 pp.

FOX, P.J. (1978). Preliminary observations on different reproduction strategies in the bullhead (*Cottus gobio* L.) in northern and southern England. J. Fish Biol., 12(1): 5-11.

FREY, H. (1961). Illustrated dictionary of tropical fishes. 768 pp. T.F.H. Publications.

FREY, H.W. (ed.) (1971). California's living marine resources and their utilization. 148 pp. California Department of Fish and Game.

FROST, G.A. (1929). Otoliths of the Neopterygian fishes. Ann. Mag. nat. Hist., (Series 10) 4: 120-130.

GABRIEL, M.L. (1944). Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*. J. exp. Zool., 95(1): 105-147.

GARSIDE, E.T. (1970). Temperature - structural responses. pp. 561-573. In: KINNE, O. Marine Ecology, 1(1): 681 pp. Wiley-Interscience.

GIBSON, R.N. (1967). The use of the anaesthetic quinaldine in fish ecology. J. Anim. Ecol., 36: 295-301.

GIBSON, R.N. & EZZI, I.A. (1978). The biology of a Scottish population of Fries' goby, *Lesueurigobius friesii*. J. Fish Biol., 12(4): 371-389.

GOKHALE, S.V. (1957). Seasonal histological changes in the gonads of the whiting (*Gadus merlangus* L.) and the Norway pout (*G. esmarkii* Nilsson). Indian J. Fish., 4: 92-112.

GLEDHILL, R. (1978). The flounders of Flookburgh. Sea Angler, January: 42-44.

GOSLINE, W.A. (1948). Speciation in the fishes of the genus *Menidia*. Evolution 2: 306-313.

GUICHENOT, A. (1850). Histoire naturelle des reptiles et des poissons. Explor. Scient., Algerie, 1840-42, Sc. Phys., Zool., 5: 148 pp.

GÜNTHER, A. (1861). Catalogue of the Acanthopterygian fishes in the collection of the British Museum. 3: 586 pp. London.

HALLIDAY, R.G. (1969). Reproduction and feeding of *Argentine sphyraena* (Isospondyli) in the Clyde sea area. J. mar. biol. Ass. U.K., 49(3): 785-803.

HARDISTY, M.W. & HUGGINS, R.J. (1975). A survey of the fish populations of the Middle Severn Estuary based on power station sampling. Int. J. Environmental Studies, 7: 227-242.

HEALEY, M.C. (1971). The distribution and abundance of sand gobies, *Gobius minutus* in the Ythan Estuary. J. Zool., Lond., 163: 177-229.

HERDMAN, W.A. & DAWSON, R.A. (1902). Fishes and fisheries of the Irish Sea. Lancashire Sea-Fisheries Memoir No. 11: 98 pp.

HICKLING, C.F. (1931). The structure of the otolith of the hake. Q. Jl. Microsc. Sci., 74: 547-561.

HICKLING, C.F. (1945). The seasonal cycle in the Cornish pilchard, *Sardina pilchardus* Walbaum. J. mar. biol. Ass. U.K., 26(2): 155-138.

HICKLING, C.F. (1970). A contribution to the natural history of the English grey mullets (Pisces, Mugilidae). J. mar. biol. Ass. U.K., 50(3): 609-633.

HICKLING, C.F. & RUTENBERG, E. (1936). The ovary as an indicator of the spawning period in fishes. J. mar. biol. Ass. U.K., 21: 311-316.

HILDEBRAND, S.F. (1924). Notes on habits and development of eggs and larvae of the silversides *Menidia menidia* and *Menidia beryllina*. Bull. U.S. Bur. Fish., 38 (1921-22): 133-118.

HOLMES, R.H.A. (1975). Fish and weed on Fawley generating station screens. February 1973-January 1974. Central Electricity Research Laboratories Note, RD/L/N 129/75: 17 pp.

HOLT, E.W.L. (1899). Notes on the reproduction of teleostean fishes in the south-western district. J. mar. biol. Ass. U.K., 5(N.S.): 107-155.

HTUN-HAN, M. (1978a). The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: gonosomatic index, hepatosomatic index and condition factor. J. Fish Biol., 13(3): 369-378.

HTUN-HAN, M. (1978b). The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: seasonal changes in the ovary. J. Fish Biol., 13(3): 351-359.

HTUN-HAN, M. (1978c). The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: seasonal changes in the testis. J. Fish Biol., 13(3): 361-367.

HUBBS, C. (1965). Developmental temperature tolerance and rates of four Southern California fishes, *Fundulus parvipinnis, Atherinops affinis, Leuresthes tenuis* and *Hypsoblennius* sp. Calif. Fish and Game, 51(2): 113-122.

HUBBS, C. (1976). The diel reproductive pattern and fecundity of *Menidia audens*. Copeia, 1976(2): 386-388.

HUBBS, C. & BRYAN, C. (1974). Effect of parental temperature experience on thermal tolerance of eggs of *Menidia audens*. pp. 431-435. In: BLAXTER, J.H.S., The early life history of fish. Springer-Verlag, Berlin.

HUBBS, C., SHARP, H.B. & SCHNEIDER, J.F. (1971). Development rates of *Menidia audens* with notes on salt tolerance. Trans. Am. Fish. Soc., 100(4): 603-610.

HUBBS, C.L. (1918). The fishes of the genus *Atherinops*, their variation, distribution, relationships and history. Am. Mus. nat. Hist., Bull., 38(13): 409-440.

HUBBS, C.L. (1921). An ecological study of the life history of the fresh water atherine fish *Labidisthes sicculus*. Ecology, 2: 262-276.

HUBBS, C.L. (1922). Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. Am. Nat., 56: 360-372.

ILES, T.D. (1974). The tactics and strategy of growth in fishes. pp. 331-345. In: HARDEN JONES, F.R. (ed.). Sea Fisheries Research. 510 pp. Elek Science, London.

IRIE, T. (1955). The crystal texture of the otolith of a marine teleost *Pseudoscianena*. J. Fac. Fish. Anim. Husb. Hiroshima Univ., 1: 1-14.

IRIE, T. (1960). The growth of the fish otolith. J. Fac. Fish. Anim. Husb. Hiroshima Univ., 3: 203-221.

JAMES, M.F. (1946). Histology of gonadal changes in the blue-gill *Lepomis macrochirus* Rafinesque, and the large-mouth bass, *Huro salmoides* Lacépède. J. Morph., 79: 63-86.

JENKINS, J.T. (1936). The fishes of the British Isles both freshwater and salt. 408 pp. Warne, London.

JOHNSON, M.S. (1973). An electrophoretic study of enzyme variation in fishes of the genus *Menidia* (Teleostei, Atherinidae). Ph.D. thesis, Yale University.

JOHNSON, M.S. (1974). Comparative geographic variation in *Menidia*. Evolution, 28: 607-618.

JOHNSON, M.S. (1975). Biochemical systematics of the atherinid genus *Menidia*. Copeia, 1975(4): 662-691.

JOHNSTON, M. (1938). Some methods of preparing teleost fish otoliths for examination. Jl. R. microsc. Soc., 58: 112-119.

JONES, A. (1974). Sexual maturity, fecundity and growth of the turbot *Scophthalmus maximus* L. J. mar. biol. Ass. U.K., 54(1): 109-125.

JONES, J.W. & HYNES, H.B.N. (1950). The age and growth of *Gasterosteus aculeatus, Pygosteus pungitius* and *Spinachia vulgaris,* as shown by their otoliths. J. Anim. Ecol., 19: 59-73.

JORDAN, D.S. (1891). Relations of temperature to vertebrae among fishes. Proc. U.S. natn. Mus., 14: 107-120.

JORDAN, D.S. & HUBBS, C.L. (1919). A monographic review of the family of Atherinidae or silversides. Stanford Univ. Ser., Stud. Ichthyol., 1-97.

JORDAN, D.S. & SNYDER, J.O. (1913). Description of the Yachats "smelt", a new species of Atherinoid fish from Oregan. Proc. U.S. natn. Mus., 45(1999): 573-576.

JORDAN, D.S. & STARKS, E.C. (1901). A review of the atherine fishes of Japan. Proc. U.S. natn. Mus., 24(1250): 199-206.

JORNÉ-SAFRIEL, O. & SHAW, S. (1966). The development of schooling in the atherinid fish, *Atherina mochon.* Publ. Stat. Zool., Napoli, 35(1): 76-88.

KELLY, G.F. & WOLF, R.S. (1959). Age and growth of the redfish (*Sebastes marinus*) in the Gulf of Maine. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin, 60(156): 1-31.

KENDALL, W.C. (1902). Notes on the silversides of the genus *Menidia* of the east coast of the United States, with descriptions of two new subspecies. Rep. U.S. Commissioner Fish and Fisheries for 1901, : 241-267.

KENNEDY, M. (1954). The sea angler's fishes. 524 pp. Hutchinson, London.

KENNEDY, M. & FITZMAURICE, P. (1969). Pelagic eggs and young stages of fishes taken on the south coast of Ireland in 1967. Irish Fisheries Investigations, Series B (Marine) 5: 5-36.

KENNEDY, M. & FITZMAURICE, P. (1972). The biology of the bass, *Dicentrarchus labrax*, in Irish waters. J. mar. biol. Ass. U.K., 52(3): 557-597.

KEYS, A.B. (1928). The weight-length relation in fishes. Proc. natn. Acad. Sci. U.S.A., 14(12): 922-925.

KIENER, A. & SPILLMANN, C.J. (1969). Contributions à l'étude systématique et écologique des athérines des cotes françaises. Mém. Mus. Hist. nat., nouv. sér., Sér. A, Zool., 40: 33-74.

KIENER, A. & SPILLMANN, C.J. (1972). Note complémentaire à l'étude systématique et écologique d'*Atherina boyeri* Risso (Poissons, Cyprinidae) dans sa zone de dispersion actuelle. Bull. Mus. natn. Hist. nat., sér. 3, No. 55, Zoologie 41: 563-580.

KIENER, A. & SPILLMANN, C.J. (1973). Atherinidae. pp. 576-578. In: HUREAU, J.C. & MONOD, T. Checklist of the fishes of the North Eastern Atlantic and of the Mediterranean. Unesco, Paris.

KISLALIOGLU, M. (1975). The feeding, ecology and behaviour of inshore fishes. 292 pp. Ph.D. Thesis, University of Stirling.

KISLALIOGLU, M. & GIBSON, R.N. (1977). The feeding relationship of shallow water fishes in a Scottish sea loch. J. Fish Biol., 11: 257-266.

KOHLER, A. (1976). Observations biologiques et biométriques sur *Atherina boyeri* Risso dans l'étang du Prévost a Palavas (Hérault). Vie Milieu, 26(1) sér A: 157-174.

KRISTENSEN, I. (1956). Koornaarvissen (*Atherina presbyter*) langs de Nederlandse kust. Levende Nat., 60(7): 159-162.

LADIGES, W. & VOGT, D. (1965). Die susswasserfische europas. Paul Parey, Hamburg.

LAGLER, K.F., BARDACH, J.E. & MILLER, R.R. (1962). Ichthyology - the study of fishes. 545 pp. John Wiley

LANGFORD, T.E., UTTING, N.J. & HOLMES, R.H.A. (1978). Factors affecting the impingement of fishes on power station cooling-water intake screens. pp. 281-288. In: McLUSKY, D.S. & BERRY, A.J. (ed.) Physiology and Behaviour of marine organisms. Pergamon Press.

LE CREN, E.D. (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol., 20: 201-219.

LE DANOIS, E. (1913). Contribution à l'étude systematique et biologique des poissons de la Manche occidentale. Ann. Inst. océanogr. Monaco, 5(5): 215 pp.

LE SUEUR, R.F. (1967). The marine fishes of Jersey, 33 pp. La Société Jersiaise.

LI, H.W., MOYLE, P.B. & GARRETT, R.L. (1976). Effect of the introduction of the Mississippi silverside (*Menidia audens*) on the growth of the black crappie (*Pomoxis nigromaculatus*) and white crappie (*P. annularis*) in Clear Lake, California. Trans. Am. Fish. Soc., 105(3): 404-408.

LINNAEUS, C. (1758). Systema Naturae (ed. 10). 1: 824. (Reprint, 1956, London).

LLOYD, A.J. (1941). The marine fish fauna of the southern shores of the Bristol Channel. Proc. Bristol Naturalist Soc., 9: 202-230.

LO BIANCO, S. (1909). Notizie biologiche riguardanti specialmente il periodo di maturita sessuale degli animali del golfo di Napoli. Mitt. zool. Stn Neapel, 19: 513-761.

LOZANO Y REY, L. (1919). Los peces de la fauna ibérica en la collección des museo. Trab. Mus. nac. Cienc. nat., Madr., 39: 1-112.

LOZANO Y REY, L. (1947). Peces Ganoideos y Fistostomos. Mems. R. Acad. Cienc. exact. fis. nat. Madr., ser: Cienc. Nat., 11: 839 pp.

LUX, F.E. (1971). Age determination of fishes (revised). U.S. Department of Commerce. N.O.A.A. - Fishery Leaflet, 637: 7 pp.

LYTHGOE, J. & LYTHGOE, G. (1971). Fishes of the sea - the coastal waters of the British Isles, Northern Europe and the Mediterranean. 320 pp. Blandford, London.

MAITLAND, P.S. (1977). Freshwater fishes of Britain and Europe. 256 pp. Hamlyn, London.

MANN, R.H.K. (1976). Observations on the age, growth, reproduction and food of the pike *Esox lucius* (L.) in two rivers in southern England. J. Fish Biol., 8: 179-197.

MARION, A.F. (1891). Oeufs flottants et alevins observés dans le Golfe de Marseille durant l'année 1890. An. Mus. Marseille, Zoologie, 4: 112-121.

MARION, A.F. (1894). Sur la pêche et la reproduction du siouclet (*Atherina hepsetus* L.). Ann. Mus. Hist. nat. Marseille, 4(1): 93-99.

MARKOWSKI, S. (1966). The diet and infection of fishes in Cavendish Dock, Barrow-in-Furness. J. Zool. Lond., 150: 183-197.

MATTHEWS, S.A. (1938). The seasonal cycle in the gonads of *Fundulus*. Biol. Bull. mar. biol. Lab., Woods Hole, 75: 66-74.

MAUL, G.E. (1949). Lista sistemática dos peixes assinalados nos mares da Madeira e indice alfabético. Vertebrados da Madeira, 2nd edition, 2: 137-181.

MAY, R.C. (1971). Effects of delayed initial feeding on larvae of the grunion, *Leuresthes tenuis* (Ayres). Fishery Bulletin, 69(2): 411-425.

MEINZ, M. & MECUM, W.L. (1977). A range extension for Mississippi silversides in California. Calif. Fish and Game, 63(4): 277-278.

MENSE, J.B. (1967). Ecology of the Mississippi silversides, *Menidia audens* Hay, in Lake Texoma. Bull. Oklahoma Fish. Res. Lab., 6: 32 pp.

MIDDAUGH, D.P. & LEMPESIS, P.W. (1976). Laboratory spawning and rearing of a marine fish, the silverside *Menidia menidia menidia*. Marine Biology, 35: 295-300.

MILLER, P.J. (1961). Age, growth and reproduction of the rock goby, *Gobius paganellus* L., in the Isle of Man. J. mar. biol. Ass. U.K., 41(3): 737-769.

MILLER, P.J. (1962). Evidence for the breeding in Manx waters of the sandsmelt, *Atherina presbyter* C. and V. Rep. mar. biol. Stn., Port Erin, 74: 27-28.

MINA, M.V. (1968). A note on the problem in the visual qualitative evaluation of otolith zones. J. Cons. perm. int. Explor. Mer., 32: 93-98.

MOFFATT, N.M. & THOMSON, D.A. (1975). Taxonomic status of the gulf grunion (*Leuresthes sardina*) and its relationship to the California grunion (*L. tenuis*). Trans. San Diego Soc. nat. Hist., 18(4): 75-84.

MOLANDER, A.R. (1947). Observation on the growth of the plaice and on the formation of annual rings in its otoliths. Svenska Hydro.-biol. komm. Skr. Ser biol. 2, 8: 3-11.

MOORE, M. (1976). The salinity tolerance of *Atherina presbyter*. Undergraduate project, Portsmouth Polytechnic.

MOREAU, E. (1881). Histoire naturelle des poissons de la France. Paris, Edit. Masson, 3 :697 pp.

MORETTI, G., GIANOTTI, F.S. & GIGANTI, A. (1959). Latterino (*Atherina mochon* Cuv.) in Lake Trasimeno. Riv. Biol. Perugia, 51: 3-38.

MOREY, F. (1909). A guide to the natural history of the Isle of Wight. County Press, Newport, Isle of Wight: William Wesley, London.

MORRIS, R.W. & SCHEER, B.T. (1957). The relation of meristic characters in fishes to temperature and water movement. Ann. Biol., 33(3-4): 159-161.

MOSELLA, R.G. (1920). Sulla *Livoneca sinuata* Koelbel parassita di *Cepola rubescens* e di *Atherina mocho*. Monitore Zool. Ital., 31 (1-2): 1-10.

MOYLE, P.B. (1974). Mississippi silversides and logperch in the Sacramento-San Joaquin river system. Calif. Fish and Game, 60(3): 144-149.

MUUS, B.J. & DAHLSTROM, P. (1974). Sea fishes of Britain and North Western Europe. 244 pp. Collins, London.

NAYLOR, E. (1965). Biological effects of a heated effluent in docks at Swansea, S. Wales. Proc. zool. Soc. Lond., 144(2): 253-268.

NELSON, J.S. (1976). Fishes of the world. 380 pp. John Wiley.

NICOL, E.A.T. (1936). The brackish water lochs of North Uist. Proc. R. Soc. Edinb., 56(3): 169-195.

NICOLL, W. (1914). The trematode parasites of fishes from the English Channel. J. mar. biol. Ass. U.K., 10: 466-505.

NIKOLSKY, G.V. (1963). The ecology of fishes. 352 pp. Academic Press.

NOBRE, A. (1935). Fauna marinha de Portugal. 1. Vertebrados. Portos.

OKERA, W. (1974). Morphometrics, condition and gonad development of the East African *Sardinella gibbosa* (Bleeker) and *Sardinella albella* (Valenciennes). J. Fish Biol., 6: 801-812.

OTSU, T. & HANSEN, R.J. (1962). Sexual maturity and spawning of the albacore in the central South Pacific Ocean. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin, 62(204): 151-161.

PALMER, C.J., CULLEY, M.B. & CLARIDGE, P.N. (1979). A further occurrence of *Atherina boyeri* Risso 1810 in North-Eastern Atlantic waters. Env. Biol. Fish., 4(1): 71-75.

PANNELLA, G. (1971). Fish otoliths: daily growth layers and periodical patterns. Science, N.Y., 173: 1124.

PANNELLA, G. (1974). Otolith growth patterns: an aid in age determination in temperate and tropical fishes, pp. 28-39. In: BAGENAL, T.B. (ed.). Ageing of fish. 234 pp. Unwin Brothers Ltd.

PLYMOUTH MARINE FAUNA (1957). 457 pp. Marine Biological Association of the United Kingdom.

POLL, M. (1947). Poissons marins. 452 pp. Musée royal d'Histoire naturelle de Belgique, Bruxelles.

PORTSMOUTH POLYTECHNIC (1976). Langstone Harbour Study. The effect of sewage effluent on the ecology of the harbour. 356 pp.

QASIM, S.Z. (1957). The biology of *Centronotus gunnellus* (L.) (Teleostei). J. Anim. Ecol., 26: 389-401.

RADAKOV, D.V. (1973). Schooling in the ecology of fish. 173 pp. John Wiley.

REAY, P.J. (1972a). The biology of sandeels (Ammodytidae) with particular reference to *Ammodytes tobianus* L. in Langstone Harbour. 278 pp. Ph.D. Thesis, University of London.

REAY, P.J. (1972b). The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. J. Cons. perm. int. Explor. Mer., 34(3): 485-504.

REYNOLDS, W.W. & THOMSON, D.A. (1974a). Temperature and salinity tolerances of young Gulf of California grunion, *Leuresthes sardina* (Atheriniformes: Atherinidae). J. mar. Res., 32(1): 37-45.

REYNOLDS, W.W. & THOMSON, D.A. (1974b). Responses of young gulf grunion, *Leuresthes sardina*, to gradients of temperature, light, turbulence and oxygen. Copeia, 1974 (3): 747-758.

REYNOLDS, W.W. & THOMSON, D.A. (1974c). Ontogenetic change in the response of the Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann), to a salinity gradient. J. exp. mar. Biol. Ecol., 14: 211-216.

REYNOLDS, W.W., THOMSON, D.A. & CASTERLIN, M.E. (1976). Temperature and salinity tolerances of larval Californian grunion, *Leuresthes tenuis* (Ayres): A comparison with gulf grunion, *L. sardina* (Jenkins and Evermann). J. exp. mar. Biol. Ecol., 24: 73-82.

RIEDL, R. (1963). Fauna und flora der Adria. 640 pp. Verlag Paul Parey, Hamburg.

RISSO, A. (1810). Ichthyologie de Nice. 388 pp. Paris.

ROULE, L. (1902). *Atherina riqueti* nov. sp., nouvelle espèce d'Athérine vivant dans les eaux douces. Zool. Anz., 25: 262-267.

RUBINOFF, I. (1958). Raising the atherinid fish, *Menidia menidia*, in the laboratory. Copeia, 1958(2): 146-147.

RUBINOFF, I. & SHAW, E. (1960). Hybridization in two sympatric species of atherinid fishes, *Menidia menidia* (L.) and *Menidia beryllina* (Cope). Am. Mus. Novit., 1999: 1-13.

RUSSELL, F.S. (1976). The eggs and planktonic stages of British marine fishes. Academic Press.

SAUNDERS, R.P. (1959). A study of the food of the Mississippi silversides, *Menidia audens*, Hay, in Lake Texoma. 42 pp. M.S. Thesis, University of Oklahoma.

SCHRIEKEN, B. (1964). De trek en het voorkomen van de koornaarvis in de Waddenzee en de Noordzee in de omgeving van Den Helder. Levende Nat., 67: 29-32.

SCHRIEKEN, B. & SWENNEN, C. (1969). *Atherina mochon* Cuv., a second species of sandsmelt (Pisces, Atherinidae) from Dutch coastal waters. Netherlands J. of Sea Res., 4(3): 372-375.

SHAW, E. (1960). The development of schooling behaviour in fishes. Physiol. Zool., 33: 79-86.

SHAW, E. (1961). The development of schooling in fishes II. Physiol. Zool., 34: 263-272.

SHUL'MAN, G.E. (1960). Dynamics of the fat content of the body of fish. Russ. Rev. Biol., 49: 209-222.

SHUL'MAN, G.E. (1974). Life cycles of fish. Wiley, New York.

SCHULTZ, L.P. (1933). The age and growth of *Atherinops affinis oregonia* Jordan and Snyder, and other subspecies of baysmelt along the Pacific coast of the U.S.A. Wash. Univ., Publ. Biol., 2(3): 45-102.

SCHULTZ, L.P. (1948). A revision of six subfamilies of atherine fishes, with descriptions of new genera and species. Proc. U.S. natn. Mus., 98(3220): 1-48.

SCOTT, T. (1906). Observations on the otoliths of some teleostean fishes. Rep. Fish. Bd. Scotl., 24 (for 1905) (3): 48-82.

SIMPSON, G.L., ROE, A. & LEWONTIN, R.C. (1960). Quantitative zoology. 440 pp. New York.

SINEL, J. (1905). The fishes of the Channel Islands. Rep. Trans. Guernsey Soc. nat. Sci., 5: 56-65.

SINHA, V.R.P. & JONES, J.W. (1967). On the age and growth of the freshwater eel (*Anguilla anguilla*). J. Zool., Lond., 153: 99-117.

SLASTENENKO, E.P. (1939). Les poissons de la Mer Noire et de la Mer d'Azov. Annls. scient. Univ. Jassy, 25, Part II (1): 1-196.

SMITH, J.L.B. (1965). Fishes of the family Atherinidae of the Red Sea and the western Indian Ocean. Rhodes Univ., Grahamstown. Ichthyological Bull., 31: 601-633.

ŠOLYAN, T. (1948). Fauna i flora jodrana I. Ribe Inst. Oceanogr. Ribarst. Jugoslavia, Zabreb, Hrvatske. 437 pp.

STEARNS, S.C. (1976). Life-history tactics: a review of the ideas. Q. Rev. Biol., 51(1): 3-47.

STEARNS, S.C. (1977). The evolution of life history traits: a critique of the theory and a review of the data. Ann. Rev. Ecol. Syst., 8: 145-171.

SUYEHIRO, Y. (1942). A study on the digestive system and feeding habits of fish. Jap. J. Zool., 10(1): 1-303.

SVETOVIDOV, A.N. (1964). The fishes of the Black Sea. Opred Faune SSSR, 86: 1-552.

TANING, A.V. (1950). Influence of the environment on number of vertebrae in teleostean fishes. Nature, Lond., 165: 28.

TANING, A.V. (1952). Experimental study of meristic characters in fishes. Biol. Rev. Cambridge Philosophical. Soc., 27(2): 169-193.

THOMPSON, W.F. & THOMPSON, J.B. (1919). The spawning of the grunion. Calif. Dept. of Fish and Game, Fish Bull., 3: 29 pp.

THOMSON, D.A. & MUENCH, K.A. (1974). Spawning rhythmicity of the Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann). Resumenes Quinto Congreso Nacional de Oceanografia, Guaymas, Sonora, Mexico. 22-25 October 1974.

THOMSON, D.A. & MUENCH, K.A. (1976). Influence of tides and waves on the spawning behaviour of the Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann). Bull. Southern Calif. Acad. Sci., 75(2): 198-203.

TILTON, J.E. & WHITE, R.L. (1964). Records of *Menidia beryllina* from several Central Texas impoundments. Texas J. Sci., 11: 321-334.

TORTONESE, E. (1967). Su alcuni pesci del Golfo di Genova. Doriana, 4(177): 1-5.

TUBBS, C.R. (1975). The Medina Estuary: an ecological appraisal. 21 pp. Report to the Isle of Wight County Council. Nature Conservancy Council, Lyndhurst.

VAAS, K.F., VLASBLOM, A.G. & DE KOEIJER, P. (1975). Studies on the black goby (*Gobius niger*, Gobiidae, Pisces) in the Veerse Meer, S.W. Netherlands. Neth. J. Sea Res., 9: 56-68.

VAN DEN BROEK, W.L.F. (1978). Dietary habits of fish populations in the Lower Medway Estuary. J. Fish Biol., 13(5): 645-654.

DE VEEN, J.F. (1976). On changes in some biological parameters in the North Sea sole (*Solea solea* L.) J. Cons. perm. int. Explor. Mer., 37(1): 60-90.

VELDE, G. VAN DER & POLDERMAN, P.J.G. (1972). De kleine koornaarvis, *Atherina mochon* Valenciennes 1835, in Nederland (Pisces, Atherinidae). Zool. Bijdr. (Leiden), 13: 37-40.

VELDE, G. VAN DER & POLDERMANN, P.J.G. (1976). *Atherina boyeri* Risso, a genuine immigrant in the Delta area. Hydrobiol. Bull. (Amsterdam) 10(2): 96-97.

WALKER, B.W. (1952). A guide to the grunion. Calif. Fish and Game, 38(3): 409-420.

WATSON, P. (1978). The tolerance of *Atherina presbyter* to lowered and raised salinities. Undergraduate Project, Portsmouth Polytechnic.

WEATHERLY, A.H. (1972). Growth and ecology of fish populations. 293 pp. Academic Press.

WEISEL, G.F. (1955). Variations in the number of fin rays of two cyprinid fishes correlated with natural water temperatures. Ecology, 36(1): 1-6.

WHEELER, A. (1969). The fishes of the British Isles and North-West Europe. 613 pp. Macmillan, London.

WHEELER, A. (1970). Notes on a collection of shore fishes from Guernsey, Channel Islands. J. Fish Biol., 2: 323-328.

WILLIAMS, G. (1954). Fauna of Strangford Lough and neighbouring coasts. Proc. R. Ir. Acad. Section B., 56: 29-132.

WILTON, J.W. (1974). Summer fun with smelt. Sea Angler, June.

WITHERS, R.G. (1972). Aspects of the ecology of marine sand dwelling macrobenthos. 205 pp. Ph.D. Thesis, University of Wales.

WITHERS, R.G. (1979). The marine macrofauna and flora of the Medina Estuary. Proc. Isle Wight Natur. Hist. Archaeol. Soc. for 1976, 7(1): 19-30.

WOODHEAD, A. (1979). Senescence in fishes. Symp. zool. Soc. Lond., 44:

WOODLING, B.A. (1968). The mysterious, dancing grunion. Sea Frontiers, 14(3): 130-137.

WOOTTON, R.J., EVANS, G.W. & MILLS, L. (1978). Annual cycle in female three-spined sticklebacks (*Gasterosteus aculeatus* L.) from an upland and lowland population. J. Fish Biol., 12(4): 331.

YAMAGUTI, S. (1961). Systema Helminthum Nematoda, 3 (1 + 2). Interscience Publishers, London.

YARRELL, W. (1836). History of British fishes. 1. 408 pp. John Van Voorst, London.

Additional reference

BRITISH RECORD (ROD CAUGHT) COMMITTEE (1979). British record fish list. 8pp. National Anglers' Council.

APPENDIX A

Appendix A1

The salinity tolerance of *Atherina presbyter* to lowered and raised salinities

The salinity tolerance of *A. presbyter* was not investigated in detail but the results of five rather crudely carried out experiments are recorded here as they give an insight into the capabilities of the species to withstand salinity changes.

Methods and materials

The *A. presbyter* were captured from Langstone Harbour by seine-net and transferred to holding tanks supplied with running seawater. The species is particularly susceptible to damage and dies quickly if not carefully handled. After several days only the undamaged, fit fish remained alive. From the time of capture, during their time in the holding tanks and through the experiments the fish were not fed. (Fish kept under laboratory conditions refused to eat for many weeks presumably until their lipid reserves were utilised).

A series of salinities were set up in white plastic basins 30 x 30 x 16cm each containing 8 litres of water with an air supply. Lowered salinities were achieved by percentage dilution with distilled water, the salinity ($^{o}/oo$) of each was then recorded using a salinometer. Raised salinities were achieved by the addition of an artificial seawater mixture ('Marinemix') to seawater and the salinity ($^{o}/oo$) recorded using a salinometer. The water temperature was recorded upon transfer of the test fish to it. Controls were carried out to determine handling stress by transferring from bowls of 100% seawater to 100% seawater, subsequent to the transfer of the test fish.

Results

Experiment 1 - Fairly rapid decrease in salinity, 10 test fish + 10 control fish, 42-60mm standard length. 9-11°C.

Time in hours	Salinity % seawater	°/oo	Fish remaining alive at end of period	Remarks
1	80	28.0	10	
1	70	24.7	10	
1	60	21.2	10	
1	50	17.9	10	
1	40	14.4	10	
1	30	10.8	10	
17½	20	7.4	10	Two fish showing distress
6	20	7.4	5	Three of remaining fish showing distress
19	20	7.4	2	Remaining two fish showing no distress

All ten control fish survived the transfers.

Experiment 2 - Rapid decrease in salinity followed by a rapid increase to 100% seawater. 6 test fish + 6 control fish, 87-106mm standard length, 9.0-11.5°C.

Time in hours	Salinity % seawater	°/oo	Fish remaining alive at end of period	Remarks (as compared to control)
0.5	100	31.2	6	As control
0.5	75	23.3	6	Increase in activity
0.5	50	15.5	6	Increase in activity
0.5	40	12.4	6	Increase in activity
0.5	30	9.3	6	Fish lie at slight angle, head up, tail down.
0.5	25	7.7	6	Fish come to the surface more often
0.5	20	6.3	6	Constant forward movement, stability further impaired.
0.5	15	4.7	6	Constant forward movement, stability further impaired.
0.5	10	3.1	6	Steering slightly affected
0.5	7.5	2.3	6	Steering slightly affected
0.5	5	1.5	6	Activity reduced, stability and steering worsened.
0.13	2.5	0.7	6	Complete loss of stability and steering. Body vibrating violently.
1.0	7.5	2.3	5	Four swimming on side or upside down, other two in less distress with only slight stability problems.
0.5	20	6.3	4	One dead, three in great distress, two almost normal.
21.0	46	14.3	2	Two remaining show normal swimming activity, steering and stability.
23.0	100	31.2	2	Two remaining show normal swimming activity, steering and stability.

Five of the six control fish survived, the other died after the fifteenth transfer.

Experiment 3 - Slow decrease in salinity at two different water temperatures, 14.0 ± 1°C and 8.0 ± 1°C. 10 test fish at each temperature + 10 control fish, 47–60mm standard length.

Time in hours	Salinity % seawater	°/oo	Fish remaining alive at end of period 14°C	8°C	Remarks
24	80	28.0	10	8	Death probably due to handling stress.
24	60	21.2	10	8	
24	50	17.9	10	8	
24	40	14.4	10	8	
24	35	12.6	9	8	
20	30	10.8	9	8	
24	25	9.2	8	6	
29	20	7.4	8	0	
24	15	5.7	8		
24	10	4.0	4		
72	5	2.4	0		

Seven of the ten control fish survived the transfers.

Experiment 4 - Rapid increase in salinity followed by a rapid decrease to 100% seawater. 6 test fish + 6 control fish, 9.0-11.0°C.

Time in hours	Salinity °/oo	Fish remaining alive at end of period	Remarks
0.50	31.4	6	
0.50	36.3	6	Increase in activity
0.75	42.1	6	Stability slightly affected
0.75	47.4	6	Swim nearer surface, stability affected, head down, tails up.
0.75	50.0	6	
0.75	53.0	6	
0.50	55.5	6	Steering slightly affected, fish have difficulty keeping below surface.
0.50	58.3	6	Further increase in angle to the horizontal.
0.50	60.8	6	Fish moving constantly at the surface but steering affected.
0.50	63.6	6	
0.50	66.3	6	
0.10	69.3	6	High activity, difficulty in keeping below surface, stability and steering greatly affected.
0.25	66.3	6	
0.50	55.5	6	Steering improved almost to normal. Stability still greatly affected. Head higher than tail in water.
28.00	46.1	2	
3.00	31.4	2	Two remaining, normal swimming activity, stability and steering.

The six control fish all survived the transfers.

Experiment 5 - slow increase in salinity. 6 test fish + 3 control, 98-103mm standard length. Temperature 7-10°C.

Time in hours	Salinity °/oo	Fish remaining alive at end of period	Remarks
24	31.4	6	Normal activity
23	36.2	6	
70	41.8	5	
75	46.6	5	Increase in activity
21	52.2	5	
19	54.7	3	Stability and steering slightly affected
78	57.6	2	
24	59.9	2	Frequent gulping
25	62.8	2	Reduced activity and more rapid gulping
48	65.0	1	
24	68.2	0	

All three controls survived the transfers.

Appendix A2

A. presbyter Relationship of gut content weight/somatic weight (x) to fullness index (y).

Correlation Coefficient (r) = 0.8487

slope = 3.4611

Intercept = -3.4031

Sample (N) = 80

Value of r to be exceeded for correlation at $p < 0.001$ is 0.357.

APPENDIX B

Appendix B.1.

Photograph of the scale from the shoulder of a III group female *A. presbyter*, 115mm SL, caught on 10 May 1979.


0·5mm

Appendix B.2. Additional otolith studies

i. *A. presbyter*

a) Otolith growth

Figure B.2.1a and b illustrates otolith growth by plotting the mean otolith total lengths for each year-class in each sample, for Langstone and Fawley respectively, from Table B.2.1.

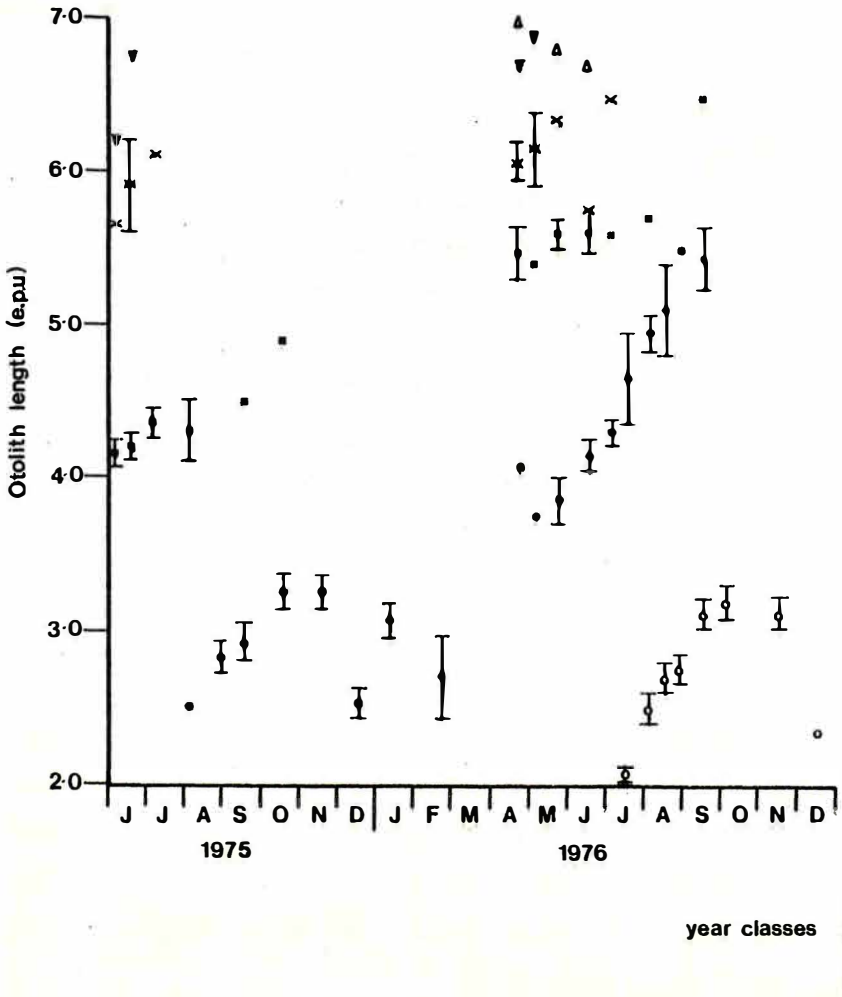
0 group. The otoliths appear to grow steadily until October, at which time, as has been previously illustrated, the hyaline zone is laid down. At this time the lengths at Langstone are significantly different from those at Fawley, however, this is probably due to the sampling bias against small fish at the latter station. The mean opaque centre length at the time of formation of this first annulus is given in Figure B.2.2, and was 3.11 and 3.31 epu for Langstone and Fawley respectively. This figure was constructed by amalgamating all the centre measurements of all age-groups and assumed that no ingrowth occurred at the interface of opaque and hyaline material. A significant difference exists between the means at the two localities. However, when the size frequency distribution of otolith opaque centres are compared (Fig. B.2.3a and b) it becomes apparent that Langstone has a higher percentage of otoliths with small centres, perhaps indicating later spawned fish. These may well correspond to the influx of small fish caught late in the year in Langstone (see Section 4.1.3).

I group. Otolith size remains fairly constant until late May when rapid growth in length occurs through to October when growth ceases at the formation of the hyaline zone. The mean otolith length at the formation of this second annulus was 5.07 and 5.34 epu for Langstone and Fawley respectively (Fig. B.2.2). Again a significant difference exists between

Figure B.2.1

A.presbyter Otolith growth

a) Langstone



b) Fawley

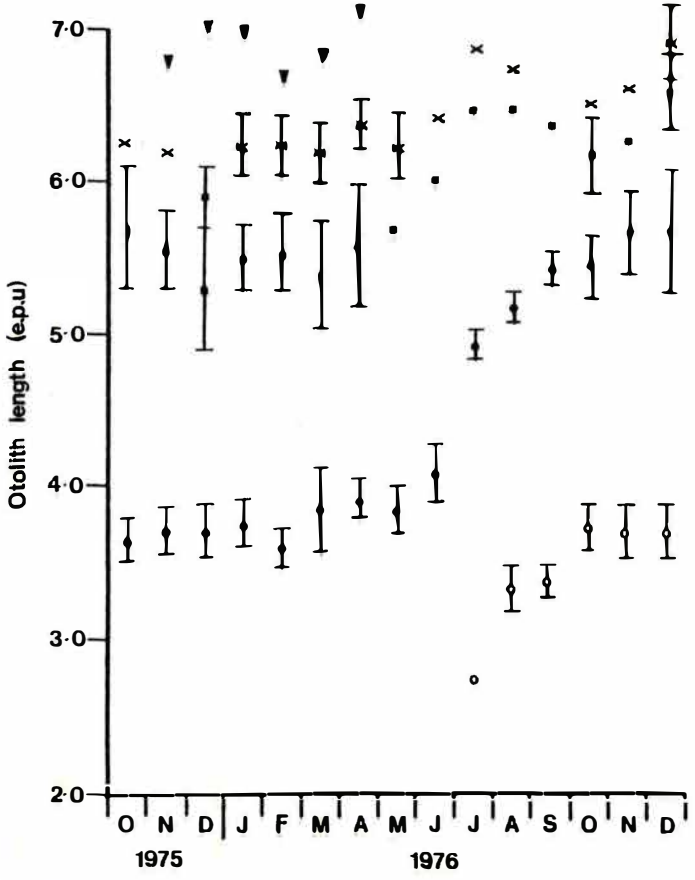


Table B.2.1. *A. presbyter*. Mean lengths (in eye-piece units, where 1.0 epu = 0.7mm) of otoliths with respect to age, sexes combined.

	0			I			II			III			IV			V		
	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N
a) Langstone																		
1975																		
6 Jun				4.14	±0.08	39	5.65		4	6.20		2						
19 Jun				4.20	0.08	37	5.82	±0.31	6	6.75		2						
7 Jul				4.36	0.10	48	6.10		1									
6 Aug	2.50		1	4.31	0.20	39												
3 Sep	2.83	±0.10	30															
17 Sep	2.93	0.12	38	4.50		1												
16 Oct	3.23	0.12	45	4.90		2												
26 Nov	3.23	0.11	41															
16 Dec	2.53	0.10	39															
1976																		
15 Jan				3.07	0.13	29												
26 Feb				2.71	0.28	9												
26 Apr				4.07		3	5.48	0.17	15	6.07	±0.16	11	6.70		1	6.97		3
7 May				3.75		2	5.40		2	6.17	0.25	10	6.90		3	6.90		3
26 May				3.84	0.15	24	5.59	0.11	12	6.37		3				6.80		2
17 Jun				4.15	0.10	41	5.62	0.15	16	5.75		2				6.70		1
5 Jul				4.31	0.08	47	5.60		1	6.50		1						
19 Jul	2.07	0.05	40	4.66	0.29	5												

Table B.2.1. continued.

	0			I			II			III			IV			V		
	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N
3 Aug	2.50	0.11	30	4.97	0.12	20	5.70		1									
17 Aug	2.69	0.09	41	5.12	0.30	6												
1 Sep	2.77	±0.10	49	5.50		1												
15 Sep	3.13	0.10	40	5.45	0.19	20	6.50		1									
4 Oct	3.22	0.12	40															
17 Nov	3.12	0.11	40															
16 Dec	2.35		2															
b) Fawley																		
1975																		
Oct	3.63	0.15	26	5.69	0.39	7	6.25		2									
Nov	3.70	0.15	21	5.55	0.33	6	6.20		4									
Dec	3.70	0.18	14	5.30	0.38	5	5.89	0.21	7									
1976																		
Jan				3.73	0.17	20	5.50	0.22	10	6.33	0.19	12	7.00		3			
Feb				3.60	0.12	20	5.53	0.26	7	6.30	0.20	11	6.70		3			
Mar				3.86	0.28	8	5.40	0.36	5	6.18	0.19	16	6.87		3	7.20		3
Apr				3.92	0.13	17	5.60	0.38	6	6.41	0.17	17	7.15		2	7.10		2
May				3.83	0.17	20	5.70		1	6.25	0.22	11						
Jun				4.08	0.19	22	6.03		4	6.43		4						
Jul	2.75		2	4.94	0.10	28	6.50		1	6.90		1						
Aug	3.33	0.17	19	5.19	0.11	39	6.50		2	6.75		2						

Table B.2.1. continued.

	O			I			II			III			IV			V		
	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N	$\bar{x}$	95%CL	N
Sep	3.40	0.11	40	5.46	0.12	22	6.40		2									
Oct	3.75	0.17	16	5.48	0.18	24	6.20	0.26	8	6.53		3.						
Nov	3.72	0.18	17	5.70	0.27	15	6.30		4	6.63		4						
Dec	3.72	0.17	18	5.70	0.41	5	6.63	0.25	6	6.95	0.25	8						

Figure B.2.2.

A.presbyter Otolith length at the formation of each annulus (data from Table B.2.2.a).

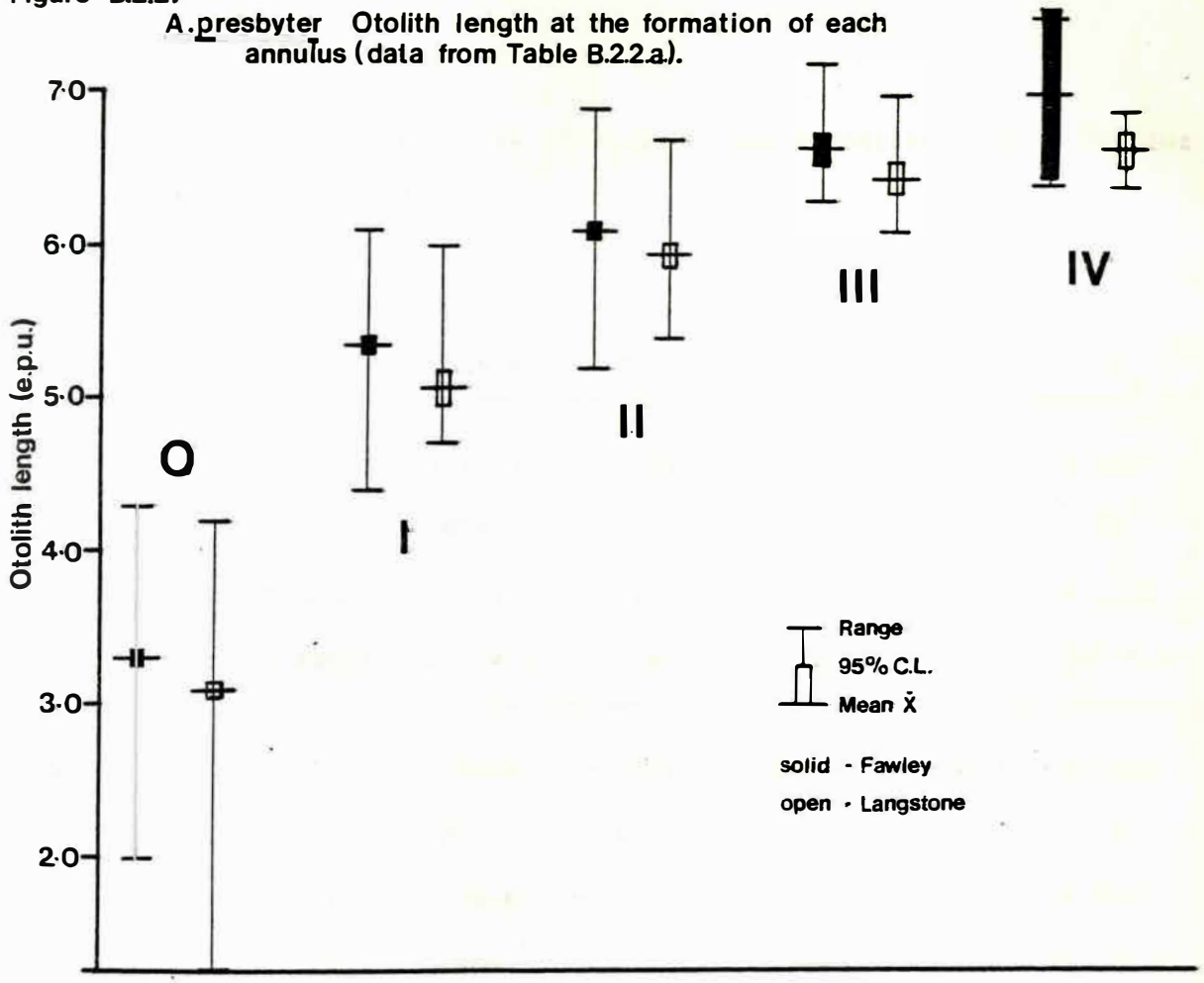


Figure B.2.3.

A.presbyter Size frequency distribution of otolith opaque centres.

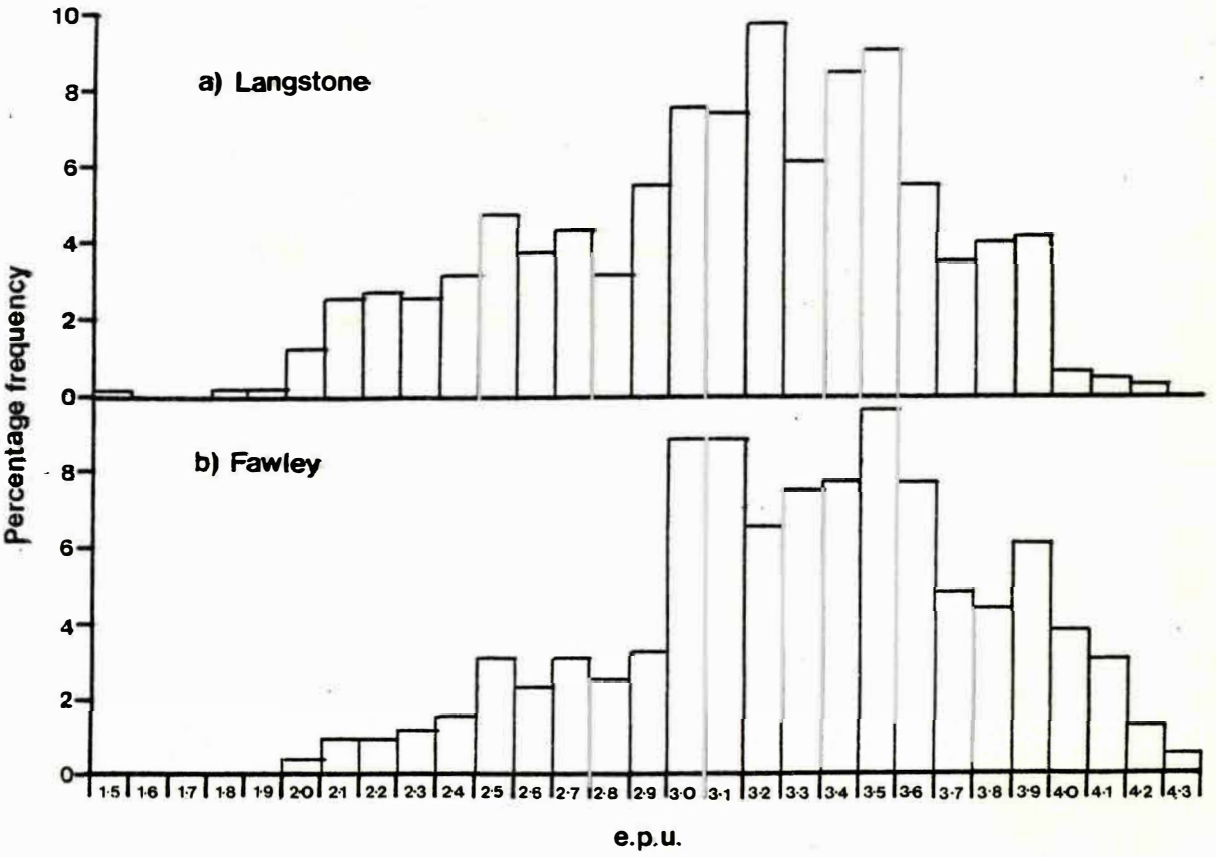


Table B.2.2. The lengths of otoliths at the formation of each hyaline annulus.

a) *A. presbyter*

		Centre	I	II	III	IV
Langstone	$\bar{x}$	3.1070	5.0698	5.9656	6.4522	6.6500
	N	679	149	64	23	10
	95%C.L.$\pm$	0.0384	0.0925	0.0742	0.0983	0.1228
	range	1.5-4.2	4.7-6.0	5.4-6.7	6.1-7.0	6.4-6.9
Fawley	$\bar{x}$	3.3096	5.3388	6.0928	6.6606	7.0000
	N	521	227	138	33	5
	95%C.L.$\pm$	0.0416	0.0459	0.0586	0.1148	0.5621
	range	2.0-4.3	4.4-6.1	5.2-6.9	6.3-7.2	6.4-7.5

b) *A. boyeri*

	$\bar{x}$	2.4983	3.5604	4.1125
	N	60	48	8
	95%C.L.$\pm$	0.1042	0.0943	0.2506
	range	1.5-3.4	2.8-4.3	3.6-4.5

these means with the Langstone mean, as for all annuli, lower than the corresponding Fawley annulus mean, although the ranges are similar (Table B.2.2a). This is probably the result of the higher percentage of late spawned fish in the Langstone population, already mentioned.

II-IV groups. The picture of otolith growth here is not as clear due to irregular and low sample numbers and because increases in length are small. However, the indications are that otolith growth takes place in summer and autumn. The decrease in otolith growth rate in these older fish is also illustrated in Fig. B.2.2 where successive mean annulus lengths are closer to one another and greater overlap in the range of lengths occur.

b) The relationship between otolith length and standard body length

From an analysis of otoliths from 140 *A. presbyter* retained at Fawley, between October 1975 and September 1976 inclusive, and representing all age-groups, the otolith length (in epu, where 1.0 epu = 0.7mm) was found to be significantly correlated ($P < 0.001$) to standard length (mm) and could be expressed by the equation.

$$\text{Otolith length} = 0.0514\ (\pm 0.0021)\ SL + 0.4568 \qquad (r = 0.9727)$$

ii. *A. boyeri*

a) Otolith growth

No analysis of seasonal otolith growth was possible due to low sample numbers. However, the mean otolith length at the formation of each hyaline annulus was determined by combining the data from all age-groups. The results are given in Table B.2.2b and show that, at the formation of each hyaline annulus represented, the otoliths of *A. boyeri* are significantly smaller than those of *A. presbyter*.

b) The relationship between otolith length and standard body length

From an analysis of the otoliths from 61 *A. boyeri* retained at Oldbury, the relationship of otolith length (epu) to standard length (mm) could be expressed by the equation,

Otolith length = 0.0516 ($\pm$0.0066) SL + 0.0969 (r = 0.8968)

and thus, was not significantly different from that found in *A. presbyter* at Fawley.

Appendix B.3. *A. presbyter*. Photographs of a selection of saccular otoliths extracted from fish from Langstone Harbour (Scale = 1mm).

a. 0 group. Female, 56mm SL, caught on 15 September 1976.

b. I group. Female, 79mm SL, caught on 23 June 1977.

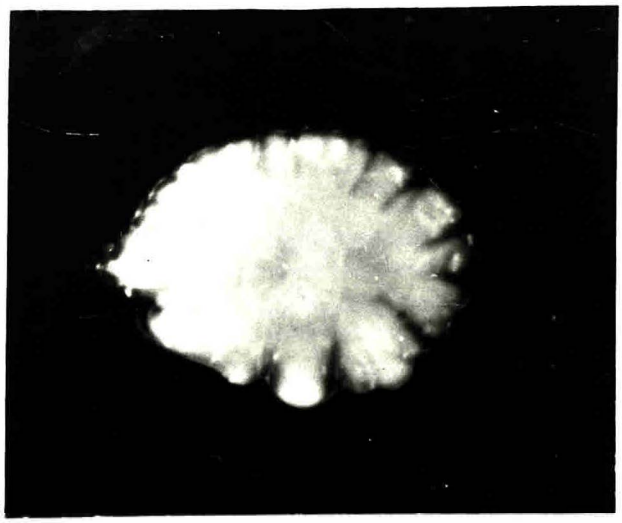
c. II group. Male, 108mm SL, caught on 23 June 1977.

d. III group. Female, 122mm SL, caught on 26 April 1976.

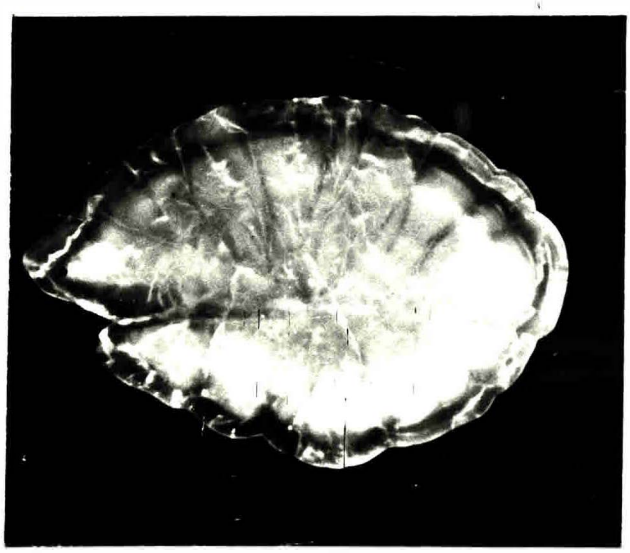
e. IV group. Female, 125mm SL, caught on 26 April 1976.

f. V group. Female, 133mm SL, caught on 26 April 1976.

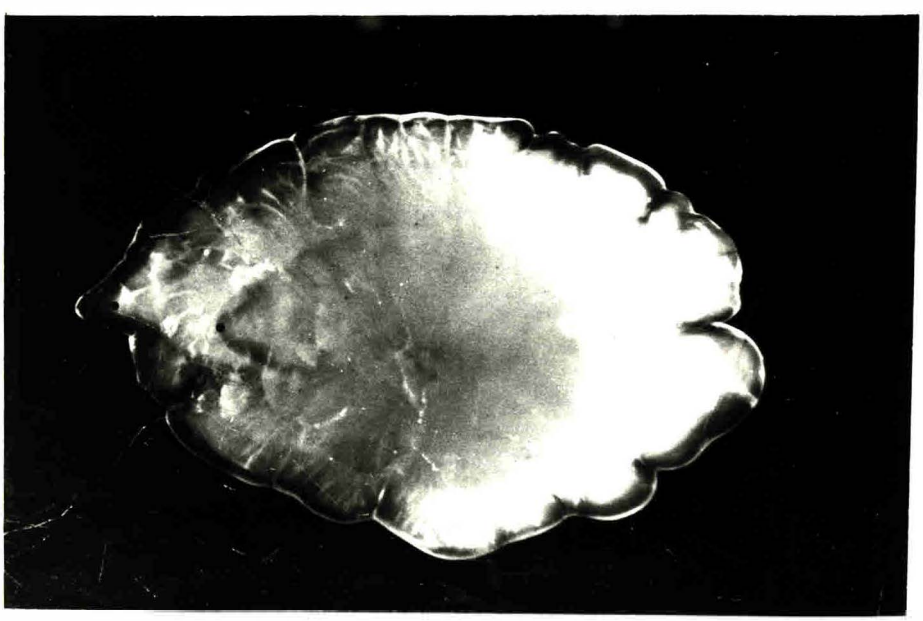
a



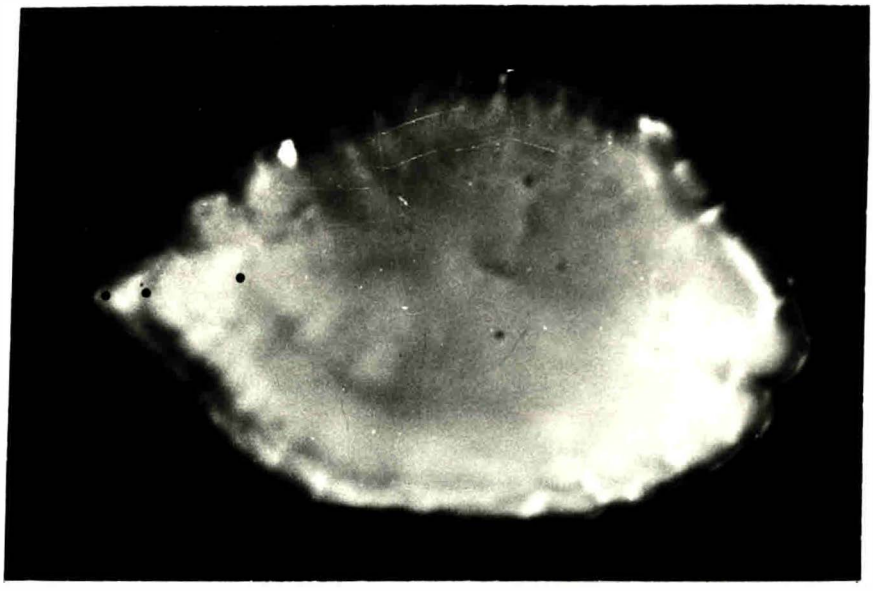
b



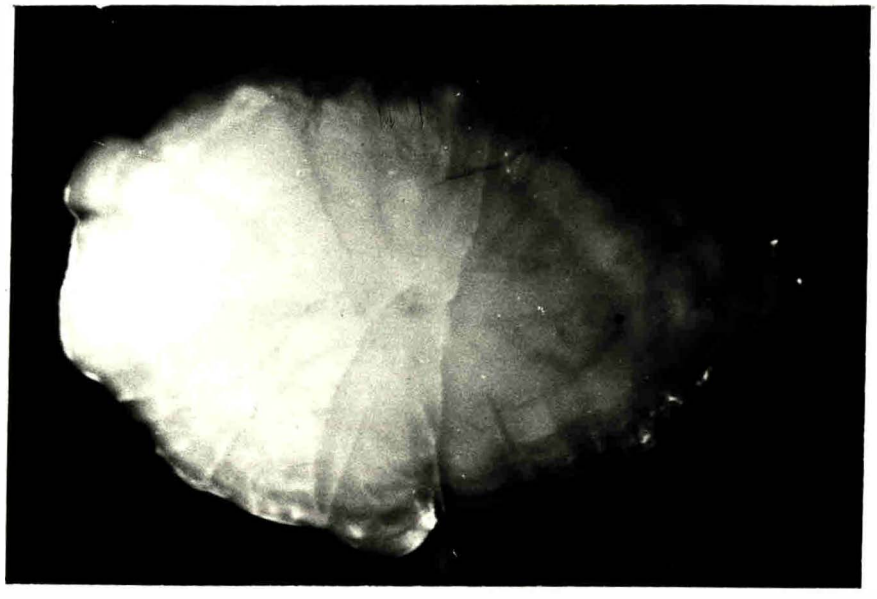
c



d



e



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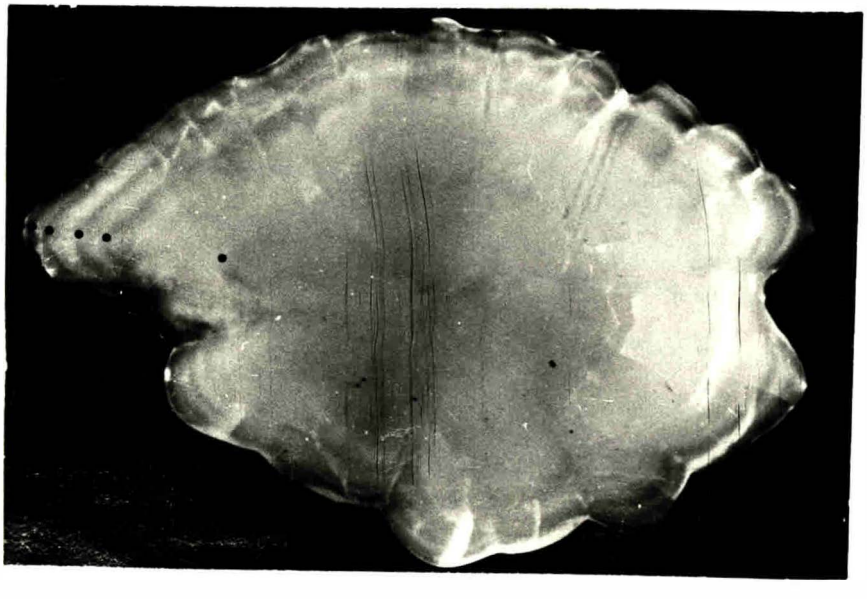


Appendix B.4. *A. presbyter*. Material at otolith edge.

a) Langstone

Date	Opaque N	Hyaline N
1975		
3 Sept	50	0
17 Sept	49	1
16 Oct	16	31
26 Nov	5	45
16 Dec	3	47
1976		
15 Jan	24	6
26 Feb	9	0
26 Apr	36	0
7 May	20	0
26 May	42	0
17 June	60	0
5 July	49	0
19 July	50	0
3 Aug	50	0
17 Aug	50	0
1 Sept	50	0
15 Sept	68	7
4 Oct	24	26
17 Nov	11	29

b) Fawley

Date	Opaque N	Hyaline N
1975		
Oct	17	18
Nov	4	29
Dec	24	6
1976		
Jan	46	0
Feb	41	0
Mar	35	0
Apr	46	0
May	33	0
June	32	0
July	33	0
Aug	63	0
Sept	64	1
Oct	22	29
Nov	0	40
Dec	0	39

Appendix B.5. *A. presbyter*. Length-frequency distribution data for Langstone Harbour

Mid points of length groups (mm)

	32 37	42 47	52 57	62 67	72 77	82 87	92 97	102 107	112 117	122 127	132 137	142 147	Total (N)
1975													
23 Apr							4	6	6	3	3	8	7	2	1		40
22 May				4	7	12	4	1	1	2	2	1	1	1	1		37
6 Jun					12	17	9	1		3	1	2					45
19 Jun			1		4	12	19	1		2	3	2	1				45
7 Jul				6	4	2	26	28	9				1				76
6 Aug		1			1	9	14	8	7	9	1						50
3 Sept		3	21	21	4	1											50
17 Sept	1	4	12	19	7	4	2		1								50
16 Oct		3	5	15	8	10	7	1		1							50
26 Nov		3	5	7	18	13	4										50
16 Dec	2	2	26	16	3	1											50

Appendix B.5. continued.

Mid points of length groups (mm)

	32	37	42	47	52	57	62	67	72	77	82	87	92	97	102	107	112	117	122	127	132	137	142	147	Total (N)
1976																									
15 Jan			3	5	12	20	9	1																	50
26 Feb			3	3	1	2																			9
26 Apr								2	1			1	5	3	3	7	2	4	2	3	3				36
7 May							1	1							2	1	5	4	4	1	1				20
26 May							2	9	10	3	1			5	7		2	1	1	1					42
17 Jun								6	11	16	7	1	2	6	4	5	1			1					60
5 Jul								2	12	17	6	6	4	1					1						49
19 Jul	12	33							1	1	2	1													50
3 Aug	2	5	11	10	2						5	5	6	4	1										51
17 Aug		3	23	12	4							3	2	1											50
1 Sept		4	19	12	12	1	1						1												50
15 Sept			3	16	13	18	2	2				3	10	1	3	3	1								75
4 Oct			1	12	21	9	5		2																50
17 Nov		1	4	9	24	9	2	1																	50

Appendix B.6. *A. presbyter*. Length frequency distribution data for Fawley

Mid points of length groups (mm)

	32 37	42 47	52 57	62 67	72 77	82 87	92 97	102 107	112 117	122 127	132 137	142 147	Total (N)
1975													
mid Jun to mid Jul				2 1	3 3	4 1		3	4 1	3			25
mid Jul to mid Aug		1 1	6 3	1		3 8	8 1			1 1			34
mid Aug to end Sept		2 2	9 8	8 2		1 5	7 4	1	1	1			51
Oct		1	4 16	7 8	4 1		1 1	3	1 2	1			50
Nov			1 10	10 11	4 2		2 3	1	4 1	1			50
Dec			1 1	6 4	2		1 2	2	2 4	2 2	1		30

Appendix B.6. continued.

Mid points of length groups (mm)

	32	37	42	47	52	57	62	67	72	77	82	87	92	97	102	107	112	117	122	127	132	137	142	147	Total (N)
1976																									
Jan					1	6	8	2	4			2	1	4	2	2	4	6	3		1				46
Feb						3	15	7	1	1		1	2	3	2	3	4	5	6						53
Mar						2	1	4		1			3	1	1	4	10	3	1	4					35
Apr						1	2	12	2	2			2	1	2	4	2	7	6	1	1		1		46
May					1		4	6	8		1				1		3	4	3	1	1				33
Jun							1	10	7	3	3		1		1	1	1	3	1						32
Jul				1	1					3	8	7	7	4			2								33
Aug			1	3	6	6	1	2		1	3	11	13	11	1		1	2	1						63
Sept			1	10	14	28	22	15	4		1		8	7	6	1	1	1							119
Oct					1	4	6	4	2	1		2	3	9	7	9	3	2	1						54
Nov					3	5	4	2	3				1	6	3	5	2	2	4						40
Dec					4	5	3	5	1					1	1	1	5	4	5	2	2				39

Appendix B.7.

a) *A. presbyter*. Occurrence of age groups by samples at Langstone

1975	0	I	II	III	IV	V	N
11 Feb		35					35
12 Mar		6					6
17 Apr		2			1		3
21 Apr			4	2	3		9
23 Apr			7	6	3		16
22 May		10	4	2	2		18
6 June		39	4	2			45
19 June		37	6	2			45
7 July		76	1				77
6 Aug	1	49					50
3 Sept	50						50
17 Sept	49	1					50
16 Oct	48	2					50
26 Nov	50						50
16 Dec	50						50
1976							
15 Jan		50					50
26 Feb		9					9
26 Apr		3	15	11	3	4	36
7 May		2	2	10	3	3	20
26 May		25	12	3		2	42
17 June		41	16	2		1	60
5 July		47	1	1			49
19 July	45	5					50
3 Aug	29	20	1				50
17 Aug	44	6					50
1 Sept	49	1					50
15 Sept	54	20	1				75
4 Oct	50						50
17 Nov	50						50
16 Dec	2						2

Appendix B.7. a) continued

	0	I	II	III	IV	V
Combined number		322*	74	41	15	10
% frequency		69.7	16.0	8.9	3.2	2.2
Annual % mortality		77.0	44.4	64.0	31.2	

* N.B. Only from samples which contained II+ fish

Appendix B.7. b) Fawley

	0	I	II	III	IV	V	N
1975							
Oct	41	7	2				50
Nov	38	6	4	2			50
Dec	14	5	7	4			30
1976							
Jan		21	10	12	3		46
Feb		27	8	14	4		53
Mar		8	5	16	3	3	35
Apr		19	7	16	2	2	46
May		20	1	11	1		33
June		24	4	3	1		32
July	2	29	1	1			33
Aug	19	39	2	3			63
Sept	94	23	2				119
Oct	18	25	8	3			54
Nov	17	15	4	4			40
Dec	18	5	10	5			39
Combined Number	-	273	75	94	15	5	
% frequency		59.1	16.2	20.3	3.2	1.1	
Annual % Mortality			72.6	-25.3	84.2	65.6	

APPENDIX C

Appendix C.1. A comparison of seasonal fluctuations in the 'wet' and 'dry' weights of body components for *Atherina presbyter*.

Introduction

In 6.3.5. the seasonal fluctuations in the 'wet' weight of mesenteric lipid, liver, intestine and gonad were recorded as body component-somatic indices. To investigate whether such fluctuations were changes in actual organic matter or were due to variations in fluid retention, corresponding 'dry' body component-somatic indices were calculated for comparison. However, these were only recorded for II+ *A. presbyter* from Fawley during 1976. This was because for 0 and I group fish the weights involved were so small that the percentage error involved was too great and II+ Langstone fish were of such restricted occurrence.

Method and Materials

After removal and the 'wet' weight recorded, the carcass, mesenteric lipid, liver, intestine and gonad were placed in separate aluminium foil containers of known weight. These were placed in an oven and dried for 48 hours at 100°C by which time a constant dry weight was achieved. Temperatures from 50 to 105°C have been recommended for drying biological samples (Winberg 1971) and the temperature of 100°C was chosen so as to decrease the time for a constant weight to be reached. Immediately after removal from the oven the containers were weighed to the nearest 0.0025 gram and the dried weights deduced. For comparative purposes each 'dry' body component weight was then expressed as a percentage of the 'dry' carcass weight.

Results

The monthly mean 'dry' and 'wet' body component indices are given in Table C.1.1 and plotted in Fig. C.1.1. Sexes were not separated.

a) Mesenteric lipid weight (Fig. C.1.1.a)

In all samples the 'dry' index was higher than the corresponding 'wet' index and showed a much larger mean variation, almost 18% compared to five and a half percent. The seasonal fluctuations in the 'dry' index mirrored those of the 'wet' index although were more exaggerated. Thus it may be concluded that seasonal fluctuations in the mean 'wet' mesenteric lipid-somatic index reflect changes in actual organic matter.

b) Gonad weight (Fig. C.1.1.b)

The mean 'wet' and 'dry' gonadosomatic indices were almost identical except during May and June, the peak spawning period, when the mean 'dry' index was slightly higher. Thus again, not surprisingly, it may be concluded that seasonal fluctuations in the mean 'wet' gonadosomatic index reflect changes in actual organic matter.

c) Liver weight (Fig. C.1.1.c)

The mean 'dry' hepatosomatic index was always higher than the 'wet' index and showed a larger mean variation. Except for the November sample seasonal fluctuations in the mean 'dry' index mirrored those in the 'wet' index, which again implies that variations in the mean 'wet' hepatosomatic index reflect changes in actual organic matter.

d) Intestine weight (Fig. C.1.1.d)

In contrast to the other body components, the 'wet' intestine-

Table C.1.1. *A. presbyter* Comparison of wet and dry body component indices of II+ fish from Fawley during 1976

	Mesenteric lipid-somatic		Gonadosomatic		Hepatosomatic		Intestinal-somatic		N
	wet	dry	wet	dry	wet	dry	wet	dry	
Mar	0.95	3.25	3.22	3.06	1.99	2.25	3.66	2.19	20
Apr	1.04	3.38	6.02	6.00	2.56	2.82	2.94	2.18	19
May	0.33	0.39	17.26	18.97	4.40	5.67	2.93	1.79	10
Jun	0.55	0.96	11.58	13.74	4.27	5.56	6.61	3.64	8
Jul									
Aug	4.08	12.03	0.28	0.26	2.83	4.40	2.88	2.62	3
Sep									
Oct									
Nov	5.80	18.15	0.72	0.74	2.50	4.58	2.69	2.49	8
Dec	4.75	15.56	1.18	1.16	2.22	3.70	2.49	2.17	16

Figure C.1.1.

A. presbyter A comparison of 'wet' and 'dried' body component indices.

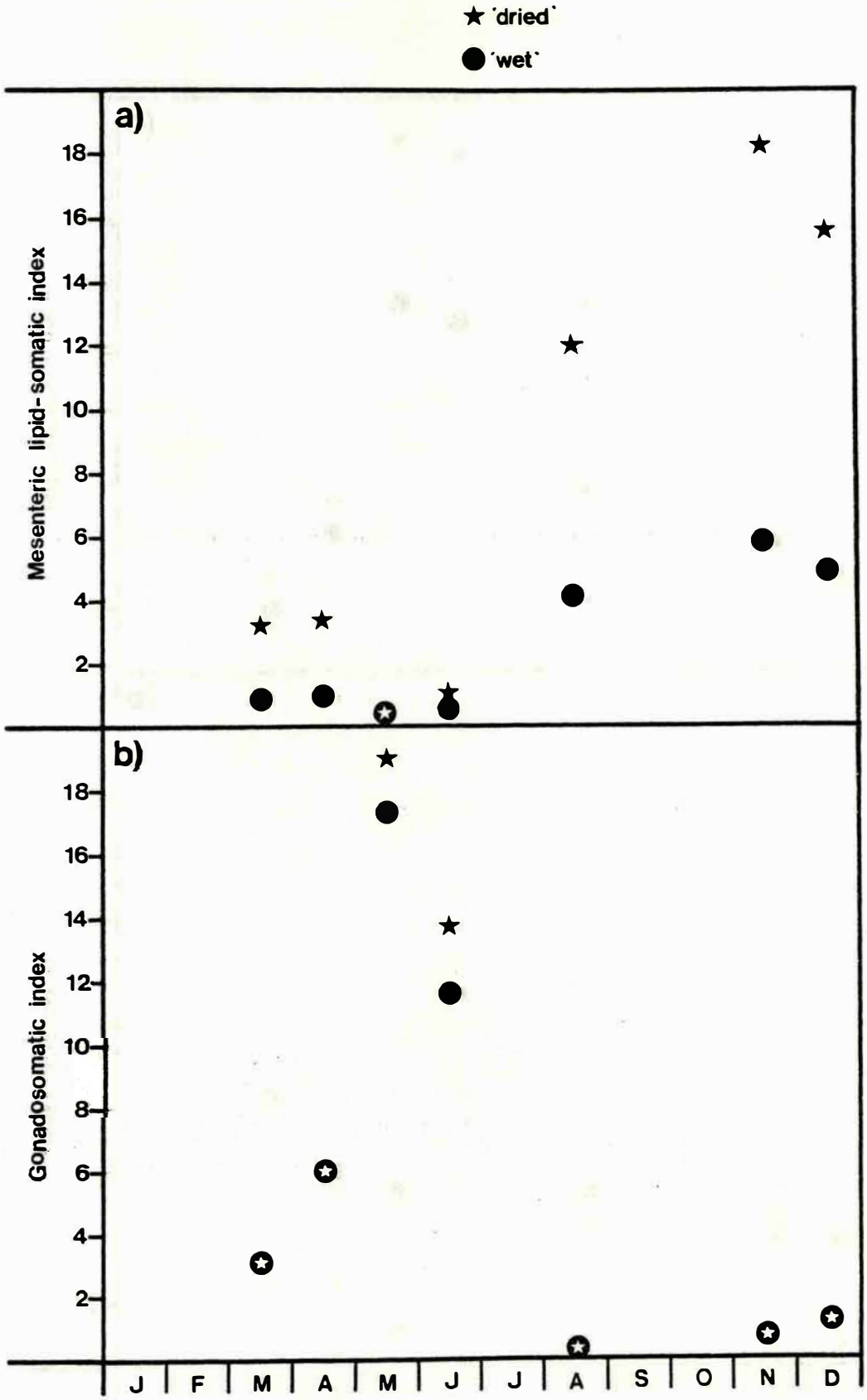
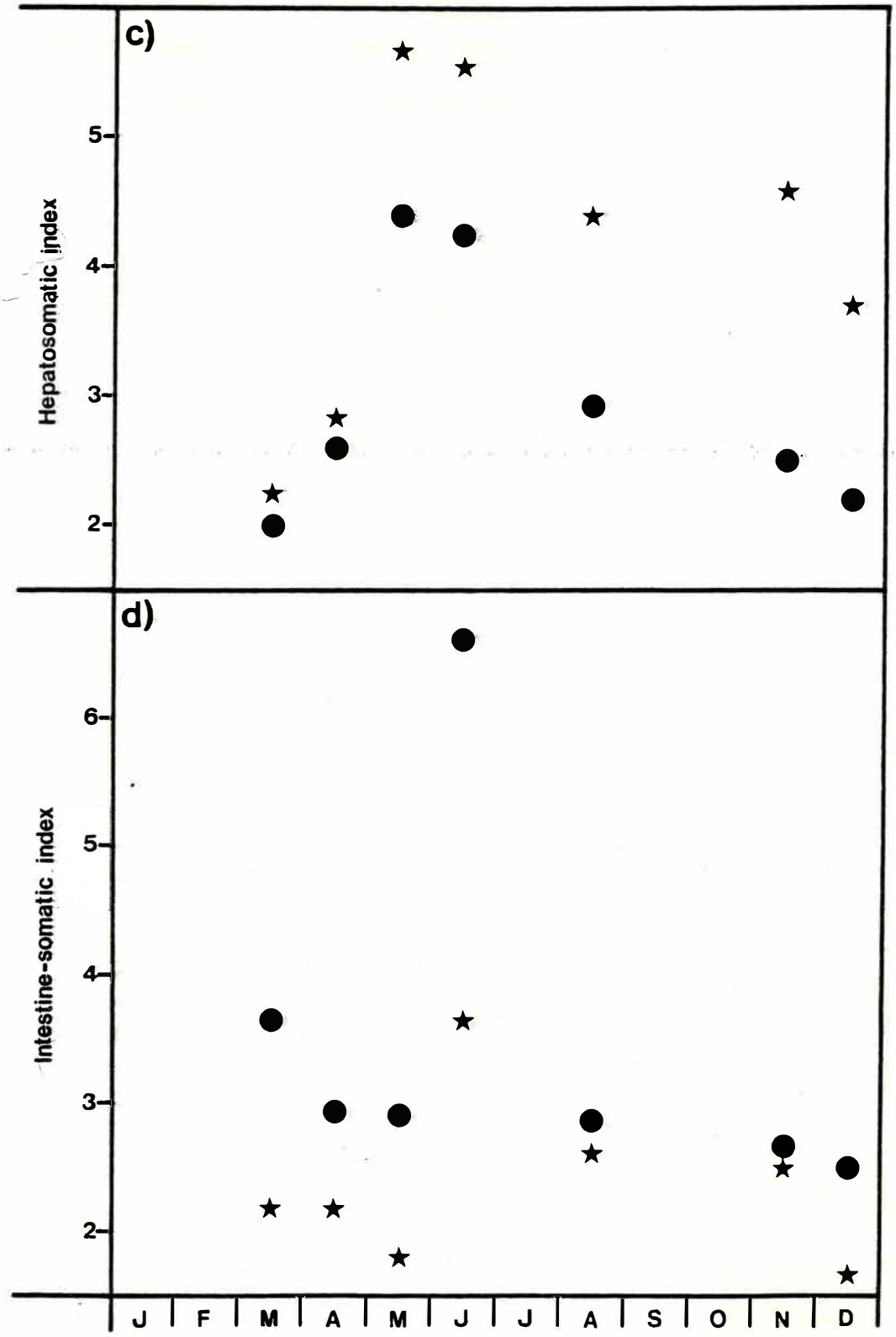


Figure C.11. continued.



somatic indices were higher than the 'dry' indices and showed a larger mean variation. There also seemed to be less correlation between the two indices implying some variation in water retention. This was not unexpected and was probably due to variation in food material and the amount of digestive juices and absorbed preservative within the gut.

Appendix C.2. *A. presbyter* Mean standard lengths (mm) of age-groups, sexes combined.

a) Langstone	$\bar{x}$	0 95% C.L.	N	$\bar{x}$	I 95% C.L.	N	$\bar{x}$	II 95% C.L.	N	$\bar{x}$	III 95% C.L.	N	$\bar{x}$	IV 95% C.L.	N	$\bar{x}$	V 95% C.L.	N
1975																		
11 Feb				57.40	±2.29	35												
12 Mar				57.33	±6.22	6												
17/23 Apr				63.00		2	104.52	±2.00	21	120.93	±2.19	14	128.53	±2.48	15			
22 May				70.26	±1.79	27	100.33	±5.04	6	121.00	-	1	135.00	-	2			
6 Jun				71.85	±1.27	39	101.25	-	4	115.50	-	2						
19 Jun				73.68	±1.43	37	101.50	±3.80	6	118.00	-	1						
7 Jul				78.55	±1.43	76	111.00	-	1									
6 Aug	46.00	-	1	81.51	±2.15	49												
3 Sep	49.66	±1.21	50															
17 Sep	52.10	±1.86	49	82.00	-	1												
16 Oct	55.75	±2.04	48	85.00	-	2												
26 Nov	56.64	±1.72	50															
16 Dec	43.88	±1.37	50															

Appendix C.2. continued.

	$\bar{x}$	0 95% C.L.	N	$\bar{x}$	I 95% C.L.	N	$\bar{x}$	II 95% C.L.	N	$\bar{x}$	III 95% C.L.	N	$\bar{x}$	IV 95% C.L.	N	$\bar{x}$	V 95% C.L.	N
1976																		
15 Jan				55.12	±1.66	50												
26 Feb				48.00	±4.37	9												
26 Apr				68.67	-	3	97.47	±3.10	15	113.27	±4.02	11	124.33	-	3	130.75	-	4
7 May				66.00	-	2	102.00		2	115.30	±3.22	10	120.67	-	3	128.33	-	3
26 May				70.00	±1.91	25	100.42	±1.15	12	113.66	-	3				123.50	-	2
17 Jun				75.20	±1.51	41	99.88	±3.45	17	110.00	-	1				128.00	-	1
5 Jul				78.23	±1.81	47	98.00	-	1	120.00	-	1						
19 Jul	35.76	±0.65	45	80.00	±4.97	5												
3 Aug	42.87	±2.00	30	89.70	±2.44	20	92.00	-	1									
17 Aug	44.77	±1.43	47	90.33	±5.30	6												
1 Sep	45.73	±1.58	49	93.00	-	1												
15 Sep	52.31	±1.50	54	94.85	±3.06	20	113.00	-	1									
4 Oct	53.30	±1.74	50															
17 Nov	51.88	±1.47	50															
16 Dec	40.00	-	2															

Appendix C.2. continued.

b) Fawley	$\bar{x}$	0 95% C.L.	N	$\bar{x}$	I 95% C.L.	N	$\bar{x}$	II 95% C.L.	N	$\bar{x}$	III 95% C.L.	N	$\bar{x}$	IV 95% C.L.	N	$\bar{x}$	V 95% C.L.	N
1975																		
mid Jul -mid Aug	53.25	±3.13	12															
mid Aug -end Sep	55.30	±2.16	30															
Oct	60.98	±1.93	41	101.14	±5.79	7	114.50	-	2									
Nov	63.53	±1.95	38	96.00	±5.59	6	112.25	-	4	123.00	-	2						
Dec	63.57	±2.93	14	97.40	±3.87	5	111.57	±2.92	7	121.75	-	4						
1976																		
Jan				63.00	±2.69	21	96.70	±4.49	10	115.33	±2.47	12	124.33	-	3			
Feb				63.33	±1.63	27	96.13	±4.57	8	113.64	±3.09	14	122.00	-	4			
Mar				65.37	±4.89	8	94.60	±5.66	5	111.20	±1.72	15	122.33	-	3	126.33	-	3
Apr				68.05	±2.26	19	98.83	±7.43	6	116.12	±2.67	17	124.50	-	2	133.00	-	1
May				67.95	±2.59	20	102.00	-	1	119.45	±3.58	11	117.00	-	1			
Jun				71.63	±2.36	24	104.25	-	4	116.67	-	3	123.00	-	1			
Jul	48.50	-	2	87.21	±2.22	29	110.00	-	1	113.00	-	1						
Aug	54.16	±2.97	19	91.00	±1.90	39	104.00	-	2	118.33	-	3						

Appendix C.2. continued.

	$\bar{x}$	0 95% C.L.	N	$\bar{x}$	I 95% C.L.	N	$\bar{x}$	II 95% C.L.	N	$\bar{x}$	III 95% C.L.	N	$\bar{x}$	IV 95% C.L.	N	$\bar{x}$	V 95% C.L.	N
Sep	58.29	±1.38	94	96.13	±2.34	23	115.50	-	2									
Oct	63.33	±3.14	18	98.64	±2.12	25	108.88	±3.30	8	116.00	-	3						
Nov	61.12	±3.41	17	101.27	±2.41	15	116.25	-	4	19.75	-	4						
Dec	60.39	±3.08	18	104.80	±8.11	5	116.86	±3.18	7	123.38	±4.69	8	132.00	-	1			

Appendix C.3. *A. presbyter* Mean body weight (g) of age-groups, sexes combined.

a) Langstone	O $\bar{x}$	O 95% C.L.	O N	I $\bar{x}$	I 95% C.L.	I N	II $\bar{x}$	II 95% C.L.	II N	III $\bar{x}$	III 95% C.L.	III N	IV $\bar{x}$	IV 95% C.L.	IV N	V $\bar{x}$	V 95% C.L.	V N
1975																		
11 Feb				1.58	±0.19	34												
12 Mar				1.45	±0.50	6												
17/24 Apr				1.95	-	2	11.28	±0.76	21	17.72	±1.91	13	20.98	±1.78	16			
22 May				3.45	±0.26	27	10.50	±1.61	6	18.15	-	1	22.15	-	2			
6 Jun				3.96	±0.23	39	10.86	-	4	16.42	-	2						
19 Jun				4.35	±0.29	37	11.98	±2.27	6	17.10	-	2						
7 Jul				5.63	±0.35	59	15.52	-	1									
6 Aug	1.09	-	1	6.57	±0.53	49												
3 Sep	1.31	±0.10	50															
17 Sep	1.53	±0.18	49	6.11	-	1												
16 Oct	1.87	±0.22	48	6.77	-	2												
26 Nov	1.87	±0.17	50															
16 Dec	0.79	±0.08	50															

Appendix C.3. continued.

	O $\bar{x}$	O 95% C.L.	O N	I $\bar{x}$	I 95% C.L.	I N	II $\bar{x}$	II 95% C.L.	II N	III $\bar{x}$	III 95% C.L.	III N	IV $\bar{x}$	IV 95% C.L.	IV N	V $\bar{x}$	V 95% C.L.	V N
1976																		
15 Jan				1.62	±0.14	50												
26 Feb				0.99	±0.30	9												
26 Apr				3.66	-	3	10.60	±0.94	15	15.95	±1.81	11	24.03	-	3	26.46	-	4
7 May				3.19	-	2	11.38	-	2	17.65	±1.98	10	20.64	-	3	24.73	-	3
26 May				3.93	±0.39	25	11.72	±0.64	12	16.24	-	3				20.08	-	2
17 Jun				4.79	±0.33	42	11.72	±1.19	17	16.48	-	1				25.36	-	1
5 Jul				5.63	±0.45	47	11.96	-	1	20.37	-	1						
19 Jul	0.46	±0.03	44	5.89	±1.43	5												
3 Aug	0.81	±0.11	30	8.60	±0.76	20	8.37	-	1									
17 Aug	0.94	±0.10	47	8.55	±2.25	6												
1 Sep	0.97	±0.11	49	9.53	-	1												
15 Sep	1.45	±0.14	54	10.04	±1.16	20	19.04	-	1									
4 Oct	1.47	±0.18	50															
17 Nov	1.38	±0.13	50															
16 Dec	0.50	-	2															

Appendix C.3. continued.

b) Fawley	O $\bar{x}$	O 95% C.L.	O N	I $\bar{x}$	I 95% C.L.	I N	II $\bar{x}$	II 95% C.L.	II N	III $\bar{x}$	III 95% C.L.	III N	IV $\bar{x}$	IV 95% C.L.	IV N	V $\bar{x}$	V 95% C.L.	V N
1975																		
mid Jul -mid Aug	1.57	±0.26	12															
mid Aug -end Sep	1.78	±0.23	30															
Oct	2.31	±0.25	41	11.84	±2.46	7	17.42	-	2									
Nov	2.60	±0.27	38	9.98	±2.34	6	16.64	-	4	22.07	-	2						
Dec	2.64	±0.39	14	10.46	±2.44	5	16.30	±0.94	7	20.09	-	4						
1976																		
Jan				2.52	±0.37	21	9.75	±1.35	10	17.52	±1.68	12	21.22	-	3			
Feb				2.31	±0.22	27	9.05	±1.39	8	15.54	±1.56	14	17.66	-	4			
Mar				2.75	±0.67	8	9.27	±1.60	5	15.38	±0.93	16	19.78	-	3	22.20	-	3
Apr				3.07	±0.35	19	10.52	±2.54	6	18.09	±1.65	17	21.89	-	2	26.74	-	2
May				3.38	±0.44	20	12.82	-	1	20.55	±2.46	11	19.40	-	1			
Jun				4.10	±0.49	24	15.29	-	4	19.17	-	3	19.11	-	1			
Jul	1.05	-	2	7.58	±0.74	28	13.48	-	1	16.74	-	1						
Aug	1.64	±0.29	19	8.58	±0.62	39	13.47	-	2	19.79	-	3						

Appendix C.3. continued.

	0			I			II			III			IV			V		
	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.	N
Sep	1.94	±0.19	65	10.05	±0.82	23	17.60	-	2									
Oct	2.54	±0.43	18	11.01	±0.78	25	15.51	±2.05	8	17.27	-	3						
Nov	2.33	±0.45	17	12.09	±1.07	15	18.34	-	4	19.65	-	4						
Dec	2.25	±0.41	18	12.51	±3.07	5	17.51	±2.10	7	21.58	±2.41	8	27.87	-	1			

Appendix C.4. *A. presbyter* Average daily instantaneous growth rates for the 1975 year-class at Fawley during 1975 and 1976.

	In body length	In body weight
1975		
mid July-mid August	0.1219	0.4050
mid Aug.-end Sept.	0.2126	0.5666
Oct.	0.1321	0.3815
Nov.	0.0021	0.0509
Dec.	-0.0291	-0.1501
1976		
Jan.	0.0169	-0.2807
Feb.	0.1093	0.6012
Mar.	0.1296	0.3551
Apr.	-0.0049	0.3207
May	0.1701	0.6229
June	0.6560	2.0484
July	0.1372	0.3997
Aug.	0.1769	0.5101
Sept.	0.0859	0.3041
Oct.	0.0849	0.3018
Nov.	0.1231	0.1138
Dec.		

Appendix C.5. *A. presbyter* Annual growth with respect to age (for conditions see text).

Age-group	$\bar{x}$	95% C.L.	N	Range	Annual growth rate
a) Length					
Fawley					
0	62.6456	±1.2190	79	52- 76	
I	98.5926	±2.3000	27	87-107	43.35
II	114.3500	±1.4455	40	106-124	14.83
III	122.8947	±2.4255	19	115-132	7.21
IV					
Langstone					
0	52.6959	±1.1209	194	33- 69	
I					
b) Weight					
Fawley					
0	2.4113	±0.1640	80	1.25- 4.44	
I	10.1679	±0.8535	28	6.39-14.41	143.91
II	16.6110	±0.7999	40	11.24-21.13	49.08
III	20.3858	±1.4728	19	16.22-23.65	20.48
IV					

Appendix C.6. *A. presbyter* Length-weight relationship

Body weights derived by substituting standard lengths into $W = aL^b$ using respective constants from Table 6.1.

S.L. mm	Langstone Body Wt (g) ♂	Langstone Body Wt (g) ♀	Fawley Body Wt (g) ♂	Fawley Body Wt (g) ♀
33	0.33			
36		0.45		
40	0.61	0.62		
43				0.71
49			1.11	
50	1.24	1.25	1.18	1.17
60	2.21	2.22	2.12	2.11
70	3.60	3.60	3.49	3.49
80	5.50	5.47	5.36	5.39
90	7.99	7.92	7.84	7.91
100	11.17	11.03	11.00	11.15
110	15.11	14.88	14.96	15.21
120	19.91	19.55	19.79	20.20
130	25.66	25.14	25.62	26.22
131	26.30			
132				27.55
133			27.57	
137		29.64		

Appendix C.7.a. *A. presbyter* Mean 'wet' ponderal and body component indices for age-groups 0, I, II+, sexes separated, at Langstone.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
1975 11 Feb	I	♂♂	3.66	±0.17	16				0.95	±0.17	10	2.59	±0.35	10	2.67	±0.32	10
		♀♀	3.40	±0.15	18				1.20	±0.19	10	2.28	±0.35	10	2.78	±0.26	10
12 Mar	I	♂♂	3.36		4				1.29		4	3.05		4	3.64		4
		♀♀	3.27		2				1.55		2	2.81		2	3.10		2
17/23 Apr	I	♂♂															
		♀♀	3.40		2				1.96		2	2.52		2	5.08		2
	II+	♂♂	3.80	±0.12	18				11.53	±1.09	5	1.66	±0.41	5	1.88	±0.26	5
		♀♀	3.88	±0.13	32				12.28	±3.05	15	3.84	±0.31	15	3.25	±0.41	15
22 May	I	♂♂	4.19	±0.31	14				6.63	±1.72	7	1.92	±0.50	7	3.42	±0.83	7
		♀♀	4.14	±0.16	7				7.17		2	3.54		2	4.26		2
	II+	♂♂	3.93		1				9.18		1	2.16		1	1.75		1
		♀♀	3.75	±0.46	7				18.16	±9.39	5	2.87	±1.24	5	2.53	±0.33	5
6 Jun	I	♂♂	4.40	±0.12	19				3.97	±0.96	15	2.14	±0.17	15	4.13	±0.29	15
		♀♀	4.59	±0.17	20				8.00	±2.58	15	3.66	±0.47	15	4.15	±0.48	15
	II+	♂♂	3.77		1				4.12		1	1.03		1	3.09		1
		♀♀	4.21	±0.17	5				12.50	±6.01	5	5.82	±0.90	5	5.66	±2.39	5
19 Jun	I	♂♂	4.43	±0.17	18	0.37	±0.23	15	1.40	±0.28	15	1.80	±0.11	15	5.05	±1.02	15
		♀♀	4.65	±0.14	19	0.70	±0.23	15	3.11	±0.99	15	3.11	±0.27	15	4.98	±0.78	15
	II+	♂♂	4.38	±0.48	5	0.31	±0.24	5	5.71	±2.36	5	2.88	±0.90	5	3.57	±0.91	5
		♀♀	4.74		3	0.79		3	7.04		3	6.61		3	5.80		3

Appendix C.7.a. continued.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
7 Jul	I	♂	4.68	±0.13	21	1.77	±0.22	15	0.57	±0.16	15	3.05	±0.38	15	3.67	±0.29	15
		♀	4.68	±0.10	28	2.46	±0.42	15	0.65	±0.17	15	3.58	±0.33	15	4.12	±0.49	15
	II+	♂															
		♀	4.42		1	1.82		1	4.91		1	6.14		1	2.68		1
6 Aug	I	♂	4.91	±0.11	21	3.57	±0.47	15	0.22	±0.04	15	3.63	±0.34	15	4.58	±0.38	15
		♀	4.92	±0.19	28	3.75	±0.68	15	0.29	±0.03	15	3.42	±0.35	15	4.07	±0.42	15
3 Sep	0	♂	4.91	±0.12	23	1.07	±0.27	15	0.00	±0.00	15	1.76	±0.18	15	5.05	±0.56	15
		♀	4.72	±0.10	27	1.24	±0.39	15	0.11	±0.05	15	1.87	±0.18	15	5.55	±0.55	15
17 Sep	0	♂	4.66	±0.09	26	1.54	±0.66	15	0.01	±0.00	15	1.72	±0.19	15	4.51	±0.45	15
		♀	4.63	±0.07	23	1.12	±0.40	15	0.15	±0.05	15	1.52	±0.09	15	4.36	±0.57	15
16 Oct	0	♂	4.57	±0.11	20	2.17	±0.60	15	0.00	±0.00	15	2.05	±0.32	15	5.73	±0.74	15
		♀	4.60	±0.10	28	2.11	±0.56	15	0.27	±0.00	15	1.96	±0.23	15	4.67	±0.45	15
26 Nov	0	♂	4.39	±0.10	28	2.88	±0.37	15	0.08	±0.03	15	2.96	±0.38	15	3.76	±0.27	15
		♀	4.45	±0.08	22	2.81	±0.39	15	0.25	±0.04	15	3.04	±0.28	15	3.64	±0.29	15
16 Dec	0	♂	4.17	±0.10	29	2.28	±0.38	15	0.00	±0.00	15	2.96	±0.37	15	3.65	±0.38	15
		♀	4.23	±0.14	21	2.08	±0.36	15	0.05	±0.06	15	3.04	±0.54	15	3.05	±0.34	15
1976																	
15 Jan	I	♂	4.22	±0.06	30	1.80	±0.38	15	0.11	±0.05	15	2.19	±0.29	15	4.12	±0.51	15
		♀	4.19	±0.11	20	1.84	±0.42	15	0.38	±0.09	15	2.16	±0.32	15	4.36	±0.54	15
26 Feb		♂	3.84	±0.25	5	0.40	±0.29	5	0.16	±0.18	5	2.48	±0.72	5	3.10	±0.69	5
		♀	4.07		4	0.53		4	0.51		4	2.41		4	3.63		4

Appendix C.7.a. continued.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
26 Apr	I	♂♂	4.83		3	0.53		3	6.97		3	2.66		3	7.10		3
		♀♀															
	II+	♂♂	4.28	±0.22	10	0.24	±0.10	10	9.89	±1.23	10	1.59	±0.25	10	4.20	±0.61	10
		♀♀	4.54	±0.13	23	0.62	±0.41	10	11.73	±2.39	10	4.78	±0.68	10	5.26	±0.73	10
7 May	I	♂♂	4.82		2	1.13		2	5.92		2	2.67		2	4.88		2
		♀♀															
	II+	♂♂	4.39		2	0.29		2	9.13		2	1.57		2	3.87		2
		♀♀	4.43	±0.25	16	0.35	±0.18	10	11.43	±1.18	10	4.94	±0.44	10	6.63	±1.09	10
26 May	I	♂♂	4.69	±0.15	10	0.91	±0.53	10	4.05	±1.82	10	1.69	±0.09	10	5.75	±1.18	10
		♀♀	4.90	±0.24	15	1.58	±0.70	10	3.68	±2.14	10	2.88	±1.18	10	5.73	±1.07	10
	II+	♂♂	4.19		4	0.14		4	9.12		4	1.86		4	5.07		4
		♀♀	4.58	±0.21	13	0.24	±0.20	10	12.84	±3.46	10	5.35	±0.47	10	5.98	±0.39	10
17 Jun	I	♂♂	4.59	±0.13	24	1.33	±0.75	10	0.77	±0.31	10	1.77	±0.23	10	5.51	±1.53	10
		♀♀	4.68	±0.12	18	2.73	±0.86	10	1.29	±1.41	10	2.29	±0.35	10	4.90	±0.67	10
	II+	♂♂	4.47		3	1.32		3	2.78		3	2.68		3	4.14		3
		♀♀	4.69	±0.15	15	0.89	±0.46	10	8.73	±1.79	10	5.13	±0.53	10	5.77	±1.10	10
5 Jul	I	♂♂	4.81	±0.10	27	4.26	±0.84	10	0.20	±0.06	10	2.72	±0.42	10	5.25	±1.53	10
		♀♀	4.80	±0.13	20	3.34	±0.59	10	0.29	±0.09	10	3.04	±0.40	10	3.93	±0.42	10
	II+	♂♂	5.08		1	3.82		1	0.59		1	4.90		1	3.44		1
		♀♀	4.52		1	1.41		1	5.00		1	2.91		1	9.19		1
19 Jul	0	♂♂	4.80	±0.17	24												
		♀♀	4.86	±0.21	21												
	I	♂♂	4.92		3	4.17		3	0.16		3	3.20		3	4.48		3
		♀♀	4.51		2	3.74		2	0.28		2	2.04		2	2.56		2

Appendix C.7.a. continued.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
3 Aug	0	♂	4.69	±0.15	11												
		♀	4.54	±0.20	19												
	I	♂	4.72	±0.19	10	5.46	±0.74	10	0.10	±0.03	10	3.02	±0.61	10	3.78	±0.44	10
		♀	4.88	±0.16	10	6.10	±1.11	10	0.25	±0.04	10	3.17	±0.61	10	3.39	±0.52	10
	II+	♂															
		♀	4.35		1	0.64		1	0.71		1	2.57		1	3.73		1
17 Aug	0	♂	4.71	±0.13	25												
		♀	4.77	±0.15	22												
	I	♂	4.60		3	5.63		2	0.27		2	3.08		2	6.42		2
		♀	4.67		3	6.39		1	0.12		1	3.86		1	4.53		1
1 Sep	0	♂	4.59	±0.18	22												
		♀	4.47	±0.15	27												
	I	♂	4.79		1	4.81		1	0.15		1	2.29		1	4.45		1
		♀															
15 Sep	0	♂	4.32	±0.12	29												
		♀	4.50	±0.13	25												
	I	♂	4.71	±0.26	10	5.27	±1.48	10	0.10	±0.03	10	2.47	±0.48	10	5.07	±1.17	10
		♀	4.58	±0.12	10	7.18	±1.13	10	0.34	±0.10	10	2.60	±0.49	10	3.04	±0.07	10
	II+	♂															
		♀	5.13		1	8.44		1	0.49		1	5.21		1	3.97		1
4 Oct		♂	4.22	±0.13	22												
		♀	4.13	±0.08	28												
17 Nov	0	♂	4.27	±0.12	26												
		♀	4.26	±0.15	24												

Appendix C.7.a. continued.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
16 Dec	0	♂♂ ♀♀	3.63		2												

Appendix C.7.b. *A. presbyter* Mean 'wet' ponderal and body component indices for age-groups 0, I and II+, sexes separated, at Fawley.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
1975	0	♂♂															
		♀♀															
mid Jun	I	♂♂	4.32	±0.47	8	1.00	±0.83	6	0.38	±0.36	6	1.60	±0.36	6	5.77	±3.45	6
-mid Jul		♀♀	4.79	±0.30	6	1.77		4	0.49		4	2.49		4	4.73		4
	II+	♂♂	4.38	±0.36	5	1.42	±1.14	5	0.75	±0.65	5	2.63	±0.80	5	4.33	±4.04	5
		♀♀	4.57	±0.48	6	0.38	±0.31	5	5.58	±2.63	5	3.44	±0.52	5	5.65	±3.34	5
	0	♂♂	4.69	±0.32	6												
		♀♀	4.53	±0.28	6												
mid Jul	I	♂♂	4.54	±0.28	11	3.46		4	0.15		4	3.34		4	2.75		4
-mid Aug		♀♀	4.21	±0.34	9	2.56	±0.97	5	0.39	±0.22	5	2.04	±0.43	5	3.26	±0.59	5
	II+	♂♂															
		♀♀	4.04		2	3.34		2	0.56		2	2.81		2	2.11		2
	0	♂♂	4.55	±0.23	16	1.28	±0.36	10	0.00		10	1.66	±0.33	10	4.26	±1.21	10
		♀♀	4.53	±0.22	14	0.83	±0.21	10	0.10	±0.07	10	1.41	±0.28	10	3.96	±0.80	10
mid Aug	I	♂♂	4.78	±0.41	9	3.55	±1.21	7	0.12	±0.05	7	3.47	±2.39	7	4.96	±1.93	7
-end Sep		♀♀	4.53	±0.19	9	3.27	±1.14	7	0.30	±0.08	7	3.31	±0.97	7	3.07	±0.72	7
	II+	♂♂	4.00		2	2.96		2	0.37		2	2.91		2	2.40		2
		♀♀															
	0	♂♂	4.23	±0.10	19	1.45	±0.55	10	0.08	±0.04	10	2.05	±0.33	10	3.28	±0.63	10
		♀♀	4.40	±0.12	22	2.18	±0.37	10	0.26	±0.09	10	2.22	±0.57	10	3.21	±0.50	10
Oct	I	♂♂	4.68		3	3.63		2	0.25		2	2.75		2	2.33		2
		♀♀	4.33		4	4.08		4	0.59		4	2.52		4	2.57		4
	II+	♂♂	5.18		1	4.55		1	0.20		1	1.82		1	3.88		1
		♀♀	4.47		2	3.79		2	0.89		2	2.74		2	3.64		2

Appendix C.7.b. continued.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
Nov	0	♂	4.36	±0.15	19	2.46	±0.29	10	0.10	±0.04	10	2.71	±0.65	10	2.81	±0.32	10
		♀	4.23	±0.14	19	2.87	±0.74	10	0.31	±0.08	10	2.68	±0.27	10	2.56	±0.28	10
	I	♂	4.49		2	4.26		2	0.26		2	2.10		2	2.11		2
		♀	4.46		4	3.59		4	0.79		4	2.18		4	3.04		4
	II+	♂	4.36		2	5.24		2	0.35		2	2.16		2	2.49		2
		♀	4.66		4	4.83		4	1.25		4	3.47		4	2.80		4
Dec	0	♂	4.34	±0.14	11	1.67	±0.45	11	0.13	±0.06	10	2.16	±0.30	10	2.90	±0.35	10
		♀	4.49		3	2.41		3	0.51		3	2.23		3	3.53		3
	I	♂	4.61		4	3.82		4	0.44		4	2.44		4	2.72		4
		♀	4.06		1	3.66		1	1.67		1	2.25		1	2.67		1
	II+	♂	4.39	±0.62	6	3.26	±2.30	6	0.70	±0.27	6	2.59	±0.88	6	3.01	±1.03	6
		♀	4.55	±0.45	5	3.50	±1.38	5	1.53	±0.38	5	2.22	±0.79	5	2.42	±0.97	5
1976 Jan	I	♂	4.22	±0.25	10	1.26	±0.51	10	0.25	±0.08	10	1.59	±0.17	10	2.93	±0.30	10
		♀	4.33	±0.18	11	1.35	±0.44	10	0.52	±0.10	10	1.58	±0.22	10	3.00	±0.46	10
	II+	♂	4.30	±0.19	15	2.82	±0.62	15	1.01	±0.24	15	2.20	±0.32	15	2.74	±0.29	15
		♀	4.36	±0.20	10	2.58	±1.16	10	1.88	±0.28	10	2.20	±0.45	10	3.33	±1.17	10
Feb	I	♂	3.96	±0.13	14	0.78	±0.36	10	0.39	±0.17	10	1.76	±0.16	10	3.21	±0.56	10
		♀	3.86	±0.15	14	0.80	±0.27	10	0.48	±0.12	10	1.87	±0.16	10	3.19	±0.54	10
	II+	♂	4.09	±0.18	15	2.06	±0.85	10	1.75	±0.65	10	2.12	±0.58	10	2.65	±0.46	10
		♀	3.87	±0.19	10	0.94	±0.46	10	2.68	±0.35	10	1.90	±0.29	10	3.15	±0.36	10
Mar	I	♂	4.27	±0.17	5	0.52	±0.62	5	0.84	±0.27	5	1.92	±0.50	5	3.35	±0.58	5
		♀	3.98		3	0.23		3	0.68		3	2.08		3	3.56		3
	II+	♂	4.35	±0.18	14	0.84	±0.39	10	3.15	±0.72	10	1.66	±0.23	10	3.64	±1.04	10
		♀	4.26	±0.17	13	1.07	±0.48	10	3.30	±0.48	10	2.32	±0.42	10	3.68	±0.70	10

Appendix C.7.b. continued.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
Apr	I	♂	4.19	±0.32	6	0.43	±0.13	6	2.48	±0.80	6	2.34	±0.29	6	3.49	±0.75	6
		♀	4.09	±0.12	13	0.49	±0.11	10	1.14	±0.27	10	2.12	±0.27	10	3.39	±0.40	10
	II+	♂	4.23	±0.23	9	1.20	±0.73	9	6.12	±1.42	9	1.96	±0.39	9	2.75	±0.57	9
		♀	4.33	±0.23	16	0.89	±0.35	10	5.93	±3.32	10	3.10	±0.52	10	3.12	±0.44	10
May	I	♂	4.41	±0.21	8	0.49	±0.23	8	6.51	±1.69	8	1.87	±0.27	8	2.83	±0.36	8
		♀	4.59	±0.35	12	0.57	±0.32	10	4.03	±2.16	10	2.93	±0.69	10	3.25	±0.35	10
	II+	♂															
		♀	4.62	±0.23	13	0.33	±0.14	10	17.26	±5.19	10	4.40	±0.37	10	2.93	±0.37	10
Jun	I	♂	4.64	±0.25	11	1.53	±0.81	10	0.80	±0.58	10	1.57	±0.24	10	5.18	±1.92	10
		♀	4.63	±0.16	13	1.49	±0.55	9	2.04	±2.10	10	2.10	±0.45	10	3.95	±0.78	9
	II+	♂															
		♀	4.89	±0.51	8	0.55	±0.36	8	11.58	±4.43	8	4.27	±0.48	8	6.61	±2.22	8
Jul	I	♂	4.54	±0.22	14	4.14	±0.76	10	0.14	±0.03	10	3.33	±0.40	10	3.57	±0.96	10
		♀	4.72	±0.28	14	2.94	±1.09	10	0.26	±0.09	10	2.91	±0.73	10	4.03	±1.25	10
	II+	♂	3.96		1	2.62		1	0.52		1	2.03		1	1.99		1
		♀	4.51		1	1.28		1	0.54		1	3.00		1	2.17		1
Aug	0	♂	4.50	±0.21	10												
		♀	4.44	±0.27	9												
	I	♂	4.45	±0.24	21	4.11	±1.31	10	0.15	±0.05	10	3.17	±1.06	10	2.39	±0.31	10
		♀	4.66	±0.16	19	4.94	±1.03	10	0.23	±0.03	10	3.20	±0.42	10	2.69	±0.57	10
	II+	♂	4.65		3	4.15		2	0.20		2	2.57		2	2.47		2
		♀	4.68		1	3.95		1	0.44		1	3.36		1	3.71		1

Appendix C.7.b. continued.

Date	Age	Sex	Ponderal $\bar{x}$	Ponderal 95%CL	Ponderal N	Mesenteric lipid-somatic $\bar{x}$	Mesenteric lipid-somatic 95%CL	Mesenteric lipid-somatic N	Gonadosomatic $\bar{x}$	Gonadosomatic 95%CL	Gonadosomatic N	Hepatosomatic $\bar{x}$	Hepatosomatic 95%CL	Hepatosomatic N	Intestinal-somatic $\bar{x}$	Intestinal-somatic 95%CL	Intestinal-somatic N
Sep	0	♂	4.10	±0.08	57												
		♀	4.14	±0.12	37												
	I	♂	4.53	±0.14	13	6.04	±0.91	10	0.15	±0.04	10	2.92	±0.50	10	2.68	±0.33	10
		♀	4.43	±0.23	10	6.27	±1.43	7	0.34	±0.10	7	3.05	±0.62	7	3.37	±0.87	7
	II+	♂															
		♀	4.43		2	7.26		1	0.49		2	6.23		2	3.48		1
Oct	0	♂	4.22	±0.32	6												
		♀	4.21	±0.21	12												
	I	♂	4.52	±0.13	12	5.14	±1.65	10	0.17	±0.05	10	2.20	±0.37	10	3.11	±0.71	10
		♀	4.58	±0.19	12	6.33	±1.55	10	0.44	±0.06	10	2.90	±0.49	10	3.66	±1.22	10
	II+	♂	4.42		3	4.28		2	0.26		2	3.60		2	3.58		2
		♀	4.50	±0.48	8	4.89	±1.26	8	0.83	±0.06	8	2.41	±0.70	8	3.31	±0.53	8
Nov	0	♂	4.16	±0.19	10												
		♀	4.43	±0.19	7												
	I	♂	4.65		4	5.94		4	0.29		4	2.66		4	3.29		4
		♀	4.57	±0.21	11	6.93	±1.72	10	0.72	±0.12	10	2.39	±0.52	10	2.77	±0.56	10
	II+	♂	4.61		3	5.58		3	0.37		3	2.26		3	2.57		3
		♀	4.36	±0.25	5	5.94	±3.45	5	0.93	±0.17	5	2.64	±1.01	5	2.76	±1.10	5
Dec	0	♂	4.35	±0.28	9												
		♀	4.30	±0.18	9												
	I	♂	4.07		1	3.35		1	0.44		1	1.53		1	1.82		1
		♀	4.28		4	5.83		4	1.17		4	2.56		4	2.35		4
	II+	♂	4.26	±0.31	7	3.37	±1.63	7	0.71	±0.39	7	2.08	±0.64	7	2.54	±0.74	7
		♀	4.37	±0.28	9	5.82	±1.59	9	1.54	±0.13	9	2.32	±0.47	9	2.44	±0.42	9

Appendix C.8. *A. presbyter* Combined ponderal indices

a) Langstone

1975	$\bar{x}$	95%C.L.	N
11 Feb.	3.52	± 0.12	34
21 Mar.	3.33	± 0.24	6
17/23 Apr.	3.83	± 0.09	52
22 May	4.07	± 0.17	29
6 June	4.45	± 0.10	45
19 June	4.54	± 0.10	45
7 July	4.68	± 0.08	50
6 Aug.	4.92	± 0.11	50
3 Sept.	4.81	± 0.08	50
17 Sept.	4.64	± 0.06	50
16 Oct.	4.58	± 0.07	50
26 Nov.	4.41	± 0.07	50
16 Dec.	4.19	± 0.08	50
1976			
15 Jan.	4.20	± 0.06	50
26 Feb.	3.94	± 0.15	9
26 Apr.	4.49	± 0.11	36
7 May	4.46	± 0.21	20
26 May	4.68	± 0.12	42
17 June	4.63	± 0.07	60
5 July	4.81	± 0.08	49
19 July	4.82	± 0.13	50
3 Aug.	4.67	± 0.10	51
17 Aug.	4.72	± 0.09	53
1 Sept.	4.53	± 0.11	50
15 Sept.	4.48	± 0.08	75
4 Oct.	4.17	± 0.07	50
17 Nov.	4.27	± 0.09	50
16 Dec.	3.63		2

b) Fawley

1975	$\bar{x}$	95%C.L.	N
mid June-mid July	4.50	± 0.19	25
mid July-mid Aug.	4.45	± 0.14	34
mid Aug.-end Sept.	4.56	± 0.13	50
Oct.	4.35	± 0.08	50
Nov.	4.35	± 0.08	50
Dec.	4.43	± 0.14	30
1976			
Jan.	4.30	± 0.09	46
Feb.	3.95	± 0.08	53
Mar.	4.27	± 0.10	35
Apr.	4.22	± 0.10	44
May	4.56	± 0.15	33
June	4.70	± 0.15	32
July	4.57	± 0.16	32
Aug.	4.53	± 0.10	63
Sept.	4.19	± 0.06	119
Oct.	4.42	± 0.10	53
Nov.	4.43	± 0.10	40
Dec.	4.31	± 0.10	39

Appendix C.9. *A. presbyter* Mesenteric lipid index, age groups and sexes combined

a) Langstone				b) Fawley			
Date	$\bar{x}$	95%C.L.	N	Date	$\bar{x}$	95%C.L.	N
1975				1975			
19 Jun	0.52	± 0.17	38	mid Jun – mid Jul	1.10	± 0.45	20
7 Jul	2.11	± 0.29	31				
6 Aug	3.59	± 0.48	31	mid Jul – mid Aug	2.48	± 0.67	16
3 Sep	1.15	± 0.23	30				
17 Sep	1.41	± 0.39	31	mid Aug – end Sep	2.08	± 0.50	36
16 Oct	2.23	± 0.39	32				
26 Nov	2.84	± 1.06	30	Oct	2.48	± 0.47	29
16 Dec	2.18	± 0.25	30	Nov	3.32	± 0.51	33
1976				Dec	2.72	± 0.57	30
15 Jan	1.82	± 0.26	30	1976			
26 Feb	0.46	± 0.23	9	Jan	2.09	± 0.39	45
26 Apr	0.44	± 0.18	23	Feb	1.17	± 0.29	41
7 May	0.45	± 0.23	14	Mar	0.80	± 0.25	28
26 May	0.82	± 0.31	34	Apr	0.78	± 0.21	35
17 Jun	1.62	± 0.43	33	May	0.46	± 0.13	28
5 Jul	3.69	± 0.52	22	Jun	1.23	± 0.37	27
19 Jul	4.00	± 0.53	5	Jul	3.47	± 0.63	23
3 Aug	5.54	± 0.78	21	Aug	3.57	± 0.69	33
17 Aug	5.15	± 1.81	6	Sep	4.00	± 0.79	38
1 Sep	4.81		1	Oct	4.82	± 0.58	46
15 Sep	6.33	± 0.93	21	Nov	5.50	± 0.74	36
				Dec	4.20	± 0.63	39

Appendix C.10. *A. presbyter* Hepatosomatic indices, with age-groups combined although sexes separated

a) Langstone

Date	♀♀ $\bar{x}$	♀♀ 95%C.L.	♀♀ N	♂♂ $\bar{x}$	♂♂ 95%C.L.	♂♂ N
1975						
11 Feb	2.28	± 0.35	10	2.59	± 0.35	10
12 Mar	2.81		2	3.05		4
17/23 Apr	3.69	± 0.36	17	1.66	± 0.41	5
22 May	3.06	± 0.85	7	1.95	± 0.43	8
6 Jun	4.20	± 0.63	20	2.07	± 0.24	16
19 Jun	3.69	± 0.35	18	2.07	± 0.29	20
7 Jul	3.74	± 0.50	16	3.05	± 0.38	15
6 Aug	3.34	± 0.44	16	3.63	± 0.34	15
3 Sep	1.87	± 0.18	15	1.76	± 0.18	15
17 Sep	1.52	± 0.09	15	1.78	± 0.22	16
16 Oct	2.02	± 0.30	16	1.96	± 0.21	16
26 Nov	3.04	± 0.28	15	2.96	± 0.38	15
16 Dec	3.04	± 0.54	15	2.96	± 0.37	15
1976						
15 Jan	2.16	± 0.32	15	2.19	± 0.29	15
26 Feb	2.41		4	2.48	± 0.72	5
26 Apr	4.78	± 0.68	10	1.84	± 0.36	13
7 May	4.94	± 0.44	10	2.12		4
26 May	4.11	± 0.83	20	1.74	± 0.08	14
17 Jun	3.71	± 0.74	20	1.98	± 0.32	13
5 Jul	2.73	± 0.37	11	2.91	± 0.58	11
19 Jul	2.56		2	3.20		3
3 Aug	3.11	± 0.55	11	3.02	± 0.61	10
17 Aug	2.97		3	2.66		3
1 Sep				2.29		1
15 Sep	2.83	± 0.69	11	2.47	± 0.48	10

Appendix C.10. continued

b) Fawley

Date	♀♀ $\bar{x}$	♀♀ 95%C.L.	♀♀ N	♂♂ $\bar{x}$	♂♂ 95%C.L.	♂♂ N
1975						
mid Jun -mid Jul	3.35	± 0.82	9	2.07	± 0.48	11
mid Jul -mid Aug	2.18	± 0.30	10	2.79	± 0.96	6
mid Aug -end Sep	2.19	± 0.62	17	2.46	± 0.87	19
Oct	2.36	± 0.47	16	2.14	± 0.31	13
Nov	2.72	± 0.36	19	2.54	± 0.53	14
Dec	2.22	± 0.38	9	2.33	± 0.27	21
1976						
Jan	1.89	± 0.28	20	1.96	± 0.23	25
Feb	1.89	± 0.15	20	1.94	± 0.29	20
Mar	2.26	± 0.34	13	1.75	± 0.23	15
Apr	2.61	± 0.36	20	2.11	± 0.26	15
May	3.67	± 0.50	20	1.87	± 0.27	8
Jun	3.06	± 0.63	18	1.57	± 0.24	10
Jul	3.30	± 1.03	12	3.21	± 0.44	11
Aug	2.42	± 0.56	18	2.60	± 0.69	18
Sep	2.43	± 0.90	19	2.12	± 0.48	20
Oct	2.44	± 0.29	28	2.22	± 0.35	18
Nov	2.38	± 0.28	22	2.31	± 0.26	14
Dec	2.22	± 0.28	22	1.82	± 0.27	17

Appendix C.11. *A. presbyter* Combined intestinal-somatic indices

a) Langstone				b) Fawley			
Date	$\bar{x}$	95%C.L.	N	Date	$\bar{x}$	95%C.L.	N
1975				1975			
11 Feb	2.73	± 0.23	20	mid Jun -mid Jul	5.17	± 1.25	20
12 Mar	3.46	± 0.69	6				
17/23 Apr	3.11	± 0.47	22	mid Jul -mid Aug	2.82	± 0.33	16
22 May	3.12	± 0.57	15				
6 Jun	4.33	± 0.40	36	mid Aug -end Sep	3.98	± 0.53	36
19 Jun	4.89	± 0.63	38				
7 Jul	3.85	± 0.33	31	Oct	3.14	± 0.29	29
6 Aug	4.38	± 0.35	31	Nov	2.69	± 0.20	33
3 Sep	5.28	± 0.38	30	Dec	2.87	± 0.31	30
17 Sep	4.38	± 0.35	31	1976			
16 Oct	5.11	± 0.45	32	Jan	2.97	± 0.28	45
26 Nov	3.70	± 0.20	30	Feb	3.04	± 0.23	41
16 Dec	3.35	± 0.27	30	Mar	3.59	± 0.42	28
1976				Apr	3.17	± 0.25	35
15 Jan	4.24	± 0.35	30	May	3.01	± 0.19	28
26 Feb	3.34	± 0.39	9	Jun	5.19	± 0.96	27
26 Apr	5.04	± 0.63	23	Jul	3.65	± 0.65	23
7 May	5.99	± 0.98	14	Aug	2.86	± 0.37	36
26 May	5.73	± 0.44	34	Sep	3.07	± 0.21	38
17 Jun	5.29	± 0.56	33	Oct	3.22	± 0.31	46
5 Jul	4.75	± 0.84	22	Nov	2.92	± 0.29	36
19 Jul	3.71	± 1.58	5	Dec	2.68	± 0.21	39
3 Aug	3.59	± 0.31	21				
17 Aug	4.71	± 1.79	6				
1 Sep	4.45		1				
15 Sep	4.80	± 0.75	1				

Appendix C.12. *A. boyeri* Annual growth with respect to age (for conditions see text)

	Age group	$\bar{x}$	95%C.L.	N	Range	Annual growth rate
a) Length						
	0	55.63	± 4.73	8	45-62	
	I	70.77	± 2.24	30	55-79	24.07
	II	80.25		4	72-86	12.57
	III					
b) Weight						
	0	1.44	± 0.47	8	0.57-1.97	
	I	3.56	± 0.42	28	1.41-5.45	90.51
	II	5.25		4	2.42-7.05	38.85
	III					

Appendix C.13. *A. boyeri*

a) Length-weight relationship.

Body weights derived by substituting standard lengths into $W = aL^b$ using respective constants from Table 6.3.

S.L. mm	Body Wt. (g) ♂♂	♀♀
45		0.6456
50	1.0777	0.9359
55	1.4615	1.3096
60	1.9299	1.7797
65	2.4924	2.3598
70	3.1584	3.0643
75	3.9375	3.9080
80		4.9063
81	5.0353	
86		6.3309

b) Combined ponderal indices

	$\bar{x}$	95%C.L.	N
January	1.7735	± 0.1173	17
February	1.6945	± 0.1250	11
March	1.4900		4
April	1.4620	± 0.1306	5
May	1.6000	± 0.2649	5
June	1.5350		2
July	1.5633		3
August		no data	
September	1.6700		1
October	1.4525		4
November	1.7400		1
December	1.7525	± 0.1441	12

Appendix C.14. *A. boyeri* Mean monthly body component indices, sexes, age-groups and years combined

	Mesenteric lipid-somatic		Hepatosomatic		Intestinal-somatic		
	$\bar{x}$	95%C.L.	$\bar{x}$	95%C.L.	$\bar{x}$	95%C.L.	N
Jan	1.69	± 0.62	2.12	± 0.31	2.77	± 0.44	17
Feb	1.51	± 0.50	2.15	± 0.34	2.91	± 0.50	11
Mar	0.89		1.74		2.43		4
Apr	0.42	± 0.42	2.12	± 0.54	4.25	± 0.82	5
May	0.31	± 0.22	1.97	± 0.70	3.23	± 0.90	5
Jun	0.18		2.50		2.22		2
Jul	1.32		1.04		1.91		2
Aug	No data		No data		No data		
Sep	2.64		1.76		2.64		1
Oct	0.59		1.65		2.52		3
Nov	2.67		1.87		3.34		1
Dec	2.09	± 0.62	2.12	± 0.45	3.10	± 0.84	11

APPENDIX D

Appendix D.1. *A. presbyter.* The seasonal occurrence of testis developmental stages.

		LANGSTONE			FAWLEY			COMBINED		
Month	Stage	0	I	II+	0	I	II+	0(%)	I(%)	II+(%)
Sept. 1975	I	29			10			39(97.5)		
	II	1	1			7	2	1(2.5)	8(100)	2(100)
	III									
	IV									
	V									
Oct. 1975	I	15			3			18(72)		
	II		1		7	2	1	7(28)	3(100)	1(100)
	III									
	IV									
	V									
Nov. 1975	I	5			2			7(28)		
	II	10			8	2	2	18(72)	2(100)	2(100)
	III									
	IV									
	V									
Dec. 1975	I	15			2			17(65)		
	II				9	4	6	9(35)	4(100)	6(100)
	III									
	IV									
	V									
Jan. 1976	I		5			1			6(24)	
	II		10			9	10		19(76)	10(67)
	III						5			5(33)
	IV									
	V									
Feb. 1976	I		2						2(13)	
	II		3			10			13(87)	
	III						10			10(100)
	IV									
	V									
March 1976	I									
	II					3			3(60)	
	III					2	9		2(40)	9(90)
	IV						1			1(10)
	V									
April 1976	I									
	II					1			1(11)	
	III		1			5	2		6(67)	2(11)
	IV		2	10			7		2(22)	17(89)
	V									

Appendix D.1. continued.

		LANGSTONE			FAWLEY			COMBINED		
Month	Stage	0	I	II+	0	I	II+	0(%)	I(%)	II+(%)
May 1976	I									
	II									
	III					2			2(10)	
	IV		12	6		6			18(90)	6(100)
	V									
June 1976	I									
	II									
	III									
	IV		9	2		8			17(89)	2(100)
	V		1			2			3(11)	
July 1976	I									
	II		3			4			7(30)	
	III									
	IV		1	1			1		1(5)	2(100)
	V		9			6			15(65)	
Aug. 1976	I				6			6(100)		
	II		13			10			23(100)	
	III									
	IV									
	V						2			2(100)

Appendix D.2. *A. presbyter*. Selected oocyte size frequency distributions.

a) Langstone

Date	Age	S.L. mm	eye piece units 0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7
26.4.76	3	116	86	52	46	32	20	27	16	22	6	3	3			2	4	5
"	2	97	66	46	47	41	52	39	26	21	6	1	2	5	8	8	5	
7.5.76	3	114	81	42	42	51	36	21	20	7	9	8	1	1				
26.5.76	1	80	29	11	21	40	56	31	19	14	10	8	6	4	4	5	7	13
"	2	99	84	42	39	49	51	45	20	7						4	7	7
"	2	101	50	49	49	50	57	39	15	6	2	1	1		1	6	10	16
17.6.76	1	64	22	19	32	44	40	33	12	5					2	1	1	3
"	2	95	91	49	43	45	50	47	21	4	1			1	6	12	8	6
"	2	103	78	42	31	35	35	48	39	11	3	1	7	13	7	7	1	1
"	2	101	71	43	37	42	51	48	14	8	13	13	9	9	5	1		
5.7.76	1	71	206	69	5													
"	3	120	73	50	43	40	40	25	25	13	3				2	12	12	2
19.7.76	1	122	11	2														
3.8.76	1	84	193	68	1													
17.8.76	1	85	223	58	2													
15.9.76	1	94	257	29	1													
"	2	113	220	33	2													

Appendix D.2. continued.

b) Fawley

Date	Age	S.L. mm	eye piece units 0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	N
1.76	3	120	220	64	52	53	51	46	44	32	5																	567
2.76	1	68	93	54	33	26	4																					210
3.76	3	108	83	45	37	35	39	49	45	26	6	1																366
4.76	1	65	65	54	39	39	11	1																				209
"	3	122	53	31	24	31	36	40	48	28	25	14	7	5	3	3	1	1										350
5.76	1	71	40	28	35	61	53	32	18	8	16	7	1					1	3	7	10	7						327
"	3	125	33	45	24	35	43	43	27	20	9	12	4	4	2	1						2	7	11	13	11	1	347
6.76	1	79	90	29	23	41	32	30	28	13	8	3	1						8	23	17	3	2	1	1	1		354
"	3	117	138	49	34	35	27	30	15	14	10	5	11	7	6	1				1	1	2	3	9	8	10	2	418
7.76	1	97	159	73	18																							250
"	3	113	240	10																								250
8.76	1	97	236	54	2																							292
"	3	116	209	39	2																							250
9.76	1	97	131	54	36	28	1																					250
"	2	114	184	55	10	1																						250
10.76	1	102	131	59	35	23	2																					250
"	3	117	146	50	38	16																						250
11.76	1	99	140	48	32	20	8	1																				250
"	3	116	48	40	28	16	2																					250
12.76	1	110	113	52	40	27	26	6	1																			265
"	2	128	103	40	35	29	24	15	3																			250

Appendix D.3. The number of ova released at a single spawning in *A. presbyter* as determined from 25 fish caught on 9.5.77.

S.L.	Age	Fish Weight	Ova Weight	No. of Ova	No/g of fish
63	1	2.70	0.075	57	21.11
71	1	3.82	0.25	125	32.72
72	1	4.07	0.23	122	29.98
72	1	3.93	0.254	94	23.92
73	1	4.02	0.28	158	39.30
73	1	4.50	0.36	218	48.44
74	1	4.31	0.30	234	54.29
89	2	8.33	0.765	370	44.42
91	2	9.17	1.28	391	42.64
96	2	10.18	1.27	408	40.08
98	2	11.15	1.06	501	44.93
105	2	13.14	1.52	705	53.65
106	2	14.66	1.27	800	54.57
106	2	14.86	3.07	783	52.69
106	2	13.45	1.22	693	51.52
107	2	14.04	2.44	673	47.93
113	4	17.27	2.48	767	44.41
116	3	18.71	2.61	827	44.20
117	3	18.97	1.86	760	40.06
118	3	20.47	2.52	861	42.06
120	4	18.99	2.19	1084	57.08
121	3	21.97	2.29	1147	52.21
121	3	18.21	1.83	782	42.94
122	4	19.31	1.81	823	42.62
123	4	23.73	2.60	1094	46.10
$\bar{x}$ 98.92		12.56	1.433	579.08	43.75

Appendix D.4. *A. boyeri* - Male sexual cycle as shown by the testis : carcass weight ratio.

Date	Age Group	S.L. mm	Total Wet weight g	Carcass weight g	Testis weight g	$\frac{\text{Testis}}{\text{Carcass}} \times 100\%$
3.12.74	1	67	2.89	2.6775	0.0225	0.84
10.12.74	1	72	3.83	3.4950	0.0300	0.86
17.12.74	1	65	2.39	2.2175	0.0125	0.56
"	1	74	4.11	3.8350	0.0250	0.65
"	1	70	3.41	3.1500	0.0250	0.79
"	1	71	3.53	3.3050	0.0350	1.06
1.75	-	63	2.57	2.3750	0.0250	1.05
"	2	70	3.75	3.5550	0.0200	0.56
"	-	70	3.48	3.2350	0.0200	0.62
18. 2.75	-	79	5.10	4.7400	0.0900	1.90
18. 3.75	2	79	4.04	3.8000	0.0675	1.78
27. 5.75	2	69	3.32	2.8500	0.3700	12.98
3. 6.75	2	68	2.20	2.0800	0.0150	0.54
29. 7.75	1	50	1.10	0.9850	0.600	6.09
30.12.75	2	81	5.61	5.2550	0.0700	1.33
13. 1.76	2	58	1.73	1.6150	0.0200	1.24
3. 2.76	2	69	2.36	2.2350	0.0200	0.89
13. 4.76	3	77	3.65	3.4000	0.0800	2.35
4. 5.76	3	79	3.84	3.5650	0.0850	2.38
"	2	66	2.57	2.4400	0.0250	1.02
13. 7.76	2	71	2.92	2.8025	0.0350	1.25
5.10.76	1	70	2.41	2.3175	0.0100	0.43
28.12.76	1	69	3.99	3.7225	0.0125	0.34
4. 1.77	2	72	3.96	3.7775	0.0150	0.40
18. 1.77	2	66	2.41	2.2450	0.0200	0.89
1. 2.77	2	73	3.62	3.3200	0.0400	1.20
"	1	61	1.92	1.8250	0.0050	0.27
"	1	62	1.97	1.8425	0.0050	0.27
15. 2.77	2	69	3.22	2.9550	0.0275	0.93
"	2	76	4.53	4.2150	0.0400	0.95
"	2	76	4.58	4.2500	0.0425	1.00
1. 3.77	2	76	4.25	3.9950	0.0250	0.63

Appendix D.5. *A. boyeri* - Female sexual cycle as shown by the ovary : carcass weight ratio.

Date	Age Group	S.L. mm	Total Wet weight g	Carcass weight g	Ovary weight g	$\frac{\text{Ovary}}{\text{Carcass}} \times 100\%$
8.10.74	1	72	2.89	2.6650	0.0500	1.88
5.11.74	1	75	4.12	3.7450	0.0800	2.14
17.12.74	1	72	3.81	3.3950	0.0800	2.36
1.75	2	76	5.01	4.5200	0.1050	2.32
"	-	78	5.45	5.0050	0.1400	2.80
"	2	73	3.78	3.5050	0.0800	2.28
"	-	78	4.80	4.4700	0.1200	2.68
11. 2.75	-	70	2.69	2.4400	0.0825	3.38
8. 4.75	2	77	4.08	3.6500	0.1600	4.38
15. 4.75	2	76	3.28	2.9500	0.1250	4.24
22. 4.75	2	72	3.00	2.6900	0.1400	5.20
6. 5.75	2	79	3.95	3.6225	0.1525	4.21
27. 5.75	2	79	4.85	3.7250	0.8900	23.89
16. 9.75	1	53	1.22	1.1350	0.0050	0.44
30.12.75	1	57	1.41	1.2825	0.0200	1.56
6. 1.76	2	55	1.44	1.3400	0.0150	1.12
13. 1.76	3	86	7.05	6.2900	0.1500	2.38
20. 1.76	3	72	2.42	2.2550	0.0550	2.44
23. 3.76	2	73	3.17	2.9850	0.0300	1.01
6. 4.76	3	85	5.68	5.0750	0.1850	3.65
22. 6.76	1	55	1.47	1.0375	0.3700	35.66
12.10.76	1	66	2.43	2.3050	0.0300	1.30
28.12.76	0	57	1.54	1.4125	0.0125	0.88
4. 1.77	2	73	3.59	3.2950	0.0400	1.21
"	3	82	5.92	5.3600	0.0700	1.31
"	1	58	1.87	1.7250	0.0200	1.16
11. 1.77	1	51	0.88	0.8250	0.0050	0.61
1. 2.77	1	58	1.86	1.7425	0.0200	1.15
15. 2.77	2	77	4.78	4.3375	0.0700	1.61
1. 3.77	1	45	0.57	0.5425	0.0050	0.92

Appendix D.6. *A. boyeri.* Selected oocyte size frequency distributions from Oldbury

Date	Age	S.L. mm	eye piece units 0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7
8.10.74	1	72	96	29	25	21	20	11	4									
5.11.74	1	75	93	53	40	54	26	9	1									
17.12.74	1	72	69	49	50	34	29	10	1									
1.75	2	73	89	59	36	34	22	7	2	1								
11. 2.75	2	70	89	72	44	42	39	33	12	1	1							
8. 4.75	2	77	75	45	40	34	41	25	1	5								
22. 4.75	2	72	90	56	59	67	47	37	15	2	1							
6. 5.75	2	79	76	47	36	54	40	30	21	6	6	1						
27. 5.75	2	79	31	32	36	36	29	27	24	13	6	4	1				2	9
30.12.75	0	57	64	25	4													
22. 6.76	1	55	42	28	32	44	43	20	11	8	7	2	4	2		4	6	12
1. 2.77	1	58	65	38	25	10	9	4										