FEEDING, UTILIZATION OF FOOD AND GROWTH IN THE LESSER SPOTTED DOGFISH, *SCYLIORHINUS CANICULA* (L.), FROM ISLE OF MAN WATERS.

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy.

by

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SYNOPSIS

Feeding relationships of the lesser spotted dogfish, Scyliorhinus canicula, were studied with reference to diet, feeding behaviour, gastric evacuation rates, assimilation efficiency, growth, and food consumption rates in the wild.

Scyliorhinus is a generalist predator that feeds opportunistically on a wide range of macrobenthic fauna. Principal prey include hermit crabs (Eupagurus), various other reptant crustacea (Macropipus, Upogebia), whelks (Buccinum), cockles (Glycymeris), pectinids and holothurians (Thyone), though typically pelagic fish (Clupea) are consumed when they are locally abundant. Molluscs and hermit crabs became more important to the diet with increasing size of dogfish. Seasonal changes in the composition of the diet were observed. "Standing crop" of stomach contents was greatest during summer and least during autumn. The feeding of the population showed no synchrony and did not correlate regularly either with time of day or state of tide.

Gastric evacuation of natural foods was investigated by means of both force-feeding and voluntary-feeding techniques. The relationship between weight of food remaining in the stomach 'residuum', and time after feeding was curvilinear but could be linearised by applying square root transformation to the residuum weight. This model implies that radial distension of the stomach may be important in controlling the rate of emptying. A partial factorial design was adopted to study the influence of temperature, fish size, meal size and type on gastric evacuation. Mathematical models expressing instantaneous rate of gastric evacuation and time to complete gastric emptying as functions of these variables were developed. Instantaneous rate of gastric evacuation increased with temperature and fish size but was little affected by meal size and meal type. In general, total gastric evacuation times were comparable to those for other elasmobranchs but slower than those reported for teleosts.

Assimilation efficiency was high and was unaffected by fish size or temperature. Different meal types were tested; molluscs were assimilated most efficiently, teleosts were intermediate and crustaceans were assimilated least efficiently.

Growth was studied under laboratory conditions for groups of dogfish fed at different ration levels and different temperatures. Growth rates were highly dependent on ration level. The effect of temperature on growth was complicated because of differences in size of dogfish and biochemical composition of diet for each experiment. Maintenance energy requirements were estimated and compared with metabolic rates determined from oxygen consumption studies. Changes in body biochemistry in relation to ration level were also monitored. Body lipid content increased while body moisture decreased with increasing ration level.

A model of feeding in the wild was proposed and in conjunction with information regarding diet and gastric evacuation, daily food consumption rates were estimated. Daily intake was maximal during summer and minimal during autumn and winter. The adequacy of the estimates was examined on theoretical grounds and the possiblity that estimates were lower than actual feeding rates in the wild was considered.

GENERAL INTRODUCTION

In the past elasmobranchs have frequently been labelled as 'primitive' or 'simple' vertebrates. However, in the latter half of the present century studies into aspects of elasmobranch biology, physiology and behaviour have indicated that such generalisations are quite misleading. For instance elasmobranchs possess comparatively large brains (Young, 1962), an array of complex sensory systems (Tester, 1963; Boord and Campbell, 1977), their genital system is highly specialised to allow for internal fertilisation and in some species embryo development is viviparous (Young, 1962), and as a group they have evolved a great diversity of feeding mechanisms (Moss, 1977).

Recently elasmobranch research received considerable impetus related to the potential threat that sharks pose to humans. In consequence much attention has been focused on the functioning of sensory systems involved with feeding. That elasmobranchs possess extremely acute olfactory sense has been recognised for many years, as has the importance that olfaction plays in feeding motivation and food location (Bateson, 1890b; Sheldon, 1911; Parker, 1914; Tester, 1963; Mathewson and Hodgson, 1972; Dijkgraaf, 1975, etc.). Lateral line receptors, which include 'ordinary' and 'ampullary' systems (Boord and Campbell, 1977) also play a significant role in feeding. The ordinary system comprises canal organs or neuromasts and pit organs or free neuromasts. While their functional significance has not been clearly defined they are mechanoreceptors sensitive to water displacements caused by other animals and inanimate objects. Probably allied with this is the ability of sharks to respond to low-frequency sounds which may simulate hydrodynamic disturbances normally associated with active predation (Richard, 1968). It is likely though that labyrinthine receptors also respond to sound stimuli (Boord and Campbell, 1977). Katsuki et al (1969) have found that pit organs are very sensitive to certain chemicals, blood and meat extracts and may therefore serve in a chemosensory function. The ampullary system includes the 'ampullae of Lorenzini' which respond to chemical, mechanical and thermal stimuli though their primary function is in the detection of bioelectric fields normally produced by living prey (Kalmijn, 1971, 1977). Unrelated to the lateral line system there are also free nerve endings over all external surfaces which are chemoreceptive (Tester, 1963). In close proximity to prey vision may be important (Gilbert, 1963) and on final contact with the food gustatory sense comes into play (Tester, 1963).

Awareness and location of prey is thus accomplished through the interaction of a complex series of complimentary sensory systems which culminate in the attack and ingestion of the food. Research interest into the utilization of food once ingested has been much less extensive and publications are limited both in scope and number. It was this obvious need to provide such information for elasmobranchs that prompted the current study. The lesser spotted dogfish, Scyliorhinus canicula, was chosen as a suitable study animal because of its abundance throughout Britain's coastal waters, its ready adjustment to laboratory conditions, the fact that a considerable amount of information already exists regarding other aspects of its physiology and that the species is frequently used for teaching purposes in educational institutions. The aims of the present study are to examine factors that influence the removal of food from the stomach, assimilation efficiency and growth in captivity. In conjunction with the experimental approach regular field collections and analysis of stomach contents will enable a detailed picture of the natural diet to be constructed. Finally, based on appropriate synthesis of these experimental and field data, rates of food consumption in the wild will be estimated. Since so little information is available for elasmobranchs, where ever possible comparison will be made between the findings of the present study and those reported for teleosts.

CHAPTER 1

Food and Feeding Habits

INTRODUCTION

The primary motivation for many studies into the food and feeding habits of elasmobranchs has been the belief that these fish either consume commercially important species or compete with them for the same food resources. Related to this and the fact that comparatively few elasmobranch species support significant fisheries there is a general dearth of literature pertaining to the feeding relationships of this group. Much of the existing published work has tended to be very restricted in scope, often little more than qualitative lists of prey items.

Only the spurdog, Squalus acanthias, has been studied intensively and even though this species is fished commercially, the principal aim of many of the studies has been to assess the influence of spurdog predation on other commercially important species, notably herring (Holden, 1966; Rae, 1967b; Jones and Geen, 1977). Various members of the Rajidae are also fished on a commercial scale (Holden, 1977). Initial interest in aspects of their feeding biology was shown at a time when the British fishery for skates and rays was expanding (Clark, 1922; Steven, 1930) but more detailed studies have been made only in more recent years at a time when the ray stocks are declining and the fishery threatened with collapse (Holden and Tucker, 1974; de Souza, 1978; Nottage and Perkins, 1980).

Despite extensive use of the lesser spotted dogfish, Scyliorhinus canicula, in educational institutions and its ready availability in the coastal waters of European and Mediterranean countries comprehensive investigations into the food and feeding habits of this species are lacking. The value of much of the early work is limited owing to small sample sizes, methods of analysis and inadequate consideration of how factors such as growth (as a function of size) and season influence the composition of the diet and feeding intensity (Ford, 1921; Steven, 1930; Eales, 1949). The later studies of Canadjija (1961) and Azouz and Capapé (1971) suffer similar criticism. More recently Jardas (1972, 1979), Capapé (1974) and Armstrong (1980) have included these factors in their analyses, but both Jardas (1972) and Armstrong (1980) examined comparatively small sample sizes, 151 and 195 individuals respectively and some of their conclusions may not, therefore, be fully representative. The only reasonably detailed studies to date are those of Capapé (1974) and Jardas (1979) based on dogfish from the north Tunisian coast and Adriatic respectively; there have been no similarly detailed studies reported in British or European waters.

Atlantic and Mediterranean populations of Scyliorhinus differ with respect to a number of morphometric features. These include the maximum length attained - the former grow in excess of 70 cm whereas the latter only reach about 50 cm, and the size at maturity, which generally occurs between 50 - 65 cm in the Atlantic stock and between 30 - 40 cm in the Mediterranean populations (Ford, 1921; Leloup and Olivereau, 1951; Harris, 1952; Capapé, 1977; Jardas, 1979, etc.). These differences accompanied by consequences of geographic variation in associated prey communities and temperature regimes emphasise the need for detailed investigations into the feeding relationships of this species in British waters.

MATERIALS AND METHODS

(i) Study Area

Dogfish were caught on a coarse ground situated 6 - 8 kilometers east of Douglas, Isle of Man, at a depth of 30 - 40 m (Figure 1.1). A preliminary grab survey ($0.1 m^2$ van Veen grab) confirmed the overall homogeneity of the substrate throughout the study area, which consisted of sandy-gravel with considerable deposits of shell (mainly *Glycymeris*) and coralline algae (*Lithothamnion*) remains.

Tidal currents, which generally run along a NE - SW axis and reach a maximum speed of 0.93m/sec during spring tides, represent an important hydrographical feature of the study area. Their significance in determining and maintaining the type of substratum has been recognised by Jones (1951).

(ii) Collection of Material

Monthly sampling was conducted between July 1979 and December 1980 from the R.V. Cuma using a Boris-Capella type otter trawl with a 70 mm cod-end mesh. Each trawl was of between 1 and 2 hours duration.

When the weather conditions permitted the catch was immediately measured and sorted into the following categories according to total lengths; (a) $\leqslant$ 39cm; (b) 40 - 52 cm; (c) 53 - 62 cm; and (d) $\geqslant$63 cm. These length classes were chosen in such a way that the weight increments for each group lay between 200 and 300 g, as determined by the length-weight relationship calculated for *Scyliorhinus* in this study (Figure 1.2).

That is: $W = 0.0024\ L^{3.069}$

(Where W is fish weight in grams, and L is length in centimeters).

Although over 95% of the individuals that fell within category (d)

Figure 1.1 Map of the Isle of Man showing the study area (stippled).

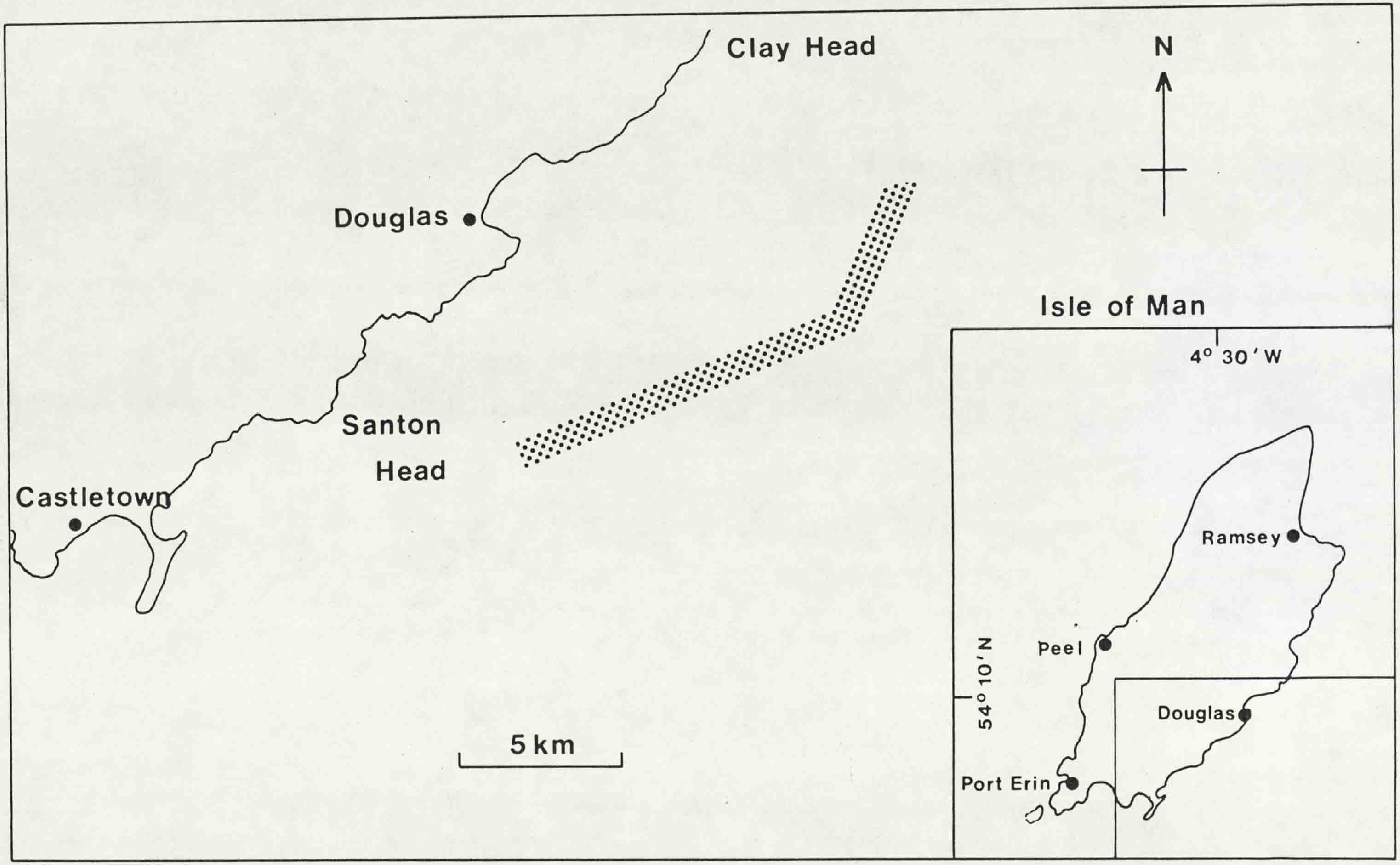

Clay Head
N
Douglas
Santon
Head
Castletown
5 km
Isle of Man
4° 30′ W
Ramsey
Peel
54° 10′ N
Douglas
Port Erin

Figure 1.2 Length-weight relationship for Scyliorhinus canicula :

Males ▲

Females △

(note several points omitted from figure for clarity)

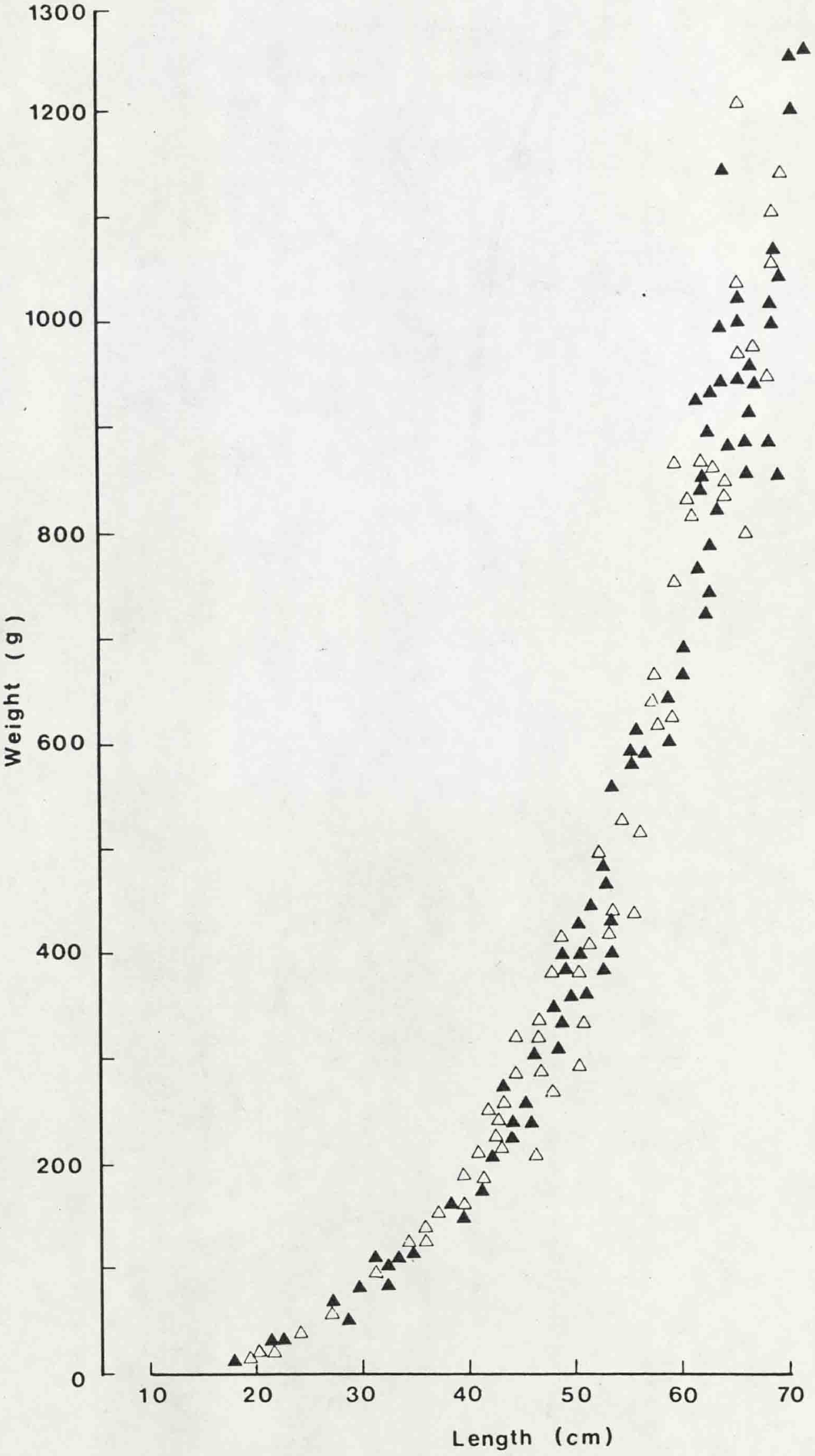
Males ; $W = 0.0023L^{3.085}$ ($n = 114$, $r = 0.997$)

Females ; $W = 0.0025L^{3.067}$ ($n = 114$, $r = 0.997$)

Combined ; $W = 0.0024L^{3.069}$

where W is weight (g) and L length (cm).

(G.M. regressions)


1300
1200
1000
800
600
400
200
0
Weight (g)
10
20
30
40
50
60
70
Length (cm)

were between 63 - 69 cm, specimens upto 74 cm long were recorded.

If catches were large, subsamples of 20 individuals for each length group and for each trawl were considered for stomach content analysis. Where possible equal numbers of males and females were retained. Stomachs were removed by opening the body cavity and severing the gut at the oesophagus and behind the pyloric constriction. The food remains contained in the cardiac portion were then squeezed into a container and preserved in 10% formalin solution. Stomach contents for each size group were pooled in this manner, although on most occasions the sexes were treated separately. Dogfish with empty stomachs were recorded while those exhibiting evidence of regurgitation were disregarded from further analysis. In fact regurgitation which may be a serious problem with some teleosts was of negligible importance in the present study with less than 0.5% of the dogfish examined for stomach content analysis showing signs of this phenomenon.

In order to investigate the diel feeding patterns, sampling was conducted over three 24-h periods; in November 1979 and February and June 1980. Trawls of roughly 1½ h duration were carried out approximately once every 4 h.

Whenever possible the bottom water temperature was taken using a Nansen-Petterson insulated water bottle.

(iii) Laboratory Procedure

From the outset it was apparent that the stomach contents included copious quantities of semifluid material, gastric juices combined with digested food remains. This was due to the fact that in *Scyliorhinus*, as in other elasmobranchs, the stomach contains many secretory glands (Leake, 1975) and represents the main site of digestive breakdown of food (Hogben, 1967), only semifluid chyme being passed on into the intestine. In analysing stomach contents the preserved material was weighed and separated into the fluid and solid components. The various prey items in the latter component were identified to species or generic level where possible. The following texts were particularly useful for this purpose, Bruce et al (1963), Allen (1967) and Wheeler (1978).

The quantitative methods used in stomach content analysis have been reviewed by Hynes (1950), Pillay (1952), Windell (1966) and Hyslop (1980), and their limitations stressed. For instance gravimetric and volumetric methods are biased in favour of large items and those that are resistant to rapid digestion, whereas numerical methods tend to over emphasise the importance of small food organisms. It is usual in feeding studies to employ more than one approach in order to account for some of these limitations. In the present study, gravimetric and numerical approaches were adopted. Prey organisms were weighed (wet weight), counted, and their 'digestion state' estimated visually on a scale from I (fresh) to V (advanced state of digestion). The carapace lengths of Eupagurus and carapace widths of Macropipus were also recorded.

The two components, i.e. the solid and fluid material, were then dried separately at 65°C, weighed, recombined and ground into a fine powder. A subsample of between 0.5 - 1.0 g was heated at 500°C for approximately 8 h to determine the ash content.

Morphometric measurements of mouth gape, in the horizontal and vertical planes, were obtained from freshly killed or anaesthetised (MS 222 Sandoz) individuals.

RESULTS

(i) The Studied Population

Seasonal length-frequency distributions and catch statistics indicate some important points relating to the studied population of Scyliorhinus (Table 1.1, Figure 1.3), despite the fact that trawl catches were often subsampled.

Firstly, the sex ratio varied seasonally; males predominated in the catches throughout the year, with the exception of the winter months. Seasonal variation in the sex ratio of adult dogfish in the Plymouth and Ilfracombe regions has been reported previously by Ford (1921) and Harris (1952) and, according to Harris (op cit.), is correlated with spawning migrations. Females are thought to move into shallow water to deposit egg capsules, after insemination in deeper water. A number of workers have noted that the egg laying season for Scyliorhinus extends throughout most, if not all, of the year with a decline or cessation of ovulation in September and October (Ford, 1921; Metten, 1941; Harris, 1952; Craik, 1978; Sumpter and Dodd, 1979). In the present study, females bearing egg capsules in the oviducts were observed from November to June, though not continuously over this period as mature females were absent from some of the intervening monthly samples. It is likely, however, that egg production in Manx dogfish was at least continuous between November and June.

By rearranging the data in Table 1.1 it became apparent that the primary cause of the unequal sex ratio was due to the disproportionately large number of adult males compared with adult females. With the exception of the winter months, and to a lesser degree spring, females were noticeably absent from the samples, accounting

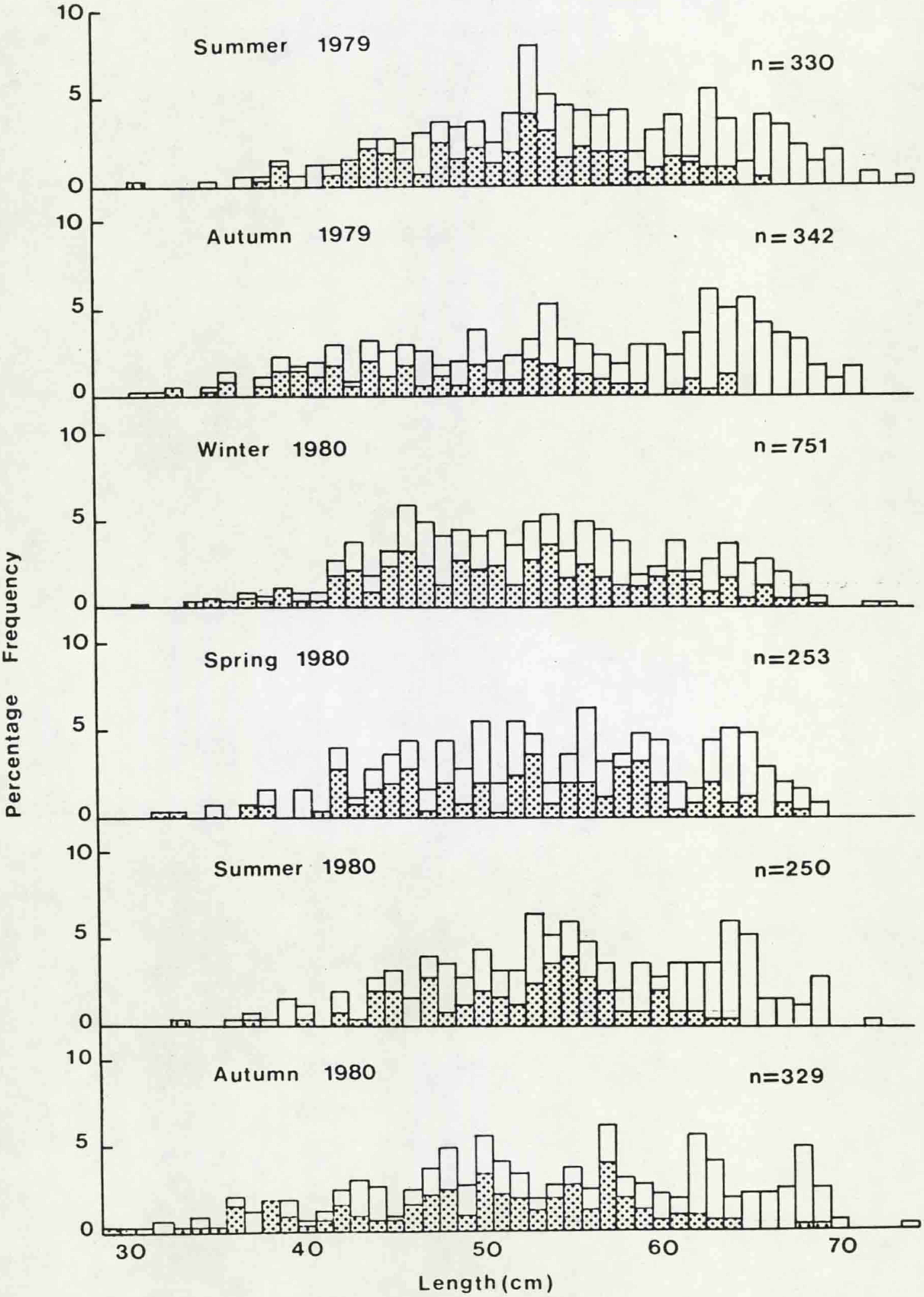
Table 1.1 Variation in sex ratio of *Scyliorhinus canicula* from east of the Isle of Man.

Season	Numbers			Percentage	
	Male	Female	Total	Male	Female
Summer 1979	203	127	330	61.5	38.5
Autumn	237	105	342	69.3	30.7
Winter 1980	366	385	751	48.7	51.3
Spring	141	112	253	55.7	44.3
Summer	158	92	250	63.2	36.8
Autumn	185	144	329	56.2	43.8
Total	1290	965	2255	57.2	42.8
Dogfish less than 60cm.					
Summer 1979	116	108	224	51.8	48.2
Autumn	108	96	204	52.9	47.1
Winter 1980	272	306	578	47.1	52.9
Spring	88	91	179	49.2	50.8
Summer	88	81	169	52.1	47.9
Autumn	100	130	230	43.5	56.5
Total	772	812	1584	48.7	51.3
Dogfish greater than 60cm.*					
Summer 1979	87	19	106	82.1	17.9
Autumn	129	9	138	93.5	6.5
Winter 1980	94	79	173	54.3	45.7
Spring	53	21	74	71.6	28.4
Summer	70	11	81	86.4	13.6
Autumn	85	14	99	85.8	14.1
Total	518	153	671	77.2	22.8

* Females in excess of 60cm were generally mature, although a single female of 59cm contained egg capsules.

Figure 1.3 Length-frequency of catches of *Scyliorhinus canicula* on a seasonal basis.

Males	☐
Females	▒


Summer 1979
n=330
Autumn 1979
n=342
Winter 1980
n=751
Spring 1980
n=253
Summer 1980
n=250
Autumn 1980
n=329
Percentage Frequency
10
5
0
30
40
50
60
70
Length (cm)

for less than 18% of the adult individuals. The fact that adult females occurred in relatively low abundance in the study area throughout all but the beginning of the spawning period, and the absence of egg-purses in trawl and dredge samples, suggests that the Douglas ground is not an important spawning site for dogfish. It may be postulated then, that the presence of adult females was only transitory, they were moving through the study area, and onto the true spawning grounds. Unfortunately this aspect of the biology of the dogfish was not fully investigated in this study and therefore remains speculative.

In addition to the general scarcity of large female dogfish, individuals of either sex less than about 40 cm in total length were poorly represented in the catches. This was almost certainly attributable to sampling bias and not to any distributional pecularities, as dogfish within this size range readily escape through the 70 mm cod end mesh. The Douglas ground thus represents a feeding site for juvenile as well as adult dogfish, although it was evident that in response to spawning movements large females were resident for only a short period.

(ii) Morphology of the Mouth

The mouth is subterminally positioned and lined with relatively small teeth (modified placoid scales) which are directed into the mouth. There are slight differences in dentition between the sexes. Females possess comparatively smaller teeth than males which do not extend to the jaw margins, whereas in males toothed areas are more widely spread.

The increase in mouth gape, in both horizontal and vertical planes, with dogfish size is found to be linear

Figure 1.4 Relationship between jaw width/height and size of *Scyliorhinus canicula* ;

Jaw width, w (mm), and dogfish size, L (cm)

Males ; $w = 0.617L + 2.036$

$(n = 38, r = 0.962)$

Females ; $w = 0.509L + 6.806$

$(n = 32, r = 0.964)$

Jaw height, h (mm), and dogfish size

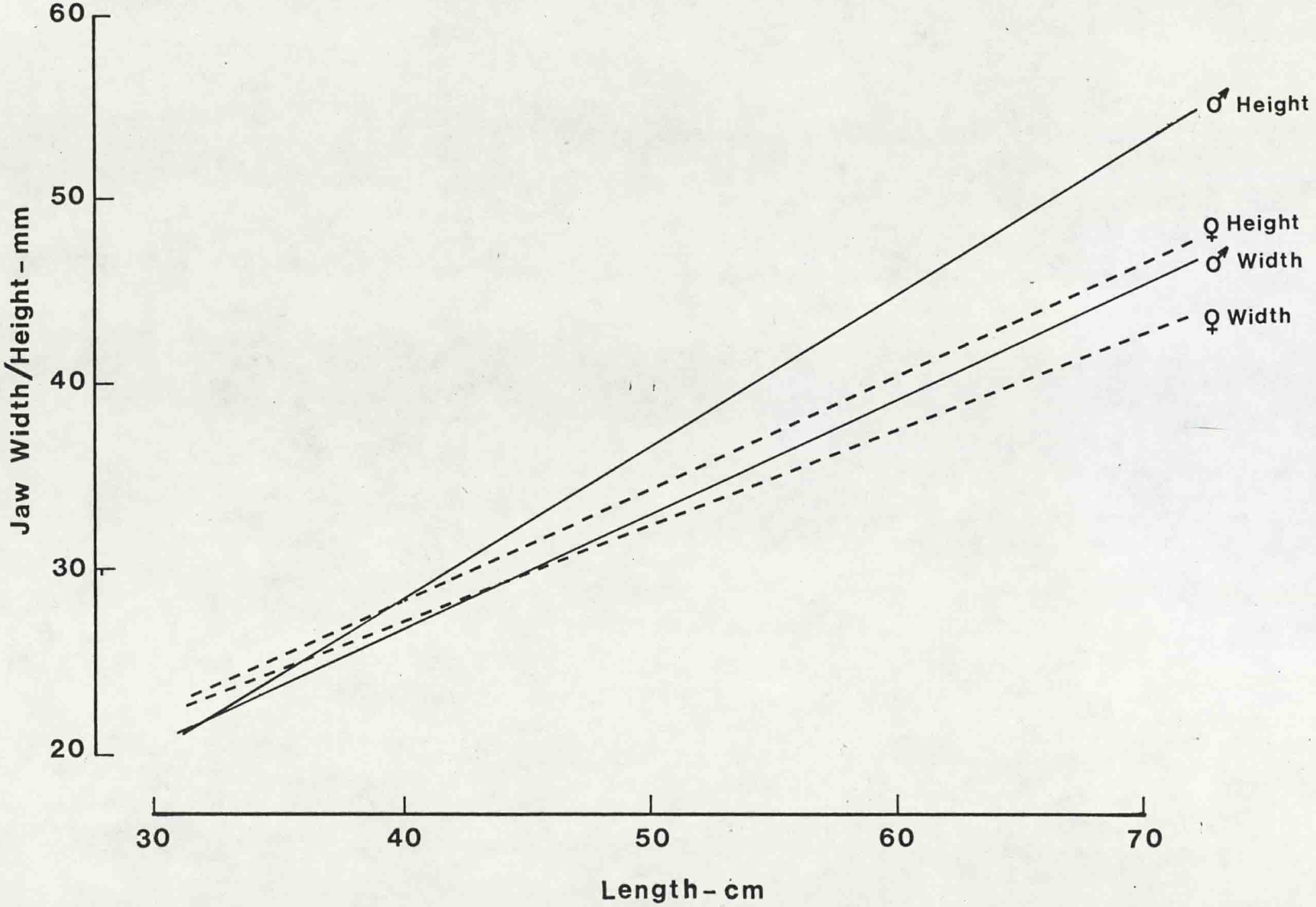
Males ; $h = 0.828L + 5.015$

$(n = 38, r = 0.955)$

Females ; $h = 0.609L - 3.854$

$(n = 32, r = 0.953)$

(note, for clarity points omitted and only regression lines drawn)


60
50
40
30
20
Jaw Width/Height - mm
30
40
50
60
70
Length - cm
♂ Height
♀ Height
♂ Width
♀ Width

(Figure 1.4). There are differences in the jaw dimensions between sexes, with jaw heights considerably larger in males.
Sexual dimorphism in the structure of the mouth has been reported previously by Arthur (1950) and is related to the fact that the anterior margin of the lower jaw is more flattened in female than in male dogfish.

(iii) Composition of the Diet

During the study period the stomach contents of a total of 2003 dogfish were examined, of which over 90% contained at least some traces of food remains. In the analyses of the diet it was decided to pool data for each sex as there were no fundamental differences in the composition of the diet for males and females. This observation was tested statistically and confirmed by the use of the Spearman rank correlation coefficient (see Appendix I).

A species list of all the prey consumed by Scyliorhinus is presented in Table 1.2 and diet composition for each size class over the whole study period summarised in Table 1.3 and Figure 1.5. For complete details refer to Appendix II. Food of the dogfish was composed of a wide range of macrobenthic organisms, with the crustaceans: Eupagurus bernhardus, Upogebia spp., Macropipus spp.; molluscs: Buccinum undatum, Glycymeris glycymeris, Chlamys sp. and a holothurian, Thyone sp., accounting for the bulk of the diet. In addition to a variety of demersal fish typically pelagic forms, e.g. Clupea harengus, were eaten.

Although in terms of species composition there was considerable uniformity in the diets of each size class of dogfish, quantitatively there were conspicuous differences. Crustacean and molluscan prey together accounted for over 85% of the diet, by weight, in all size

TABLE 1.2 List of all identified organisms consumed by *Scyliorhinus canicula* from a sandy-gravel ground east of the Isle of Man.

- POLYCHAETA
  - *Nereis* spp.
  - Aphroditidae
  - *Harmothoe* sp..
  - *Aphrodite aculeata*
  - *Nephthys* spp.
  - *Glycera convoluta*
  - *Glycera* spp.
  - Eunicidae
  - *Notocirrus scoticus*
  - *Lumbriconereis* sp.
  - *Ammotrypane aulogaster*
- CRUSTACEA
  - Decapoda
    - Reptantia
      - *Eupagurus bernhardus*
      - *E. prideauxi*
      - *E. pubescens*
      - *E. cuanensis*
      - *Upogebia stellata*
      - *U. deltaura*
      - *Macropipus pusillus*
      - *M. corrugatus*
      - *M. depurator*
      - *M. holsatus*
      - *M. puber*
      - *Galathea dispersa*
      - *G. intermedia*
      - *Porcellana longicornis*
      - *Atelecyclus rotundatus*
      - *Pinnotheres pisum*
      - *Hyas araneus*
      - *Ebalia tumefacta*
      - Xanthidae
    - Natantia
      - *Eualus pusiolus*
      - *Pandalina brevirostris*
      - *Dichelopandalus bonnieri*
      - *Pandalus montagui*
      - *Crangon allmanni*
  - Amphipoda
    - Gammaridae
  - Isopoda
  - Mysidacea
  - Euphausiacea
- MOLLUSCA
  - Gastropoda
    - *Buccinum undatum*
    - *Neptunea antiqua*
  - Lamellibranchia
    - *Glycymeris glycymeris*
    - *Chlamys opercularis*
    - *Pecten maximus*
    - *Ensis* sp.
    - *Cardium* sp.
    - *Mya* sp.
    - *Lutraria lutraria*
  - Cephalopoda
    - *Sepiola atlantica*
- ECHINODERMATA
  - *Thyone fuscus*
  - *Ophiura* sp.
  - *Asterias rubens*
- SIPUNCULOIDEA
  - *Goldfingia* sp..
- COELENTERATA
  - Hydroida
- CEPHALOCHORDATA
  - *Branchiostoma lanceolatum*
- PISCES
  - *Clupea harengus*
  - *Sprattus sprattus*
  - *Callionymus lyra*
  - Pleuronectidae
  - *Glyptocephalus cynoglossus*
  - *Diplecogaster bimaculata*
  - *Pholis gunnellus*
  - *Ammodytes* sp.
  - *Trisopterus luscus*
  - *Agonus cataphractus*
  - Cottidae
  - *Gobius microps*
  - *Lumpenus lampetraeformis*
  - *Scyliorhinus canicula*

TABLE 1.3 *Scyliorhinus canicula*: diet composition by percentage digested weight and percentage numbers.

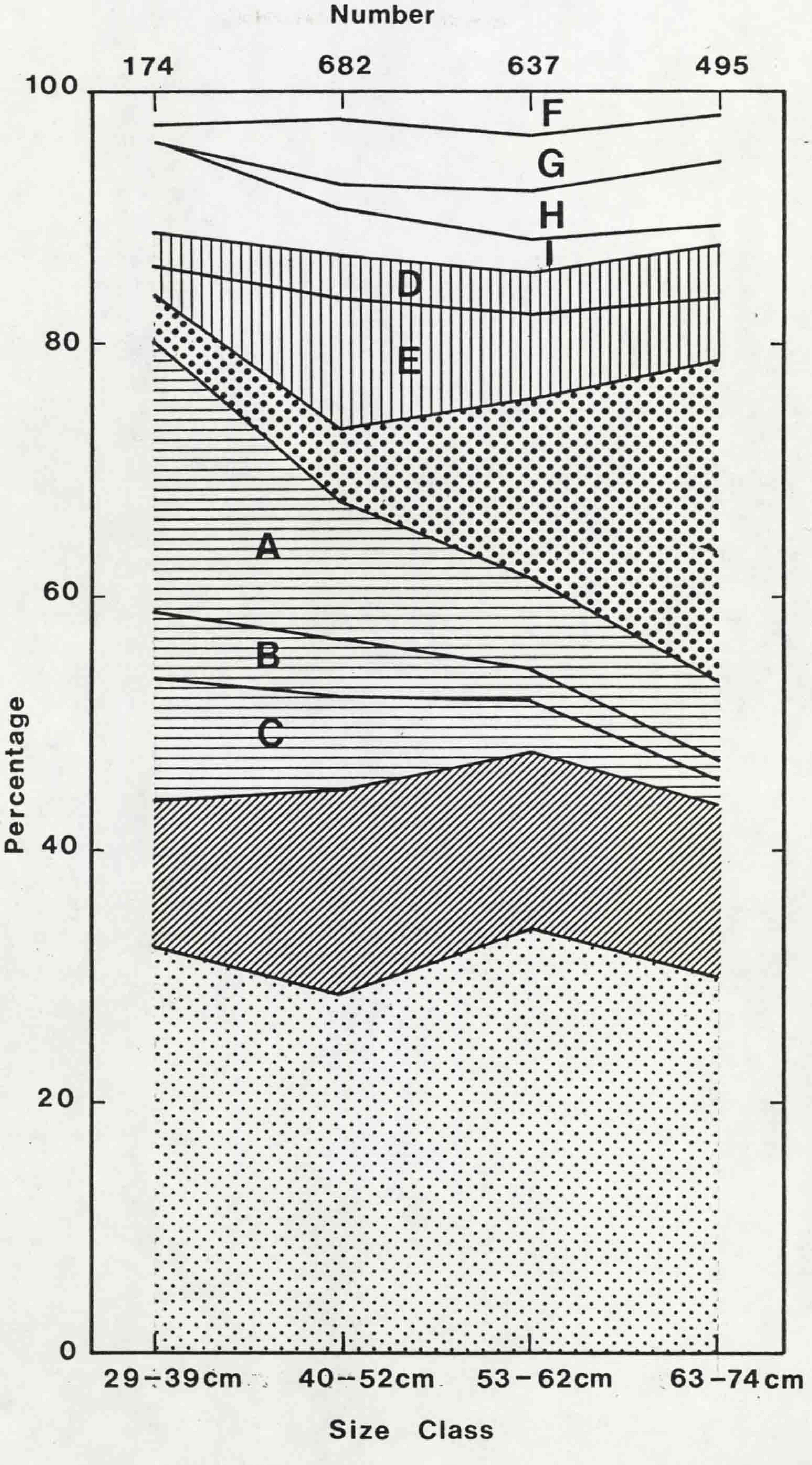
Dogfish size class	29-39 cm		40-52 cm		53-62 cm		63-74 cm	
	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
CRUSTACEA	68.29	64.39	51.15	43.98	47.46	31.43	39.31	27.86
Eupagurus bernhardus	30.39	4.26	25.04	7.43	32.77	9.65	27.92	10.82
Other Pagurids	1.67	1.43	3.49	2.43	1.14	1.69	1.87	1.52
Upogebia spp.	9.92	3.28	7.27	4.45	3.87	4.20	1.85	3.04
Macropipus spp.	5.08	6.23	4.59	6.91	2.53	5.82	1.51	4.61
Galathea spp.	2.21	18.25	0.50	8.72	0.26	3.46	0.08	2.37
Maiidae	3.16	1.75	0.81	1.10	0.79	0.98	0.92	1.61
Other Reptantia	1.48	4.81	0.59	2.98	0.26	1.62	0.41	0.71
Natantia	2.54	19.24	0.64	6.50	0.12	2.79	0.11	2.63
Other Crustacea	0.75	5.14	0.23	3.46	0.06	1.22	+	0.55
Unident. remains	11.09		7.99		5.66		4.64	
MOLLUSCA	20.58	9.84	36.06	25.87	38.44	37.13	48.83	48.14
Buccinum undatum	4.01	0.77	6.02	1.72	14.21	4.57	25.59	8.11
Neptunuea antiqua	0.49	0.33	0.27	0.09	0.40	0.18	1.58	0.34
Glycymeris glycymeris	11.75	6.45	16.22	18.91	14.10	26.14	14.00	33.47
Chlamys sp.	2.23	1.09	8.36	3.38	5.49	3.95	4.73	3.89
Pecten maximus	-	-	1.75	0.06	0.98	0.09	0.31	0.04
Ensis sp.	-	-	1.93	0.86	1.51	1.13	0.96	0.97
Mya sp.	-	-	0.38	0.06	0.22	0.09	0.89	0.55
Other Mollusca	2.10	1.20	1.13	0.79	1.53	0.98	0.77	0.77
POLYCHAETA	7.11	22.40	3.51	21.71	2.49	21.17	1.46	14.69
Ammotrypane aulogaster	0.60	11.91	0.13	6.41	0.04	3.28	0.01	1.14
Harmothöe spp.	0.52	2.95	0.37	5.46	0.22	5.39	0.09	3.25
Other Polychaeta	5.99	7.54	3.01	9.84	2.23	12.50	1.36	10.30
PISCES	2.83	1.97	2.62	1.57	6.56	1.80	6.27	1.90
Clupea harengus	-	-	1.97	0.21	3.78	0.28	4.97	0.59
Other Pisces	2.83	1.97	0.65	1.36	2.78	1.52	1.30	1.31
OTHER TAXA	1.19	1.42	6.65	6.89	5.01	8.43	4.08	7.39
Goldfingia sp.	0.12	0.44	0.98	1.38	0.34	1.84	0.26	1.39
Thyone spp.	1.07	0.87	5.24	4.76	4.50	5.46	3.67	4.61
Other	+	0.11	0.43	0.75	0.17	1.13	0.15	1.39
No. examined	175		686		642		500	
No. with food	174		682		637		495	

\+ values less than 0.01%

Figure 1.5 Composition of the diet based on percentage weight and in relation to size class of _Scyliorhinus canicula_.

KEY

Eupagurus spp.	░
Upogebia spp.	C
Macropipus spp.	B
Other Crustacea	A
Glycymeris glycymeris	▨
Buccinum undatum	▓
Pectinidae	E
Other Mollusca	D
Polychaeta	I
Clupea harengus	H
Thyone spp.	G
Other	F


Number
174
682
637
495
100
80
60
40
20
0
Percentage
F
G
H
I
D
E
A
B
C
29-39cm
40-52cm
53-62cm
63-74cm
Size Class

groups. There was, however, a significant decline in that portion of the diet comprised of crustaceans, offset by an increase in the importance of molluscs, in the food of bigger dogfish (Figure 1.5).

Gravimetrically, hermit crabs (predominately Eupagurus bernhardus) were the principal prey consumed, being of more or less equal importance for all sizes of dogfish (approximately 30% of all food identified). In general though, greater numbers were taken by bigger dogfish and there was some evidence for size selectivity (Figure 1.6, Appendix IIb). Of the other crustacean prey only Upogebia and Macropipus accounted for over 5% of the diet, by weight, in any size class. In each case they became progressively less important with increasing dogfish size. None of the other crustaceans eaten contributed significantly in terms of weight, though considerable numbers of squat lobsters, Galathea intermedia, and shrimps, Eualus pusiolus, were present in the stomachs of smaller dogfish.

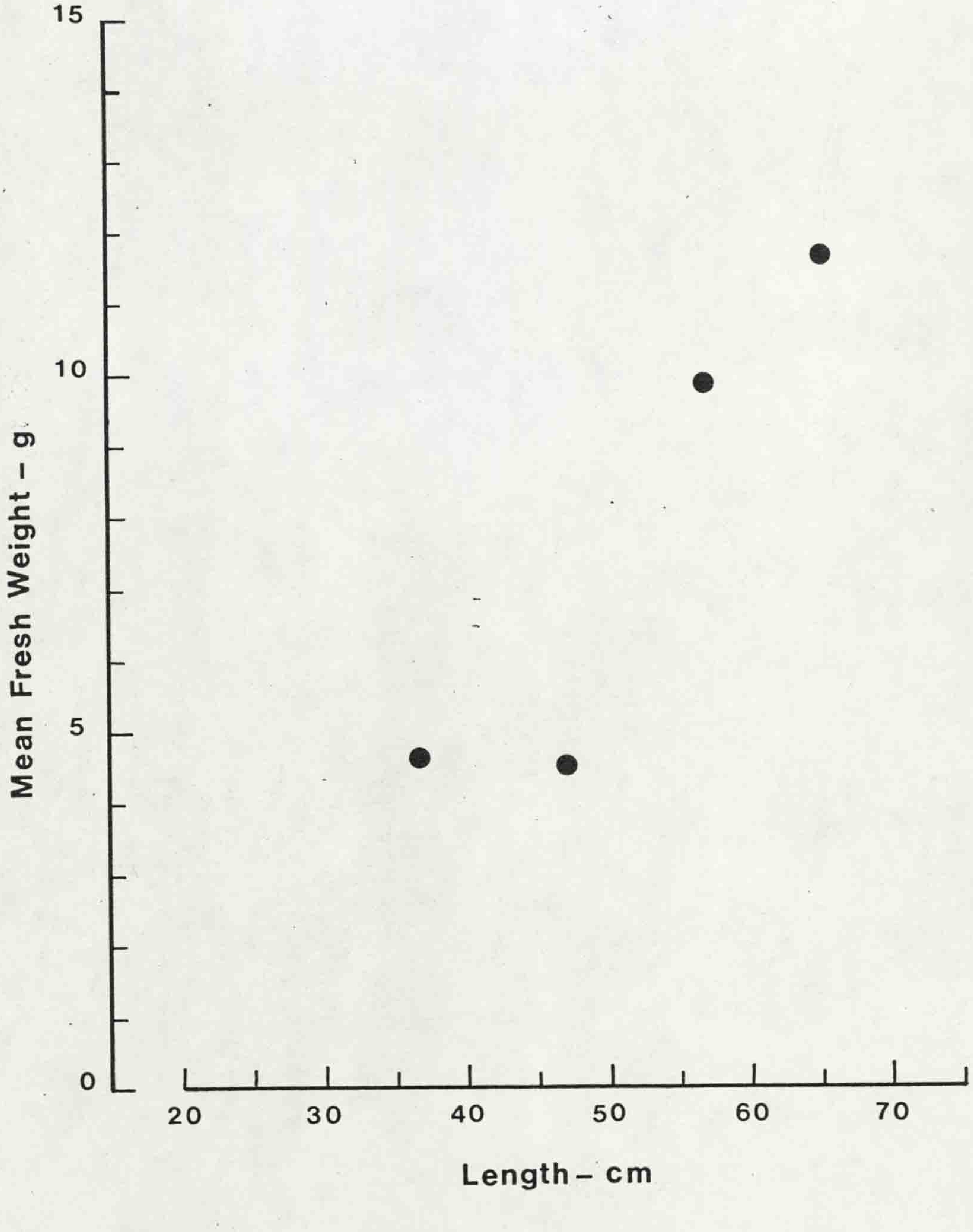
The cockle, Glycymeris, which represented an equally important source of food by weight to all size groups (approximately 15%) was preyed upon more intensively, i.e. numerically, by larger dogfish. The whelk, Buccinum, too was clearly more favoured by the larger individuals, and contributed over 25%, by weight, to the diet of the 63 - 74 cm size group. Interestingly none of the molluscs consumed were ingested with their shells intact. Only the muscular foot (including operculum) and often head regions of Buccinum and Neptunea were eaten (visceral mass accompanied only 2.6% of the whelks eaten). Glycymeris, Ensis and Cardium were represented in the stomach contents by the foot region; Chlamys by the mantle fringe (only 9.4% also included the adductor muscle and/or gonads); and Mya and Lutraria by the siphons (the former including the

Figure 1.6 Mean fresh weight of Eupagurus bernhardus consumed by Scyliorhinus canicula , in relation to dogfish size.

E. bernhardus fresh weight calculated from length-weight relationship ;

$$\log_{10}W = 3.090\log_{10}L - 2.988$$

where W is fresh weight (g) and L carapace length (mm).


15
10
5
0
Mean Fresh Weight – g
20
30
40
50
60
70
Length – cm

periostracal sheath).

With the exceptions of the holothurian, Thyone, and the herring none of the remaining taxa were particularly important by weight. Polychaetes (Ammotrypane, Harmothoe, Nereis etc.) did however, makeup over 7% of the diet, by weight, in the 29 - 39 cm group but dropped to less than 1.5% in the 63 - 74 cm dogfish. As most polychaetes examined were at an advanced stage of digestion it was probable that their role in the overall diet was underestimated; their numerical contribution of between 15 - 22% suggested this to be the case.

(iv) Seasonal Changes in the Composition of the Diet

For the purpose of studying seasonal variation in the relative composition of the diet, the year was split into quarters which roughly correspond to the seasons: winter - January to March; spring - April to June; summer - July to September; and autumn - October to December. Complete details of the composition of the diet on a seasonal basis are presented in Appendix III and summarised in Figure 1.7. Bottom water temperatures over the study period are shown in Figure 1.8.

On a seasonal basis hermit crabs, and especially Eupagurus bernhardus, were heavily preyed upon by all sizes of dogfish at all times of the year. Numerically and gravimetrically there was only slight evidence for seasonal fluctuations with peaks during spring and autumn for most of the dogfish size groups. In the 29 - 39 cm group a particularly high value, by weight, obtained for Eupagurus during summer 1979 was almost entirely attributable to two large hermit crabs which had been ingested just prior to the time of capture.

The prominence of Buccinum in the diets of the larger dogfish has already been established. As with Eupagurus there was little

Figure 1.7 Seasonal variation in relative importance of selected prey to the diet of _Scyliorhinus canicula_, expressed as percentage by weight of average stomach contents.

A : 29-39 cm size group
B : 40-52 cm size group

KEY

Eupagurus spp.	░
Glycymeris glycymeris	▧
Upogebia spp.	▤
Buccinum undatum	▒
Pectinidae	▥
Clupea harengus	□

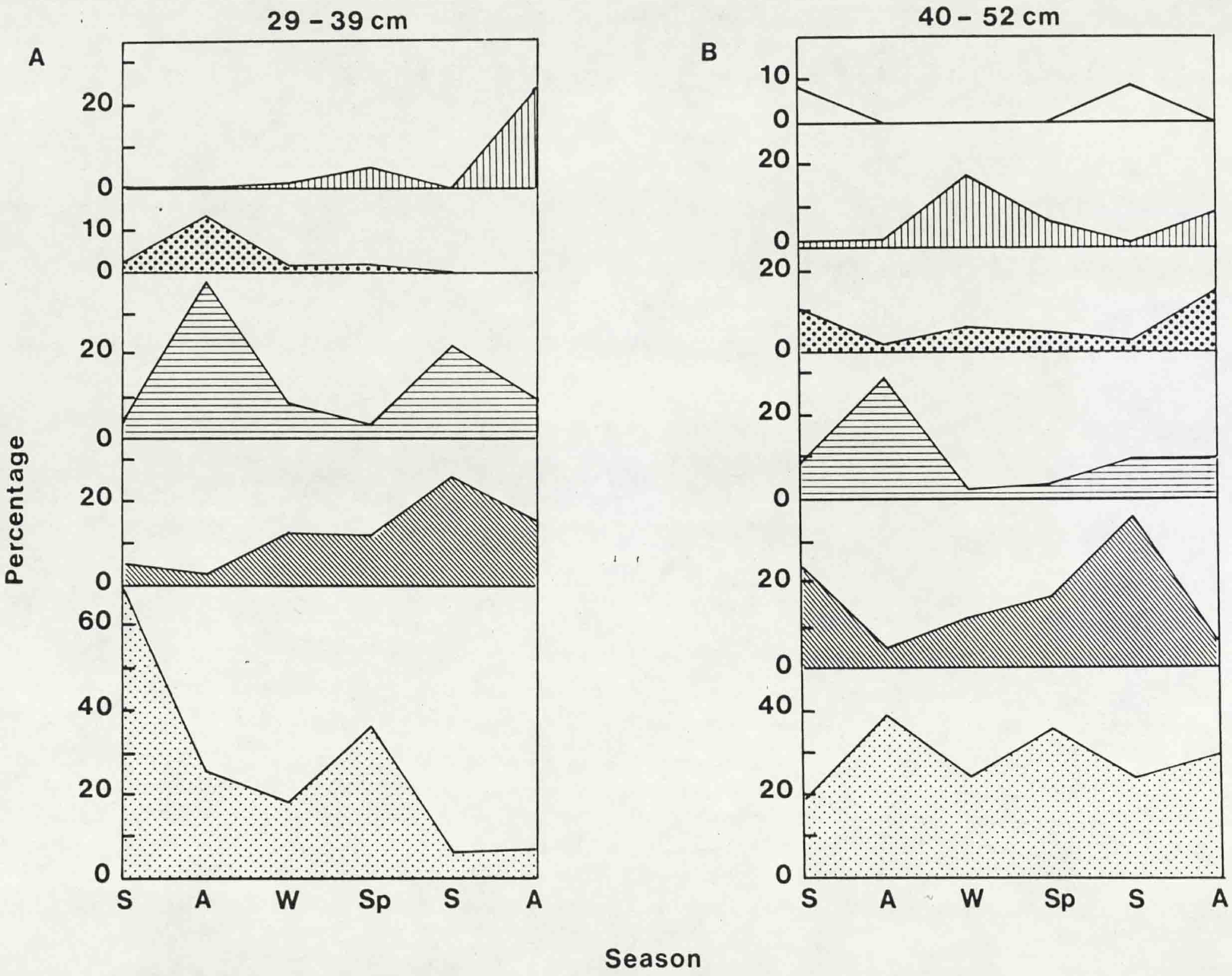

A
29 - 39 cm
B
40 - 52 cm
Percentage
20
0
10
0
20
0
20
0
60
40
20
0
10
0
20
0
20
0
20
0
20
0
40
20
0
S
A
W
Sp
S
A
S
A
W
Sp
S
A
Season

Figure 1.7 (continued) Seasonal variation in relative importance of selected prey to the diet of Scyliorhinus canicula, expressed as percentage by weight of average stomach contents.

C : 53-62 cm size group
D : 63-74 cm size group

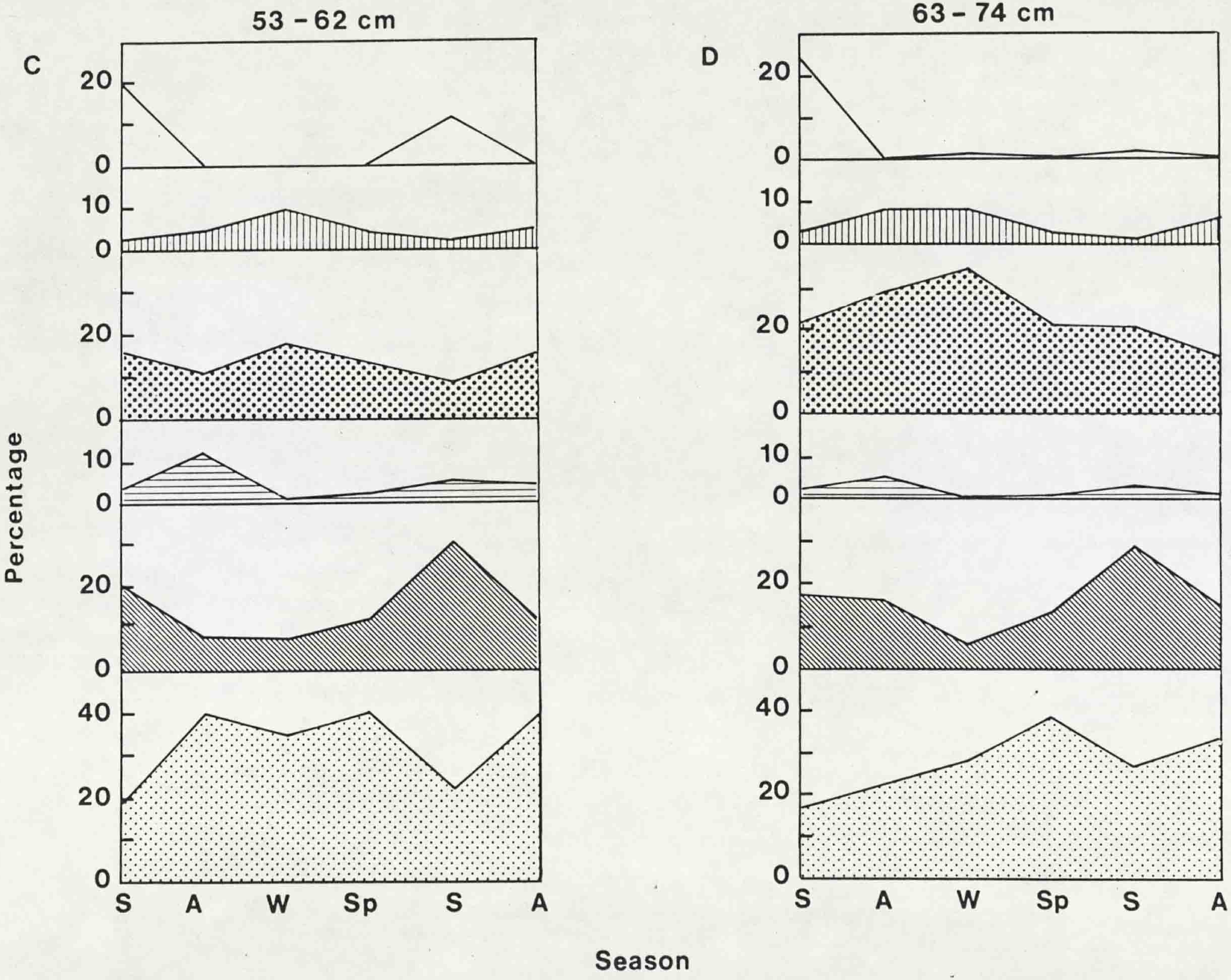
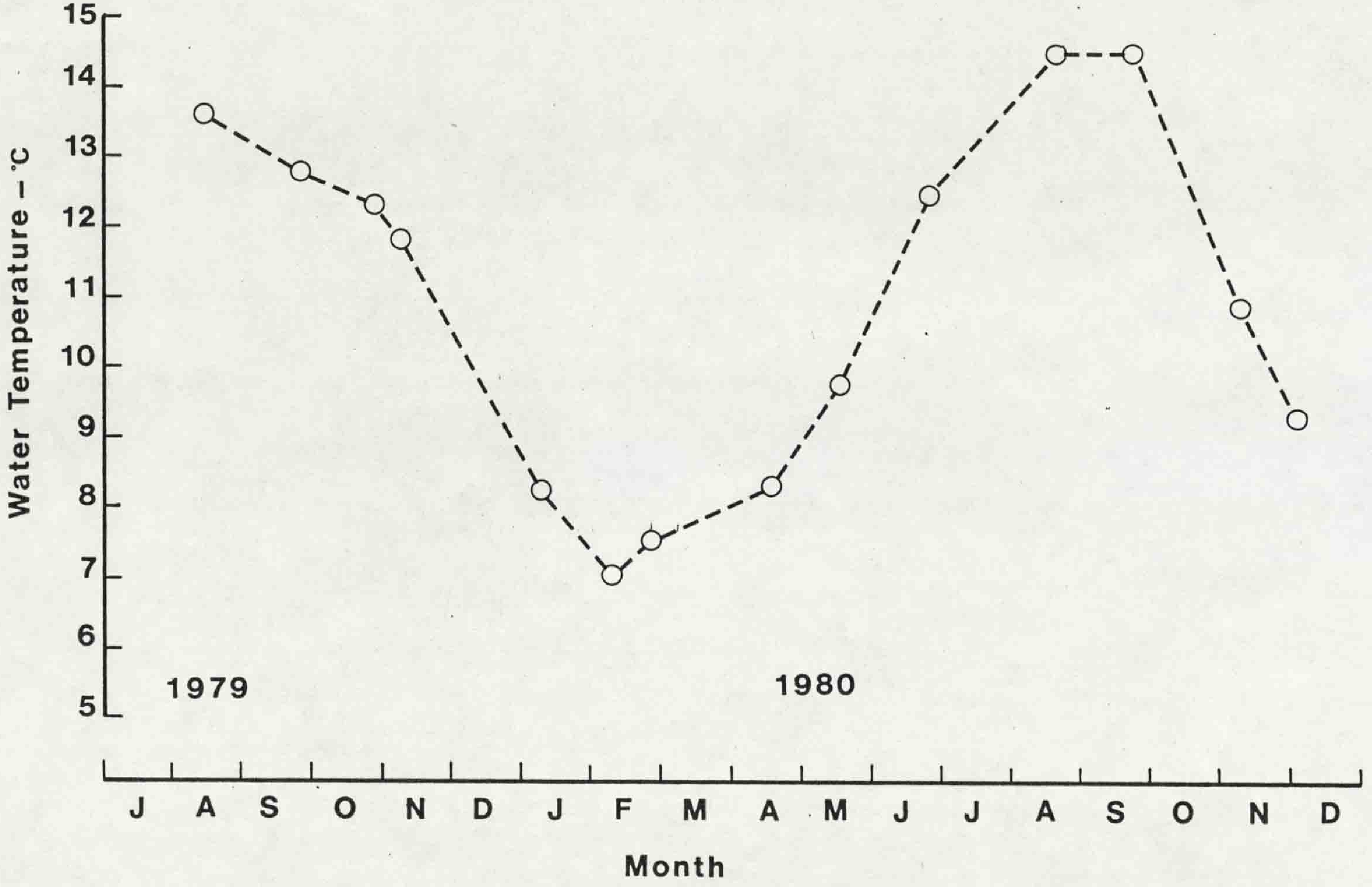

53 - 62 cm
63 - 74 cm
C
D
Percentage
20
0
10
0
20
0
10
0
20
0
40
20
0
S
A
W
Sp
S
A
Season

Figure 1.8 Bottom water temperatures throughout the study period.


15
14
13
12
11
10
9
8
7
6
5
Water Temperature – °C
1979
1980
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
Month

evidence for definite seasonal variation, although there was a slightly higher reliance on this species during the winter. Lack of marked seasonality is hardly surprising as hermit crabs and whelks were present in considerable numbers throughout the year (personal observations) and presumably are readily accessible as a potential food source.

Consumption of Glycymeris, however, exhibited pronounced seasonal variation, being greatest during summer when it accounted for up to 30% of the diet by weight and over 50% by numbers. This peak was followed by a sharp decline in importance during autumn and winter and a slight increase in the spring months.

As suggested previously the contribution by weight of Upogebia tended to decrease as the size of the dogfish increased. Overlying this trend the seasonal pattern of consumption was characterised by a general increase in the summer and autumn months of both years, accompanied by an appreciable drop during the remainder of the year. Clear seasonal patterns were also apparent for the herring, which was essentially a summer food, the pectinids, Chlamys and Pecten, which were generally more important during the autumn and winter, and the holothurian, Thyone, which was most heavily exploited during winter and spring.

In order to describe these observed patterns in more absolute terms, the data were also treated as mean weight and mean number of each prey per feeding dogfish. Results for the more important prey species are tabulated in Appendix IV and mean weights are presented in histogram form in Figure 1.9. As well as affirming the trends already discussed this analysis demonstrates that for the prey that show marked seasonality in their occurrence in the diet of the dogfish, the distribution of peaks and troughs were

Figure 1.9 Seasonal variation in mean wet weight of selected prey contained in the stomachs of different size groups of *Scyliorhinus canicula*.

KEY

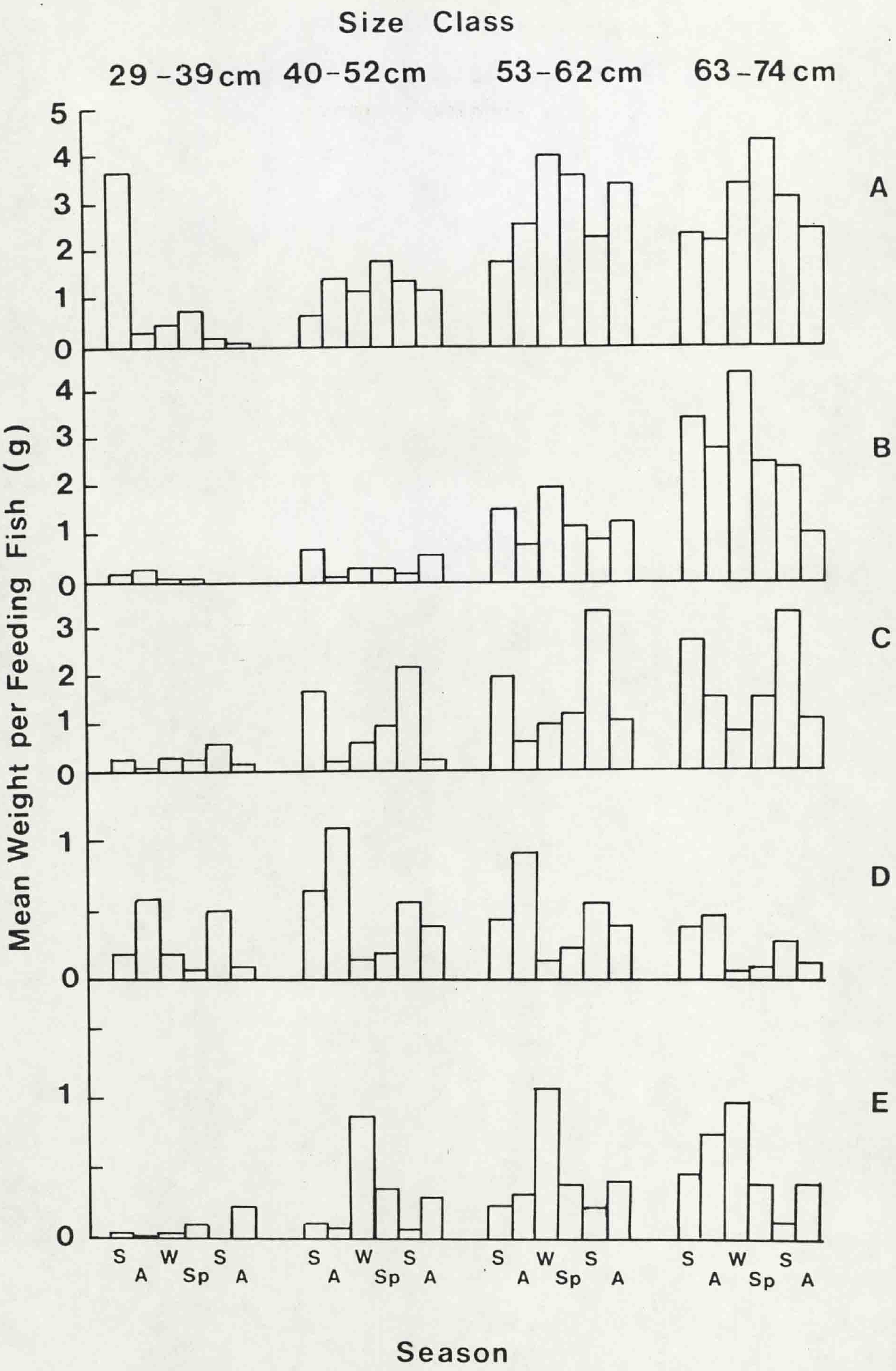
A : *Eupagurus bernhardus*

B : *Buccinum undatum*

C : *Glycymeris glycymeris*

D : *Upogebia* spp.

E : *Chlamys* cf. *opercularis*


Size Class
29 - 39 cm
40 - 52 cm
53 - 62 cm
63 - 74 cm
Mean Weight per Feeding Fish (g)
5
4
3
2
1
0
A
4
3
2
1
0
B
3
2
1
0
C
1
0
D
1
0
E
S
A
W
Sp
S
A
Season

very similar for all sizes of dogfish even though the absolute quantities eaten differed.

Some of the smaller prey items whose weight contributions were essentially insignificant featured very abundantly in the food of the dogfish at various times of the year. For instance the squat lobster *Galathea intermedia* was encountered in large numbers during winter and spring, while the shrimp *Eualus pusiolus* and polychaete *Ammotrypane aulogaster* were most numerous in the autumn samples.

(v) Seasonal Variation in Feeding Intensity

The seasonal variation in feeding intensity, as judged by mean stomach content weights, indicated a peak during summer followed by a distinct minimum during autumn for all sizes of dogfish. Winter and spring values tended to fall between those of summer and autumn, with the exception of a high winter value for the 53 - 62 cm dogfish (Table 1.4, Figure 1.10). It was apparent that the summer maxima in 1980 were generally reduced in relation to corresponding values for 1979. If, however, the semifluid digested material also contained in the stomach was considered then the total weights for the two summers were more comparable. These summer peaks were primarily due to consumption of herring during September. Mean stomach content weights for the other summer months, July and August, were in fact very comparable to those determined for the remainder of the year, with the exception of autumn. For instance, in the 63 - 74 cm dogfish herring consumed in September 1979 contributed 3.16 g (wet weight) to the mean stomach content weight for that summer whereas in 1980, when the summer peak was very much reduced, the contribution was only 0.20 g. Copious quantities of oily chyme characteristically accompanied the

Table 1.4 Seasonal variation in mean weight of stomach contents (g)
(Note: empty stomachs included in calculations .)

A. Solid component

Size class (cm)		1979		1980			
		Summer	Autumn	Winter	Spring	Summer	Autumn
29-39	Wet wt.	5.41	1.58	2.62	2.25	2.38	0.99
	Dry wt.	1.16	0.31	0.59	0.40	0.50	0.20
40-52	Wet wt.	6.75	3.78	5.19	5.74	6.06	4.25
	Dry wt.	1.40	0.77	1.05	1.16	1.33	0.87
53-62	Wet wt.	9.80	6.88	11.47	8.97	10.49	8.76
	Dry wt.	2.44	1.47	2.67	1.95	2.48	2.04
63-74	Wet wt.	15.36	9.37	12.63	11.41	11.49	6.67
	Dry wt.	4.12	2.39	2.98	2.73	2.84	1.64

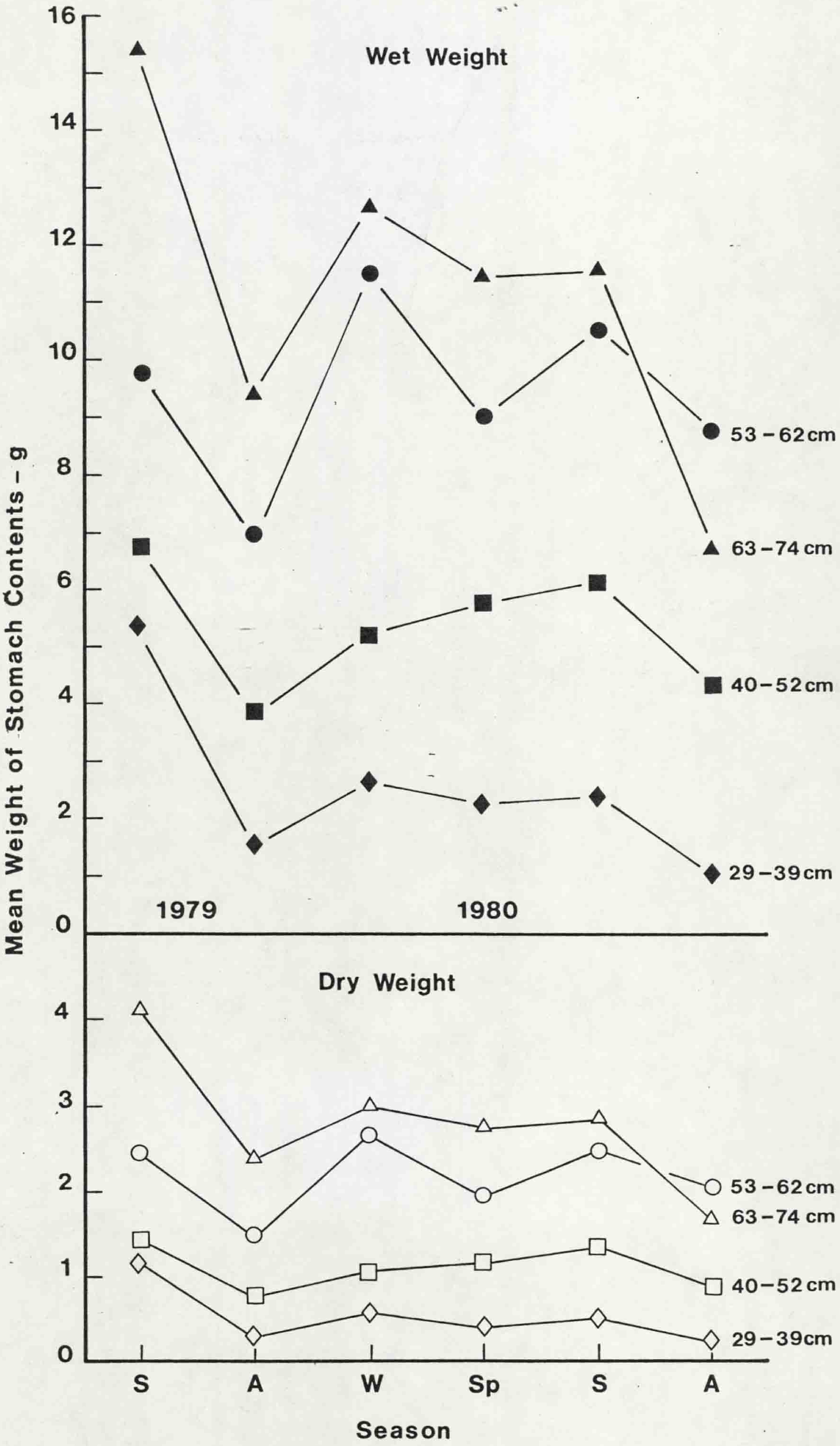
B. Semi-fluid component

29-39	Wet wt.	4.34	2.93	4.36	3.44	3.27	3.54
	Dry wt.	0.93	0.36	0.59	0.83	0.51	0.39
40-52	Wet wt.	9.22	7.84	8.90	8.28	12.50	9.11
	Dry wt.	1.27	0.94	1.02	0.95	2.18	1.07
53-62	Wet wt.	17.62	15.16	17.97	15.66	19.23	17.15
	Dry wt.	2.85	1.97	2.16	1.87	3.79	2.19
63-74	Wet wt.	24.73	20.48	17.10	19.48	27.34	16.99
	Dry wt.	4.50	4.14	2.16	2.44	6.93	3.05

C. Ash-free dry weight of total stomach contents .

29-39	1.87	0.53	0.90	0.68	0.78	0.48
40-52	2.29	1.39	1.60	1.71	3.07	1.59
53-62	4.62	2.88	3.70	3.09	5.50	3.50
63-74	7.60	5.83	4.16	4.32	9.00	4.21

Figure 1.10 Seasonal variation in mean weight of stomach contents (solid component) in relation to size class of *Scyliorhinus canicula*.


Wet Weight
Dry Weight
Mean Weight of Stomach Contents – g
16
14
12
10
8
6
4
2
0
4
3
2
1
0
1979
1980
53 – 62 cm
63 – 74 cm
40 – 52 cm
29 – 39 cm
S
A
W
Sp
S
A
Season

presence of herring in dogfish stomachs and this was reflected in high summer values for the semifluid portion of the stomach contents.

The relationship between time of year and mean number of prey items per stomach for each size group was also examined (Table 1.5.). While these data demonstrate no marked or consistent trends for all size groups the mean numbers of prey were generally higher during summer, 4.7 - 6.6, and slightly lower during autumn and winter, 3.9 - 5.8.

(vi) Feeding Chronology

Of the three occasions when sampling was continued over a 24-h period, both the November and February trips had to be completed over two separate days owing to the deterioration of weather conditions. This lack of continuity could have introduced extraneous factors which would bias the observed patterns of feeding. One such factor envisaged is a possible variation in prey availability on a short term basis, between the two sampling dates, accompanied by a corresponding change in the intensity of feeding. As there were no major differences in the observed trends for each of the three 24-h series this criticism does not appear to be supported.

The data for the 24-h trips are summarised in Appendix V and mean weights of the stomach contents for each haul and each length group of dogfish are presented in Figures 1.11, 1.12, 1.13. Because undigested and digested semifluid portions are related, the latter arising from gastric breakdown of the former, both components were considered in the analysis. It might be expected that

Table 1.5 Seasonal variation in mean numbers of prey items per feeding dogfish.

	Size group (cm)			
Season	29-39	40-52	53-62	63-74
Summer 1979	4.73	5.43	5.71	5.80
Autumn	5.00	4.17	4.04	4.80
Winter 1980	5.75	4.19	5.14	3.98
Spring	5.71	5.04	5.10	4.67
Summer	4.89	5.47	6.56	6.38
Autumn	4.26	5.15	4.15	3.89

Table 1.6 Mann-Whitney U-test for 24-h samples comparing day (D) and night (N) periods (see text).

A- Dry weight of solid material.

Date	Size group (cm)			
	29-39	40-52	53-62	63-74
November 1979	-	-	n.s.	n.s.
February 1980	n.s.	n.s.	n.s.	n.s.
June 1980	p=0.05*	n.s.	n.s.	n.s.

B- Dry weight of semifluid material.

Date	29-39	40-52	53-62	63-74
November 1979	-	-	n.s.	n.s.
February 1980	n.s.	p=0.05*	n.s.	n.s.
June 1980	n.s.	n.s.	n.s.	n.s.

* D>N

these two components are inversely proportional and the relative proportions of each could be of some importance in the demonstration of feeding patterns.

Three general statements can be made with regards to the way the stomach contents varied throughout the 24-h periods:

(a) the weight of stomach contents fluctuated, with peaks and troughs apparent,

(b) the patterns of fluctuation were not consistent between the different sizes of dogfish or between the different sampling dates,

and (c) the undigested and digested components were not consistently related in their pattern of fluctuation.

The results obtained in June (Figure 1.13), for example, showed that peaks in the standing crop of undigested food occurred just prior to sunset and just after sunrise for the 29 - 39 cm and 63 - 74 cm dogfish. Two peaks were also recorded for the 40 - 52 cm and 53 - 62 cm size groups, the first occurred for both groups at about midday with the second at about midnight for the 40 - 52 cm dogfish and just prior to sunrise for the 53 - 62 cm size class.

A firm conclusion regarding the presence or absence of feeding chronology thus could not be made based solely on these results. The data were tested using the Mann-Whitney U-test to determine whether there was any statistically signficant evidence for nocturnal or diurnal feeding. In each case the results were split into 'day' and 'night' periods, the former defined for this purpose as lying between 0801 - 2000 h and the latter between 2001 - 0800 h. The results of the test are presented in Table 1.6. With only two exceptions, differences between the

Figure 1.11 Variation in mean dry weight of stomach contents of different size classes of Scyliorhinus canicula with time of day - November 1979.

Dry weight of solid component □—□

Dry weight of semifluid chyme ○—○

(Numbers indicate sample size; HW time of high water; SS sunset, SR sunrise and shaded area hours of darkness)

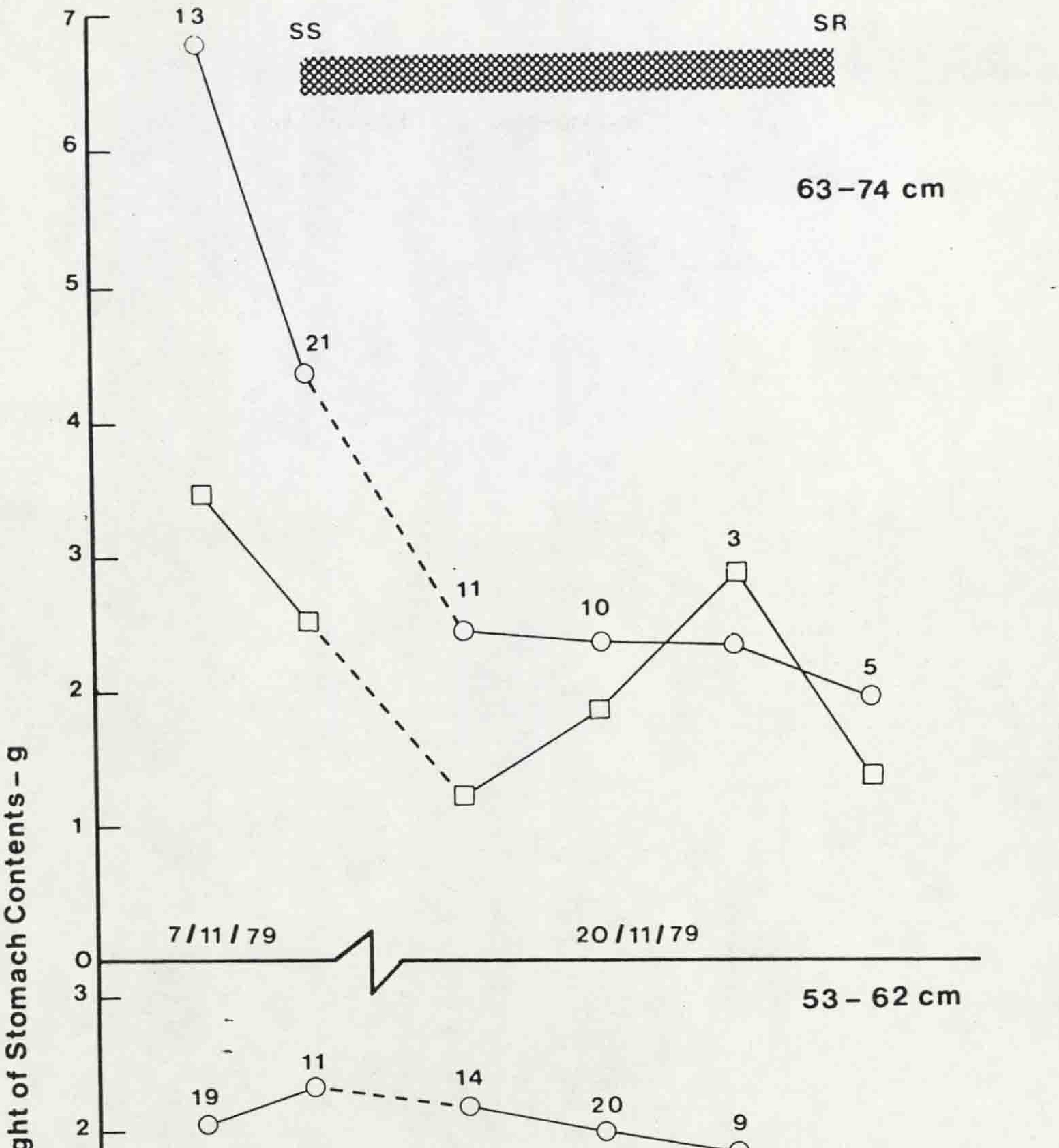

Mean Weight of Stomach Contents - g
Time of Day - h
SS
SR
63-74 cm
53 - 62 cm
40 - 52 cm
7/11/79
20/11/79
13
21
11
10
3
5
19
11
14
20
9
7
20
3
20
20
3
0
1
2
3
4
5
6
7
1200
2400
0600
1200
HW
HW
HW

Figure 1.12 Variation in mean dry weight of stomach contents of different size classes of Scyliorhinus canicula with time of day - February 1980.

Legend same as Figure 1.11 .

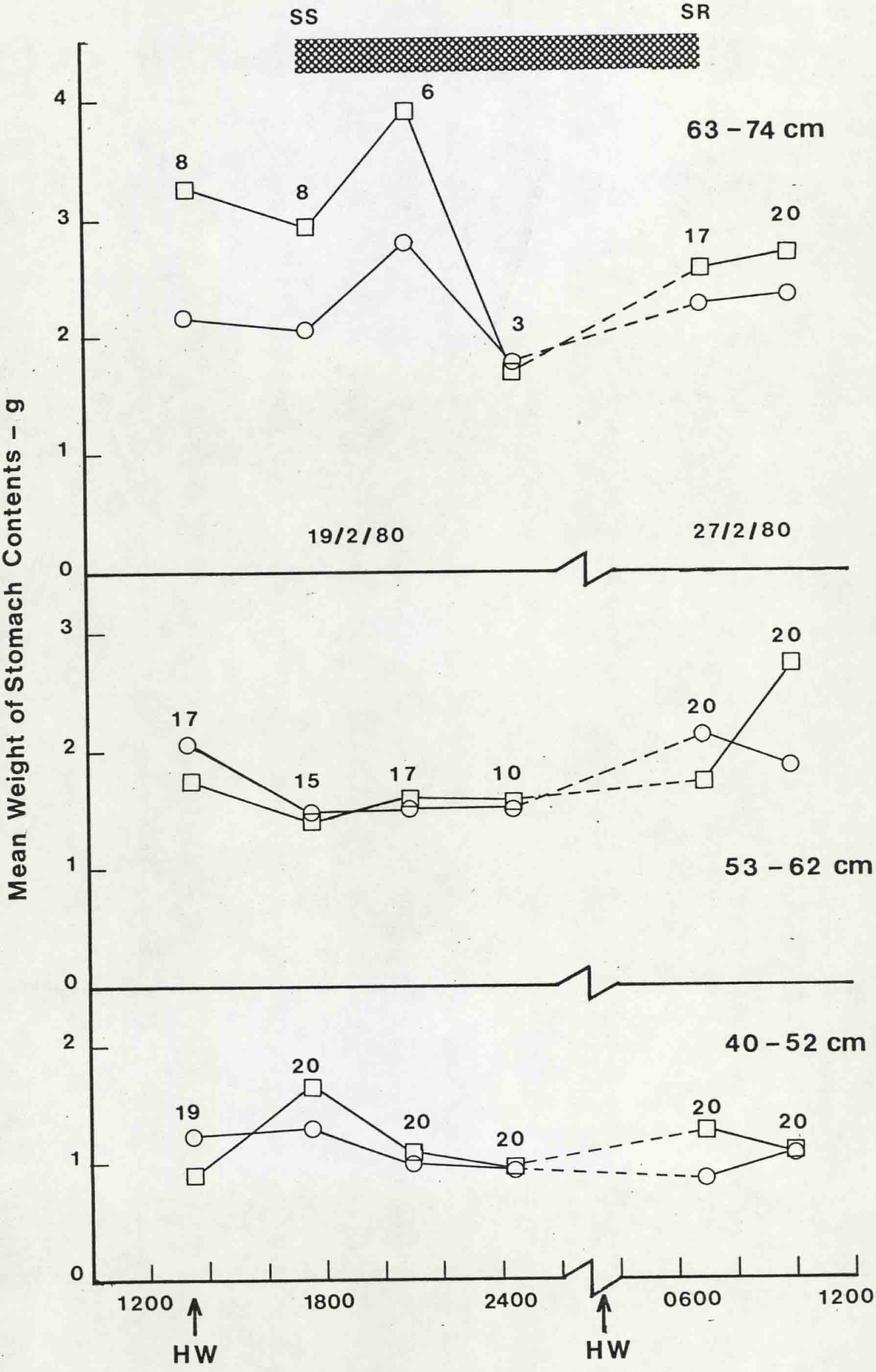

SS
SR
63 - 74 cm
19/2/80
27/2/80
53 - 62 cm
40 - 52 cm
Mean Weight of Stomach Contents - g
4
3
2
1
0
3
2
1
0
2
1
0
8
8
6
3
17
20
17
15
17
10
20
20
19
20
20
20
20
20
1200
1800
2400
0600
1200
HW
HW
Time of Day - h

Figure 1.13a Variation in mean weight of stomach contents of 29-39 cm and 40-52 cm size groups of *Scyliorhinus canicula* with time of day - June 1980.

Wet weight of solid component	■——■
Dry weight of solid component	□——□
Wet weight of semifluid chyme	●——●
Dry weight of semifluid chyme	○——○

(Further details see Figure 1.11)


SS
SR
29 - 39 cm
40 - 52 cm
Mean Weight of Stomach Contents - g
Time of Day - h
0
1
2
3
4
5
0
2
4
6
8
10
12
1200
1800
2400
0600
1200
HW
HW
9
15
8
5
11
5
20
22
22
20
20
16

Figure 1.13b Variation in mean weight of stomach contents of 53-62 cm size group of *Scyliorhinus canicula* with time of day - June 1980.

Legend same as Figure 1.13a

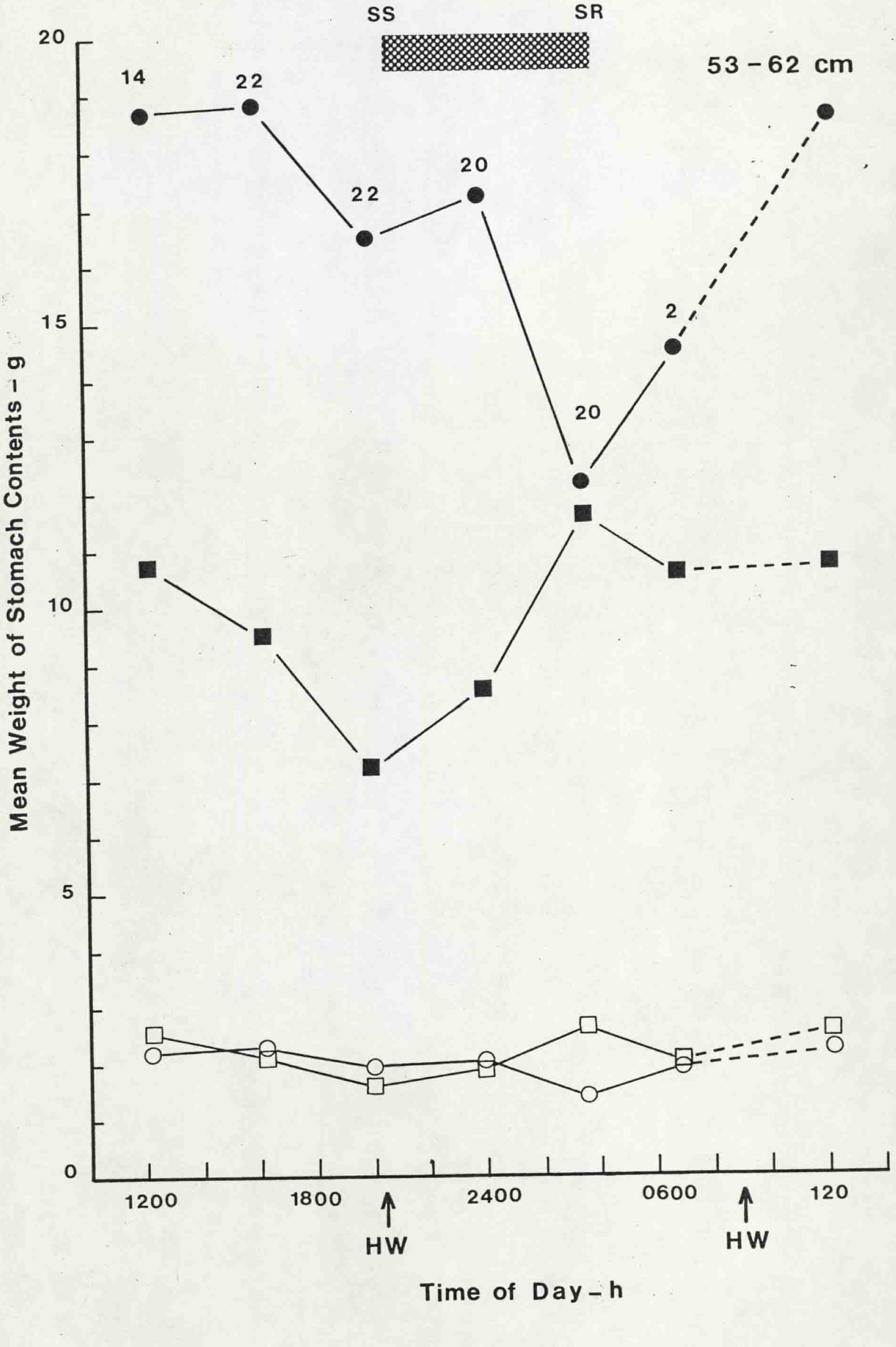
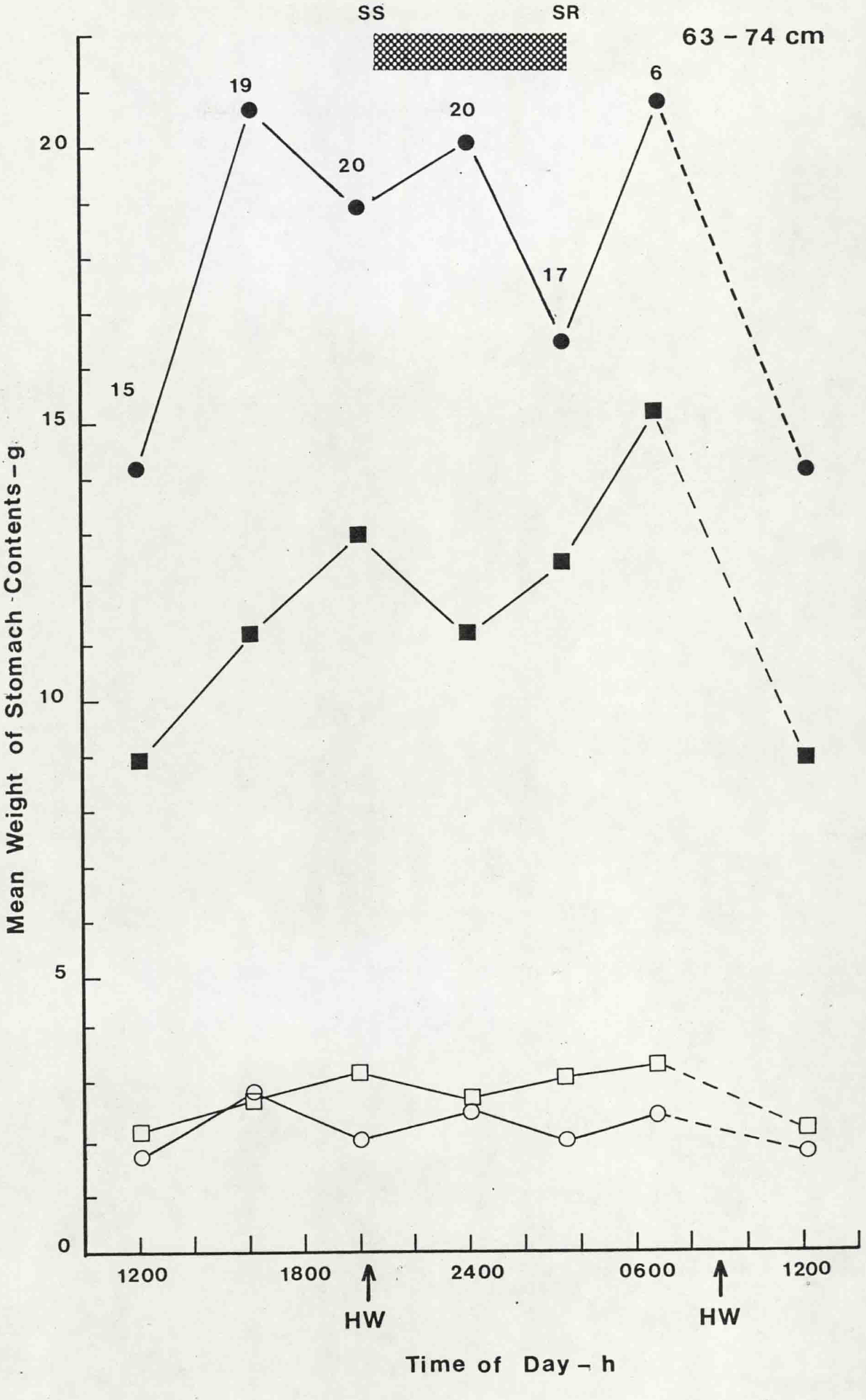

SS
SR
53 - 62 cm
20
15
10
5
0
14
22
22
20
20
2
Mean Weight of Stomach Contents - g
1200
1800
2400
0600
120
HW
HW
Time of Day - h

Figure 1.13c Variation in mean weight of stomach contents of 63-74 cm size group of *Scyliorhinus canicula* with time of day - June 1980.

Legend same as Figure 1.13a

SS
SR
63 - 74 cm
19
20
20
17
6
15
Mean Weight of Stomach Contents - g
0
5
10
15
20
1200
1800
2400
0600
1200
HW
HW
Time of Day - h

day and night samples for both the undigested and semifluid portions were not significant at 95% confidence. There was, therefore, no evidence to indicate marked diurnal or nocturnal feeding activity in the dogfish. In further support of this conclusion there were no clear trends in the state of digestion of the various prey in the stomachs over the sample periods to indicate a general synchrony of feeding activity.

DISCUSSION

The diet of Scyliorhinus canicula around the Isle of Man indicates that it is a generalist predator consuming more or less whatever is available. It eats a wide range of benthic and demersal species and also preys on typically pelagic fish when they are locally abundant; food items of importance in the diet are numerous and varied. Previous workers have reached similar conclusions regarding the feeding habits of Scyliorhinus based on different populations from around Britain (Ford, 1921; Steven, 1930; Eales, 1949; Armstrong, 1980) and throughout the Mediterranean (Canadjija, 1961; Azouz and Capapé, 1971; Jardas, 1972, 1979; Capapé, 1974). The main features of the diets from the various localities are presented in Table 1.7.

Epibenthic crustacea and in particular decapods, represent a significant source of food for the dogfish. The results for the present study and those of Ford (1921), Steven (1930), Eales (1949) and Armstrong (1980) indicate that reptant decapods such as Eupagurus, Upogebia, Macropipus, and in the latter two studies Nephrops norvegicus dominate the crustacean element. Canadjija (1961), Jardas (1972, 1979) and Capapé (1974) on the other hand found that natant decapods, in particular Alpheus and Penaeus, and to a lesser extent stomatopods,

Table 1.7 Main features of the diet of Scyliorhinus canicula from various localities around Britain and throughout the Mediterranean.

Source	Present Study•				Armstrong (1980)•		Ford (1921)+	Steven (1930)+	Canadjija (1961)•	Capape (1974)+	Jardas (1972)•	Jardas (1979)•
Location	IRISH SEA (East coast, Isle of Man)				IRISH SEA (West coast, I.O.M.)		ENGLISH CHANNEL (Plymouth)	ENGLISH CHANNEL (Plymouth)	ADRIATIC	MEDITERRANEAN (Tunisia)	ADRIATIC (Central)	ADRIATIC (Central)
Size range (cm)	29–39	40–52	53–62	63–74	50–64	65–79	na	Adults and juveniles	11–49	Adults and juveniles	8–48	21–46
CRUSTACEA	64.4	44.0	31.4	27.9	58.6	61.3	36.5	47.2	76.1	38.5	54.3	62.7
Paguridae	5.7	9.9	11.3	12.3	6.4	1.2	18.7	18.2	–	1.4	0.7	–
Nephrops	–	–	–	–	39.1	50.0	–	–	0.002	–	–[a]	–
MOLLUSCA	9.8	25.9	37.1	48.1	10.2	9.3	9.7	3.0	7.4	20.9	18.7	13.9
Cephalopoda	0.2	0.1	0.3	0.2	2.6	2.8	1.7	na	7.1	17.1	8.3	13.9
PISCES	2.0	1.6	1.8	1.9	21.4	16.5	20.3	34.2	11.4	33.7	19.2	22.4
POLYCHAETA	22.4	21.7	21.2	14.7	6.0	7.7	20.3	13.9	5.1	4.9	7.7	0.9
HOLOTHURIOIDEA	0.9	4.8	5.5	4.6	na	na	6.1	1.7	–	–	–	–
OTHER	0.6	2.1	3.0	2.8	3.8	5.2	7.0	–	–	2.0	–	–
Number with food	174	682	637	495	100	75	146	142	334	1177	151	276

• Percentage by numbers

+ Percentage of total occurrences

[a] Nephrops was not recorded in dogfish stomachs although they were singly the most abundant crustacean throughout the study area – cf. Armstrong (1980)

na data not available

Squilla, as well as various crabs, e.g. Goneplax, were the most important crustacean prey eaten.

Molluscs and typically demersal fish are also preyed upon although there are considerable differences in the relative importance of these groups to the diet of dogfish from different regions. These differences are no doubt attributable to qualitative and quantitative variability in associated benthic communities. An investigation of bottom fauna around the south of the Isle of Man by Jones (1951) encompassed the southern half of the present study area (his ground 'A4') and the muddy ground (ground 'D') studied by Armstrong (1980). Jones (op cit.) determined species abundance semi-quantitatively as the number of dredge or grab hauls in which a particular species occurred and expressed it as a percentage of the total number of hauls for that ground. This revealed some very significant differences between the faunistic components of the two grounds (Table 1.8). Diversity and abundance of suitable molluscan prey species appears to be a characteristic of the Douglas ground while general paucity of molluscs is typical of the muddy ground (D) west of the Isle of Man. The relative importance of molluscs in the diets of dogfish from these two grounds very obviously reflect these differences (Table 1.7). Steven (1930) also reported that molluscs played only a minor role in the diet of dogfish from the Plymouth area, 3% of the total occurrences, but did note that molluscs were poorly represented in the fauna on the grounds he studied.

Fish accounted for only about 2% of the total number of prey noted in the present study whereas other workers have found that fish were considerably more prominent. Capapé (1974), for instance, recorded that fish comprised nearly 35% of the diet, and in a study of predominately adult dogfish Azouz and Capapé (1971) found fish in 80% of the stomachs examined.

Table 1.8 Relative abundance of crustacean and molluscan fauna from coarse and muddy grounds around the Isle of Man (data from Jones, 1951) that feature in the diet of *Scyliorhinus canicula* .*

Locality :	East of Langness (southern half of present study area)	Approx. 16 km west of Isle of Man .
	Ground "A4"	Ground "D"
Substrate :	Gravel,shell and stones	Mud
FAUNA :		
CRUSTACEA		
Crangon allmanni	-	13
Pandalus montagui	18	13
Dichelopandalus bonnieri	-	13
Pandalina brevirostris	24	-
Nephrops norvegicus	-	22
Calocaris macandreae	-	70
Galathea intermedia	40	-
G. dispersa	6	-
Porcellana longicornis	18	-
Eupagurus bernhardus	41	-
E. prideauxi	53	-
E. cuanensis	41	-
E. pubescens	24	-
Macropipus pusillus	35	-
MOLLUSCA		
Glycymeris glycymeris	65	-
Pecten maximus	18	-
Chlamys opercularis	71	-
Buccinum undatum	53	-
Sepiola atlantica	6	9

* Abundance measured semi-quantitatively as the number of dredge or grab hauls in which each species occurred and expressed as a percentage of the total number of hauls for that ground .

In any attempt to explain the major differences in the diets of the various dogfish populations the question of feeding selectivity arises. By comparing the prey eaten by *Scyliorhinus* (Table 1.3) with their abundance in the benthic community (Jones, 1951; and Table 1.8) it can be seen that the principal prey, *Eupagurus bernhardus*, *Glycymeris glycymeris*, *Buccinum undatum* and *Chlamys opercularis*, were correspondingly very abundant on the ground studied, with values in excess of 40%. Numerically important prey, such as *Galathea intermedia* and *Macropipus pusillus*, were also frequently recorded in Jones's samples. On the basis of this evidence it seems likely that within the limits imposed by the structural morphology of the mouth and innate behavioural patterns, *Scyliorhinus* feeds indiscriminately consuming those species that are most readily available. Steven (1930) reached a similar conclusion regarding the feeding habits of several demersal fish species, including *Scyliorhinus*. Jardas (1972) on the other hand postulated that dogfish quite positively selected for *Alpheus glaber*, *Squilla desmaresti* and *Upogebia* sp. The possibility that the abundance of these species might have been underestimated in his benthic sampling programme must be considered, since the first two species are very active crustaceans and the last a burrowing form. In a later more detailed study Jardas (1979) concluded that there was no evidence for selection of the various prey groups, which agrees with the present findings.

Examination of the type of prey consumed and its condition in the stomach enables a number of points to be inferred with regards to the actual feeding behaviour employed by the dogfish. Kalmijn (1971) established that *Scyliorhinus* was capable of digging for buried prey. It is interesting to note, however, that the parts of the burrowing molluscs consumed suggest that dogfish essentially crop organs protruding from the shells and presumably exposed at the surface of the substrate, rather than actually digging for them. Only the foot regions of *Glycymeris*, *Ensis* and *Cardium* and the siphons of *Mya* and *Lutraria* were recorded in the stomach contents. Similarly the virtual absence of the adductor muscle and gonads of *Chlamys* is probably due to the fact that dogfish tackle this prey by grasping the mantle fringe, exposed in the queenie's feeding posture, which is then torn free from the body. Such a procedure would tend to leave the organs that are firmly attached to the shells intact and inaccessible.

In aquaria, Brightwell (1953) observed a dogfish knock over a crawling whelk to expose the head and foot regions. The dogfish then gripped the foot and shook until the head and foot were torn away from the visceral mass which remained in the shell. This feeding mode is clearly utilized in the wild, attested by the occurrence of the head and foot of *Buccinum* and *Neptunea* in the stomachs, rarely accompanied by the visceral mass. Brightwell (op cit.) also reported that hermit crabs were extracted from their shells in a similar manner. This would account for the frequent absence of the abdomen in the stomach contents. The chitinous opercula of the whelks resist digestion and in several instances large numbers were contained in individual stomachs. As the opercula were too large to pass through the pyloric sphincter and were never found in the intestine they must be periodically regurgitated to avoid interference with the normal stomach contractions associated with digestion. Other elasmobranchs are thought to remove indigestible material from the stomach in a similar manner (Gudger, 1949; Clarke and Stevens, 1974).

A common feature of the feeding habits of many teleosts (Tyler, 1972; Daan, 1973; etc.) and various groups of elasmobranchs, for instance *Raja* (Holden and Tucker, 1974; McEachran *et al*, 1976; de Souza, 1978), *Squalus acanthias* (Jones and Geen, 1977) and *Scyliorhinus canicula* (Jardas, 1972, 1979; Capapé, 1974; Armstrong, 1980), is that the composition of the diet alters with growth. In the present study it was noted that bigger dogfish ate greater numbers and larger individuals of *Eupagurus bernhardus* while the quantity of other benthic crustacea decreased. Molluscs and to a lesser extent, teleosts became gradually more important in the diets of larger dogfish. These trends reflect the increasing ability of bigger dogfish to tackle larger prey, such as *Buccinum undatum*, *Eupagurus bernhardus* and *Clupea harengus*, no doubt a consequence of larger mouths and increased swimming speed. Smaller prey, *Galathea intermedia*, *Upogebia* spp., *Macropipus pusillus* (the mean carapace width of which varied only between 10 - 16 mm for the four size classes of dogfish), *Eualus pusiolus* and various polychaetes were more a feature of the diets of smaller dogfish.

The present findings accord with those of Capapé (1974) who noted that crustaceans declined in importance in the diet of larger dogfish, while concurrently the quantity of cephalopods and teleosts increased. Rather than this marked drop in the role of crustaceans Jardas (1972, 1979) observed a switch in the composition of the crustacean element, from mysids and amphipods to decapods, stomatopods and isopods. Cephalopods and teleosts were more heavily exploited by the bigger dogfish. A similar pattern was obtained for dogfish from west of the Isle of Man (Armstrong, 1980) in this case increase in importance of the prawn, *Nephrops norvegicus*, offset the decrease of other crustacean prey in the diet. Armstrong (op cit.) did report that Buccinum was taken more frequently by larger dogfish which is corroborated by the present findings.

By confining the sampling programme to a small area of comparatively homogeneous substrate it was hoped that the influence that geographic varation might have on prey abundance would be reduced to a minimum. It was, therefore, likely that seasonal changes in the composition of the diet were a true reflection of seasonal patterns of prey availability. This premise is supported by the fact that the most conspicuous patterns of consumption were similar in all size classes of dogfish. Allen (1941) and Ware (1972) emphasise that in determining the risk of potential prey to predation both the behaviour of the prey, its activity and degree of exposure, as well as its numerical abundance are important.

Behavioural changes in the prey may be associated with reproduction, for instance Upogebia stellata and U. deltaura were apparently least susceptible to predation during winter and spring when berried females occurred. The marked seasonal pattern of consumption of Glycymeris, characterised by a peak during summer and followed by a distinct minimum during autumn and winter, suggests that there was some seasonal variation in the degree of exposure to dogfish predation. The fact that Glycymeris make irregular migrations to the surface of the substrate has been reported under laboratory conditions by Morris (1978) and the digging process, which commences with 'pedal probing', has been described by Ansell and Trueman (1967). As only the muscular foot and occasionally the body, but never the shell, were recorded in dogfish stomachs it seems probable that they were eaten whilst on or just under the substrate surface and during digging activity. Trawl and dredge damage to Glycymeris shells could also expose them to dogfish predation, but this is unlikely to be very significant as the study area is not intensively fished. The most plausible explanation seems to be that migrations to the substrate surface are more frequent during the spring and summer months, possibly in response to endogenous activity patterns and rising water temperatures. In support of this suggestion preliminary field observations of another burrowing bivalve, Arctica islandica, suggest that there is a seasonal pattern in the numbers found at the substrate surface, with a peak occurring during summer (M. Bates, pers. comm.).

The numerical abundance of a prey species is influenced most directly by recruitment or migration into or out of an area. The occurrence of herring in the diet during summer, or more precisely September, was in response to the migration of spawning shoals into the study area. At this time herring are concentrated in large numbers near the seabed (Bowers, 1969).

Feeding intensity of a species may undergo marked seasonal changes. These changes may be related to changes in availability of appropriate food organisms (Raymont, 1947; Nikolsky, 1969), endogenous cycles, e.g. spawning (Homans and Vladijkov, 1954; Rae, 1967a) and/or a variety of environmental factors, e.g. water temperature (Jones, 1973), light intensity (Blaxter, 1968), etc. Seasonal variation in the quantity of food in the stomachs of Scyliorhinus was characterised by a summer maximum, which was primarily due to an apparent increase in available food (herring), followed by a minimum during autumn (Figure 1.10). This minimum may in fact be a physiological response to falling water temperatures and/or to the relative scarcity of prey such as Glycymeris during autumn.

Jardas (1972, 1979) and Capapé (1974) using different criteria, i.e. stomach fullness and the proportion of stomachs containing food respectively, have also reported seasonal variation in feeding intensity for Scyliorhinus. Jardas (1972) found that Scyliorhinus fed most heavily during autumn through to early spring, at a time when spawning was most intensive. These conclusions, however, must be viewed very critically as they were based on few samples, for instance the apparent summer minimum was based on only three specimens. In contrast, Jardas (1979), found that maximum feeding intensity occurred during summer and autumn. Capapé (1974) also observed a greater feeding intensity during the summer and autumn months for juveniles and adult females. He suggested that the pattern obtained for juveniles was a consequence of seasonal changes in food availability whereas the pattern for adult females was partly related to reproduction. That is, during the period of reduced vitellogenesis and egg production (summer and autumn) they fed most heavily, building up energy reserves necessary for the subsequent reproductive demands. The fact that there was no seasonal variation in the feeding intensity of the adult males supported this suggestion. As a consequence of the short residence time of adult females in the present study area it was not possible to confirm these observations.

Bateson (1890b) and Brightwell (1952) have observed that Scyliorhinus is basically night-active in aquaria while Kuchnow (1971) found that the pupillary reponse to light is typical of nocturnal selachians. The species might thus be expected to exhibit a nocturnal feeding pattern. There was, however, no evidence for any discrete diel feeding patterns in the present study. Evidence presented in this study suggested rather that the weight of stomach contents fluctuated randomly about a mean value, which was determined by the time of year and by the size of dogfish in question. The extremely low occurrence of completely empty stomachs, and presence of several prey at various stages of digestion in individual stomachs provided further support for the conclusion that *Scyliorhinus* feeds at any time of the day. Based on mean stomach fullness, Jardas (1972), concluded that *Scyliorhinus* fed most intensively in the early afternoon but as the hauls were conducted between 0700 and 1800 h and the sample sizes were small, these finding were unlikely to be tru~~e~~ly representative.

An absence of marked diel periodicity of feeding has also been reported for some ray species, e.g. *Raja erinacea*, *R. ocellata* and *R. radiata* (McEachran *et al*, 1976) and *R. clavata* (de Souza, 1978). The feeding strategies adopted by these demersal elasmobranchs contrast with that for the predominately pelagic feeder, *Squalus acanthias*. Holden (1966) and Jones and Geen (1977) concluded that *Squalus* feeds only intermittently, ceasing to feed until digestion is completed, and that even then the fish may not necessarily feed again immediately.

The control and timing of feeding behaviour of fish is a very complex process. Endogenous activity rhythms will be important, but the ultimate timing of intake will be mediated by factors including the rate of appetite return, activity and consequent exposure of potential prey organisms, and various environmental cues. The importance of appetite return which is to a large extent related to gastric emptying, in synchronising feeding chronology, has been demonstrated in various teleost species (e.g. Magnuson, 1969; Brett, 1971a; Reshetnikov *et al*, 1972; Elliott, 1975b; Grove *et al*, 1978; Grove and Crawford, 1980; Gwyther and Grove, 1981). No similar studies have been conducted on elasmobranchs, although Kalmijn (1971) noted that even though *Scyliorhinus* was generally inactive during the day individuals would become spontaneously active when hungry. With regards to the activity patterns of prey consumed by the dogfish both diurnally active forms, e.g. *Eupagurus bernhardus* (Mitchell, 1974) and nocturnally active forms, e.g. *Macropipus pusillus*, *Porcellana longicornis* (Bateson, 1890a), were included in the diet.

Olfactory stimuli represent a powerful factor in motivating exploratory feeding behaviour in *Scyliorhinus* (Bateson, 1890b; Teichmann and Teichmann, 1959; Kalmijn, 1971, 1977; Dijkgraaf, 1975) although precise prey location may involve electrolocation (ampullae of Lorenzini) (Kalmijn, 1971, 1977). In the wild dogfish tend to face into the prevailing tidal current while during slack water they become more randomly positioned (C. Briggs, pers. comm.). Thus orientation pattern would be optimal for the detection of food odours dispersed by unidirectional currents (tides), with rheotaxis contributing significantly to food location (Dijkgraaf, 1975). Preliminary results for acoustically tagged dogfish also indicate that a relationship exists between swimming activity and tidal currents (Greer Walker *et al*, 1980). Rae (1967b) has reported circumstantial evidence which emphasises the possible relationship between tidal currents and feeding for another elasmobranch, *Squalus*. Damage to gill-netted herring by spurdogs was apparently most severe during strong tidal movements but minimal at slack tide. Although tidal water movements represent an important hydrographical feature of the present study area no direct relationship between the state of tide and quantity of food contained in the stomach was apparent (Figures 1.11, 1.12, 1.13). This finding is not altogether surprising as any such relationship would probably be masked by the slow rates of gastric evacuation (Chapter 2), and the fact that feeding rates in pooled subsamples of the population were considered and not the feeding pattern of the individual over a 24-h period.

CHAPTER 2

Gastric Evacuation Rates

INTRODUCTION AND LITERATURE REVIEW

The rate of elimination of food in fish is of considerable interest to fisheries biologists as it has bearing on a variety of parameters relating to fish production. Several workers have used this information to produce estimates of food consumption in the wild (Darnell and Meierotto, 1962; Seaburg and Moyle, 1964; Magnuson, 1969; Healey, 1971; Swenson and Smith, 1973; Thorpe, 1977; Doble and Eggers, 1978; Elliott and Persson, 1978; Diana, 1979; etc.) while such information can be used in aquaculture to determine feeding schedules in order to optimise production (Shrable _et al_, 1969; Brett and Higgs, 1970; Brett, 1971a; Elliott, 1975b; Grove _et al_, 1978; Flowerdew and Grove, 1979; Vahl, 1979).

In discussing elimination of a meal from the stomach or entire digestive tract, terms such as 'rates of digestion' and 'gastric digestion' have been used and imply physiological digestion and absorption. It is more appropriate in such studies to refer to the process as 'evacuation', 'elimination', 'emptying' or 'clearance'.

Most investigations of gastric evacuation rates have been conducted under controlled laboratory conditions, though a number of field studies have been attempted. There are two main approaches to field estimations; (a) by isolating a sample of fish in a food free environment and following the decrease in mean stomach content weight of subsamples examined at various times after capture (Seaburg and Moyle, 1964; Healey, 1971; Thorpe, 1977) or, (b) by following the decline in stomach content weight of samples taken over an established non-feeding period (Doble and Eggers, 1978).

A variety of experimental techniques have been employed in laboratory studies though the basic plan of the fish consuming a meal of known size and subsequent examination of this meal is common throughout.

(i) Methods used to Measure Evacuation Rates/Time.

Removal of Stomach Contents after a meal: Partially digested meal may be retrieved for examination by killing the fish or alternatively the stomach may be emptied either by causing the fish to vomit (Markus, 1932) or by stomach lavage (Hunt, 1960; Seaburg and Moyle, 1964; Elliott, 1972; Swenson and Smith, 1973; Steigenberger and Larkin, 1974; Griffiths, 1976; Persson, 1979). The degree of digestive breakdown of the food has been assessed visually (Pierce, 1936; Darnell and Meierotto, 1962; Armstrong and Blackett, 1966), by water displacement (Hunt, 1960; Seaburg and Moyle, 1964), by wet or dry weights (Pandian, 1967; Magnuson, 1969; Shrable *et al*, 1969; Windell *et al*, 1969; Jones, 1974; Griffiths, 1976), by dry weight of organic matter (Windell, 1966; Windell and Norris, 1969; Brett and Higgs, 1972; Elliott, 1972; Persson, 1979, 1981), or by calorific and biochemical analysis of the residue (Beamish, 1972; Gerald, 1973; Jobling and Davies, 1979; Jobling, 1980 a, c).

In situ observation of stomach contents: The movement of a meal from the stomach of fish has been observed by direct visual observation, possible in transparent fish larvae (Laurence, 1971) and by X-ray techniques, through examination of prey's skeletal structures (Molnár and Tölg, 1962; Fábian *et al*, 1963; Molnár *et al*, 1967) or through the incorporation of a contrast medium, such as barium sulphate, into paste diets or soft bodied invertebrates (Edwards, 1971, 1973; Goddard, 1974; Grove *et al*, 1978; Flowerdew and Grove, 1979; Grove and Crawford, 1980; Gwyther and Grove, 1981).

Other Methods: A number of workers have measured the total time between food intake and defaecation. In fish such as Rutilus and Misgurnus this approach has proven very straightforward as a small meal subsequently appears as a single dropping (Scheuring, 1928; Bokova, 1938; cited by Fänge and Grove, 1979). In microphagous feeders which feed more or less continuously a 'quantum' of food may be labelled with a dye (Laurence, 1971), or sandwiched between a prey that is easily recognisable in the faeces (Rosenthal and Paffenhöfer, 1972), or observed directly in transparent larvae (Rosenthal and Hempel, 1970). In most macrophagous fishes faeces from the meal appear over a considerable period of time and the time lapse cannot, therefore, be judged accurately.

Radioactive labels have also been used, for instance Kevern (1966) employed cesium isotope (^{137}Cs) while Peters and Hoss (1974) used radioactive cerium (^{144}Ce).

(ii) Factors influencing Evacuation Rates/Time

A variety of factors have been demonstrated to be of importance in influencing gastric evacuation rates, these include water temperature, fish size, meal size and digestibility, feeding frequency and physiological state of the fish. The roles of these factors have been reviewed by Kapoor et al (1975), Windell (1978), and Fänge and Grove (1979), and the results of some of the published data are summarised in Table 2.1.

Temperature: In poikilotherms, physiological and physio-chemical processes such as digestion are highly dependant on the environmental temperature and previous thermal history of the animal. Gastric evaucation rates are positively related to the water temperature and tend to increase in a curvilinear fashion with

TABLE 2.1 Time to complete gastric emptying (GET) in fishes (based on Fänge and Grove, 1979).

Species	Fish Size	Temp. (°C)	GET + (hours)	Meal Type	Method •	Reference
ELASMOBRANCHII						
Squalus acanthias		18	48–72	Chopped beef	FF	Van Slyke & White (1911)
	70–107 cm	10	124	120 g *Clupea*	FF	Jones & Geen (1977)
Raja clavata	186 g	8	106.5	1% *Crangon*	FF	de Souza (1978)
		12.5	78			
		16	63.5			
HOLOSTEI						
Lepisosteus platyrhynchus	70–132 g	23–26	25	0.7% *Gambusia*, *Molliensia*	FF	Hunt (1960)
Chaenobrytus gulosus	72–113 g	23–26	26	2.7% *Gambusia*, *Molliensia*	FF	Hunt (1960)
Amia clava	11–33 g	21	32	4.9% *Gambusia*, *Molliensia*	FF	Herting & Witt (1968)
TELEOSTEI						
Salmo trutta	90 g	5.2	49	1% *Gammarus*	Vol	Elliott (1972)
		7.6	37			
		9.8	29			
		12	22			
		15	16			
Salmo gairdnerii	75–85 g	8.5	26.5	1% Paste	Vol/FF	Grove *et al* (1978)
		13.5	18.2			
		18	15			
Oncorhynchus nerka	30–40 g	3.1	147	1.5–2.7 pellets	Vol	Brett & Higgs (1970)
		5.5	79			
		9.9	38			
		14.9	23			
		20.1	18			
Gadus morhua	150–373 g	2	72	0.45–0.64 *Pandalus*	Vol	Tyler (1970)
		5	58			
		10	25			
		15	20			
		19	20			

	Fish Size	Temp. (°C)	GET⁺ (hours)	Meal Type	Method•	Reference
Pleuronectes platessa	280–320 g	1	36	1.3–1.5 g *Arenicola*	FF	Edwards (1971)
		5	35			
		9	16			
		14	12			
		20	10			
	16–25 g	5	67	0.5 ml paste	FF	Jobling & Davies (1979)
		10	36			
		15.5	31			
		17.5	26			
		21	20			
Limanda limanda	100 g	8.5	18	1% paste	FF	Jobling *et al* (1977)
		16.5	12			
	85 g	12	22.5	1.6–1.7% paste	FF	Gwyther & Grove (1981)
		13.5	21.8			
		15.5	19.5			
Perca fluviatilis	35–40 cm	17	20	0.85–1.30 g *Gobiomorphus*	Vol	Griffiths (1976)
	8.9–17.4 cm	21.7	9.5	27–39 mg dry wt. *Gammarus*	Vol	Persson (1979)
		13.5	28.9			
		10.4	41.3			
Perca flavescens	6 cm	15	6–12	*Daphnia*	Vol	Nobel (1973)
	3–4 cm	22	1.5–6.5			
Stizostedion vitreum	18–38 cm	14.5	16–25	0.1–2.2% *Pimephales*	Vol	Swenson & Smith (1973)
Ptychocheilus oregonensis	230 g	6	111	2–8 g *Salmo*	FF	Steigenberg & Larkin (1974)
		10	38			
		15	14			
		20	10			
		24	8			
Ictalurus melas	4–6 cm	6	24	1% *Hyalella*	Vol	Darnell & Meierotto (1962)
Gobius minutus	3–5 cm	5	18–20	6 mg *Corophium*	Vol	Healey (1971)
		10	16–18			
		15	14			
Lepomis macrochirus	34–64 g	17–21	18–21	0.6–1.8% mixed inverts.	Vol	Windell (1966)
Katsuwonus pelamis	900–2400 g	23–26	12	32–295 g Osmeridae	Vol	Magnuson (1969)

• FF denotes force fed   Vol denotes voluntary feeding

⁺ Gastric evacuation time: time for complete stomach emptying.

rising temperatures towards a maximum rate near the species upper limit of temperature tolerance (Molnár and Tölg, 1962; Fábian et al, 1963; Molnár et al, 1967; Shrable et al, 1969; Brett and Higgs, 1970; McKone, 1971; Elliott, 1972; Jones, 1974; Persson, 1979, 1981; Jobling and Davies, 1979; Jobling, 1980c). Findings for Gadus (Tyler, 1970), however, suggest that there may be an optimum temperature for gastric evacuation which occurs near the upper thermal limit, beyond which the rate drops and the fish become lethargic and cease to feed. It follows from the above that total emptying times are negatively related to temperature.

As a general rule temperature and gastric evacuation rates follow an exponential curve or power law such that a positive linear relationship exists between temperature and log (gastric evacuation rate) (Elliott, 1972; Jones, 1974; Persson, 1979, 1981) while for log (gastric evacuation time) a negatively linear relationship exists with temperature (Windell et al, 1969; Windell et al, 1976). Several workers have found that a log-log transformation produces a straight line between gastric evacuation time and temperature (Molnár and Tölg, 1962; Edwards, 1971; Maliyenko, 1975; Grove et al, 1978). By summarising previously published data on gastric evacuation times Backiel (1971) represented the effect of temperature in the form of Krogh's curve with a respiratory quotient (Q_{10}) value of about 2.6. Fábian et al (1963) plotted the reciprocal of the evacuation time against the reciprocal of the temperature and were able to demonstrate that their data changed in accordance with the Arrhenius equation (enzyme kinetics). The only report of a linear relationship between temperature and evacuation time has been that of Laurence (1971), but as the temperature range studied was limited, 18 - 23°C, it may in fact have represented the straightening of part of a curve.

A further complicating factor is the possible existence of some form of metabolic compensation for seasonal temperatures (Molnár *et al*, 1967; Smit, 1967; Brett and Higgs, 1970; Owen and Wiggs, 1971; Fonds, 1978), and therefore use of experimental findings to extrapolate to other temperatures, or determination of evacuation rates at unseasonal experimental temperatures may lead to spurious results. Brett and Higgs (1970), for instance, estimated gastric evacuation rates for *Oncorhynchus* at 3°C by extrapolation of evacuation rates determined at summer temperatures. When tested experimentally in the winter, the actual evacuation time was 33% less than expected. Metabolic compensation has not been demonstrated in *Salmo* (Windell and Norris, 1969) or *Perca* (Persson, 1979); both studies failed to show significant differences in evacuation rates conducted at similar temperatures but in different seasons.

Meal Size: The effect of increased meal size is to increase the gastric evacuation rates (g/h) in fish (Hunt, 1960; Windell, 1966; Kitchell and Windell, 1968; Tyler, 1970; McKone, 1971; Beamish, 1972; Elliott, 1972; Rosenthal and Paffenhöfer, 1972; Swenson and Smith, 1973; Jones, 1974; Bagge, 1977; Flowerdew and Grove, 1979; Jobling and Davies, 1979; Grove and Crawford, 1980; Gwyther and Grove, 1981). An exception to this general case is that reported for *Ptychocheilus* by Steigenberger and Larkin (1974) who found that the digestion rate decreased as meal size increased.

In a few fish species, *Lepomis macrochirus* (Windell, 1966) *L. gibbosus* (Kitchell and Windell, 1968), young *Belone* (Rosenthal and Paffenhöfer, 1972) and *Blennius* (Grove and Crawford, 1980), gastric evacuation rates have been shown to increase such that total evacuation time for a given size of fish at a stated temperature is the same regardless of meal size. In general, however, compensation for increased meal size is only partial, which necessarily implies that while the rate increases so does the total evacuation time, but not in linear proportion to the meal size. For instance, for *Micropterus* (Beamish, 1972) a four-fold increase in meal size only doubled the time to empty the stomach, while a five-fold increase in meal size trebled the emptying time in *Limanda* (Jobling *et al*, 1977).

Fish Size: The relationship between fish size and gastric evacuation is quite variable and dependent on the species under study. Results for *Lepomis* (Windell, 1966), *Gadus* (Tyler, 1970), *Salmo*, (Elliott, 1972), *Ptychocheilus* (Steigenberger and Larkin, 1974), *Perca* (Persson, 1979), *Blennius* (Grove and Crawford, 1980) and *Pleuronectes* (Jobling, 1980c) have indicated that gastric evacuation rates and total elimination times are unaffected by different sizes of fish when fed a standard meal (g). On the other hand, for species such as *Stizostedion* (Swenson and Smith, 1973), various gadoids (Jones, 1974), *Limanda* (Jobling *et al*, 1977), and *Scophthalmus* (Flowerdew and Grove, 1979) larger fish evacuate a given weight of food more rapidly than smaller fish. An exception to these trends has been reported for *Lepisosteus* (Hunt, 1960) force-fed with a single *Gambusia*, where large fish evacuated the meal more slowly than smaller fish. This observation may, however, be an anomaly as no significant differences in the rates occurred between different sized fish when fed multiple-unit meals.

Recently, Jobling *et al* (1977) have suggested that since a linear relationship exists between stomach volume and body weight for Limanda it is more appropriate to compare meals of equal stimulus, that is expressed in terms of percentage body weight, when considering the influence of fish size on gastric evacuation. In this context smaller fish tend to eliminate a % body weight meal quicker than larger fish, though there may be some compensation by larger fish through increased elimination rate (Pandian, 1967; Gerald, 1973; Jobling et al, 1977; Grove et al, 1978; Flowerdew and Grove, 1979; Grove and Crawford, 1980; Gwyther and Grove, 1981).

Meal Type: Digestibility of ingested food is a further variable that can significantly affect gastric evacuation rates, such that food items with exoskeletons or surrounded by a dense layer of scales are evacuated at slower rates than more easily digestible items (Windell, 1966; Pandian, 1967; Kitchell and Windell, 1968; Windell et al, 1969; Western, 1971; Elliott, 1972; Kionka and Windell, 1972; Reshetnikov et al, 1972; Jones, 1974). In fact there is evidence to suggest that indigestible material, such as chitin, is moved more slowly from the stomach than the more readily digestible fraction and thus delays emptying, (Kapervitch and Bokova, 1937; Windell, 1966; Pandian, 1967; Western, 1971; Kionka and Windell, 1972).

The biochemical composition, and in particular lipid content, of food can influence digestive capability in fish. In mammals lipids are known to inhibit the pyloric sphincter region (Quigley and Meschan, 1941) and for fish lipids act to reduce gastric motility such that diets with high fat levels tend to be removed at comparatively slow rates (Kapervitch and Bokova, 1937; Kitchell and Windell, 1968; Windell et al, 1969; Western, 1971; Elliott, 1972).

Recently Grove *et al* (1978) for *Salmo*, Flowerdew and Grove (1979) for *Scophthalmus*, and Jobling (1980a) for *Pleuronectes* have found that meals diluted with kaolin are evacuated from the stomach faster than untreated meals. Jobling (op cit.) has suggested that reduction in the energy content of food elicits an increased emptying rate, such that within limits, the evacuation of dietary energy remains relatively constant. It seems then, that it may be the energy content of the gastric chyme, rather than its specific nutrient composition which influences the rate of gastric emptying. The general applicability of this model waits to be tested.

Often preceding gastric evacuation there may be a delay before the weight of the meal decreases (Armstrong and Blackett, 1966; Herting and Witt, 1968; Windell and Norris, 1969; Jones, 1974; Persson 1981), the magnitude of which is dependent upon both temperature and digestibility of the food (Jones, 1974). For example Jones (op cit.) found that pieces of fish fed to gadoids remained unaltered for 1.5 - 3 h while with crustaceans, such as *Crangon*, *Nephrops* and *Carcinus* a delay of between 10 - 40 h occurred.

(iii) Experimental Procedure - Limitations

In view of the difficulties of inducing several fish to eat a precisely measured meal at the same time, many workers have resorted to force-feeding a meal to the test animals (Markus, 1932; Hunt, 1960; Molnár and Tölg, 1962; Fábian *et al*, 1963; Seaburg and Moyle, 1964; Armstrong and Blackett, 1966; Molnar *et al*, 1967; Herting and Witt, 1968; Shrable *et al*, 1969; McKone, 1971; Edwards, 1971; 1973; Steigenberger and Larkin, 1974; Griffiths, 1976; Jobling *et al*, 1977; Flowerdew and Grove, 1979; Jobling, 1980 a, b, c;

Gwyther and Grove, 1981). Windell (1966) and Swenson and Smith (1973) have, however, demonstrated that force-feeding significantly reduces evacuation rate when compared with fish allowed to feed voluntarily.

The previous feeding history of a fish may introduce further complications. It is usual to deprive a fish of food for a period prior to feeding the experimental meal in order to allow for complete emptying of previous meals. Deprivation may lead to reduced gastric acid secretion (Western, 1971) and a reduction in intestinal motility (Goddard, 1974). A number of workers have shown that deprivation periods in excess of seven days may depress the rate of gastric evacuation (Windell, 1966; Elliott, 1972; Griffiths, 1976; Jobling, 1980b). Possibly the most serious limitation of most studies on gastric evacuation has arisen from the fact that many are based on the elimination of a single meal. There is evidence that the evacuation rate of fish fed on continuous feeding regimes may be between 1.5 to 2 times faster than that for a single meal (Rozin and Mayer, 1964; Laurence, 1971; Noble, 1973; Jones, 1974), though this does not seem to be the general case for all species (Elliott, 1972; Persson, 1981).

These biases may impose severe limitations on experimental results, particularly important if the gastric evacuation rates are to be extrapolated to estimate food consumption rates in the wild. Despite the possible magnitude of these errors, very few workers have attempted to account for their effects.

It is clear from the above review that most of our understanding of gastric evacuation in fish has been derived from work on teleosts. Published accounts of gastric evacuation in elasmobranchs remain extremely limited, only <u>Raja clavata</u> has been studied in any detail (de Souza, 1978) and superficial accounts exist for *Squalus acanthias* (van Slyke and White, 1911; Jones and Geen, 1977). Neglect of elasmobranchs can be attributed to their relative unimportance commercially and to difficulties encountered in maintaining them in captivity. The principal aims of the present study were to provide a detailed account of gastric evacuation for a common elasmobranch, *Scyliorhinus canicula*, and to use this information in conjunction with stomach content analysis data (Chapter 1), to produce estimates of daily food intake in the wild (Chapter 5).

MATERIALS AND METHODS

(i) Experimental Tanks and Maintenance Schedule

Experimental fish were caught by trawl and longline from various localities around the Isle of Man. During initial acclimation to laboratory conditions, and between experiments, dogfish were held in a 2.4 x 1.2 x 0.7 m deep and a 3.7 x 1.2 x 0.7 m deep tank, supplied with flowing seawater and aeration. They were fed *ad lib* on a variety of food - sprat, herring, whiting, and *Chlamys* adductor muscle - twice a week for water temperatures above 8°C and once a week at lower temperatures. Under this regime individuals were maintained in a healthy state for the duration of the study.

Related to limitations imposed by available time and facilities a partial factorial design was adopted to study the relationships between temperature, meal size, fish size and meal type and gastric emptying in *Scyliorhinus*. Five size classes were considered -

(a) 70 - 140 g; (b) 200 - 349 g; (c) 350 - 500 g; (d) 650 - 850 g, and (e) $>$ 900 g. Prior to experiments dogfish were weighed, without anaesthetic, to the nearest 0.5 g then placed into the experimental tanks and left undisturbed, except for tank cleaning and feeding, for at least one week. Gastric evacuation experiments were conducted at ambient sea temperatures in tanks similar to the holding tanks but netlon barriers were used when necessary to partition the tanks into two or three compartments. A number of additional experiments were conducted in a larger tank, 3.7 x 3.7 x 0.6 m, which was partitioned into eight equally sized compartments. This tank had the additional advantage of temperature control (Full details given in Chapter 4). A standard 12 L : 12 D photoperiod was used for all experiments, with light intensity at the water surface between 0.01 - 0.05 W/m^2. Salinity of incurrent water ranged between 33.01‰ and 34.82‰.

(ii) Experimental Procedure

It became apparent early in the study that deprivation periods of upto seven days were generally insufficient to allow for complete emptying of the stomach. It was deemed necessary, therefore, to follow the deprivation period which proce~~e~~ded each experiment (2 - 4 days above 10°C, and 4 - 7 days below 10°C) by stomach lavage using a stomach pump modified after Seaburg (1957) to remove remnants of previous meals. Force-feeding and voluntary-feeding techniques were used. Force-feeding was employed because of difficulty in inducing dogfish to feed simultaneously and the fact that experiments were conducted with groups of dogfish in each tank and extreme difficulty was encountered in ensuring that each individual ate the prescribed quantity of food. For force-fed meals dogfish were anaesthetised in MS 222, Sandoz (approx 1 : 18,000), the stomach flushed and the experimental meal inserted into the stomach via a stomach tube as outlined by Dodd *et al* (1959). In order to account for handling stress resulting from the force-feeding procedure a number of voluntary-feeding experiments were conducted. Dogfish were stomach pumped 24 h prior to meal presentation. Experimental procedures did not appear to stress the dogfish unduly and the same individuals were used on several occas~~s~~ions.

At predetermined times after feeding, groups of one to four dogfish were removed from the tanks and stomach contents flushed out and meal residuum collected. The efficiency of this recovery method was tested and found in almost all cases to be 100%. Washings from the stomach were filtered through a pre-weighed 280μ plankton net and further rinsed with distilled water. The net and meal residuum were dried in an oven at 65°C, cooled in a desiccator and weighed to the nearest milligram.

(iii) Experimental Meals

The muscular foot of *Buccinum undatum* (minus operculum) was chosen as a standard test food because of its importance in the diet of wild dogfish (Chapter 1) and because it was readily available and easily 'trimmed' into blocks of predetermined weight. A number of other prey species were also tested for comparisons with results obtained for *Buccinum*. Prey were killed by freezing, then thawed and sorted into individual meal units, as required, and refrozen. All meals were weighed such that the maximum deviation was to within 0.05 g of the desired wet weight, and for each experiment a subsample of food was dried to determine **water** content. Where ever possible whole organisms or single pieces of food were presented, thus approximating to the form of the food encountered in the wild. In some experiments crustacean prey, Eupagurus bernhardus and Palaemon elegans, were presented, in which case the chitin content of the residuum was also determined, using the method outlined by Richards (1951).

(iv) Stomach Volume

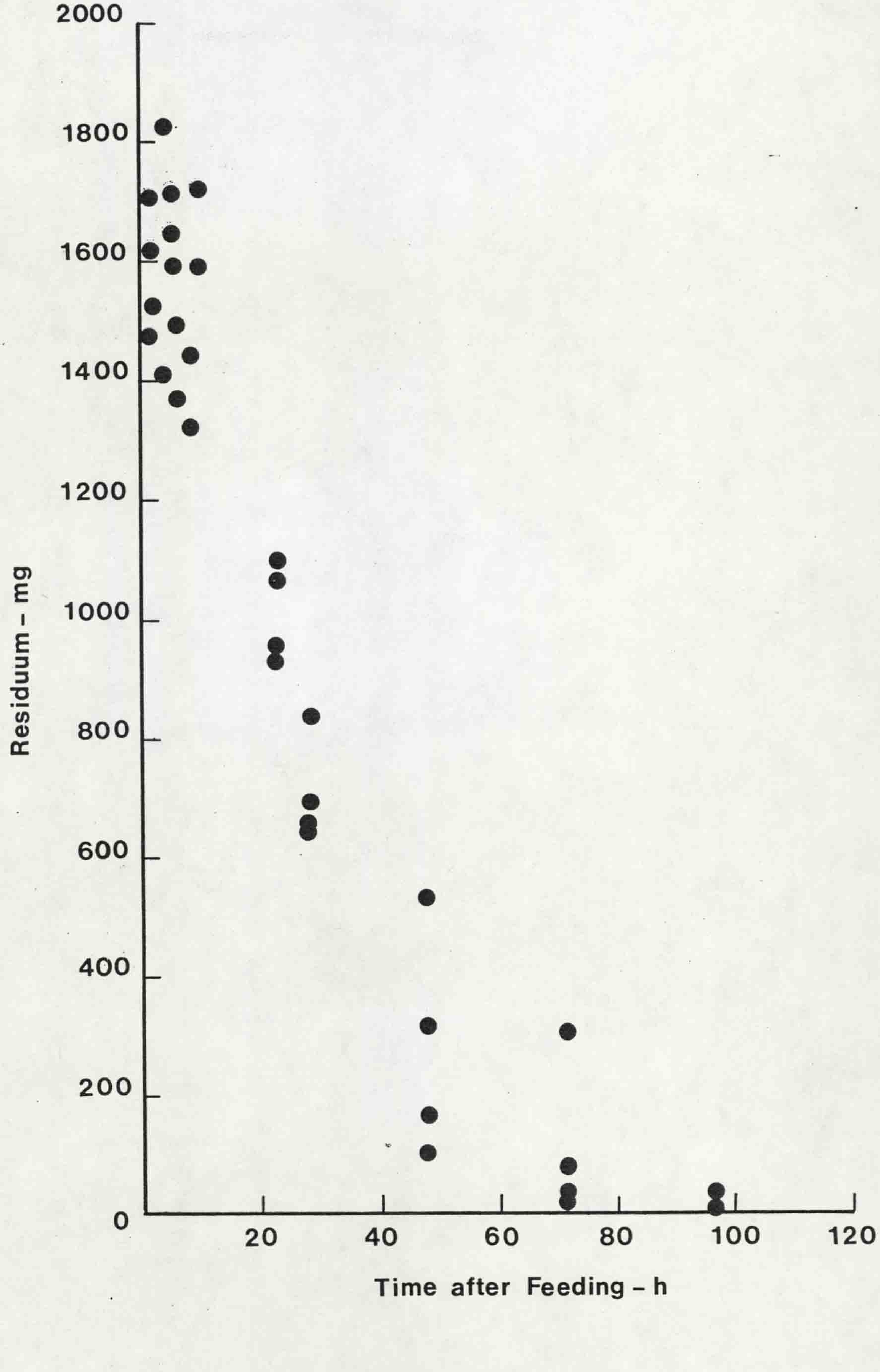
The relationship between stomach volume and body weight was determined by removing and emptying stomachs of freshly killed dogfish. The stomach was ligatured at the junction of the cardiac and pyloric limbs and a syringe needle, attached by narrow bore rubber tubing to a burette, placed into the gastric lumen via the oesophagus. The oesophagus was then ligatured at the oesophageal sphincter. Stomach volume was taken as the volume of water required for complete dilation of the cardiac portion at atmospheric pressure and supporting a 40 ml head of water.

RESULTS

(i) Pattern of Gastric Emptying

The relationship between the dry weight of food remaining in the stomach, i.e. 'residuum', and the time interval after feeding was found to be curvilinear on an arithmetic scale for all experimental conditions; Figure 2.1 shows one example. The curves may be transformed into near linear form by applying various mathematical functions to observed values of the weight of the

Figure 2.1 Relationship between the dry weight of food remaining in the stomach, "residuum" , and time after feeding, for 732.7±60.8 g Scyliorhinus canicula force-fed 1% b.w. meal of Buccinum at 13.6°C.


2000
1800
1600
1400
1200
1000
800
600
400
200
0
Residuum - mg
20
40
60
80
100
120
Time after Feeding - h

residuum. In Table 2.2 and Figure 2.2, semilog (Brett and Higgs, 1970; Tyler, 1970; Elliott, 1972 etc.), square root (Hopkins, 1966; Jobling and Davies, 1979), and cube root of square (Fänge and Grove, 1979) transformations are compared with a linear regression. All transformations gave a reasonably good fit to the data, but the square root and cube root of square accounted for more of the variance than did the semilog transformation.

The square root model fitted the data over the greater part of the experimental range and was powerful in predicting the time for complete evacuation (gastric evacuation time; GET), giving predicted values close to those indicated by experimental results. The early stages of gastric emptying tended to proceed faster than predicted by the model, a phenomenon noted by Jobling and Davies (1979). As a consequence the predicted meal weight (intercept with Y-axis) was frequently less than the actual weight of food presented. Despite these limitations the square root transformation was accepted as an adequate model of gastric emptying in Scyliorhinus and is defined by the regression equation:

$$S_t^{0.5} = a - Rt$$

where S_t is weight of residuum (mg) at time t after feeding, a is the intercept with the Y-axis (i.e. square root of the predicted meal weight), and R is the slope or 'relative' gastric evacuation rate.

Regressions were not constrained to go through the point representing known meal size and all results, unless otherwise stated, are based on regressions calculated directly from experimental findings.

Table 2.2 Analysis of variance and coefficient of determination (r^2) for the relationship between dry weight of food remaining in the stomach, Y (mg), and the time since meal ingestion, t (h).*

			Type of regression equation			
Temp. (^{o}C)			Linear $Y = a - Rt$	Semilog $\ln(Y+1) = a - Rt$	Square root $Y^{0.5} = a - Rt$	Cube root squar $Y^{0.67} = a - Rt$
6.6	15	r^2	0.923	0.897	0.937	0.937
		F	154.9	115.8	191.0	192.4
10.3	20	r^2	0.928	0.812	0.942	0.947
		F	233.3	77.8	291.5	320.8
13.6	36	r^2	0.862	0.925	0.935	0.915
		F	212.0	418.7	488.9	364.5
15.6	12	r^2	0.780	0.850	0.863	0.842
		F	35.4	56.5	63.2	53.4

* All F-values highly significant, $p < 0.001$

Table 2.3 Weight of gastric juices at various times after feeding with sponge. Mean water temperature: 14.7°C (14.0 - 15.5)
Mean dogfish weight ± SD: 735.5 ± 52.5 g

	Time after feeding (h)			
	4.5	24.0	48.0	72.0
Weight of gastric juices (mg)	132	248	353	307
		305	434	

Figure 2.2 Comparison of regression lines for different transformations of residuum weight against time after feeding for data presented in Figure 2.1. (Note each point represents the mean of two determinations)

A : No transformation; linear regression

$y = 1529.8 - 18.849x \qquad (r = -0.928)$

B : Semilog transformation

$y = 7.735 - 0.050x \qquad (r = -0.962)$

(Arrows indicate transformed initial meal weight)

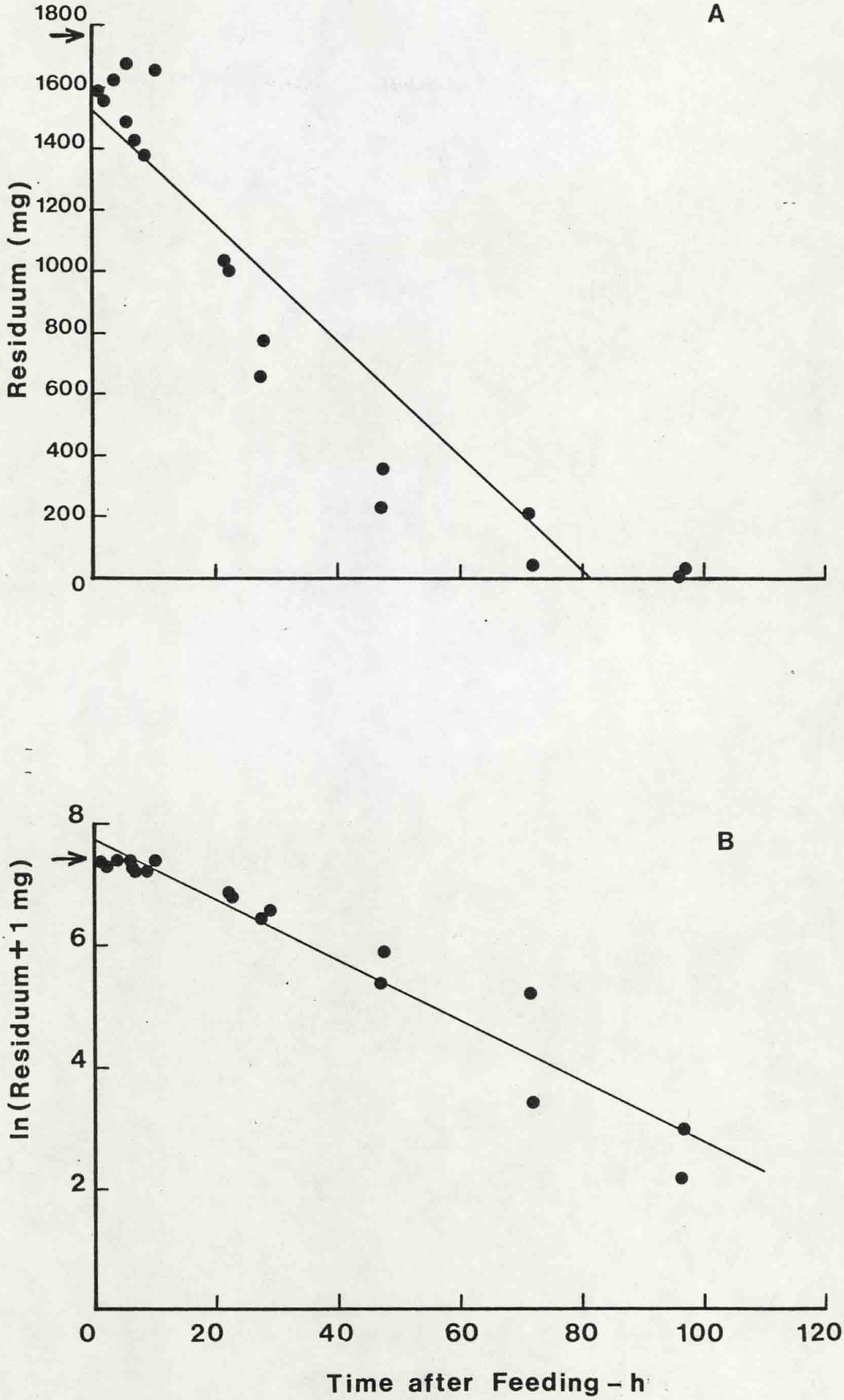

A
Residuum (mg)
1800
1600
1400
1200
1000
800
600
400
200
0
B
ln(Residuum + 1 mg)
8
6
4
2
0
20
40
60
80
100
120
Time after Feeding – h

Figure 2.2 (Continued) Comparison of regression lines for different transformations of residuum weight against time after feeding for data presented in Figure2.1. (Note each point represents the mean of two determinations)

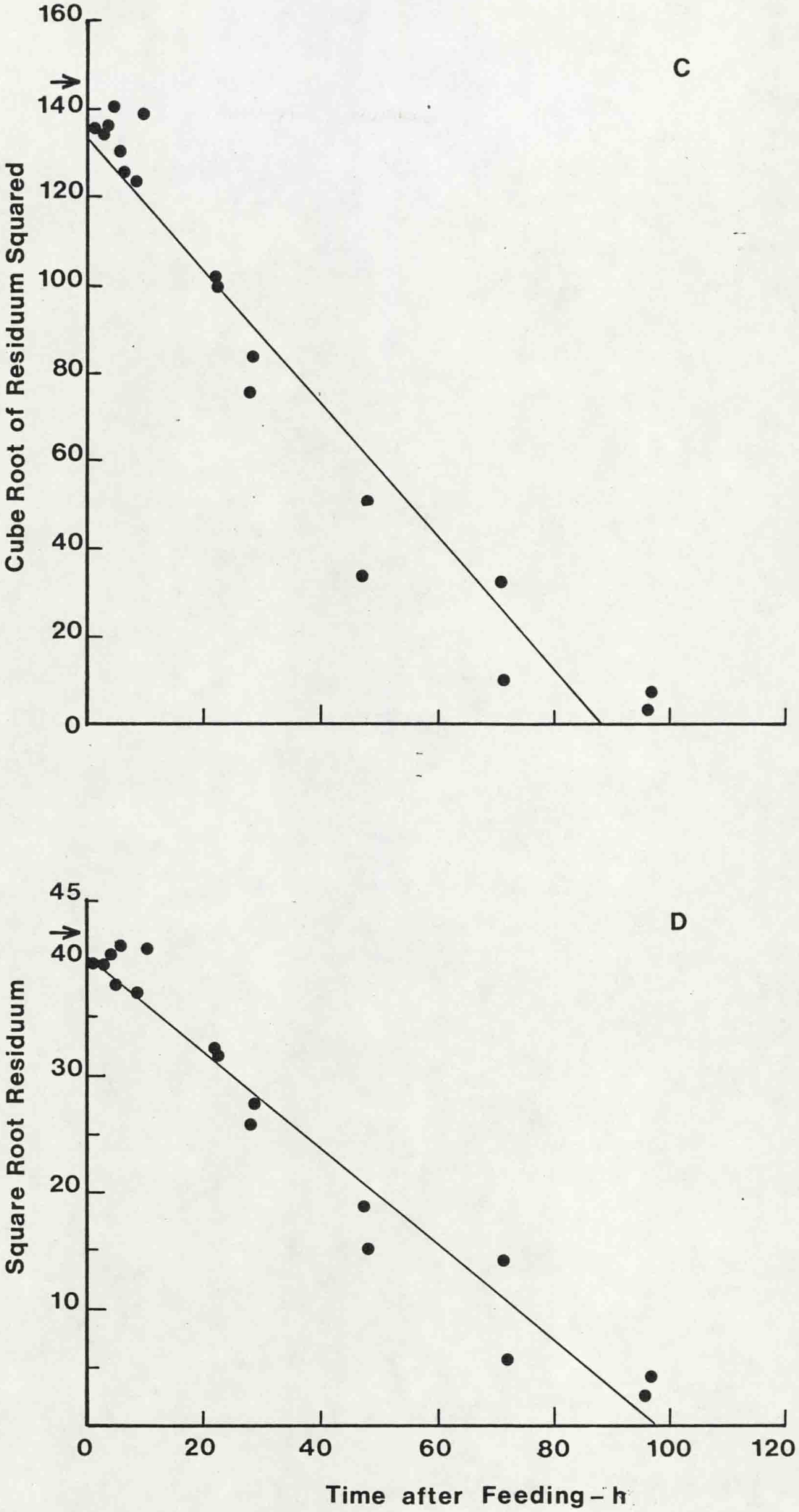
C : Cube root of the square of the residuum (mg)

$y = 136.142 - 1.532x$ $(r = -0.956)$

D : Square root of residuum (mg)

$y = 40.588 - 0.418x$ $(r = -0.967)$

(Arrows indicate transformed initial meal weight)


C
Cube Root of Residuum Squared
160
140
120
100
80
60
40
20
0
D
Square Root Residuum
45
40
30
20
10
0
20
40
60
80
100
120
Time after Feeding – h

(ii) Influence of Gastric Juices

The actual process of gastric breakdown and removal of food from the stomach was characterised by softening and digestion of the surface layers of the bolus. Accompanying these processes was a build up of partly digested particulate material and relatively large quantities of gastric secretions in the stomach (see also Chapter 1). In an attempt to assess the importance of gastric secretion a group of six dogfish, 670 - 830 g, were force-fed pieces of preweighed sponge which approximated, by dimensions, a standard meal of Buccinum. At various intervals after 'feeding' stomachs were flushed with distilled water and the entire washings dried at 65°C (Table 2.3). There was an obvious and significant rise in dry weight resulting from gastric juice secretion. As the sponge only afforded tactile stimulus to the stomach it is probable that these values were minimal and in a normal feeding situation gastric juices would contribute more heavily to overall stomach content weight. It was for these reasons that it was considered necessary to filter off gastric juices through 280μ plankton filter as outlined in Materials and Methods.

(iii) Influence of Acclimation Period

Gastric emptying rate (R) for a meal of Buccinum, equivalent by wet weight to 1% of the mean body weight, was independent of the length of time in captivity (Table 2.4a). For convenience a minimum acclimation period of four weeks was adopted for all dogfish prior to use in gastric evacuation experiments.

Table 2.4 Comparison of instantaneous gastric evacuation rates'R' for dogfish force-fed 1% b.w. meals of *Buccinum*.

(a) Influence of duration in captivity.

Water temp. : 13.5°C (13.0 - 14.0)

Dogfish wt. ± SD : 732.7 ± 67.2 g

Acclimation period	n	Regression a	 R ± 95% CL	Comparison of slopes
2 weeks	12	41.0815	0.3742 ± 0.0492	t = 0.017 df = 20 n.s.
>6 weeks	12	37.3083	0.3751 ± 0.1038	

(b) Influence of sex.

Water temp. : 13.6°C (12.7 - 13.9)

Dogfish wt. ± SD : 732.7 ± 60.8 g

Sex	n	Regression a	 R ± 95% CL	Comparison of slopes
Female	12	39.4358	0.4057 ± 0.0822	t = 0.112 df = 20 n.s.
Male	12	39.4902	0.3994 ± 0.0934	

(iv) Influence of Sex

There was no statistically significant difference in gastric emptying patterns with regard to sex and in all subsequent experiments no distinction based on sex was necessary (Table 2.4b).

(v) Influence of Temperature

A series of experiments was conducted over a temperature range of 6.5 - 16.1°C to assess the effect of temperature on gastric emptying. Dogfish of 650 - 850 g were force-fed standard 1% body weight (b.w.) meals of Buccinum and the regression for each experiment calculated and presented in Table 2.5. To facilitate visual interpretation, results at only four temperatures are compared in Figure 2.3. The gastric evacuation rate, i.e. slope 'R', increased, while gastric emptying time (GET) decreased with rising temperature (Table 2.6, Figure 2.4). The relationships between temperature, T (°C), and R, and temperature and GET (h) for 1% b.w. meals were basically exponential, with:

$$R = 0.087e^{0.115T}$$

$$(n = 15,\ r = 0.950,\ p < 0.001)$$

and

$$GET = 555.462e^{-0.128T}$$

$$(n = 15,\ r = -0.962,\ p < 0.001)$$

Since R is an 'instantaneous' rate, the absolute rate of elimination of food (mg/h) continually changes and is determined by the weight of food remaining in the stomach at any particular instant in time. It is of some value to express the emptying rate in mg/h by solving regressions in Table 2.5 over a stated time interval after feeding. For this anlysis gastric emptying

Table 2.5 Values for intercept 'a' and instantaneous rate of gastric evacuation 'R' (± 95% confidence limits) for 650 - 850 g Scyliorhinus canicula force-fed 1% b.w. meals of Buccinum at different temperatures. Actual meal sizes (mg dry wt.) and correlation coefficients (r) are given for each experiment.

Fish weight ± SD		Mean temp. (°C)	Meal size	Regression *		
(g)	n	+ (range)	(mg dry wt.)	a	R ± 95% CL	r
774.7 ± 47.7	15	6.6 (6.0 - 7.6)	2162	46.2488	0.2166 ± 0.0339	-0.9676
756.8 ± 53.4	11	7.7 (7.0 - 8.4)	1853	44.2183	0.1765 ± 0.0570	-0.9193
755.4 ± 53.1	12	8.6 (8.0 - 9.0)	1979	45.2362	0.2207 ± 0.0618	-0.9292
745.0 ± 53.1	12	8.7 (8.5 - 9.0)	1805	35.2799	0.2159 ± 0.0685	-0.9021
775.8 ± 49.1	20	10.3 (9.0 - 11.2)	1830	44.1559	0.2879 ± 0.0354	-0.9705
723.4 ± 48.4	10	12.0 (11.1 - 13.0)	2074	44.0372	0.3839 ± 0.1183	-0.9354
723.4 ± 48.4	10	12.3 (11.7 - 13.0)	1814	44.2804	0.3622 ± 0.0569	-0.9820
764.2 ± 55.6	10	12.4 (11.7 - 13.4)	1653	39.7199	0.4043 ± 0.1126	-0.9436
752.4 ± 60.2	14	12.7 (11.9 - 13.4)	2157	46.0327	0.4670 ± 0.1362	-0.9072
732.7 ± 67.2	12	13.5 (13.0 - 14.0)	1784	37.3083	0.3751 ± 0.1039	-0.9307
732.7 ± 60.8	36	13.6 (12.7 - 13.9)	1781	40.5876	0.4177 ± 0.0384	-0.9669
735.3 ± 52.5	11	14.7 (14.0 - 15.5)	1708	39.5660	0.4258 ± 0.1223	-0.9345
744.0 ± 55.3	12	15.0 (14.5 - 15.5)	1872	43.2460	0.4346 ± 0.0501	-0.9869
739.4 ± 50.4	12	15.6 (15.1 - 16.5)	2034	40.5336	0.5614 ± 0.1573	-0.9292
717.6 ± 53.1	11	16.1 (16.0 - 16.2)	1712	35.6015	0.5409 ± 0.2147	-0.8849

* All regressions highly significant, $p < 0.001$

Table 2.6 Predicted gastric evacuation time 'GET' and gastric evacuation rates 'GER' for 650 - 850 g *Scyliorhinus canicula* force-fed 1% b.w. meals of *Buccinum* at different temperatures. Based on regression equations given in Table 2.5.

Temp (°C)	GET (h)	GER (mg/h)*	Temp (°C)	GET (h)	GER (mg/h)*
6.6	213.5	18.91	12.7	98.6	37.76
7.7	250.5	14.86	13.5	99.5	24.61
8.6	205.0	18.80	13.6	97.2	29.72
8.7	163.4	14.11	14.7	92.9	29.34
10.3	153.4	23.44	15.0	99.5	33.06
12.0	114.7	30.27	15.6	72.2	37.95
12.3	122.3	28.93	16.1	65.8	31.49
12.4	98.2	28.19			

* Based on the predicted quantity of food eliminated from the stomach between 9h and 15h after feeding, divided by 6 .

Figure 2.3 Relation between square root of residuum (mg) and time after feeding, with fitted regression lines, at different temperatures for 650-850 g _Scyliorhinus_ _canicula_ force-fed 1% b.w. meals of _Buccinum_. (Refer to Table 2.5)

(Each point represents a single determination or mean of 2-4 determinations)

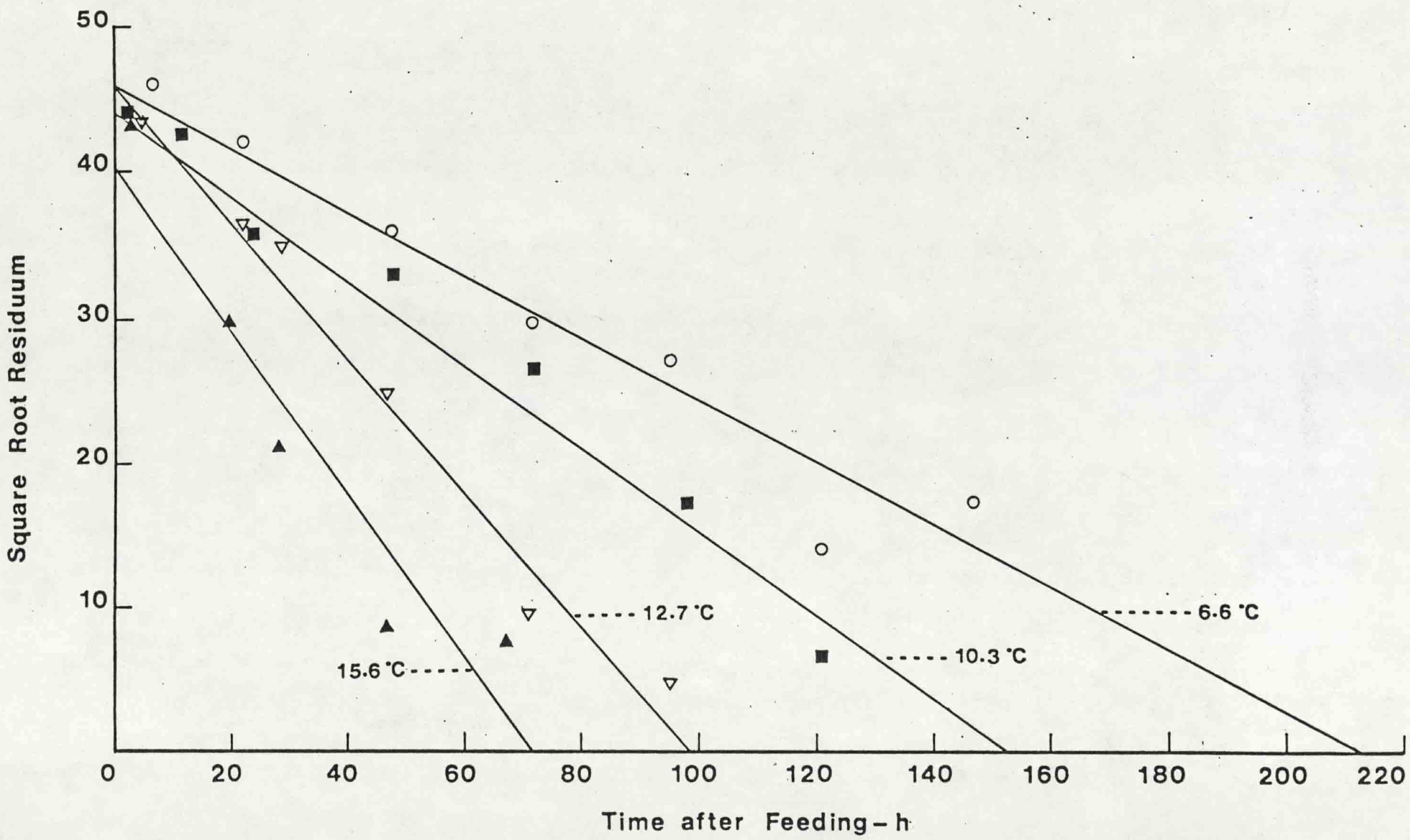
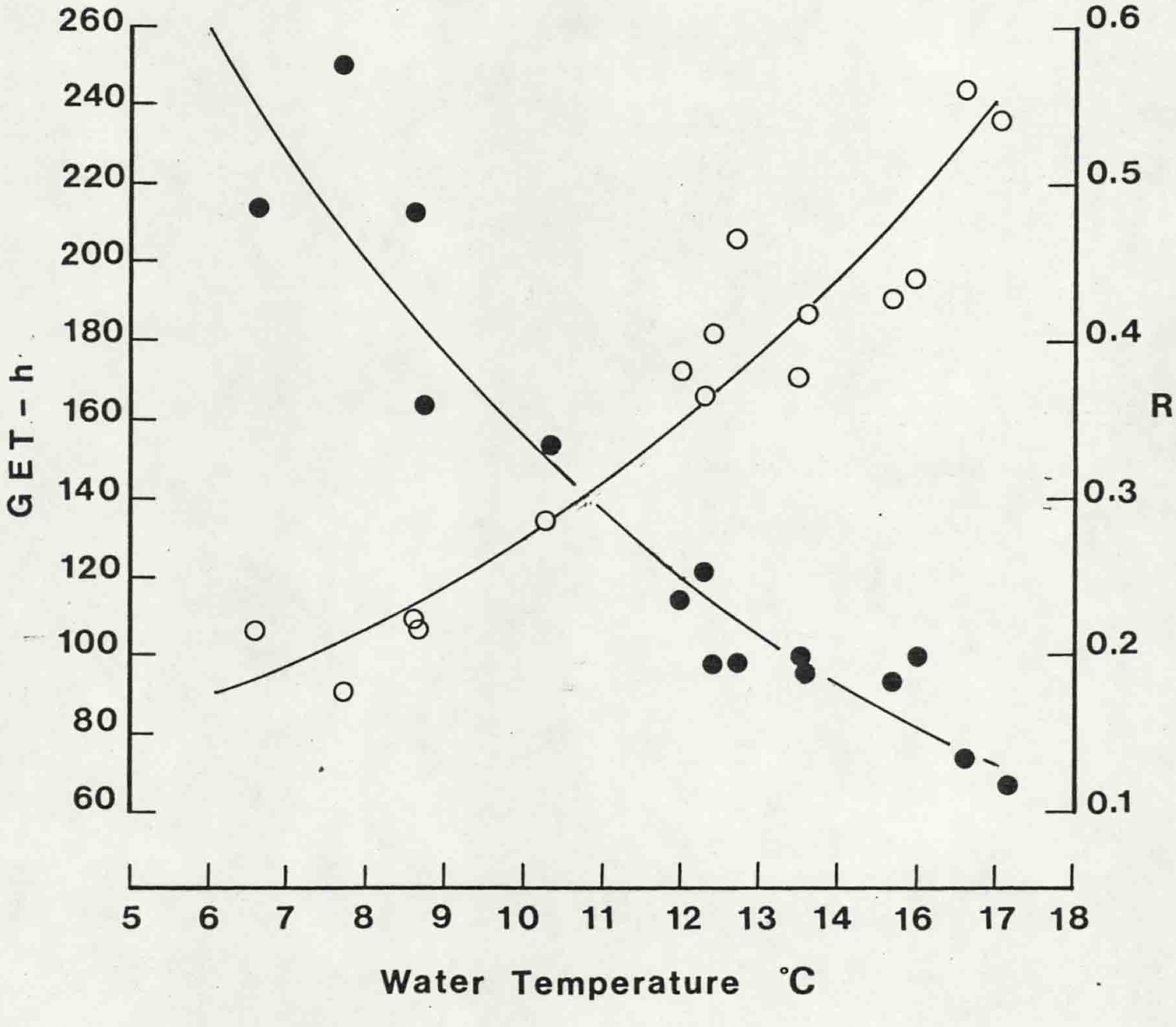

Square Root Residuum
50
40
30
20
10
0
20
40
60
80
100
120
140
160
180
200
220
Time after Feeding – h
6.6 °C
10.3 °C
12.7 °C
15.6 °C

Figure 2.4 Effect of temperature on gastric evacuation rates (R) and total gastric evacuation time (GET) for 650–850 g Scyliorhinus canicula force-fed 1% b.w. meals of Buccinum. Regression curves fitted.

R : ○
GET : ●



260
240
220
200
180
160
140
120
100
80
60
GET - h
0.6
0.5
0.4
0.3
0.2
0.1
R
5
6
7
8
9
10
11
12
13
14
16
17
18
Water Temperature °C

rates (GER) were defined as the difference between the residuum at 9 h after feeding and that at 15 h, divided by the time interval in hours (Table 2.6). GER (mg/h) increased exponentially with temperature as:

$$GER = 8.851e^{0.089T}$$
$$(n = 15, r = 0.852, p < 0.001)$$

(vi) Influence of Meal Size

The influence of meal size on gastric emptying was examined at two experimental temperatures, 7.7°C and 13.5°C, for 650 - 850 g dogfish force-fed 1%, 2% and 4% b.w. meals of Buccinum (Table 2.7 and Figure 2.5). At each temperature the rates of evacuation (R) varied only slightly with meal size and comparison of slopes by covariance analysis showed that these differences were not significant. The regressions could, therefore, be described by a common regression coefficient (Table 2.7). This implies that for dogfish of a given size and at a specified temperature the pattern of removal of a small meal corresponds to the latter stages of evacuation of a larger meal, as depicted in Figure 2.6.

While R remains independent of meal size it is implicit that GER (mg/h) at a specified time after feeding would increase with meal size (Table 8.8). GER was related to the actual meal size ingested (So) by:

$$GER = 1.312\ S_o^{0.360} \quad \text{at } 7.7°C$$
$$(r = 0.989)$$

and

$$GER = 0.683\ S_o^{0.494} \quad \text{at } 13.5°C$$
$$(r = 0.995)$$

Table 2.7 Values for intercept 'a' and instantaneous rate of gastric evacuation 'R' (± 95% confidence limits) for 650 - 850 g *Scyliorhinus canicula* force-fed meals of *Buccinum* equivalent to 1%, 2%, and 4% b.w. Gastric evacuation rates compared by covariance analysis.

y = square root residuum at specified time after feeding.

x = time after feeding.

Mean temp. °C (range)	Dogfish wt. (g) ± SD	Meal size % b.w.	Meal size Dry wt. (mg)	n	Regression * a	Regression * R ± 95% CL	Covariance analysis	Calculated with common slope
7.7	756.8 ±	1	1853	11	44.2183	0.1765 ± 0.0570	F_{slopes} 2.357	y = 49.0334 - 0.2161x
(7.0 - 8.4)	53.4	2	4081	11	58.6675	0.2039 ± 0.0614	df = 2,25	y = 60.2037 - 0.2161x
		4	8163	9	89.0146	0.2810 ± 0.1173	n.s. ($p>0.1$)	y = 81.9710 - 0.2161x
13.5	732.7 ±	1	1784	12	37.3083	0.3751 ± 0.1039	F_{slopes} 1.119	y = 38.4660 - 0.4000x
(13.0 - 14.0)	67.2	2	3568	10	54.5023	0.4079 ± 0.1154	df = 2,31	y = 54.6762 - 0.4000x
		4	7141	13	74.0352	0.4269 ± 0.0913	n.s. ($p>0.25$)	y = 71.6020 - 0.4000x

* All regressions highly significant $p<0.001$

Table 2.8 Gastric evacuation time 'GET' and gastric evacuation rate 'GER' for 650 - 850 g Scyliorhinus canicula force-fed different meal sizes. Calculated from regressions fitted to common slopes : refer to Table 2.7.

Temperature (°C)	Meal size (% b.w.)	GET (h)	GER (mg/h)*
7.7	1	226.9	20.07
	2	278.6	24.90
	4	379.3	34.31
13.5	1	96.2	26.94
	2	136.7	39.90
	4	179.0	53.44

* Based on the predicted quantity of food eliminated from the stomach between 9 h and 15 h after feeding, divided by 6.

Figure 2.5 Relationship between the square root of residuum (mg) and time after feeding for 650–850 g Scyliorhinus canicula force-fed 1% b.w.(□), 2% b.w.(●), and 4% b.w.(○) meals of Buccinum at 7.7°C and 13.5°C. Regression lines fitted (see Table 2.7).

(Arrows indicate square root of initial meal weight, and each point represents a single determination or mean of 2–3 determinations.)

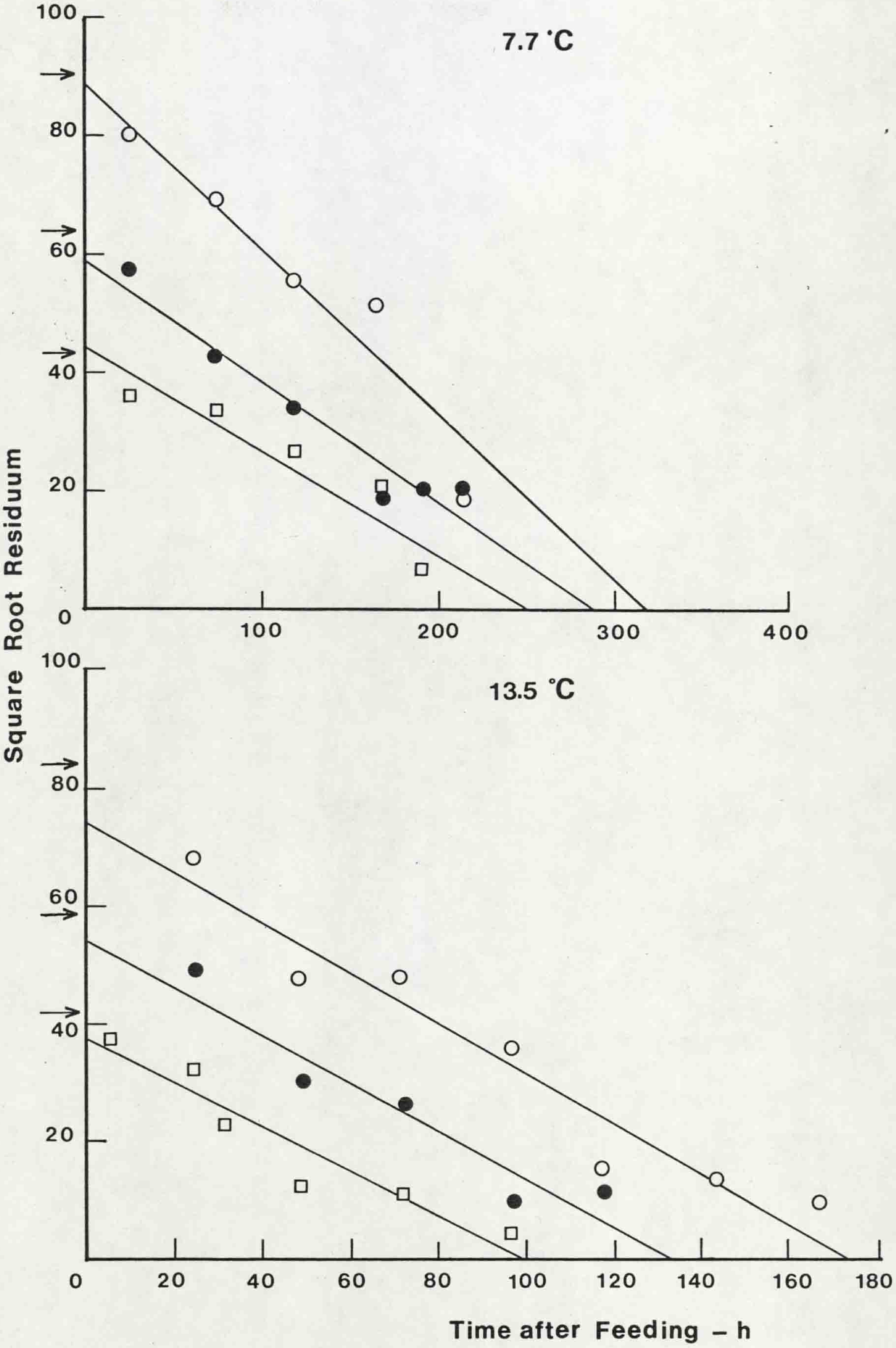
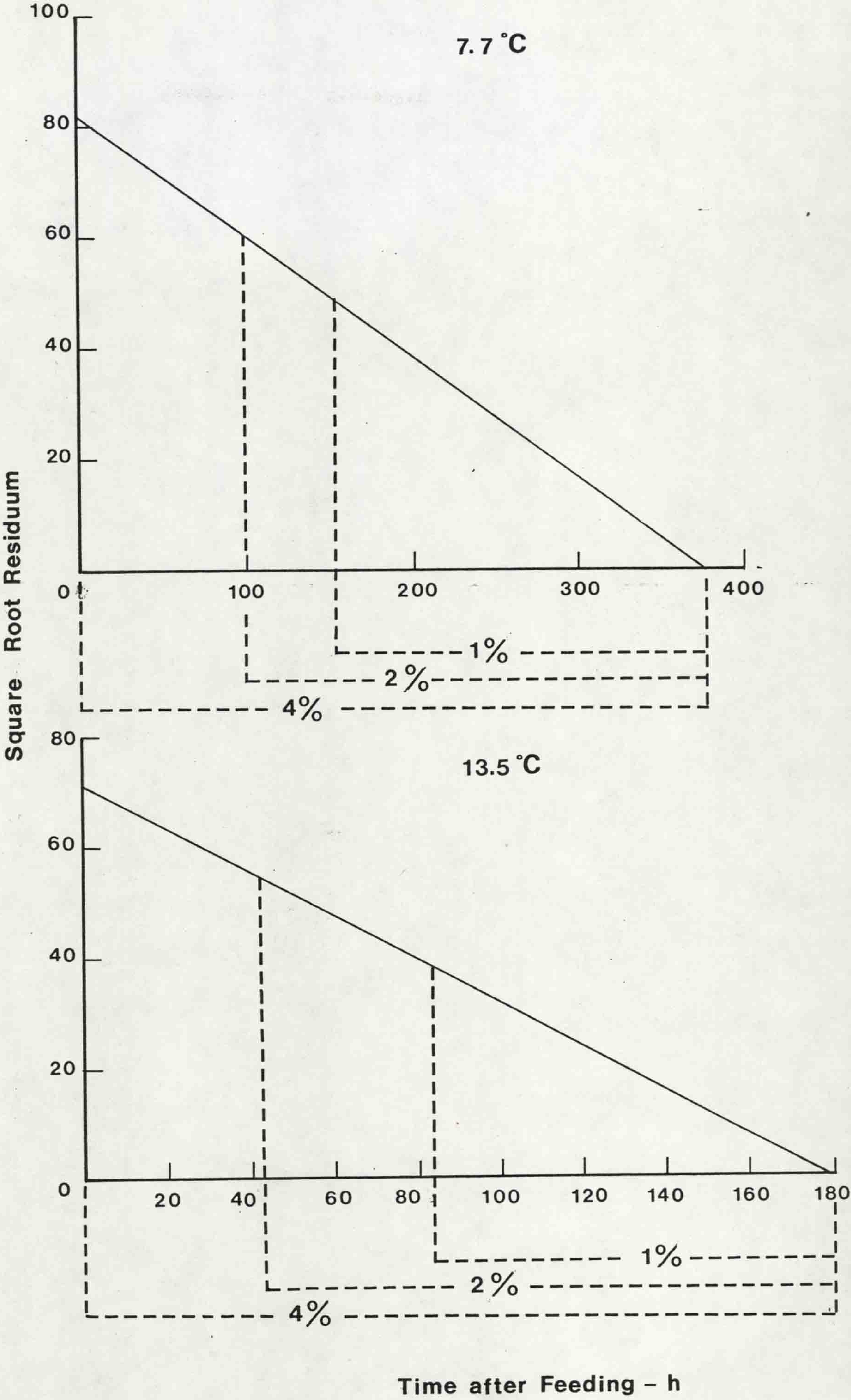

7.7 °C
13.5 °C
Square Root Residuum
Time after Feeding – h
100
80
60
40
20
0
100
200
300
400
100
80
60
40
20
0
20
40
60
80
100
120
140
160
180

Figure 2.6 Regression lines replotted to common slopes and superimposed to demonstrate the relationship between meal size and gastric evacuation. Based on data presented in Figure 2.5.

$7.7^{\circ}C$: Common slope of -0.2161

$13.5^{\circ}C$: Common slope of -0.4000


7.7 °C
13.5 °C
Square Root Residuum
Time after Feeding – h
0
20
40
60
80
100
0
100
200
300
400
1%
2%
4%
0
20
40
60
80
20
40
60
80
100
120
140
160
180
1%
2%
4%

In consequence of the above, GET did not increase in direct proportion with meal size (Table 2.8), and is given by:

$$GET = 16.616\ S_o^{0.345} \quad \text{at } 7.7°C$$

$$(r = 0.988)$$

and

$$GET = 3.416\ S_o^{0.448} \quad \text{at } 13.5°C$$

$$(r = 0.997)$$

(vii) Influence of Fish Size

Within the size range considered, stomach volume V (ml), was found to be directly proportional to dogfish weight W (g):

$$V = 0.115\ W + 9.262$$

$$(n = 24,\ r = 0.874) \qquad \text{(Figure 2.7)}$$

A meal based on a known proportion of fish live weight should thus present the same stimulus on the gut, regardless of fish size, enabling direct comparisons to be made between fish of different sizes (Jobling *et al*, 1977; Flowerdew and Grove, 1979).

Gastric emptying of 1% b.w. meals of *Buccinum* by dogfish of different sizes was examined at three experimental temperatures; 6.6°C, 12.4°C and 15.0°C (Table 2.9, Figure 2.8). The influence of dogfish size was not well defined, lack of consistent trends related in part to the high degree of individual variability evident in many experiments. Smaller dogfish generally completed elimination of a 1% b.w. meal slightly quicker than larger individuals though gastric evacuation rates increased with dogfish size (Table 2.9)[1]. In fact at 6.6°C and 12.4°C statistically

---

[1] Note the slope of 0.2166 for 650 - 850 g dogfish (mean weight 774.7 g) at 6.6°C was greater than that for the largest size group and is apparently inconsistent with the reported trend. Compared with predicted value of 0.1861 (Section (v)) this result was clearly higher than expected.

Table 2.9 Values for intercept 'a' and instantaneous rate of gastric evacuation 'R' (± 95% confidence limits) for different size groups of *Scyliorhinus canicula* force-fed meals of *Buccinum* equivalent to 1% b.w. Actual meal sizes (mg dry wt.) and correlation coefficients (r) are given for each experiment. Gastric evacuation rates compared by covariance analysis. Gastric evacuation time 'GET' and evacuation rate 'GER' are calculated from the regression equations.

Mean temp. + (range)°C	Fish wt. ± SD g	n	Meal wt. mg	Regression* a	Regression* R ± 95% CL	Covariance analysis	r	GET (h)	GER (mg/h)**
6.6	282.0 ± 43.8	8	789	28.9705	0.1249 ± 0.0486	F_{slopes} 5.220 df = 3,45 ($0.0025 < p < 0.005$)	-0.9318	231.9	6.86
(6.0 - 7.6)	449.6 ± 39.4	15	1256	33.1295	0.1399 ± 0.0269		-0.9523	236.8	8.80
	774.7 ± 47.7	15	2162	46.2488	0.2166 ± 0.0339		-0.9676	213.5	18.91
	1052.9 ± 120.7	15	2945	53.8804	0.1998 ± 0.0462		-0.9331	269.7	20.57
12.4	290.5 ± 39.9	12	630	19.6965	0.1956 ± 0.0867	F_{slopes} 5.822 df = 3,37 ($0.001 < p < 0.0025$)	-0.8463	100.7	6.78
(11.7 - 13.4)	425.0 ± 40.0	12	920	26.2986	0.2486 ± 0.1036		-0.8606	105.8	11.59
	764.2 ± 55.6	10	1653	39.7198	0.4043 ± 0.1126		-0.9463	98.2	28.19
	1036.8 ± 122.1	11	2242	45.2203	0.4135 ± 0.1108		-0.9422	109.4	33.29
15.0	111.9 ± 22.2	10	282	17.2965	0.2520 ± 0.0661	F_{slopes} 12,203 df = 3,37 ($p < 0.0005$)	-0.9519	68.6	7.19
(14.5 - 15.5)	275.3 ± 42.6	11	692	25.6618	0.3056 ± 0.0853		-0.9378	84.0	13.44
	744.0 ± 55.3	12	1872	43.2460	0.4346 ± 0.0501		-0.9869	99.5	33.06
	1043.8 ± 132.0	12	2624	48.6921	0.4783 ± 0.0477		-0.9901	101.8	41.09

* All regressions highly significant $p < 0.001$; ** Based on the predicted quantity of food eliminated from the stomach between 9h and 15h after feeding, divided by 6.

Figure 2.7 Relationship between stomach volume, V(ml), and live weight of Scyliorhinus canicula, W(g):

$$V = 0.115W + 9.262 \qquad (n = 24, r = 0.874)$$

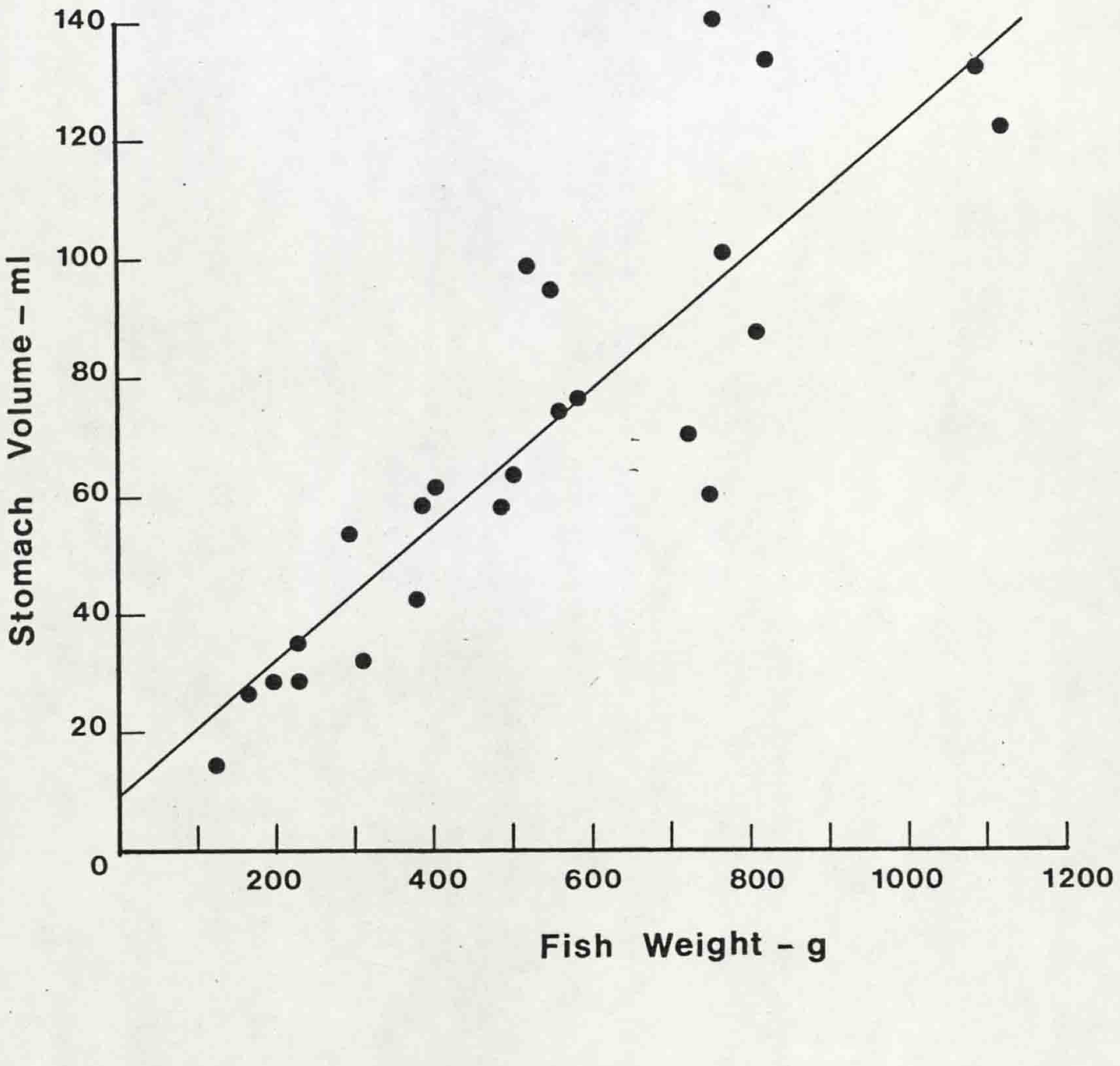

140
120
100
80
60
40
20
0
200
400
600
800
1000
1200
Stomach Volume - ml
Fish Weight - g

Figure 2.8 Relationship between square root of the residuum (mg) and time after feeding for different sized *Scyliorhinus canicula* force-fed 1% b.w. meals of *Buccinum*. Regression lines fitted.

Size class 6.6°C

282.0 ± 47.8g : ■-------■ : $y = 29.971 - 0.125x$
($n = 8$, $r = -0.932$)

449.6 ± 39.4g : □———□ : $y = 33.129 - 0.140x$
($n = 15$, $r = -0.952$)

774.7 ± 47.7g : ●-----● : $y = 46.240 - 0.217x$
($n = 15$, $r = -0.968$)

1052.9 ± 120.7g : ○———○ : $y = 53.880 - 0.200$
($n = 15$, $r = -0.933$)

(Arrows indicate square root of initial meal weight)

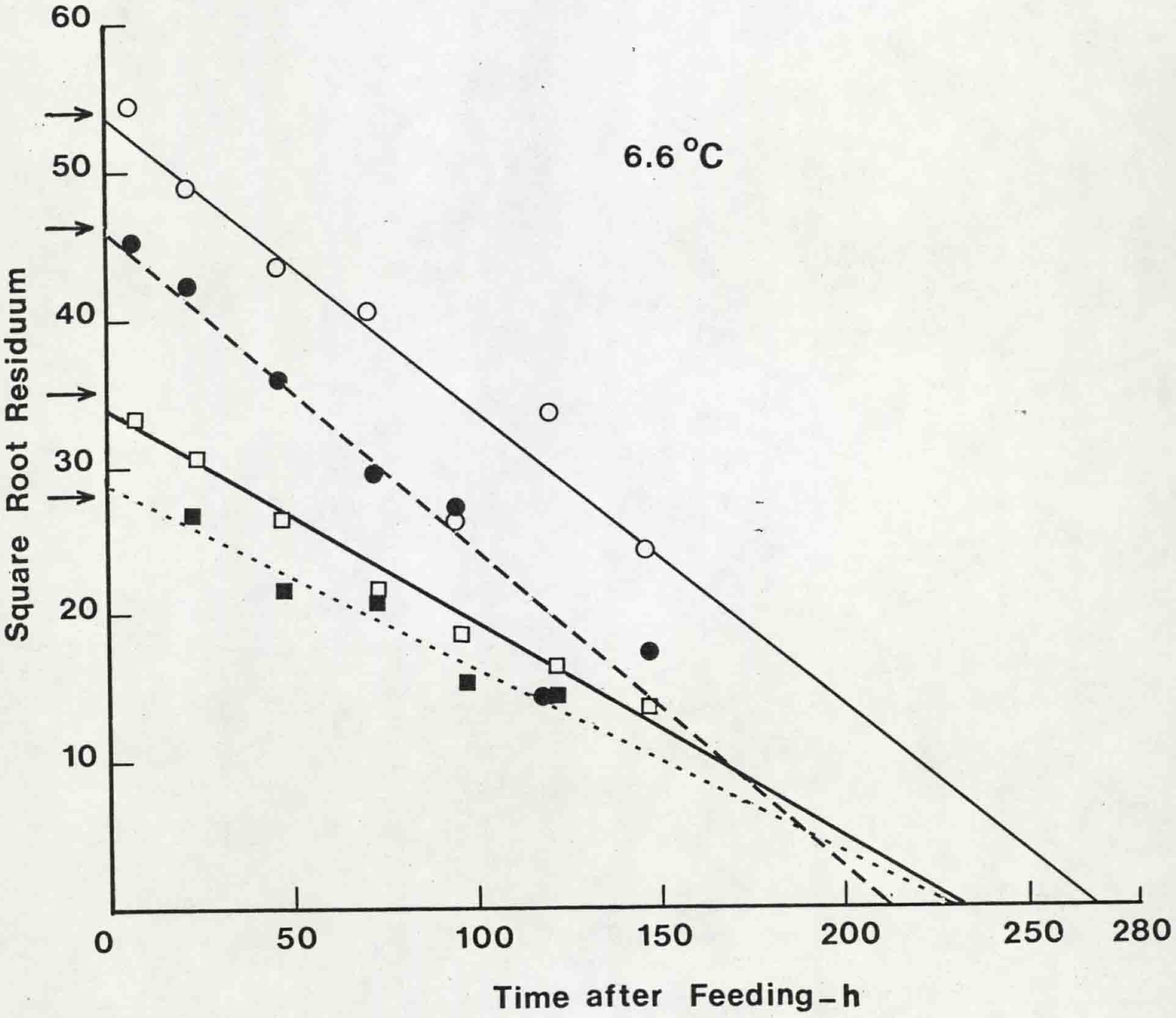

6.6 °C
Square Root Residuum
60
50
40
30
20
10
0
50
100
150
200
250
280
Time after Feeding-h

Figure 2.8 (Continued) Relationship between square root of the residuum (mg) and time after feeding for different sized Scyliorhinus canicula force-fed 1% b.w. meals of Buccinum. Regression lines fitted.

Size class

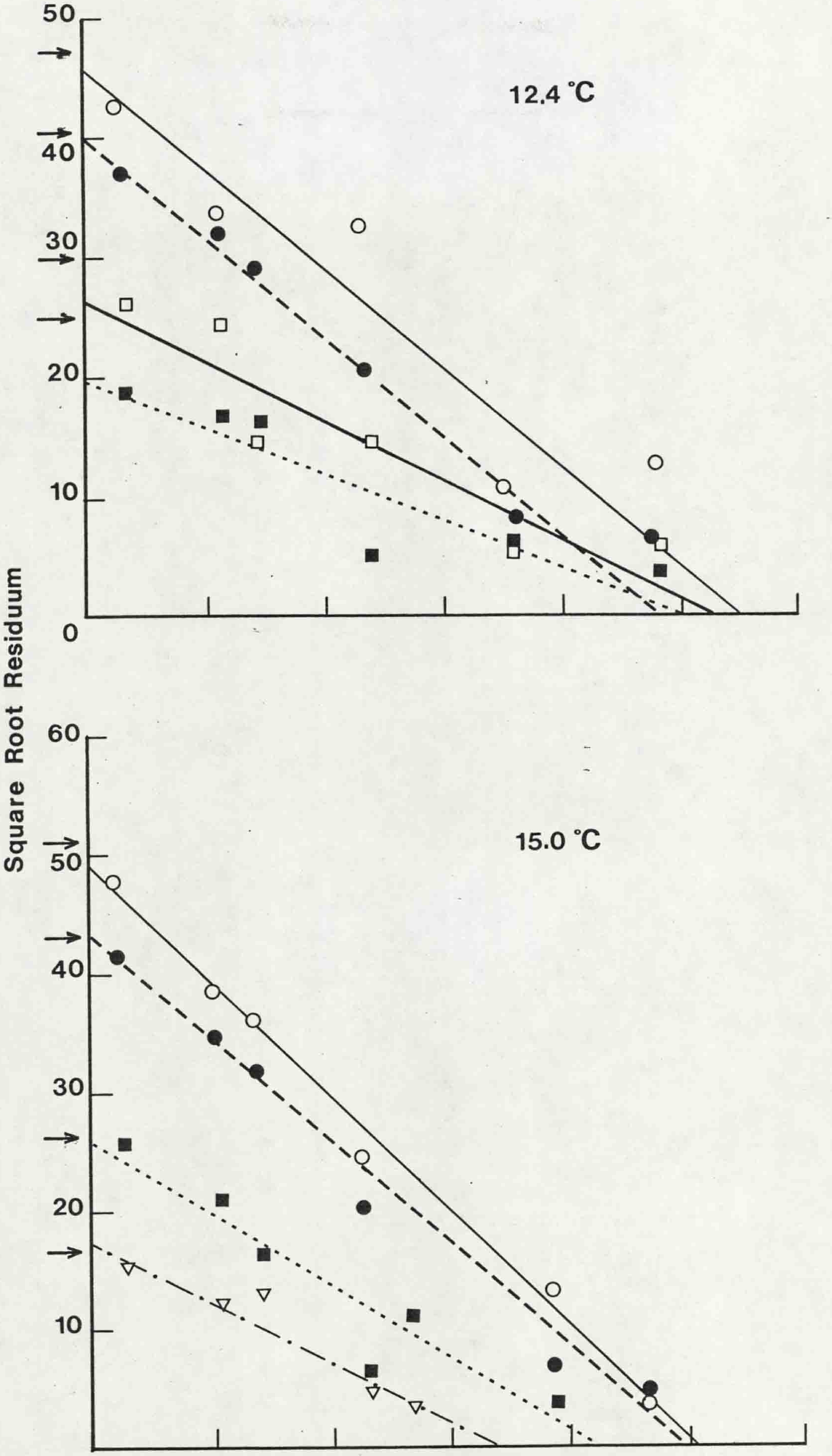
<u>12.4°C</u>

290.5 ± 39.9g : ■-------■ : $y = 19.697 - 0.196x$
($n = 12$, $r = -0.846$)
425.0 ± 40.0g : □———□ : $y = 26.299 - 0.249x$
($n = 12$, $r = -0.861$)
764.2 ± 55.6g : ●----● : $y = 39.720 - 0.404x$
($n = 10$, $r = -0.946$)
1036.8 ± 122.1g : ○———○ : $y = 45.220 - 0.414x$
($n = 11$, $r = -0.942$)

<u>15.0°C</u>

111.9 ± 22.2g : ▽—·—·▽ : $y = 17.297 - 0.252x$
($n = 10$, $r = -0.952$)
275.3 ± 42.6g : ■-------■ : $y = 25.662 - 0.306x$
($n = 11$, $r = -0.938$)
744.0 ± 55.3g : ●----● : $y = 43.246 - 0.435x$
($n = 12$, $r = -0.987$)
1043.8 ± 132.0g : ○———○ : $y = 48.692 - 0.478x$
($n = 12$, $r = -0.990$)

(Arrows indicate square root of initial meal weight)


12.4 °C
15.0 °C
Square Root Residuum
Time after Feeding - h
50
40
30
20
10
0
60
50
40
30
20
10
0
20
40
60
80
100
120

insignificant relationships existed between GET (h) and dogfish weight, W (g):

$$GET = 160.645\ W^{0.061} \quad \text{at } 6.6°C$$

$$(r = 0.371)$$

$$GET = 105.130\ W^{-0.003} \quad \text{at } 12.4°C$$

$$(r = -0.227)$$

At 15.0°C compensation through increased evacuation rates was less complete and smaller dogfish eliminated a 1% b.w. meal significantly faster than larger individuals:

$$GET = 0.033\ W^{0.179}$$

$$(r = 0.992)$$

An alternative approach to the study of the relationship between fish size and gastric evacuation is to feed fish of different sizes a meal of given weight. For this purpose four size groups of dogfish were force-fed 3.00 g (wet weight) of Buccinum at 14.2°C (Table 2.10). The biggest dogfish emptied the meal fastest, while there was little difference in the rates of evacuation between the three smaller size groups. These results were somewhat unexpected as the relationships between meal size and gastric emptying (Section (vi)) and dogfish size and removal of 1% b.w. meals predicted that bigger dogfish would eliminate a given quantity of food more rapidly than smaller individuals. Support from experimental findings was only partial.

Table 2.10 Values for intercept 'a' and instantaneous rate of gastric evacuation 'R' (± 95% confidence limits) for different size groups of Scyliorhinus canicula force-fed 3.00 g (wet wt.) meals of Buccinum.* Correlation coefficients and predicted GET's are given for each experiment. Instantaneous evacuation rates are compared for differences.

Temp. : 14.2°C (14.0 - 15.0)

Dogfish wt. ± SD (g)	n	Regression** a	R ± 95% CL	r	GET(h)
258.9 ± 50.1	9	26.0442	0.3330 ± 0.0934	-0.9547	78.2
427.2 ± 29.5	11	26.7839	0.3363 ± 0.1063	-0.9221	79.6
745.5 ± 50.6	10	27.0793	0.3487 ± 0.0887	-0.9475	77.7
1058.7 ± 142.1	10	30.8774	0.4556 ± 0.0906	-0.9715	67.8

Comparison of slopes.

Size group	258.9	427.2	745.5
258.9	-		
427.2	ns ($p > 0.5$)	-	
745.5	ns ($p > 0.5$)	ns ($p > 0.5$)	-
1058.7	$p < 0.05$	$0.1 > p > 0.05$	$0.1 > p > 0.05$

* Equivalent to 764 mg dry wt.

** All regressions highly significant $p < 0.001$

(viii) Meal Type

At 12°C groups of 650 - 850 g dogfish were force-fed one of seven different prey species, representatives of four phyla. Although standard 1% b.w. meals were presented (except for Eupagurus) the dry weight of food ingested varied because of differences in moisture content of each prey species (Table 2.11). As demonstrated previously (Section (vi)) evacuation rates (R) were independent of the actual meal size ingested. Thus direct statistical comparison of slopes was possible for different foods despite variation in the weight of dry matter consumed. Except for Chlamys, evacuation rates of all prey groups did not differ significantly from those for Buccinum. It may be assumed then that evacuation rates determined for the elimination of a meal of Buccinum will adequately represent evacuation rates (R), for most other prey species. GET's did differ, with Nereis being completely removed from the stomach quicker than any other prey.

Loss of taxonomic identity through digestive breakdown has bearing on stomach content analysis and was most rapid for Nereis and Sprattus; within 24 h for the former and 48 h for the latter. The rapid breakdown of Sprattus was accompanied by a build up of semidigested particulate material in an oily chyme, removal of which proceeded comparatively slowly, giving a GET of 128 h.

With crustacean prey, the proportion of chitin remaining in the stomach tended to increase with time after feeding (Table 2.12). This suggests that more readily digestible matter was eliminated from the stomach at a faster rate than the chitin. Note that because the heavily chitinised walking appendages and chelae of

Table 2.11 Values for intercept 'a' and instantaneous rate of gastric evacuation 'R' (± 95% confidence limits) for 650 - 850 g *Scyliorhinus canicula* force-fed 1% b.w. meals of different prey species. Initial meal size (mg dry wt.) and predicted gastric evacuation time (GET) are given for each experiment. Rates of gastric evacuation are compared statistically with those determined for the elimination of *Buccinum* meals. Mean dogfish wt. : 723.4 g

Temp. 12.0°C (11.1 - 13.0)		Initial	Regression*			Comparison of R with
Prey	n	meal size (mg)	a	R ± 95% CL	GET (h)	that for *Buccinum* meal
Buccinum undatum	10	2074	44.0372	0.3839 ± 0.1183	114.7	-
Chlamys opercularis	10	1559	30.2755	0.2368 ± 0.0653	127.9	t = 2.492 ; $0.02 < p < 0.05$
Glycymeris glycymeris	12	1777	43.7756	0.3133 ± 0.0737	139.7	t = 0.147 ; n.s.
*Eupagurus bernhardus***	12	2739	45.4382	0.3385 ± 0.1132	134.2	t = 1.595 ; n.s.
Temp. 12.3°C (11.7 - 13.0)						
Buccinum undatum	10	1814	44.2804	0.3622 ± 0.0569	122.2	-
Sprattus sprattus	11	2268	43.1494	0.3361 ± 0.1637	128.4	t = 0.416 ; n.s.
Nereis virens	11	1319	29.2433	0.3675 ± 0.1027	79.6	t = 0.106 ; n.s.
Palaemon elegans	11	1980	45.3353	0.4113 ± 0.1563	110.2	t = 0.673 ; n.s.

* All regressions significant $p < 0.005$; ** wet wt. fed 9.97 g (not 1% b.w.), cephalothorax and abdomen only.

Table 2.12 Proportion of chitin in residuum with time after feeding for *Scyliorhinus canicula* force-fed crustacean food. Values represent the mean of 3 determinations.

Prey species : *Eupagurus bernhardus* Temp. : 12.0°C

	Time after feeding (h)				
Chitin	0	24.75	46.50	71.75	96.50
(% residuum)	6.56	9.21	18.61	22.72	25.52

Prey species : *Palaemon elegans* Temp. : 12.3°C

	Time after feeding (h)					
Chitin	0	6.00	24.25	48.00	72.00	96.00
(% residuum)	15.24	20.88	24.06	26.48	24.48	24.79

Eupagurus were removed prior to feeding it is probable that the delay in GET arising from differential movement of chitin would be considerably reduced when compared to that for intact hermit crabs.

(ix) Voluntary Feeding - Correction Factor

Regressions describing the gastric elimination of 1% b.w. meals of *Buccinum* fed voluntarily to 650 - 850 g dogfish are presented in Table 2.13. Comparison of these results with those obtained for force-fed meals under similar experimental conditions (refer to Tables 2.5 and 2.6) indicate that voluntary-fed dogfish eliminated a meal at a faster rate than force-fed individuals. An example is shown in Figure 2.9. It is possible to relate R and GET with temperature for voluntary-fed meals in the same form as for force-fed meals[2]:

$$R_V = 0.141\ e^{0.089T}$$

$$(n = 7,\ r = 0.925,\ p < 0.01)$$

(Compare with $R = 0.087\ e^{0.115T}$, for force-feeding)

and

$$GET_V = 287.867\ e^{-0.089T}$$

$$(n = 7,\ r = -0.841,\ p < 0.05)$$

(Compare with $GET = 555.462\ e^{-0.128T}$ for force-feeding)

By dividing predicted values for R_V by R at specified temperatures a correction factor for the bias arising from force-feeding can be applied to the data obtained in force-feeding experiments. The magnitude of this correction factor was itself temperature dependent (Figure 2.10a); the effects of stress arising from force-feeding

---

[2] The subscript 'V' has been used in order to distinguish results for voluntary-feeding from those for force-feeding.

Table 2.13 Values for intercept 'a' and instantaneous rate of gastric evacuation 'R' (± 95% confidence limits) for 650 - 850 g *Scyliorhinus canicula* voluntary-fed 1% b.w. meals of *Buccinum* at different temperatures. Actual meal sizes (mg dry wt.) and correlation coefficients (r) are given for each experiment.

Fish weight ± SD		Mean temp.(°C)	Meal size	Regression		
(g)	n	+ (range)	(mg dry wt.)	a	R ± 95% CL	r
760.0 ± 59.4	8	8.4 (8.0 - 8.6)	1959	46.7835	0.2583 ± 0.0358	-0.9905 **
755.4 ± 53.1	9	8.6 (8.0 - 8.9)	1979	44.3513	0.3356 ± 0.1940	-0.8397 *
745.0 ± 53.1	9	8.7 (8.5 - 9.0)	1805	32.3188	0.3019 ± 0.1467	-0.8786 *
752.4 ± 60.2	10	12.7 (11.9 - 13.4)	2157	38.8360	0.5337 ± 0.3314	-0.7955 *
729.1 ± 49.6	6	14.3 (14.0 - 14.5)	1736	40.6159	0.5046 ± 0.1681	-0.9724 **
754.6 ± 65.7	10	14.3 (14.0 - 14.9)	1711	39.5791	0.4663 ± 0.1036	-0.9648 **
739.4 ± 50.4	4	15.6 (15.1 - 16.5)	2034	40.5742	0.5365 ± 0.1986	-0.9927 **

* $p < 0.01$; ** $p < 0.001$

Figure 2.9 Comparison between square root of residuum (mg) and time after feeding for force-fed and voluntary-fed 1% b.w. meals of <u>Buccinum</u>.

755.4±53.1 g <u>Scyliorhinus</u> <u>canicula</u>.

Force-fed : $y = 45.236 - 0.221x$

($n = 12$, $r = -0.929$)

Voluntary-fed : $y = 44.351 - 0.336x$

($n = 9$, $r = -0.840$)

(Arrow indicates square root of initial meal weight)

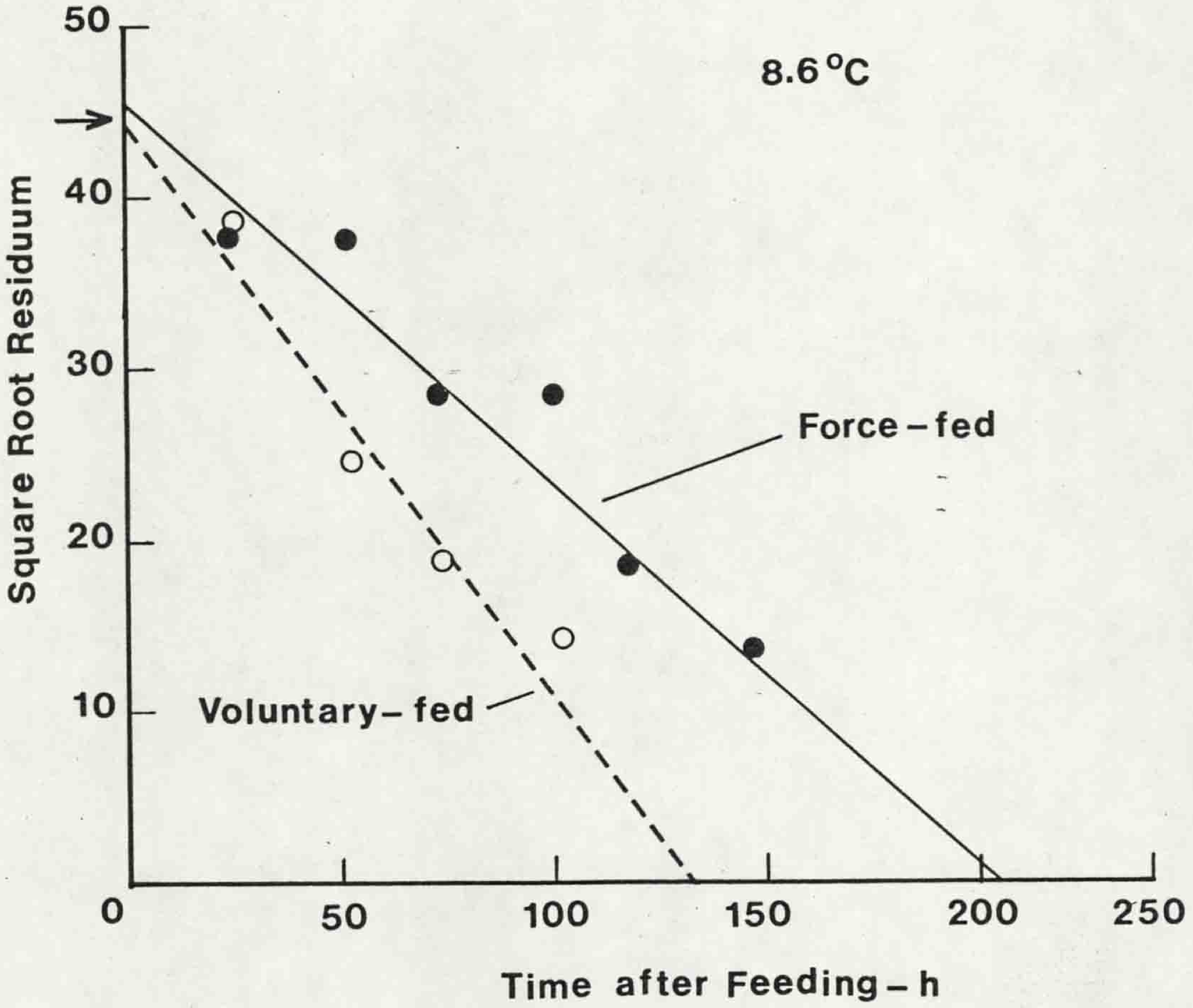
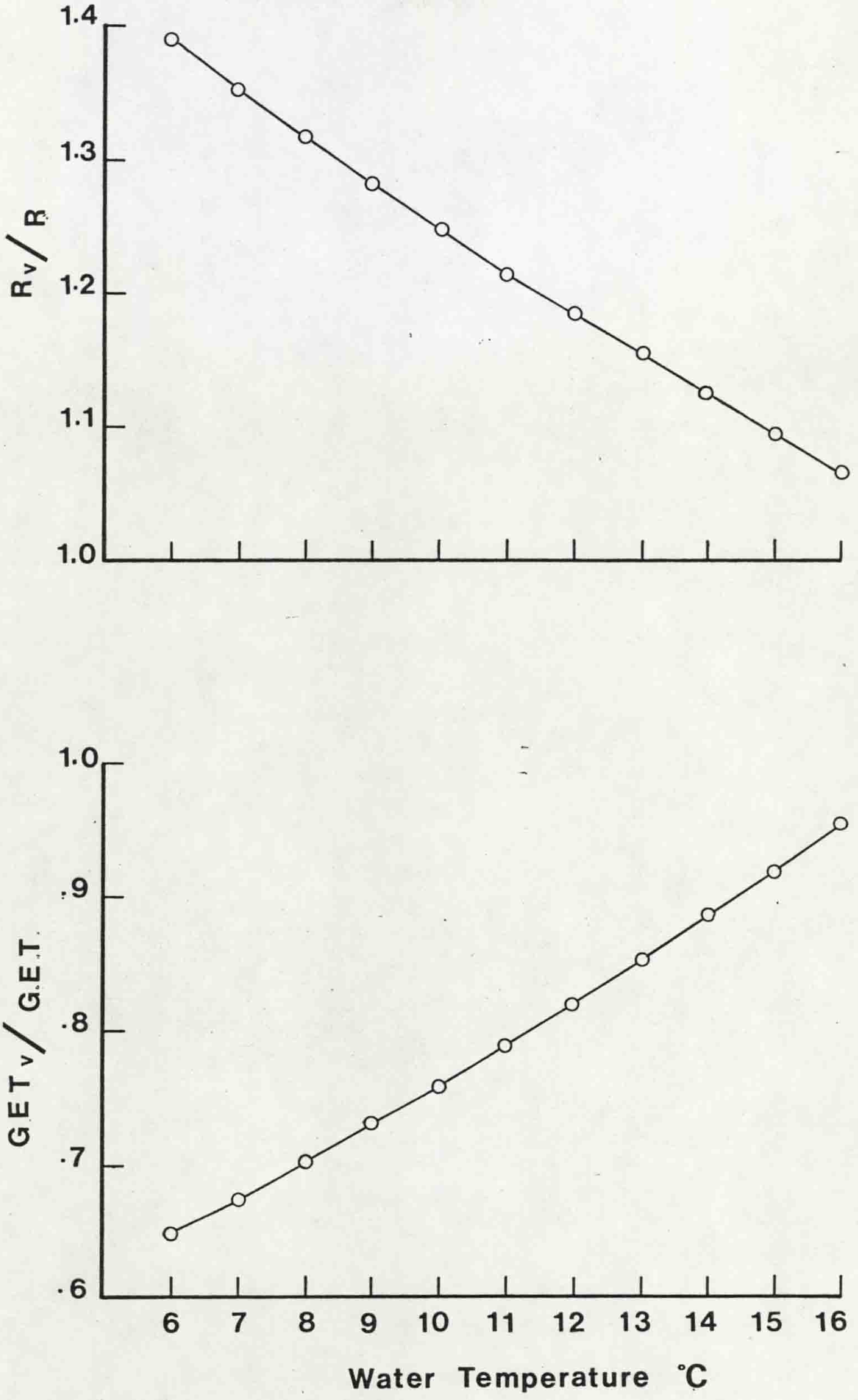

8.6 °C
Force - fed
Voluntary - fed
Square Root Residuum
50
40
30
20
10
0
50
100
150
200
250
Time after Feeding - h

Figure 2.10 Relationships between rate correction factor (R_v/R) and temperature and gastric evacuation time correction factor (GET_v/GET) and temperature .

(See text for explanation)


1.4
1.3
1.2
1.1
1.0
Rv/R
1.0
.9
.8
.7
.6
GETv/G.E.T.
6
7
8
9
10
11
12
13
14
15
16
Water Temperature °C

being most marked at low temperatures. For example actual values at 8.6°C were $R = 0.2207$ and $R_V = 0.3356$, while at 12.7°C $R = 0.4670$ and $R_V = 0.5337$. A correction factor for GET can be calculated in a similar fashion, i.e. GET_V/GET (Figure 2.10b). The relationships between these correction factors and temperature can be described as follows:

$$\ln (R_V/R) = 0.4869 - 0.0263T$$

and

$$\ln (GET_V/GET) = 0.0383T - 0.6573$$

Assuming that correction factors determined in this manner are unaffected by dogfish size and meal size it is possible to 'correct' values for R and GET given in Tables 2.5, 2.6, 2.7, 2.9, 2.10. Corrected values of R and GET and results for voluntary-feeding can be related to temperature, meal size and dogfish size by multiple non-linear regression, such that:

$$\ln(R) = 0.0910T + 0.2552 \ln(W) + 0.1392 \ln (S) - 4.7444$$

$$(n = 39, r = 0.947)$$

which is equivalent to $R = 0.0087\ e^{0.091T}\ W^{0.2552}\ S^{0.1392}$

and $\ln(GET) = 4.6111 - 0.0862T - 0.2005 \ln (W) + 0.3132 \ln(S)$

$$(n = 39, r = 0.948)$$

or $GET = 100.595\ e^{-0.0862T}\ W^{0.2005}\ S^{0.3132}$

Similarly GET may be written as a function of meal size expressed as % b.w. (M), temperature and dogfish size:

$$\ln (GET) = 4.9305 - 0.0885T + 0.1125 \ln (W) + 0.3161 \ln (M)$$

$$(n = 39, r = 0.950)$$

(Correlation matrix is presented in Table 2.14)

Table 2.14 Correlation matrix for multiple non-linear regressions relating instantaneous rate of gastric evacuation (R) or gastric evacuation time (GET) with temperature (T); dogfish size (W); and meal size (S and M). See text for explanation.

	Variable			
	lnR	lnGET	T	lnW
T	0.750	-0.862	-	-
lnW	0.452	0.229	-0.121	-
lnS	0.296	0.574	-0.272	0.713
lnM	-	0.548	-0.212	-0.018

- Multiple Meals

A number of experiments were initiated to establish whether there were significant differences between gastric emptying rates for dogfish fed single or multiple meals. Considerable difficulties were encountered and several experiments had to be abandoned, due mainly to the reluctance of dogfish to feed readily and to limitations imposed by available tank space.

In one experiment a group of dogfish was fed a single 1% b.w. meal while a second group was also fed a second meal 29.5 h after ingesting the first meal (Table 2.15a, Figure 2.11). Comparison of slopes suggest only a slight increase in evacuation rate for the group fed two meals. An alternative approach adopted was to feed a group of dogfish 1% b.w. meals on four consecutive days and follow the subsequent clearance of the stomach (Table 2.15b). Compared with the predicted value of R for a single voluntarily fed meal of Buccinum of 0.4077 (95% confidence limits of 0.3608 to 0.4610) the actual value of 0.3258 was slightly lower than expected.

DISCUSSION

A number of mathematical models have been proposed to describe the rate at which food is eliminated from the stomach in fish. The simplest of these is represented by a linear decrease in stomach contents with time. This implies that the rate of gastric evacuation (g/h) remains constant, and such a model adequately describes gastric elimination for Lepisosteus (Hunt, 1960), Megalops (Pandian, 1967), Gobius (Healey, 1971), Stizostedion (Swenson and Smith, 1973), various gadoids (Daan, 1973; Jones, 1974),

Table 2.15 Results for multiple meals fed voluntarily to 650 -850 g <u>Scyliorhinus</u> <u>canicula</u>.

(a) Weight of residuum with time after feeding for a group of dogfish fed a single 1% b.w. meal of <u>Buccinum</u> compared with another group fed a second 1% b.w. meal 29.5 h after ingesting the first meal. Regression equations are given. y = residuum (mg) at specified time; x =time after feeding.

Temp °C : 15.6 (15.1 - 16.5)

Dogfish wt. ± SD : 739.4 ± 50.4 g

	Time after first meal (h)			Regression
	22.75	47.50	69.25	
Residuum (mg)	843 855	167	21	$y = 40.5743 - 0.5365x$ $(r = -0.992)$

	Time after second meal (h)			
	18.00	40.00	66.00	
Residuum (mg)	1240	480	50 85	$y = 44.9409 - 0.5597x$

(b) Group of dogfish fed 1% b.w. meals of <u>Buccinum</u> on 4 consecutive days. Weight of residuum with time after the final meal. Regression equation is given.

Temp °C : 11.9 (11.5 - 12.4)

Dogfish wt. ± SD : 754.6 ± 65.7 g

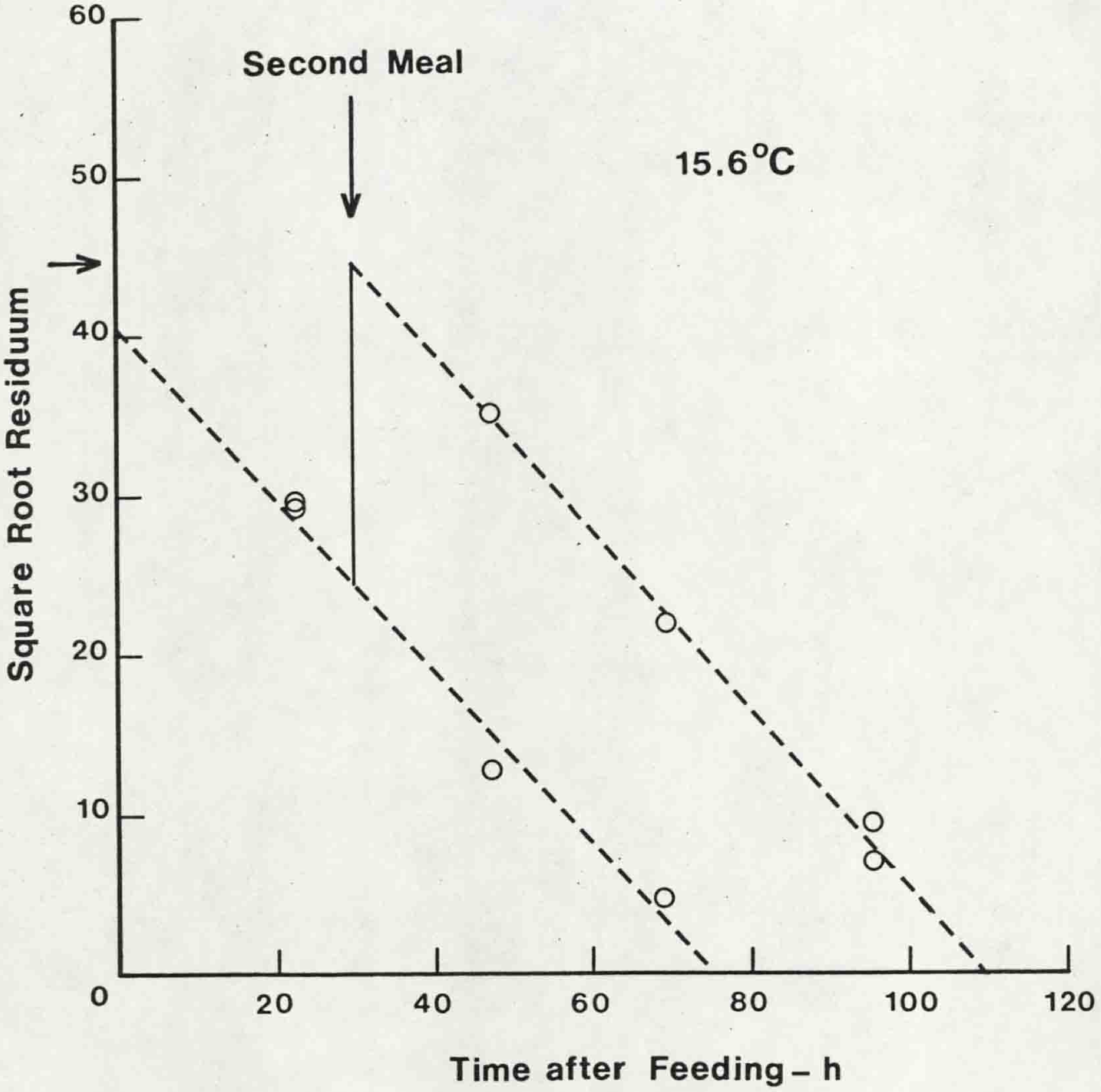
	Time after final meal (h)				
	18.50	43.00	68.00	92.00	136.50
Residuum : (mg)	3719	3277	1473	1136	630

Regression : $y = 66.4086 - 0.3258x$

$(r = -0.960)$

Figure 2.11 Square root of residuum (mg) with time after feeding for two groups of Scyliorhinus canicula : one fed a single 1% b.w. meal of Buccinum and the other fed a second 1% b.w. meal 29.5 h after ingesting the first meal. Regression lines fitted. (See Table 2.15a)

Temp. °C : 15.6 (15.1 - 16.5)
Dogfish wt. ± SD : 739.4 ± 50.4 g


Second Meal
15.6°C
Square Root Residuum
Time after Feeding – h
0
10
20
30
40
50
60
0
20
40
60
80
100
120

and Squalus (Jones and Geen, 1977). More often, however, the relationship between the weight of residuum and time after feeding is curvilinear and consequently the gastric evacuation rate (g/h) continually changes. Tyler (1970) and Fänge and Grove (1979) have postulated that as enzyme attack occurs at the surface of the bolus the evacuation rate might be expected to be a function of the surface area of the food remaining, such that:

$$dS/dt = -f\, S^{0.67} \qquad (1)$$

where the differential dS/dt describes the rate of emptying, S is the amount of food in the stomach and f is a constant. On the basis of published accounts of gastric evacuation Jobling (1981b) has questioned the validity of such a model and argues that the instantaneous rate of evacuation is more dependent on the volume rather than surface area of food in the stomach. There are two volume-dependent models. The first assumes that the emptying rate is in constant proportion to the instantaneous volume of food remaining in the stomach. That is to say:

$$^{dS}/_{dt} = -f\, S \qquad (2)$$

or

$$S_t = S_o\, e^{-Rt}$$

Where S_o is initial meal size, S_t is meal residuum at time t after feeding and R is the instantaneous evacuation rate. The exponential model has been applied to gastric emptying in Oncorhynchus (Brett and Higgs, 1970), Gadus (Tyler, 1970), Salmo (Elliott, 1972), Ptychocheilus (Steigenberger and Larkin, 1974), Perca (Griffiths, 1976; Thorpe, 1977; Persson, 1979, 1981), Lagodon (Peters and Hoss, 1974), and Blennius (Grove and Crawford, 1980). The second volume-dependent model was applicable to gastric evacuation in Scyliorhinus, and can be summarised mathematically as:

$$dS/_{dt} = - f\ S^{0.5} \qquad (3)$$

or

$$S_t^{\ 0.5} = S_o^{\ 0.5} - Rt$$

The rationale for this 'square root' or 'radial distension' model is that gastric motility is linked with the radial distension of the stomach and that the circumferential tension so developed is proportional to the radius. Since the radius of a cylinder of constant height varies in direct proportion with the square root of its volume and by the Law of Laplace circumferential tension is proportional to the radius (Hopkins, 1966) then the tension developed in the stomach wall will also vary with the square root of the volume (or weight) of food in the stomach. The square root model has been applied to the gastric elimination of fluids in man (Hopkins, 1966), as well as to the pattern of gastric evacuation in Raja (de Souza, 1978) and Pleuronectes (Jobling and Davies, 1979). In fact, recent re-examination of the literature by Jobling (1981b) has indicated that the data given in several previous studies would also be best described by the 'square root' model (refer to his Table I).

Temperature was the most significant single factor found to influence gastric evacuation in Scyliorhinus. In accordance with findings reported for other fish groups (references given in Introduction) gastric evacuation rate increased with rising water temperature, and consequently gastric emptying times were negatively correlated with temperature (Table 2.5, Figure 2.3). At least five temperature-dependent processes are thought to control digestive functioning, these include feeding rate, secretory rate of digestive juices, hydrolytic activity of digestive enzymes, gastric and intestinal motility and the rate of intestinal absorption (Kapoor _et al_, 1975). Smit (1967) has demonstrated experimentally that the secretory rate of gastric juices is temperature dependent and that the composition of the juices is influenced by the rate of secretion. It is possible then that the digestive power of gastric juices also increases with increasing temperature (Smit, op cit.). In elasmobranchs, rising temperature is known to cause an increase in the rate of spontaneous contractions of all parts of the stomach (Nicholls, 1933), which would enhance evacuation rates.

Within the temperature range considered, the instantaneous rate of gastric evacuation for _Scyliorhinus_ increased exponentially with temperature (Figure 2.4). Similar relationships have been found for _Salmo_ (Elliott, 1972) and _Perca_ (Persson, 1979, 1981), but apparently contrast those for _Oncorhynchus_ (Brett and Higgs, 1970), _Pleuronectes_ (Jobling, 1980a) and _Gadus_ (Tyler, 1970). For _Oncorhynchus_ and _Pleuronectes_ R approached a plateau at high temperatures while for _Gadus_ R attained a maximum value and then declined at higher temperatures. Nevertheless over part of the temperature ranges considered by these workers R increased more or less exponentially with temperature. Deviation from the exponent occurred only as the limits of temperature tolerance were approached.

In the present study temperatures considered fell within the thermal tolerance range for Scyliorhinus, so it is possible that had the limits been approached, the pattern of R with temperature would have altered and thus conform with trends reported elsewhere. As a consequence of the evacuation rate-temperature relationship gastric evacuation times decreased exponentially with rising temperature.

Based on corrected values, gastric evacuation rate and evacuation time for Scyliorhinus were related to temperature by $e^{0.091T}$ and $e^{-0.086T}$ respectively, giving Q_{10} values of 2.48 and 2.37. These findings fall within the range of 2 to 3 normally associated with thermochemical (enzymatic) reactions (Hoar, 1966) and compare favourably with Q_{10} values for other fishes; e.g. 3.1 for Salmo trutta (Elliott, 1972), 2.5 for S. gairdneri (Windell et al, 1969), 2.2 for gadoids (Jones, 1974) and Scophthalmus (Flowerdew and Grove, 1979), 2.0 for Pleuronectes (Jobling and Davies, 1979) and 1.9 for Sarotherodon (Ross and Jauncey, 1981).

When Scyliorhinus of given weight were fed different sized meals the time to complete gastric emptying increased with increasing meal size, but the instantaneous gastric evacuation rate R remained unchanged (Table 2.7). Similar responses to varying meal size have been reported by Hopkins (1966) in man, and Jobling and Davies (1979) in Pleuronectes. Tyler (1970), Elliott (1972) and Persson (1981) have also shown in their experiments based on the exponential model of gastric evacuation (equation (2)) that R was unaffected by meal size.

Since a single curve (i.e. in terms of untransformed data) adequately described the gastric evacuation of a meal for dogfish of given size, large meals will be emptied more rapidly (mg/h) during the early stages of gastric evacuation than smaller meals (Figure 2.6). The increase in GET will not, therefore, be in direct proportion to the increase in meal size and was found to vary as $(\text{meal size})^{0.35}$ at 7.7°C and as $(\text{meal size})^{0.46}$ at 13.5°C. Similarly the evacuation rate, expressed as mg/h, increased with $(\text{meal size})^{0.36}$ at 7.7°C and with $(\text{meal size})^{0.49}$ at 13.5°C. Grove and Crawford (1980) point out that the square root model of gastric emptying can be related to the original meal size (S_o) and that integration between $t = o$ and $t = \text{GET}$ (i.e. when $S = o$) gives:

$$\text{GET} = f \, . \, S_o^{\,0.5} \qquad (4)$$

Similarly for gastric evacuation rate (mg/h) at a specified time t after feeding:

$$\text{GER} = f \, . \, S_o^{\,0.5} \qquad (5)$$

Alternatively, Fänge and Grove's (1979) surface area model predicts that:

$$\text{GET} = f \, . \, S_o^{\,0.33} \qquad (6)$$

and

$$\text{GER} = f \, . \, S_o^{\,0.67} \qquad (7)$$

In the present experiments the actual exponents for meal size at 13.5°C were in good agreement with the values predicted by the square root model while at 7.7°C values were lower than expected for this model.

Similar analysis of published data by Jobling (1981b) has provided a certain amount of empirical support for these predicted consequences of the square root model, with gastric evacuation time varying as the following exponents of meal size; 0.43 for Salmo (Windell et al, 1969), 0.42 - 0.63 for Scophthalmus (Flowerdew and Grove, 1979), 0.52 for Pleuronectes (Jobling and Davies, 1979) and Lepisosteus (Hunt, 1960) and 0.53 for Micropterus (Beamish, 1972). There are a number of exceptions and in some cases the time required to complete gastric evacuation is more or less the same irrespective of meal size; e.g. Lepomis macrochirus (Windell, 1966), L. gibbosus (Kitchell and Windell, 1968), Belone (Rosenthal and Paffenhöfer, 1972), Raja (de Souza, 1978) and Blennius (Grove and Crawford, 1980); while for other species the exponent for meal size is greater than 0.5; e.g. 0.74 - 0.83 for Limanda (Jobling et al, 1977).

The relationship between fish size and gastric evacuation for Scyliorhinus was ambiguous, partly due to the high level of individual variability encountered in the experiments. In general though, smaller dogfish emptied 1% b.w. meals more quickly than larger individuals. These findings agree with published reports for various species fed meals based on a known proportion of fish live weight; e.g. Megalops (Pandian, 1967), Ophiocephalus (Gerald, 1973), Limanda (Jobling et al, 1977; Gwyther and Grove, 1981), Salmo (Grove et al, 1978), Scophthalmus (Flowerdew and Grove, 1979), Blennius (Grove and Crawford, 1980) and Sarotherodon (Ross and Jauncey, 1981). Gastric evacuation rates for Scyliorhinus, however, increased with dogfish size, and at 6.6°C and 12.4°C estimated GET's for all size groups were very similar, in spite of the fact that the actual weight of food ingested differed. Comparable results have been found for Raja force-fed 1.1% b.w. meals of Crangon (de Souza, 1978). At 15.0°C compensation was weaker and GET increased significantly with dogfish size; GET varied as (fish size)$^{0.179}$. Since a linear relationship exists between stomach volume and fish size the square root model predicts that for different sized fish fed the same relative meal size M (% b.w.) (Grove and Crawford, 1980):

$$GET = f \ W^{0.5} \qquad (8)$$

which compares with the surface area model (Fänge and Grove, 1979):

$$GET = f \ W^{0.33} \qquad (9)$$

In this respect the results for Scyliorhinus do not conform to the square root model. Factors such as the compensatory increase in gastric evacuation rates with increasing dogfish size are not accounted for in the model. Review of available literature by Fänge and Grove (1979) and subsequent publications reveals that total elimination times for M% b.w. meals vary by the following exponents of fish size: 0.23 for Ophiocephalus (Gerald, 1973), 0.27 for Blennius (Grove and Crawford, 1980), 0.36 for Scophthalmus (Flowerdew and Grove, 1979), 0.39 for Limanda (Jobling et al, 1977; Gwyther and Grove, 1981), 0.40 for Megalops (Pandian, 1967), and 0.7 for Salmo (Grove et al, 1978). From results for Scyliorhinus and other published work it seems that the physiological implications of varying fish size on gastric evacuation may be more complex than suggested by either the square root or surface area models.

It follows from the relationships between meal size and evacuation rate R, and the elimination of 1% b.w. meals and fish size, that the larger dogfish will eliminate a meal of given weight more rapidly than smaller individuals. While the largest size group did evacuate a 3 g meal faster than the other groups, as predicted, no significant differences in evacuation rates were detected amongst the other size groups. If experimental variation is discounted a possible explanation for this discrepancy might be that since a 3 g meal represents a comparatively small stimulus (less than 0.4% b.w.) to the two larger size groups control mechanisms other than radial distension might come into play, and in such circumstances evacuation rates would deviate from those determined for larger meals. The predicted value for R based on the relationship with temperature for the 650 - 850 g size group force-fed 1% b.w. meals was infact greater than that actually determined for the elimination of a 3 g meal (0.4466 compared with 0.3487). This being the case results based solely on comparatively small meal sizes may produce misleading conclusions when extrapolated to include larger meals, and *vice versa*. For teleosts the influence of fish size on gastric emptying of a given weight of food is variable, elimination times may be unaffected by fish size; e.g. *Lepomis* (Windell, 1966), *Gadus* (Tyler, 1970), *Salmo* (Elliott, 1972), *Ptychocheilus* (Steigenberger and Larkin, 1974), *Perca* (Persson, 1979), *Blennius* (Grove and Crawford, 1980) and *Pleuronectes* (Jobling, 1980c), while for other species larger fish evacuate a standard weight of food quicker than smaller individuals; e.g. *Stizostedion* (Swenson and Smith, 1973), various gadoids (Jones, 1974), *Limanda* (Jobling *et al*, 1977), *Scophthalmus* (Flowerdew and Grove, 1979) and *Sarotherodon* (Ross and Jauncey, 1981). The influence of fish size on gastric evacuation is clearly very complex and more work is necessary on this aspect.

Gastric evacuation rates (R) at 12°C were not significantly different ($p > 0.1$) for meals of Buccinum, Glycymeris, Sprattus, Nereis, Eupagurus and Palaemon. It can be assumed that instantaneous evacuation rates for Buccinum adequately describe rates for many of the organisms encountered in the diet (See Chapter 1). The studies of Windell (1966), Elliott (1972) and Persson (1979, 1981) have also indicated that groups of different prey species maybe evacuated at similar instantaneous rates. Other workers have found that different foods are evacuated at different rates. Differences may be influenced by the biochemical composition of the food, and in particular lipid (or more specifically energy) content (Kapervitch and Bokova, 1937; Kitchell and Windell, 1968; Windell et al, 1969; Western, 1971; Elliott, 1972; Jobling, 1980a). Probably related to the inhibitory effect that high fat content has on gastric evacuation was the finding that despite rapid disintegration of Sprattus muscle in the stomach the resulting semidigested chyme was removed at a comparatively slow rate. This observation is supported by stomach content analysis (Chapter 1); several dogfish had fed on herring and even though gastric breakdown of the body was almost complete, copious quantities of oily chyme remained in the stomach. Elimination of a meal of Nereis was completed within about half the time of other prey species. This coupled with rapid loss of taxonomic identity probably led to underestimation of the importance of polychaetes in general to the diet of dogfish.

Experimental evidence suggested that chitin was evacuated, or more correctly digested (see Alliot and Boquet, 1967), at a slower rate than the readily digestible material. This conclusion was supported by the presence of considerable quantities of crustacean remains, essentially fragmented and partially digested exoskeletons, in the stomachs of wild dogfish (Chapter 1). Comparable findings have been reported for other species by Karpevitch and Bokova (1937), Windell (1966), Pandian (1967), Western (1971) and Kionka and Windell (1972).

Force-feeding techniques have been extensively utilized in gastric evacuation studies, but evidence presented in this study and by Windell (1966) and Swenson and Smith (1973) show that force-feeding depresses gastric evacuation rates when compared with fish which consume food voluntarily. Further bias may arise because most gastric evacuation studies are based on the elimination of single meals preceded by a period of food deprivation. Preliminary experimental evidence for Scyliorhinus suggested that gastric evacuation rates R for single and multiple meals did not differ markedly. Similar conclusions have been obtained for Salmo (Elliott, 1972) and Perca (Persson, 1981). In contrast other workers have reported that continuous feeding results in an increase in evacuation rates over those for single meals by a factor of 1.5 to 2 times; e.g. Carassius (Rozin and Mayer, 1964), larval Micropterus (Laurence, 1971), young Perca (Noble, 1973) and various gadoids (Jones, 1974).

Application of an empirically determined correction factor to account for the effect of force-feeding enabled the formulation of a model expressing gastric evacuation rates/times as functions of temperature, meal size and fish size. As discussed above there are several consequences implicit in the square root model which relate fish size and meal size with GET, as shown in equations (4) and (8). These can be described as a multiple non-linear correlation equation including temperature effect such that when fish of different sizes are fed meals of the same relative size M (% b.w.) the square root model gives:

$$\ln (\mathrm{GET}) = A + 0.5 \ln M + 0.5 \ln W - bT \qquad (10)$$

where A and b are constants (after Gwyther and Grove, 1981). This compares with the surface area model which predicts, from equations (6) and (9), that:

$$\ln (\mathrm{GET}) = A + 0.33 \ln M + 0.33 \ln W - bT \qquad (11)$$

Data for Scyliorhinus subjected to multiple regression analysis gave lower coefficients for M and W than predicted by either model (viz, 0.113 and 0.316, respectively). It is interesting to note that inherent to the exponential model of gastric emptying is the fact that the coefficient for M will be less than 0.33 (Grove and Crawford, 1980; Jobling, 1981b). While the square root transformation represents a convenient model for describing the pattern of removal of food from the stomach, the mathematical consequences represent an oversimplification of the physiological processes involved in gastric evacuation for **Scyliorhinus**.

Innervation of the gut of elasmobranchs is incompletely understood (Fänge and Grove, 1979; Young, 1980) as is the physiological control of gastric digestion and emptying in teleosts and elasmobranchs. Certainly factors such as the quantity and quality of food, rate of gastric juice secretion, and gastric motility are important. The quantity of food in the stomach may influence the gastric secretory rate and by doing so increase the digestive power of the gastric juices (Smit, 1967). Distension of the stomach arising from the presence of food may stimulate gastric motility (Kapoor _et al_, 1975; Fänge and Grove, 1979) and is known to cause an increase in the amplitude of gastric peristaltic contractions (Jobling _et al_, 1977). Kapoor _et al_ (op cit.) have also postulated that the presence of chyme in the intestine may, via feed-back systems (nervous or hormonal), inhibit stomach motility. Without identifying the control mechanisms, Jobling (1980a) demonstrated that the rate of energy flow from the stomach into the intestine plays an important role in determining gastric evacuation rates in _Pleuronectes_. The fact that gastric breakdown of the bolus proceeds more rapidly than the elimination of resulting chyme, which tends to build up in the stomach, offers circumstantial evidence for some form of intestinal 'rate limiting' mechanism in _Scyliorhinus_. Clearly there is need for further investigations into the physiological mechanisms that control gastric motility in fish and from such work it is probable that apparent discrepancies noted in this study and reported elsewhere throughout the literature might be satisfactorily explained.

Finally as so little published information is available for elasmobranchs, comparison of gastric evacuation data with that for teleosts is desirable. Because experimental conditions (temperature, fish size, meal size and type, mode of presentation, form of data representation, etc.) are variable between studies direct comparison of gastric evacuation rates are extremely difficult. However, gastric evacuation times determined for _Scyliorhinus_ are generally greater than those for teleosts but comparable with those for other elasmobranchs (refer to Table 2.1). Without taking into account factors such as fish size, meal size, handling stresses, etc., published data for teleosts summarised in Table 2.1 suggest that at 10°C gastric evacuation is completed within 40 h. In contrast, gastric clearance for elasmobranchs takes about twice this time. The comparatively slow evacuation rates of elasmobranchs are no doubt linked with their general level of metabolism which is considerably lower than for most teleosts (Pérès and Rigal, 1970; Brett and Blackburn, 1978). Another contributing factor is that food is retained in the stomach until such a time that intragastric digestion renders it semifluid, with only semifluid chyme being passed into the intestine (Hogben, 1967; Young, 1980; personal observations).

CHAPTER 3

Assimilation Efficiency

INTRODUCTION

Following digestion much of the nutritive value of food is absorbed through the wall of the gut, the remainder, including any undigested remains, being defaecated. 'Assimilation efficiency' refers to the efficiency with which organisms extract energy or specific nutrients from ingested food. In the literature various other terms have been used synonymously to describe assimilation, these include 'absorption efficiency' (Gerking, 1952), 'extraction efficiency' (Davies, 1964) and 'digestibility' (Hastings, 1969).

Previous assimilation studies in fish have been directed towards teleosts and generally form part of a broader investigation into energetic and/or growth relationships (Gerking, 1952, 1955; Menzel, 1958, 1960; Davies, 1964; Pandian, 1967; Birkett, 1969; Beamish, 1972; Kelso, 1972; Smith, 1973; Cowey et al, 1974; Elliott, 1976 b,c; Flowerdew and Grove, 1980). In addition to the physiological and ecological significance of such research a knowledge of assimilation is an important consideration in aquaculture, particularly with regards to diet formulation (Inaba et al, 1962; Nose and Mamiya, 1963; Nose and Toyama, 1966; Nose, 1967; Hastings, 1969; Smith, 1971; Rychly and Spannhof, 1979; Jobling, 1981a).

As the portion of the food assimilated is difficult to estimate directly, assimilation studies have involved the collection and analysis of faeces for comparison with corresponding analysis of the food. Previous studies have been based on one of two approaches; the 'direct gravimetric method', or the 'indirect method'. The direct method requires a precise knowledge of the quantity of food ingested and the quantity of faeces produced. Assimilation efficiency is given by:

$$\text{Assimilation efficiency \%} = \frac{\text{nutrient in food - nutrient in faeces}}{\text{nutrient in food}} \times 100$$

This method has been employed for fish by several authors (Gerking, 1952, 1955; Menzel, 1958, 1960; Davies, 1964; Pandian, 1967; Birkett, 1969; Mann, 1969; Smith, 1971; Beamish, 1972; Kelso, 1972; Brocksen and Bugge, 1974; Elliott, 1976b). For the indirect method a physiologically inert reference material (e.g. chromic oxide, Cr_2O_3) is incorporated into the diet. From the ratio of the concentrations of the reference material to that of a given nutrient in the food, and the corresponding ratio in the faeces, the assimilation efficiency can be calculated without quantifying either food input or faeces output. Assimilation is calculated by:

$$\text{Assimilation efficiency \%} = 100 \times \left(1 - \frac{Cr_2O_3 \text{ : nutrient ratio in food}}{Cr_2O_3 \text{ : nutrient ratio in faeces}} \right)$$

The indirect method has been applied successfully to fish (e.g. Inaba _et al_, 1962; Nose and Mamiya, 1963; Nose and Toyama, 1966; Nose, 1967; Page and Andrews, 1973; Gwyther, 1978; Rychly and Spannhof, 1979; Flowerdew and Grove, 1980; Jobling, 1981a) and crustaceans (e.g. Nose, 1964; Forster and Gabbott, 1971) as well as higher vertebrates (e.g. Schürch _et al_, 1950, Dansky and Hill, 1952). The general applicability of the indrect method for fish has, however, been questioned by Bowen (1978) who found that juvenile _Sarotherodon_ eliminated the Cr_2O_3 from the gut at a faster rate than the food. This led to a gross underestimation of assimilation. McGinnis and Kasting (1964) compared the indirect and direct gravimetric methods for two species of phytophagous insects and concluded that the indirect method was simpler to apply and produced more reliable results than the direct method.

The present investigation was prompted by the apparent absence of any published accounts of assimilation efficiency in elasmobranchs. Comparison with findings obtained for teleosts is desirable in view of the marked anatomical differences in the alimentary tracts of the two groups and differences in gastric evacuation rates (Chapter 2). A consideration of assimilation also has implications on the aspects of growth and energetics (see Chapter 4).

MATERIALS AND METHODS

(i) Experimental Techniques

The indirect method, using Cr_2O_3 as the inert reference material, was adopted for the present study. Diets were prepared by homogenising natural foods into a paste consistency, to which 2% w/w Cr_2O_3 was added.

Prior to experiments dogfish were weighed and groups of three to five individuals placed into experimental tanks (1.2 x 0.6 x 0.3 m deep), supplied with flowing seawater and aeration. A 12L : 12D photoperiod was imposed in all experiments[1]. Light intensity at the water surface ranging between 0.01 - 0.03 W/m^2. Experiments were conducted at ambient sea temperatures with a single exception in which the water temperature was raised to the desired level at the rate of 1C degree per day. The fish were allowed a minimum of two weeks acclimation to the experimental conditions and were only disturbed for feeding during this period (Chapter 2).

Three meals, each equivalent to 2% body weight, were force-fed on alternate days. At low temperatures it was necessary to precede the first test meal by stomach lavage to prevent contamination arising from the undigested remnants of previous meals.

[1] Defaecation occurred almost exclusively during the dark period. For convenience, the light and dark periods were reversed with respect to the natural photoperiod

Collection of faeces was commenced on the day following the third meal and was continued for five days for temperatures in excess of 10°C and for upto eight days at lower temperatures. Defaecation generally continued for longer periods . In order to reduce the leaching of nutrients that might have arisen from excessive standing in water, faecal material was removed by siphon, generally within one hour of defaecation, but with a maximum standing period of two hours in a few instances. Faecal samples were washed in distilled water and immediately frozen at -20°C. At the completion of the collection period the faeces and samples of the food were freeze-dried and then finely ground in a mortar and pestle in preparation for chemical analysis.

(ii) Chemical Analyses

Samples of faeces and food were analysed for chromic oxide, total nitrogen and caloric content. For nitrogen and caloric determinations subsamples were diluted in the ratio 1 : 10 w/w with silica gel HR. Silica gel was chosen as a diluent because it is essentially free from organic matter and inorganic ions. Dilution enabled samples equivalent to between 1 - 2 mg to be weighed accurately and conveniently.

(A) Chromic oxide : Cr_2O_3 in the samples was oxidised to dichromate and chromium levels determined directly by atomic absorption spectrophotometry.

Reagent. Wet oxidation mixture. 20 g of sodium molybdate was dissolved in 300 ml distilled water. 300 ml concentrated sulphuric acid was added followed by 400 ml of 70% perchloric acid (McGinnis and Kasting, 1964).

The samples, between 5 - 20 mg, were heated in 10 ml of wet oxidation mixture for 30 min at 200°C. The resulting mixture was then diluted with distilled water and chromium levels compared with a set of known standards at 358 nm by a Pye Unicam SP90A Series 2 Atomic Absorption Spectrophotometer. Chromic oxide retention by this method varied between 83 - 108% with a mean of (±SE) of 96.9 ± 3.08%.

(B) Total Nitrogen : Nitrogen content of the samples was determined by a standard micro-Kjeldahl method[2]. Samples were digested in sulphuric acid and resulting ammonium nitrogen determined spectrophotometrically by the phenol-hypochlorite reaction, using ammonium sulphate as a standard (Forster and Gabbott, 1971).

> Reagents. Digestion mixture. 300 mg selenium dioxide dissolved in 15 ml water and mixed with 85 ml of nitrogen free sulphuric acid (BDH). Resulting solution was made upto 250 ml with distilled water.
>
> Phenol reagent. (Prepared daily) 2.5 ml of 80% aqueous phenol and 10 mg sodium nitroprusside were made up to 200 ml with distilled water.
>
> Hypochlorite reagent. (Prepared daily) 2 ml sodium hypochlorite [1N in 0.1N NaOH (BDH)] was added to 80 ml 2.5% NaOH and made up to 200 ml with distilled water.

The samples, diluted 1 : 10 with silica gel (10 - 20 mg), were heated in 1 ml of digestion mixture at 120°C overnight and then for a further six hours at 300°C. The mixture was cooled and diluted to 50 ml with distilled water. To 1 ml of diluted

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[2] The oily nature of Sprattus food meant that representative samples, on a micro-scale, could not be assured. A Macro-Kjeldahl method was, therefore, employed on undiluted samples - see Chapter 4 for method.

digestion mixture were added successively 2 ml of 2.5% NaOH, 4 ml phenol reagent and 2 ml of the hypochlorite reagent. The resulting mixture was made upto 10 ml with water and centrifuged to remove silica gel particles. The colour was allowed to develop for 25 minutes at room temperature. Absorbance was read at 635 nm in a 10 mm path-length cell.

A series of standards containing 3, 6, 12, 18, 24, and 30 µg/ml ammonium sulphate were prepared in 2% diluted digestion mixture. Separate calibration curves were prepared for each set of analyses. Protein content was determined by multiplying the total nitrogen by a factor of 6.25.

(C) Total Calories : Total calories were determined by a wet oxidation method[3]. Organic matter was oxidised with potassium dichromate and the unreduced dichromate determined spectrophotometrically (Forster and Gabbott, 1971).

Reagent. Oxidation mixture. 2.5 g potassium dichromate was mixed with 10 ml of water and the solution made up to 500 ml with concentrated sulphuric acid.

The samples, diluted 1 : 10 with silica gel (10 - 20 mg) were mixed with 2 ml of the oxidation mixture and heated at 100°C for one hour. The mixture was allowed to cool, diluted to 50 ml with water and centrifuged to remove silica gel particles. Absorbance was read at 347 nm in a 10 mm path-length cell. Standard solution of 0.5% potassium dichromate in sulphuric acid (250 mg $K_2Cr_2O_7$ mixed with 1 ml of water and made up to 50 ml with sulphuric acid) was diluted (2 ml to 50 ml) with water and treated in the same

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[3] Caloric content of undiluted Sprattus food was determined directly by bomb calorimetry (Gallenkamp Ballistic Bomb Calorimeter).

manner as the unknowns. The absorbance was corrected for an appropriate diluted sulphuric acid blank.

Calculation of total calories. Complete reduction of the dichromate corresponds to 10 mg potassium dichromate while partial reduction corresponds to a proportionate amount of potassium dichromate.

If the absorbance of the corrected standard = E_1,

and absorbance of the unknown = E_2

Then the reduced dichromate will be equivalent to:

$$\frac{E_1 - E_2}{E_1} \times 10 \text{ mg } K_2Cr_2O_7$$

Since 3 mg potassium dichromate = 0.489 mg O_2 and taking a mean oxycaloric coefficient of protein/carbohydrate/fat of 3.38 calories, then 1 mg $K_2Cr_2O_7$ = 0.552 cals. The caloric content of the sample can be expressed as :

$$\frac{E_1 - E_2}{E_1} \times 5.52 \text{ cals.}$$

Forster and Gabbott (1971), however, noted that a correction factor must be applied to account for incomplete oxidation of protein. A general figure of 60% protein oxidised was used by Gwyther (1978) and was adopted in the present study. The correction factor was calculated as follows :

If the quantity of protein (Nitrogen x 6.25) in the sample is X mg, then the unoxidised protein is equivalent to 0.4X mg. Since the caloric coefficient for protein is 5.65 cals per mg, then the total calories in the sample (corrected) is given by the expression:

$$\text{Total calories} = 5.52 \frac{(E_1 - E_2)}{E_1} + 2.26X \text{ cals.}$$

All of the above analyses were carried out in triplicate, although in some cases additional replicates were analysed. Mean values were used in the final calculations of assimilation efficiency.

RESULTS

Assimilation efficiency of protein nitrogen and total calories for four size groups of dogfish at different temperatures are given in Table 3.1. Assimilation of the test food, Buccinum, was unaffected by fish size and water temperature, giving overall mean values (±SE) of 94.9 ± 0.36% for protein and 91.0% ± 0.48% for calories.

Meal type exerted some influence on assimilation efficiencies in the dogfish, although values remained consistently high ($>$ 80%) (Table 3.2). Protein assimilation was maximal for the molluscs, Buccinum and Glycymeris, intermediate for the fish, Sprattus[4], and minimal for the crustacean, Palaemon. The pattern for assimilation of total calories followed a similar trend to that reported for protein, except for an intermediate value for Glycymeris.

Gerking (1952, 1955) and Pandian (1967) have suggested that since chitin present in food is effectively indigestible and contains 6.9% non-protein nitrogen, chitin nitrogen should be excluded in the estimation of nitrogen assimilation. No correction was applied to the present data for Palaemon because chitinase enzymes occur in the digestive tract of Scyliorhinus (Alliot and Bocquet, 1967), and the primary product of chitin breakdown, N-acetyl-D-glucosamine, is probably of some nutritive value since it is resorbed faster than glucose by the intestine (Alliot , 1967).

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[4] There were no apparent differences in assimilation efficiency for two sprat diets, despite differences in their gross biochemistry (Table 3.2).

Table 3.1 Assimilation efficiency (%) of protein and calories for dogfish fed Buccinum meals at different temperatures.

	Temperature (°C)											
Size group	8.2		8.5		10.2		14.0		15.0		15.4	
(g)	Prot	Cals	Prot	Cals	Prot	Cals	Prot	Cals	Prot	Cals	Prot	Cals
200-350	95.3	92.9	-	-	-	-	92.6	88.0	-	-	-	-
351-500	94.0	90.2	93.6	92.2	95.6 96.1	90.1[a] 90.5[b]	94.6	90.4	93.6	90.1	95.8	91.8
650-850	96.2	93.3	-	-	-	-	96.8	91.6	-	-	-	-
>900	96.2	93.8	-	-	-	-	94.0	88.7	-	-	-	-

a :- males ; b :- females

Note: two-way analysis of variance was not possible with this data because of the partial factorial design. Instead, the effects of temperature and fish size on assimilation were studied separately and in each analysis of variance the second, unconsidered variable was assumed to exert no influence on the assimilation efficiency. These assumptions enabled all values to be used in the analysis of variance.

Variable	Analysis of variance	
	Protein	Calories
Temperature	$F_{5,7}=1.16$ n.s	$F_{5,7}=1.81$ n.s.
Fish size	$F_{3,9}=1.62$ n.s.	$F_{3,9}=1.94$ n.s.

Table 3.2 Assimilation efficiency of protein and total calories for dogfish (351-500g) fed different natural foods.

	Temperature (°C)					
	8.5		15.0		15.4	
Food	Prot	Cals	Prot	Cals	Prot	Cals
Buccinum undatum	93.6	92.2	93.6	90.1	95.8	91,8
Glycymeris glycymeris	90.4	86.0	94.2	88.7	90.9	84.2
Sprattus sprattus[c]	-	-	88.3	89.7	-	-
Sprattus sprattus[d]	88.7	84.4	88.0	90.3	-	-
Palaemon elegans	84.4	80.7	-	-	-	-

c,d : distinguished because of differences in gross biochemistry.

c :- 7.396 kcal/g dry wt. ;protein 40.17% dry wt.

d :- 6,609 kcal/g dry wt. ;protein 45.70% dry wt.

DISCUSSION

Survey of the literature indicates that fish are very efficient in their ability to extract available protein nitrogen and total energy from their diets (Table 3.3). Assimilation efficiencies for protein usually range between 80 and 97% and for total calories between 70 and 98% depending upon the species and food in question, though values in excess of 85% are usual. The levels for assimilation efficiency in Scyliorhinus, 84.4 to 96.8% for protein nitrogen and 80.7 - 93.8% for energy, are in good agreement with those reported for teleosts.

Comparatively few workers have examined the influence that temperature has on assimilation. Brocksen and Bugge (1974) demonstrated that the ability of juvenile rainbow trout, Salmo gairdneri, to assimilate useable energy from their food increased with temperature. They postulated that increased enzymatic activity at higher temperatures enabled greater utilization of energy, necessary to meet increased metabolic requirements. A similar trend has been reported for brown trout, S. trutta, fed Gammarus at different temperatures (Elliott, 1976b). On the other hand the results obtained in this study for Scyliorhinus and those for Holacanthus (Menzel, 1958), Epinephelus (Menzel, 1960) and Stizostedion (Kelso, 1972) suggest that efficiency of assimilation is essentially unaffected by temperature changes.

Body size did not significantly effect the efficiency with which Scyliorhinus assimilated protein and energy from food. Comparable findings have been obtained for Lepomis megalotis, L. cyancellus, L. macrochirus (Gerking 1952, 1955), Holacanthus,

Table 3.3 Assimilation efficiency of protein and energy from various diets reported for teleosts.

Species	Fish Size	Temp. (°C)	Assimilation efficiency % Protein	Assimilation efficiency % Energy	Food	Method	Reference
Salmo gairdneri	15 g	5	-	71.8	*Tubifex*	Direct	Brocksen and Bugge (1974)
	"	17	-	77.9			
	"	20	-	84.8			
	29-68 g	16	87.6	-	Flatfish meal	Indirect	Nose and Mamiya (1963)
	18-78 g	16	65-78	-	Brownfish meal	"	Nose and Toyama (1966)
	10 and 100 g	11	91.0	-	Whitefish meal	"	Inaba *et al*. (1962)
	"	11	83.7	-	Soyabean meal	"	
	38-136 g	19	98.3	-	Casein-gelatin	"	Rychly and Spannhof (1979)
	250-500 g	15	86.6	-	Casein-gelatin	Direct	Smith (1971)
S. trutta	10-298 g	42	-	71-85	*Gammarus*	"	Elliott (1976b)
	12-300 g	20.4	-	79-89			
S. clarki		10	-	85.5	Midge larvae	"	Brocksen *et al*. (1968)
Crenimugil labrosus	5-10 g	18	-	73.9	Tess 'starter' pellets	Indirect	Flowerdew and Grove (1980)
Limanda limanda	37-120 g	12	81.5	73.6	Whitefish meal	"	Gwyther (1978)
Solea vulgaris	0.2-1.2 g	17	96.0	-	*Enchytraeus*	Direct	Birkett (1969)
	5-57 g	17	85.0	-	*Arenicola*	"	
Pleuronectes platessa	11-30 g	17	91.8	-	*Arenicola*	"	"
	20-150 g	10	93.0	84.0	Whitefish meal	Indirect	Jobling (1981)
	150-200 g	15	91.0	-	Cod	Direct	Cowey *et al*. (1974)
	"	15	86.0	-	Whitefish meal	"	

Species	Fish Size	Temp. (°C)	Assimilation efficiency %		Food	Method	Reference
			Protein	Energy			
Ictalurus punctatus	500 g	27	80–90	–	Compounded diet	Indirect	Page and Andrews (1973)
Lepomis macrochirus	19–31 g	24.6	97.2	–	Tenebrio	Direct	Gerking (1955)
L. megalotis	9–103 g	25.5	97.4	–	"	"	Gerking (1952)
L. cyanellus	7–49 g	25	95.7	–	"	"	"
Holacanthus bermudensis	49–302 g	19 + 28	85.0	77.7	Algae	"	Menzel (1958)
Epinephelus guttatus	135–710 g	19	96.4	96.1	Anchoa	"	Menzel (1960)
	"	23	90.6	91.8	Sardinella	"	
	"	28	97.3	96.9	Harengula	"	
Micropterus salmoides	7 g	25	97.3	–	Notropis	"	Beamish (1972)
	91 g	25	95.7	89.6	"	"	
Stizostedion vitreum	113–502 g	12–20	–	82.1	Gammarus	"	Kelso (1972)
	"	"	–	83.5	Orconectes	"	
	"	"	–	96.9	Perca	"	
	"	"	–	97.9	Notropis	"	
Ophiocephalus striatus	2–124 g	28	97.1	90.6	Metapenaeus	"	Pandian (1967)
Megalops cyprinoides	1–150 g	28	97.2	91.5	"	"	"
Carassius auratus	6–7 cm	12	–	92–94	Enchytraeus	"	Davies (1964)
	"	21.5	–	92–94	"		
Histrio histrio	1 g	21–24	–	72.3	Latreute and	"	Smith (1973)
	13 g	"	–	73.9	Leander	"	
	28 g	"	–	82.3		"	

Epinephelus (Menzel, 1958, 1960), Ophiocephalus, Megalops (Pandian, 1967), Micropterus (Beamish, 1972), Salmo trutta (Elliott, 1976b), S. gairdneri (Staples and Nomura, 1976) and Limanda (Gwyther, 1978). In contrast, Kelso (1972) for Stizostedion reported that the assimilation efficiency of energy declined with increasing size of fish, such that: -

$$E = 96.851 - 0.0045W.$$

where E is assimilation efficiency and W fish weight. This gives actual differences in assimilation between large fish (502 g) and small fish (113 g) of less than 2% (94.6 and 96.3%). It seems doubtful then that these results are in fact substantially different to those found for other species of fish. Birkett (1969) also reported a decline in assimilation efficiency in larger fish. He found that yearling sole, Solea, (0.2 - 1.2 g) assimilated nitrogen more efficiently than small sole (5 - 57 g), with values of 96% and 85% respectively. These findings were, however, confounded by the use of different diets, Enchytraeus for the yearling sole and Arenicola for the small sole, which may have accounted for part of the difference.

Although not considered in the present work, the relationship between assimilation and ration level has been studied in several teleost species. A number of workers have observed that fish held on high ration levels apparently excrete partially digested food (e.g. Kinne, 1960; Windell, 1966; Windell et al, 1969; etc.) and Elliott (1976b) found that assimilation efficiency decreased significantly with increasing ration size. Other published results for assimilation do not support these observations, for instance Gerking (1952, 1955), Beamish (1972), Kelso (1972), Staples and

Nomura (1976) and Gwyther (1978) were unable to detect any differences in assimilation at different ration levels tested, while Davies (1964) found that assimilation efficiency in Carassius increased to a plateau as food intake increased.

A number of factors have been demonstrated to influence rates of gastric emptying (Chapter 2) and therefore the total retention time of food in the gut. In the absence of some form of physiological compensation, any factor that causes accelerated elimination rates would also result in lowered assimilation efficiency. The general ability of many fish species to maintain the level of nutrient assimilation regardless of fish size, ration level and temperature reflects the existence and degree of effectiveness of such compensation. Although the actual mechanisms involved have not been described, compensation may be achieved in part through increased activity and secretion of digestive enzymes (Smit, 1967; Owen and Wiggs, 1971).

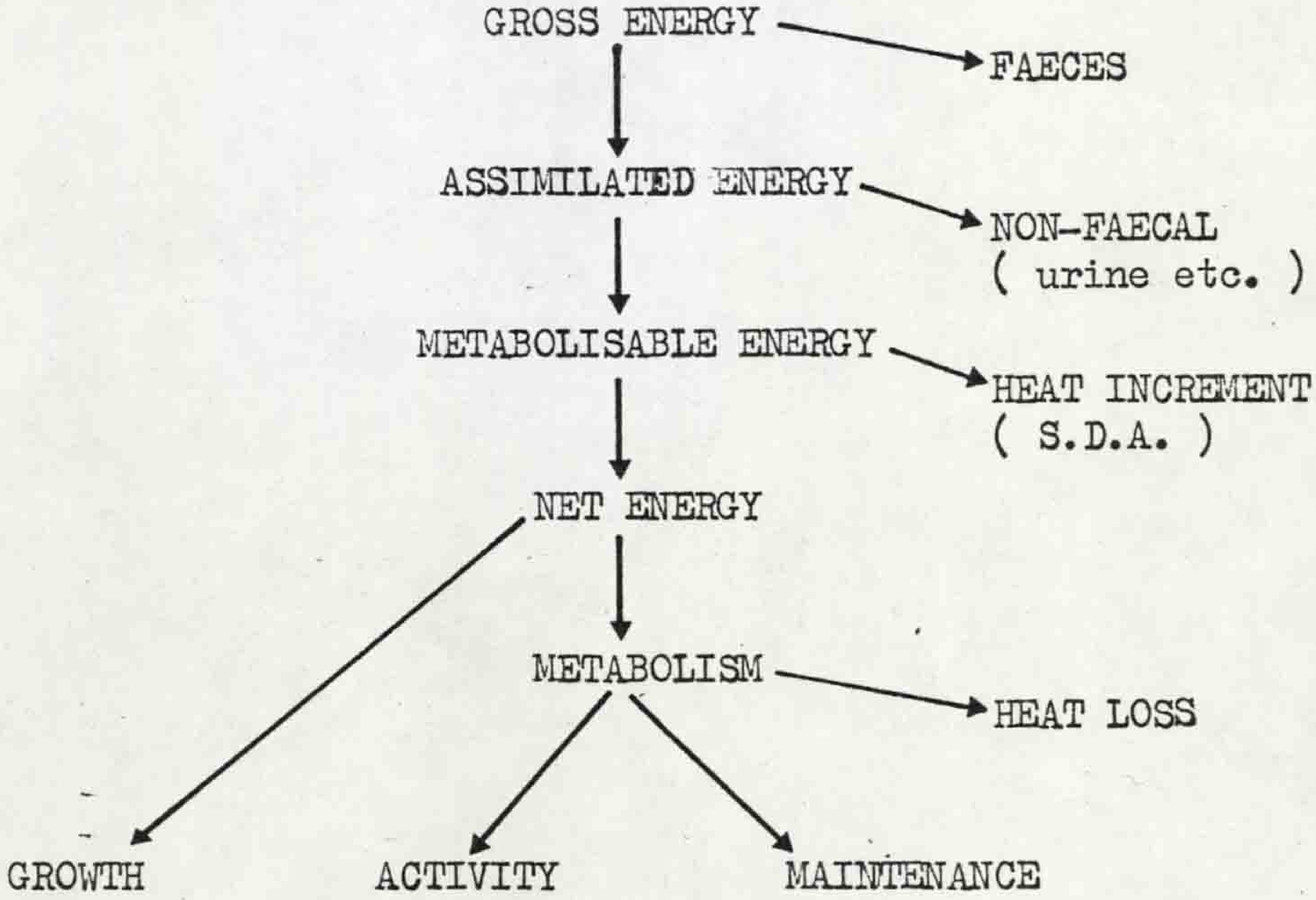
The fact that different foods are assimilated at different levels has been observed by several workers (Inaba et al, 1962; Nose and Mamiya, 1963; Nose and Toyama, 1966; Nose, 1967; Kelso, 1972; Cowey et al, 1974; Jobling, 1981a). Summarising available literature for teleosts fed on natural diets, Brett and Groves (1979) report that soft bodied invertebrates (polychaetes, squid - but not Tubifex) are assimilated most efficiently in terms of energy (95.5%). Fish meals had a mean value of 93.9 ± 3.4% (SD) while invertebrates with hard exoskeletons (crustaceans and insect larvae) were relatively poorly digested, 83.2 ± 5.9% (SD). Findings for Scyliorhinus in the present study conform very closely to these conclusions. Assimilation was most efficient for molluscan food, intermediate for fish and least efficient for crustacean prey.

With a particular emphasis on aquaculture, there has been considerable attention focused on how the nutrient composition of the diet influences assimilation. Direct correlations between protein assimilation and the level of protein in the diet have been reported by Nose and Mamiya (1963) and Nose (1967). Some workers have found that inclusion of carbohydrates into diets results in lowered protein assimilation (Kitamikado et al, 1964; Nose, 1967; Jobling, 1981a) while others have failed to detect any such reduction (Smith, 1971; Rychly and Spannhof, 1979). The presence and level of oil in food appears to have no appreciable effect on assimilation (Nose and Mamiya, 1963; Kitamikado et al, 1964; Nose and Toyama, 1966). In the current investigation, assimilation of two samples of sprat were compared. In spite of differences in gross biochemistry (energy, protein and presumably lipid content) there were no detectable differences in the assimilation of energy or protein.

Determination of egested nitrogen described in the present work did not take into account the possible influence of metabolically derived nitrogen in the faeces. Metabolic faecal nitrogen (MFN) can arise from the breakdown of digestive enzymes, alimentary tract tissue breakdown, elimination of gut parasites and bacterial residues (Gerking, 1952). Nose (1967) found that MFN levels for rainbow trout ranged between 50 - 150 mg N/100 g diet while Forster and Gabbott (1971) gave a value of 185 mg N/100 g diet for the prawn, Palaemon serratus. At relatively high protein levels, comparable to those fed to Scyliorhinus, resulting underestimation of 'true' protein assimilation arising from the failure to account for MFN is very small, generally less than 1%, and can therefore be effectively ignored (Nose, 1967; Forster and Gabbott, 1971; Rychly and Spannhof, 1979). At low protein levels, however, the importance of MFN is considerable. Nose (1967) concluded that decrease of 'apparent' protein digestibility at reduced protein levels (Nose and Mamiya, 1963; Nose, op cit.) was in fact attributable to disregard of MFN, and that the true assimilation efficiency remained constant regardless of the protein level in the diet.

The fate of assimilated food has been discussed by Winberg (1956), Davies (1964), Niimi and Beamish (1974), Brett and Groves (1979), etc., and can be summarised by Figure 3.1. A proportion of the assimilated energy is excreted as non-faecal energy (urine etc.) while the actual energy 'cost' of assimilation, is known as specific dynamic action (S.D.A.) (see Brody, 1945; Muir and Niimi, 1972; Beamish, 1974; Jobling and Davies, 1980). The remainder, net energy, is then split between metabolism (activity and maintenance) and growth (Chapter 4). Growth and metabolic requirements compete for the net energy such that increased metabolism will result in relative decrease in growth, particularly if fish are unable to compensate through increased food intake. It is apparent then that the efficiency with which fish assimilate their food has important bearing in the determination of the amount of energy potentially available for metabolism and growth.

Figure 3.1 Energy flow through the body of a fish (after Davies, 1964; Niimi and Beamish, 1974; Brett and Groves, 1979)



CHAPTER 4

Food Intake and Growth Studies

INTRODUCTION

Knowledge of growth relationships is of fundamental importance in the assessment of fish production in nature and in fish-culture. Growth, the net increase of tissue, represents the outcome of a series of behavioural and physiological processes; food intake, digestion, assimilation, metabolism and excretion; and has been defined in terms of length, weight, nitrogen (protein) or energy change depending on the objectives of different studies.

Feeding and growth are influenced by the interaction of a variety of biotic and abiotic factors, the most influential being ration, fish size and temperature (see Brett, 1979). Other factors that affect food consumption, growth and conversion efficiency in fish include diet composition (Brett, 1971b; Lee and Putnam, 1973; Cowey et al, 1974), feeding frequency (Shelbourne et al, 1973; Andrews and Page, 1975), stocking density (Brown, 1946a, b; Katre and Reddy, 1977), salinity (Kinne, 1960), oxygen concentration (Herrmann et al, 1962), photoperiod (Gross et al, 1965) and light intensity (Kwain, 1975). Any consideration of growth in fish must, therefore, be viewed in the proper context of the external factors imposed during the study.

By relating food consumption, growth rate, and metabolic rate the bioenergetics of the growth processes can be determined, providing a measure of food conversion efficiency and of energy loss via metabolism and excretion (Winberg, 1956; Paloheimo and Dickie, 1966; Warren and Davis, 1967; Brett and Groves, 1979). Only a few studies based on this energetic approach have been attempted (e.g. Edwards et al, 1969, 1972; Niimi and Beamish, 1974; Elliott, 1976c; Staples and Nomura, 1976; Flowerdew and Grove, 1980).

Most of the work on food intake, growth and conversion has been carried out on salmonids (Brown, 1946a, b, c; Brett et al, 1969; Elliott, 1975 c, d; Wurtsbaugh and Davis, 1977a, b) although several other teleost groups have been the subject of studies, e.g. pleuronectids (Edwards et al, 1969; Pandian, 1970; Tyler and Dunn, 1976), gadoids (Edwards et al, 1972; Jones and Hislop, 1972, 1978), centrarchids (Gerking, 1952, 1954, 1955; Niimi and Beamish, 1974), etc. There are only few and brief references to consumption and growth of elasmobranchs in captivity (Clark, 1963; Graeber, 1974; Jones and Geen, 1977) and no detailed accounts could be located. The general neglect of this group is largely due to lack of commercial importance, slow growth rates (Holden, 1974), and problems of laboratory maintenance. The aim of the present investigation was to examine the influence of ration level and temperature on growth and conversion in Scyliorhinus and from such data to estimate maintenance energy requirements. In addition changes in proximate body composition with ration level and food intake of different sized dogfish were studied.

MATERIALS AND METHODS

(i) Experimental Tank

Growth and feeding rate experiments were conducted in a 3.7 x 3.7 x 0.6 m deep tank partitioned by 'netlon' barriers into four equal divisions. Sea water was recirculated through a gravel filter at the rate of 0.42 l/sec and supplemented with additional inflow of between 0.08 - 0.37 l/sec. Temperature control was achieved by heating recirculated water in a header tank before return to the main tank. A 12L : 12D photoperiod was imposed in all experiments, with light intensity at the water surface of 0.1 - 0.4 W/m^2.

(ii) Experimental Procedure

Dogfish were trawled immediately prior to use in each experiment, usually from a single locality around the Isle of Man. Individuals falling within the desired size groups were placed into the experimental tank and allowed to acclimate to laboratory conditions for a minimum of four weeks. During this time they were maintained on a diet of chopped whiting and queenie adductor muscle (approximately 1% b.w. per day). When necessary the water temperature was raised at the rate of 1C degree per day.

Experiments were conducted at four temperatures - 16.6°C, 14.1°C, 10.9°C and 9.8°C - and were of either six or eight weeks duration. Following acclimation, dogfish were anaesthetised (MS 222, 1 : 18.000), blotted dry with absorbent paper and weighed to the nearest 0.1 g. An effort was made to distribute dogfish as evenly as possible, in terms of number and weight distribution, between the four experimental treatments. The standard size group used in all but one of the experiments was 200 - 550 g; at 10.9°C, the relationship between dogfish size and daily intake was investigated and for this pupose three additional size groups were used; 95 - 190 g, 690 - 870 g and 950 - 1040 g. In growth studies wide weight ranges, such as used in the present study, are not desirable. Owing to difficulties encountered in procuring large enough samples of dogfish within narrow weight limits it was necessary to adopt a compromise.

Experimental approach was basically that of Niimi and Beamish (1974), with some modifications. Each group of dogfish was fed every second day for eleven days (i.e. six feedings) at a ration level ranging from 'satiation' (i.e. food presented in excess of maximum voluntary intake at each feeding) to below maintenance. Food was withheld for four days then the dogfish weighed to determine 'initial weight'. During the course of the experiments dogfish were fed for eleven days at the ration level previously established, left without food for three days, reweighed and ration level reestablished. This procedure was repeated until the final weighing was due when food was withheld for four days, then 'final weight' determined. Deprivation periods of this length were necessary to reduce the amount of partially digested food remaining in the gut. Gastric emptying was rarely completed within these periods so it was assumed that the weight of residual food was more or less equal, on average, from one weighing to the next. It was on the basis of these assumptions that it was necessary to feed dogfish at their prescribed ration levels prior to the commencement of the experiments.

(iii) Diet and Feeding Regime

The diet used was frozen sprat (*Sprattus sprattus*) which was thawed, washed in freshwater and chopped into pieces of appropriate size. Sprat was chosen because of its acceptability to the dogfish, its availability, and the fact that clupeids feature in the diets of wild dogfish (Chapter 1).

Two batches of sprat, distinct in their gross biochemical composition (Table 4.1), were used in the experiments, batch 'A' at 16.6°C and 9.8°C, and batch 'B' at 14.1°C and 10.9°C. Variability within each batch was minimised as each was collected from a single shoal. Food was presented on alternate days at 09.30 h and any uneaten food removed at 16.30 h on the same day. In calculating the quantity of food eaten an appropriate correction was applied to account for weight increase arising from absorption of water.

TABLE 4.1 Gross biochemical composition of sprat used in growth studies.

Batch	Water Content (%)*	Energy Content (k cal/g dry wt)*	Protein Content (% dry wt)	Ash (%)
A	61.19 ± 0.80	7.143 ± 0.178	38.01	5.60
B	68.44 ± 1.31	6.854 ± 0.171	49.58	6.96

*Moisture and energy contents determined several times during the course of the growth experiments, these values represent overall means (± SD).

To ensure that individuals on restricted rations had equal opportunity to feed, food was first presented to the group on satiation rations. Food odours rapidly induced exploratory feeding behaviour in other groups such that by the time food was introduced most if not all individuals were already searching for food. At satiation and near satiation levels initial response to the presence of food was considerably weaker, individuals often took food only after it had been available for 5 - 6 hours.

(iv) Biochemical Analysis

At the commencement of the 16.6°C, 14.1°C and 9.8°C growth experiments, subsamples of between eight and twelve dogfish were killed for biochemical analysis, while on completion of experiments a further three or four individuals from each treatment were killed. The viscera and body musculature (i.e. minus head, spine and skin), were homogenised and water, ash, protein, crude lipid and energy content estimated. Samples of food were also analysed for water, protein and energy content.

Water content was estimated by drying samples at 65°C, and ash content by heating samples in a muffle furnace at 550°C for 8 h.

Protein nitrogen: Protein was estimated using the macro-Kjeldahl method (see Pearson, 1976). Samples were digested by wet combustion in sulphuric acid and the resulting acid solution was then made alkaline by addition of sodium hydroxide. Ammonium nitrogen was removed by distillation and collected in a measured amount of 0.2 N sulphuric acid. Unneutralised acid was assessed by titration against a solution of 0.1 N sodium hydroxide. Blank titrations indicated that reagents were nitrogen free. Since 1 ml of 0.1 N sulphuric acid corresponds to 1.4 mg nitrogen it was possible to estimate the nitrogen content of the sample. Protein content was calculated by multiplying the amount of nitrogen by a factor of 6.25 and was expressed as a percentage of the sample weight[1].

Crude lipids: Lipids were estimated using the Werner-Schmidt method (Pearson, 1976). Samples were digested in hydrochloric acid to break down proteins. The separated fats were extracted with a diethylether-petroleum ether mixture (equal proportions, V/V), and

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[1] The suitability of this factor in calculating protein content of elasmobranch tissue is open to criticism(Pearson, 1976). The amount of urea present in fresh elasmobranch muscle varies between 1.2 and 2.2% (cf teleosts 0.01%) and Pearson and Muslemuddin (1969) report that values for nitrogen are high due to the formation of ammonia derived from the decomposition of urea in addition to that which results from protein breakdown. Protein values will tend, therefore, to be overestimates. Techniques were not available to calculate non-protein nitrogen and protein values for dogfish are useful only for comparison between individuals and between treatments.

emulsions reduced by addition of ethanol. Ether extraction was repeated three times and the solvent removed by heating. Lipid residue was dried at 65°C, weighed and expressed as a percentage of the sample weight.

Caloric content: Caloric content of samples was determined by oxygen bomb calorimetry (Gallenkamp Ballistic Bomb Calorimeter CB.370). The bomb calorimeter was calibrated daily using benzoic acid (1 mg benzoic acid = 6.32 calories)[2]. Three to six replicates were analysed, giving a mean value with a standard error of less than 1%.

(v) Disease and Mortality

During experiments at 16.6°C, 14.1°C and 9.8°C, a number of dogfish developed a vibrio-type infection, manifest as small ulcerated spots on the body surface (see Appendix VI). There was, however, no evidence to indicate that feeding or growth were adversely affected and in many instances dogfish showed signs of complete recovery during the course of experiments. Only two dogfish became badly ulcerated and were consequently discarded from the experiments.

There were no mortalities during the course of the experiments though three dogfish were removed because of deteriorated condition. Data on these dogfish were included in all calculations up until the time that they were removed.

[2] For conversion into joules; 1 cal = 4.19 joules

RESULTS

(i) Food Intake

Food intake, expressed as a percentage of mean body weight, for dogfish fed to satiation showed considerable variation, as illustrated in Figure 4.1. It is evident that a stable feeding level was not attained at any of the experimental temperatures. On closer inspection, some similarity in the pattern of consumption over each two week period and between temperatures could be discerned. In the majority of cases feeding was most intense immediately after weighing, in response to the period of food deprivation. Reduced feeding followed, with the quantity of food eaten then gradually increasing to a second peak. At 16.6°C and 14.1°C such bimodal pattern of feeding intensity prevailed over most of the experimental period. Generally the second peak occurred at the fourth feeding at 16.6°C and at the fifth feeding at 14.1°C. The pattern at 9.8°C was considerably more variable. Similar results were attained at 10.9°C but are not included in Figure 4.1.

(ii) Growth

Results for growth and food consumption are summarised in Table 4.2, and are presented in more detail in Appendix VII. At 16.6°C dogfish were tagged with Petersen-type tags attached to the first dorsal fin, thereby enabling the growth of individuals to be calculated. Such analysis demonstrated that the responses of the individuals varied considerably as indicated by large standard deviations (Table 4.2). At all ration levels some individuals

Figure 4.1 Food intake at each feeding session for Scyliorhinus canicula maintained on 'satiation' rations at 3 different temperatures.

W indicates dogfish weighed.

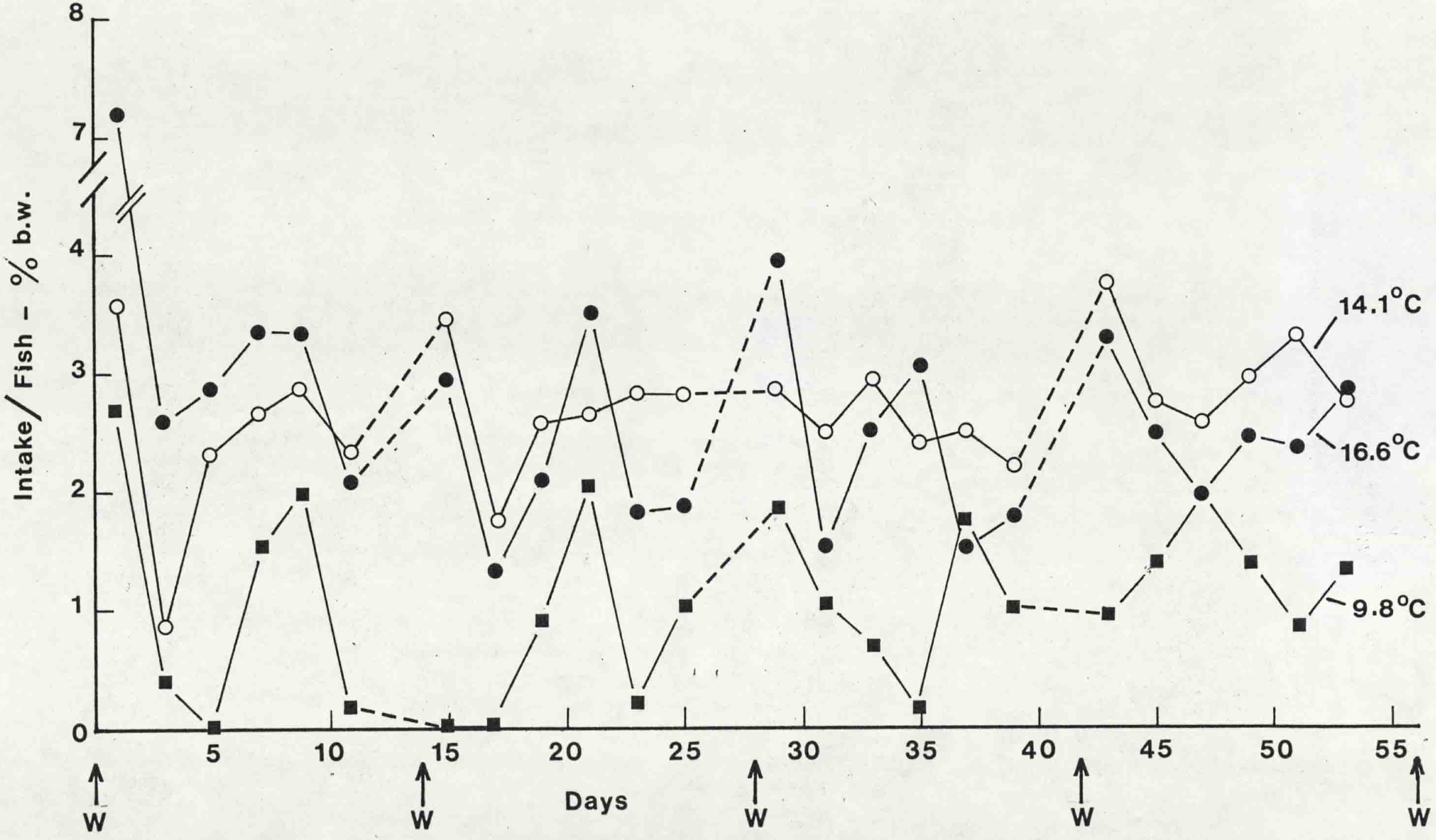

Intake/Fish - % b.w.
0
1
2
3
4
7
8
Days
5
10
15
20
25
30
35
40
45
50
55
W
W
W
W
W
14.1°C
16.6°C
9.8°C

TABLE 4.2 Growth, specific growth rate, conversion efficiency and food consumption at four different temperatures for <u>Scyliorhinus canicula</u> fed on a diet of chopped sprat.

Temp. (°C)	Duration (weeks)	Number of dogfish		Mean weight (g) ± SD		Total food intake/ dogfish (g)	Daily intake/dogfish			Mean growth/ dogfish ± SD[+] (g)	Gross conv. efficiency (%)	Specific growth rate ± SD G%/day
		Initial	Final	Initial	Final		FR* %	Dry wt. (g)	Energy (kcal)			
16.6	8	11	11	452.82 ± 81.66	507.10 ± 103.4	309.57	1.15	2.139	15.821	54.28 ± 35.36	17.5	0.19 ± 1.13
(16.0–17.0)	8	11	11	444.01 ± 54.56	506.56 ± 62.13	261.42	0.98	1.806	12.897	62.55 ± 21.36	23.9	0.24 ± 0.08
	8	12	12	412.06 ± 68.28	433.07 ± 56.72	166.31	0.70	1.149	8.206	21.01 ± 30.83	12.6	0.10 ± 0.16
	8	12	12	426.25 ± 67.37	414.21 ± 71.90	94.05	0.40	0.650	4.640	-12.04 ± 16.75	-	-0.06 ± 0.07
14.1	8	10	10	344.59 ± 68.17	375.62 ± 83.52	227.66	1.13	1.299	8.825	31.03 ± 24.77	13.6	0.14 ± 0.15
(13.0–15.5)	8	10	9	347.96 ± 67.70	347.79 ± 81.75	135.84	0.70	0.774	5.261	5.85	4.3	0.02 ± 0.14
	8	9	9	344.20 ± 85.55	321.42 ± 93.27	75.60	0.40	0.431	2.926	-22.98 ± 14.64	-	-0.14 ± 0.10
	8	11	11	319.57 ± 70.33	283.62 ± 56.86	34.57	0.20	0.197	1.338	-35.95 ± 18.37	-	-0.20 ± 0.09
10.9	6	9	9	422.50 ± 49.15	405.59 ± 37.99	94.72	0.53	0.697	4.808	-16.91 ± 25.99	-	-0.09 ± 0.15
(10.0–11.6)												
9.8	8	9	8	337.69 ± 81.37	345.21 ± 77.68	85.81	0.44	0.597	4.264	-8.06	-	-0.09 ± 0.18
(8.5–10.5)	8	8	7	348.79 ± 69.50	340.74 ± 80.22	71.38	0.37	0.496	3.543	-11.84	-	-0.07 ± 0.12
	8	8	7	372.15 ± 78.10	329.53 ± 60.92	70.45	0.34	0.488	3.491	-40.78	-	-0.19 ± 0.12
	8	9	8	311.44 ± 74.53	296.22 ± 62.40	34.33	0.20	0.238	1.703	-28.80	-	-0.21 ± 0.17

* Feeding rate: $FR\% = \frac{\bar{2}\ I}{W_T + W_t} \times 100$

where W_T and W_t are mean body weights (g) at the start and finish of each period, and I is mean daily intake per dogfish per day (g).

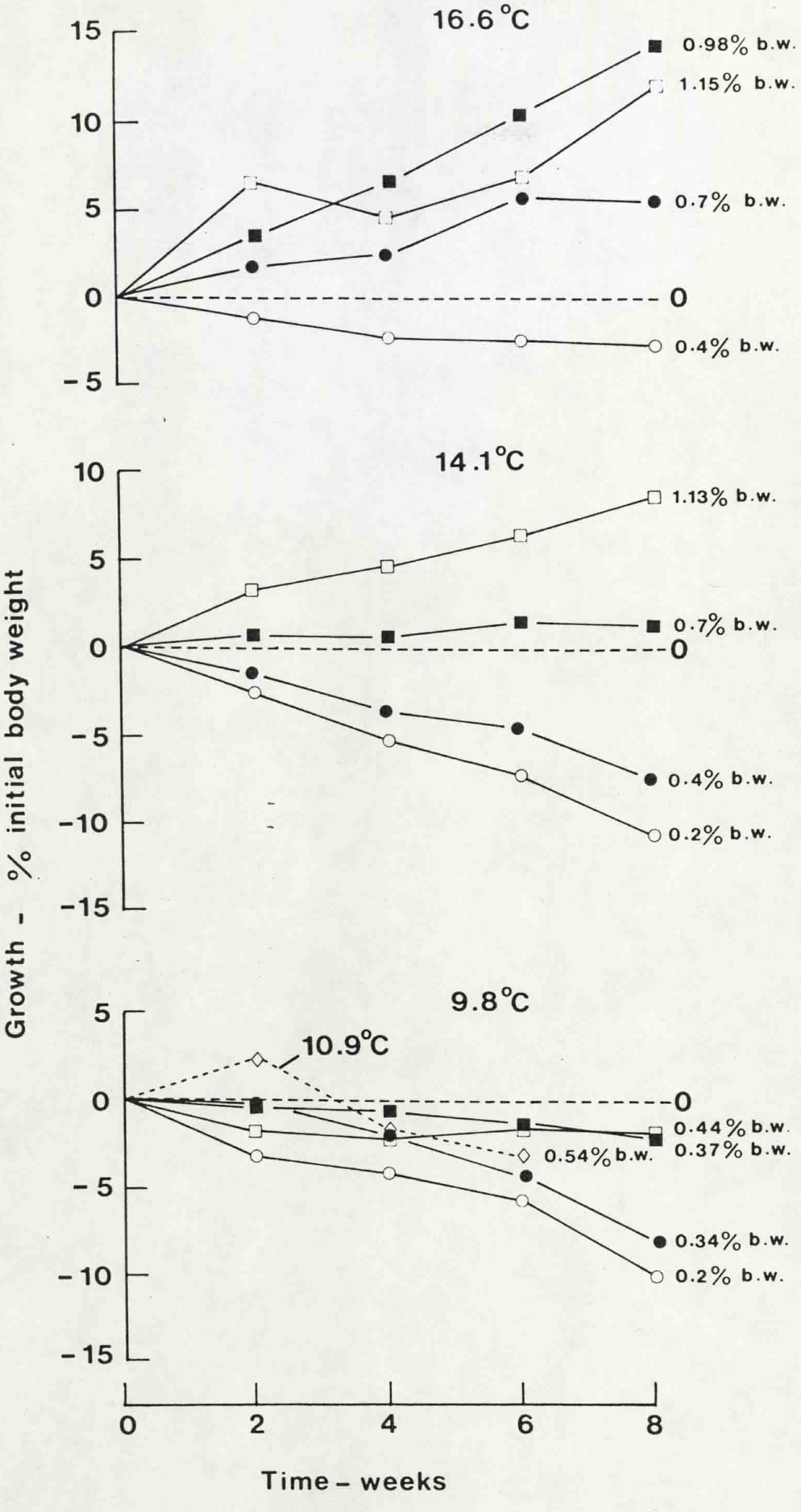
[+] Only means are presented where individuals were removed during the course of experiments.

gained weight while others lost weight. For rations below maintenance this clearly indicated that despite precautions to ensure that all dogfish had equal opportunity to feed, some individuals consumed more food than others. A further complicating factor, mentioned in Materials and Methods, was the influence of undigested food on dogfish live weight. For instance on satiation (unrestricted) rations there was an apparent loss of weight between the second and fourth week of the experiment. Rather than a net loss of body substance this was almost certainly related to the reduction in feeding rate, from 1.53%to 0.96%, and consequently to quantity of food remaining in the gut.

For other experiments it was assumed that each dogfish remained in the same rank-order of descending weight of the group throughout the experiment (Brown, 1946a, b, c; de Silva and Balbontin, 1974). Treatment of data in this manner was further facilitated by identification of individuals based on their sex and morphological pecularities, e.g. coloration, healed wounds, etc.

The magnitude of weight changes in all experiments were highly dependent on the feeding level (Figure 4.2, Appendix VII). Increase in mean body weight occurred on ration levels in excess of 0.7% b.w. per day at 16.6°C and 14.1°C while at 10.9°C and 9.8°C there was no sustained growth; even on satiation rations the dogfish apparently did not ingest enough food to meet their body maintenance requirements (Figure 4.2). Rates of weight loss increased with decreasing ration. During both of these experiments appetite was poor when compared with higher temperatures and even on restricted ration level food was left uneaten. For example at 9.8°C groups with mean feeding rates of 0.37% and 0.34% b.w., which were lower than maximum (0.44% b.w.)

Figure 4.2 Change in mean body weight, expressed as percentage of initial b.w., for *Scyliorhinus canicula* fed at different ration levels and different temperatures on a diet of sprat. Feeding rates, % b.w./day are indicated.


16.6 °C
15
10
5
0
-5
0.98% b.w.
1.15% b.w.
0.7% b.w.
0
0.4% b.w.
14.1 °C
10
5
0
-5
-10
-15
1.13% b.w.
0.7% b.w.
0
0.4% b.w.
0.2% b.w.
9.8 °C
5
0
-5
-10
-15
10.9 °C
0
0.44% b.w.
0.54% b.w.
0.37% b.w.
0.34% b.w.
0.2% b.w.
Growth - % initial body weight
0
2
4
6
8
Time - weeks

were presented with food at rates equivalent to 0.4% and 0.7% b.w. per day, respectively.

In growth studies on fish, instantaneous growth rates may be calculated on the assumption of exponential growth, from the equation:

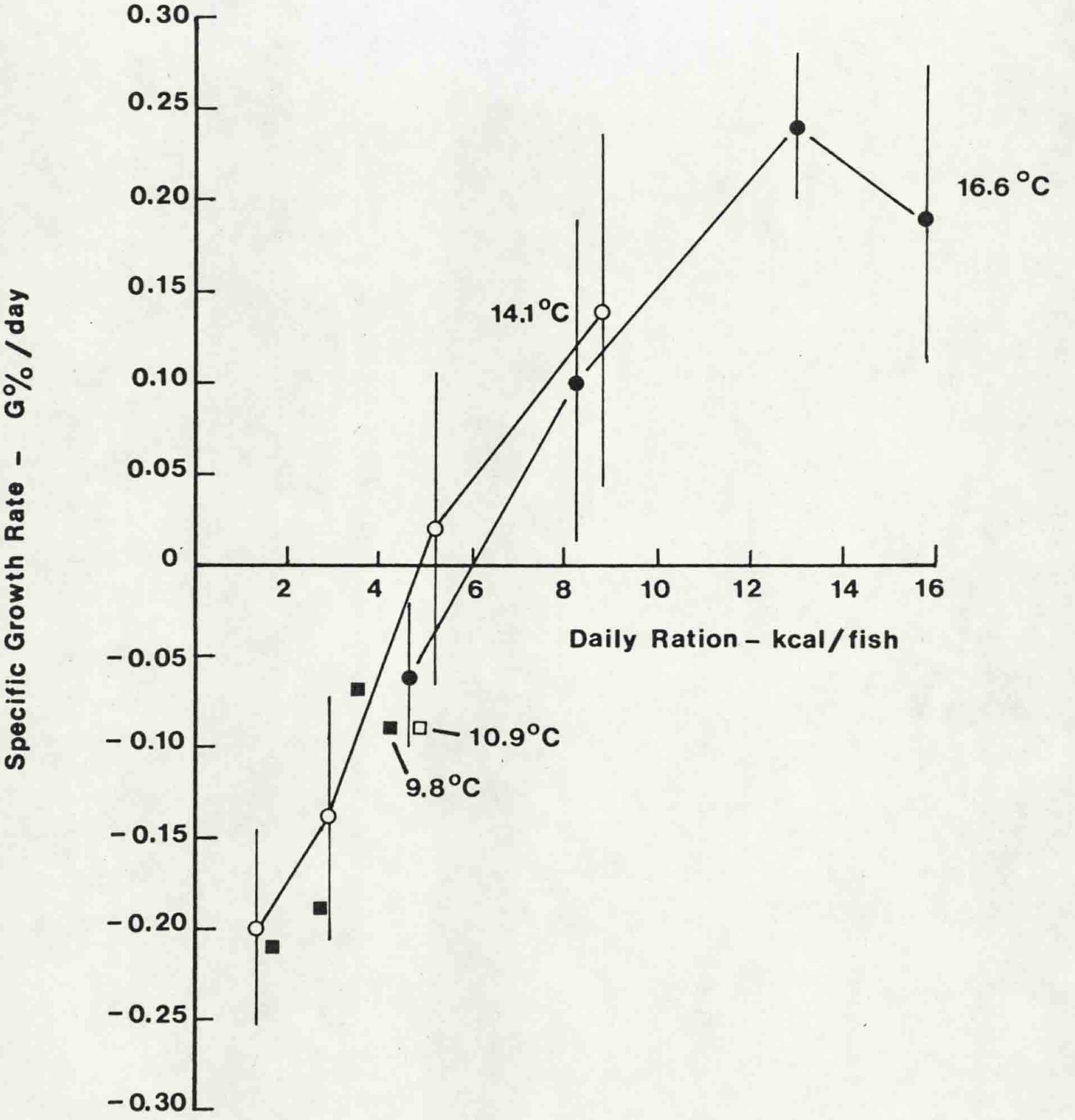
$$G\% = \frac{\ln (W_T) - \ln (W_t)}{T - t} \times 100$$

where G is instantaneous or specific growth rate, W_T and W_t are fish weights (g) at time T and time t (days).

Specific growth rates, expressed as G%/day, at each temperature and feeding level are tabulated in Table 4.2. A growth-ration curve (GR) (Brett, 1979) can be constructed for each temperature by plotting mean specific growth rates (G%/day) against ration (expressed as k cal/fish/day) (Figure 4.3). Direct comparisons between different experiments are not strictly possible because of differences in dogfish size and biochemical composition of the diet (protein : energy ratio). At all three temperatures growth rate (G%/day) tended to increase with ration though at 16.6°C on ration levels in excess of 12.90 k cal/fish/day the growth rate apparently declined. Results at 9.8°C were inconsistent with those for higher temperatures in that no net increase in body weight occurred. In fact, the efficiency of food utilization and willingness to feed were affected at temperatures below 10.9°C. During the 9.8°C experiment four dogfish had to be removed on account of poor condition and disease, which suggested that physiologically some of the individuals used in this experiment were unduly stressed. Interestingly, no sustained growth occurred at 10.9°C even though all dogfish remained

Figure 4.3 Relationship between mean specific growth rate and ration level for Scyliorhinus canicula fed sprat at different temperatures.

(Vertical lines represent 2 standard errors)


0.30
0.25
0.20
0.15
0.10
0.05
0
−0.05
−0.10
−0.15
−0.20
−0.25
−0.30
Specific Growth Rate – G% / day
2
4
6
8
10
12
14
16
Daily Ration – kcal/fish
16.6 °C
14.1°C
10.9°C
9.8°C

disease free and healthy throughout the duration of the experiment. Adequate explanation for these results was not apparent.

By interpolation of GR curves at 16.6°C and 14.1°C it was possible to estimate maintenance rations, defined as amount of food necessary to maintain body weight (i.e. G%/day = 0). At 16.6°C dogfish of overall mean weight of 450 g required approximately 6.0 k cal/day and at 14.1°C maintenance requirement for 335 g dogfish was approximately 4.5 k cal/day.

Gross conversion efficiency, defined as the percentage of ingested food material converted into fish flesh, are given in Table 4.2. Maximum conversion efficiency of 23.9% at 16.6°C was considerably higher than at 14.1°C, though conversion efficiency at comparable levels of energy intake (8 -9 k cal/fish/day) were very similar for the two temperatures, 12.6% and 13.6% respectively.

(iii) Changes in Body Composition

Results of biochemical analyses of dogfish at the commencement and termination of 16.6°C, 14.1°C and 9.8°C growth experiments are presented in Appendix VIII. Changes in body composition at different feeding levels, compared with the composition of the initial population are shown in Figure 4.4. (Note data for 9.8°C have not been considered because of apparently anomalous growth responses).

Biochemical analyses indicate that there was considerable variation in moisture, protein, lipid and energy content between individuals. In spite of this variation and the fact that small sample sizes were considered several trends could be discerned. Total lipids increased while water content decreased with increasing

Figure 4.4a Body moisture, protein and lipid content at the completion of growth experiment conducted at 16.6°C for groups of Scyliorhinus canicula maintained at different ration levels.

Mean values at the beginning of the experiments are indicated (broken line). Open circles represent mean values and vertical bars indicate standard deviation of initial mean.

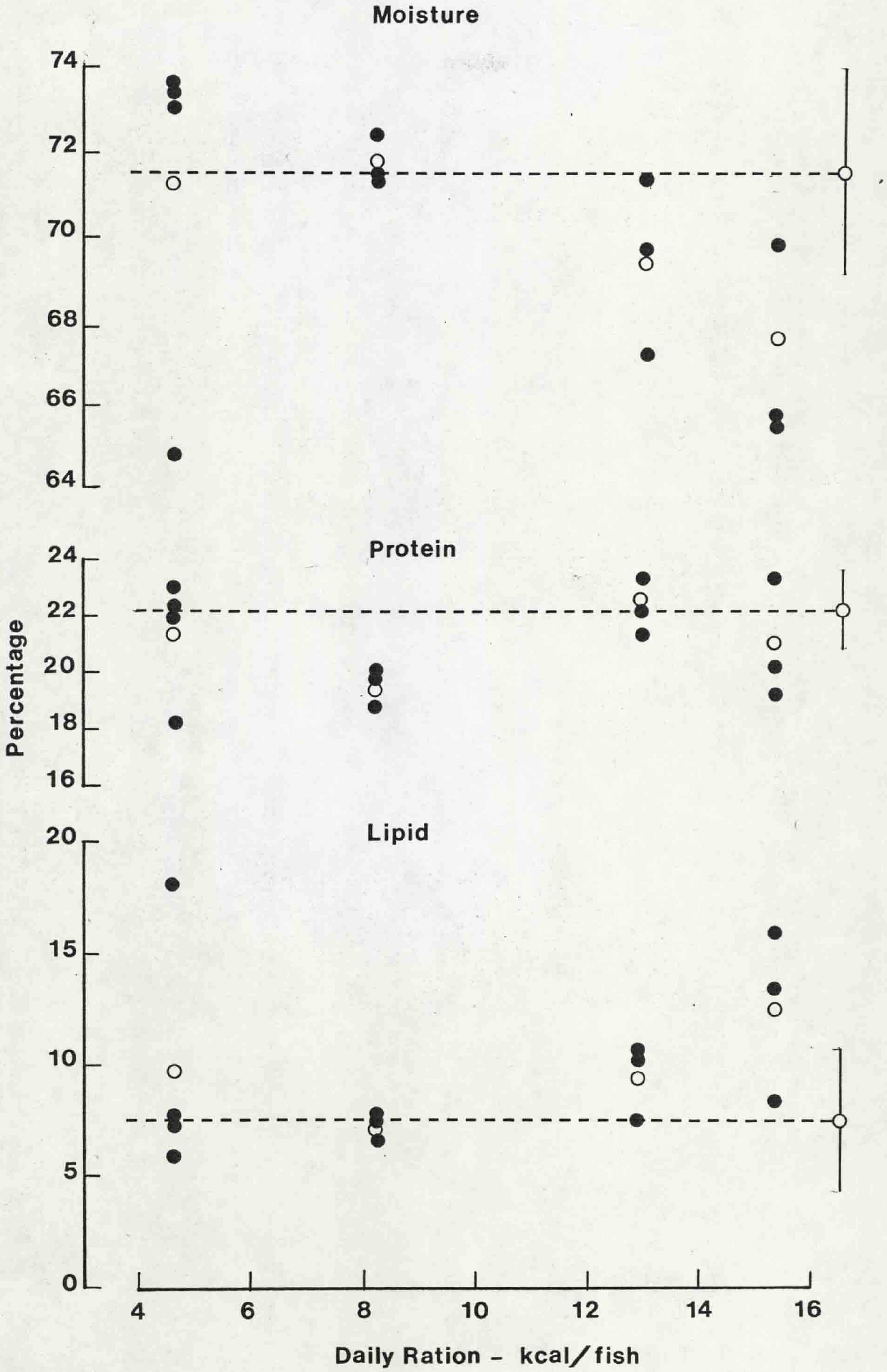
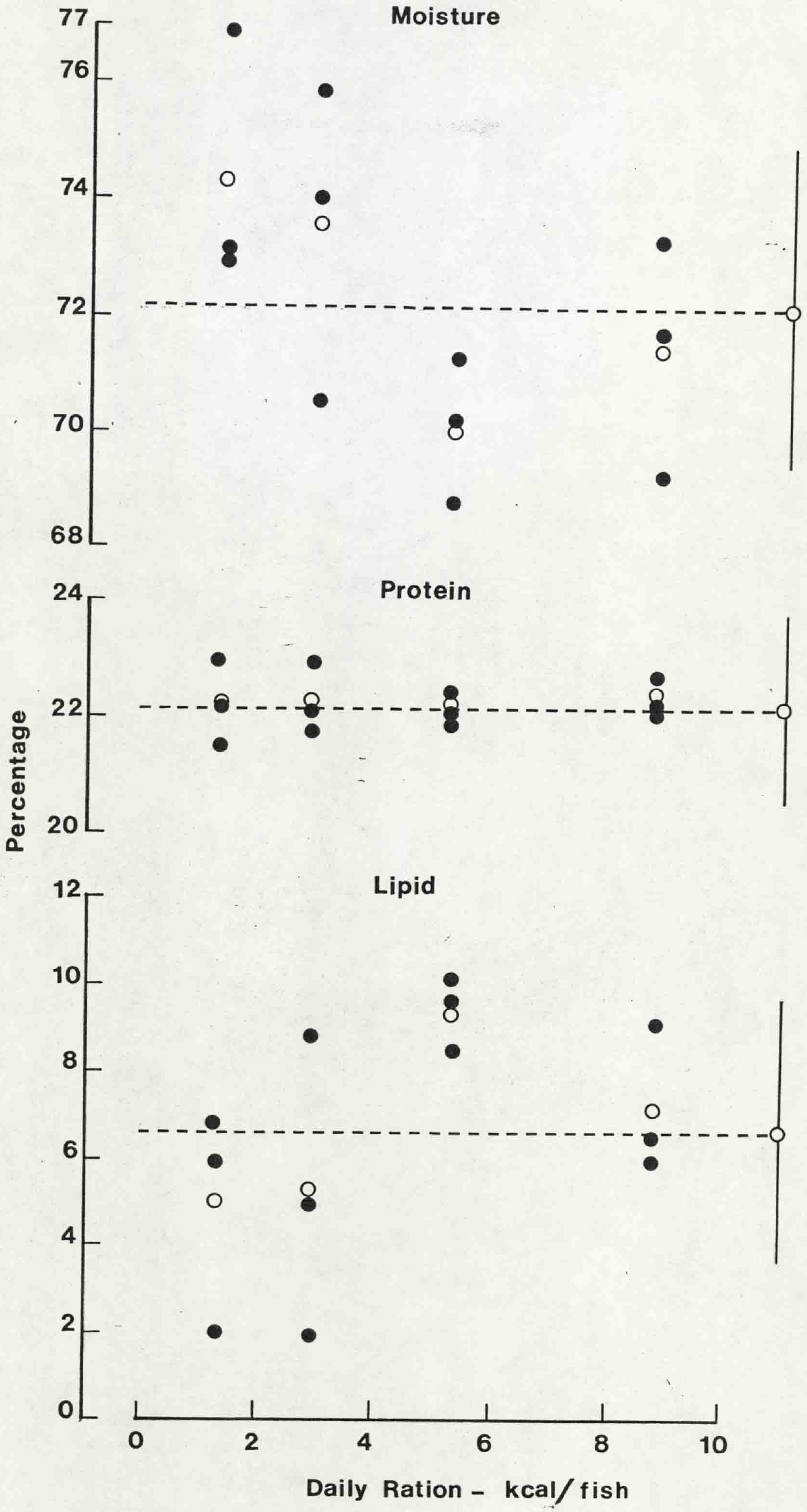

Moisture
74
72
70
68
66
64
Protein
24
22
20
18
16
Lipid
20
15
10
5
0
Percentage
4
6
8
10
12
14
16
Daily Ration - kcal/fish

Figure 4.4b Body moisture, protein and lipid content at the completion of growth experiment conducted at 14.1°C for groups of Scyliorhinus canicula maintained at different ration levels.

Mean values at the beginning of the experiments are indicated (broken line). Open circles represent mean values and vertical bars indicate standard deviation of initial mean.


Moisture
77
76
74
72
70
68
Protein
24
22
20
Percentage
Lipid
12
10
8
6
4
2
0
0
2
4
6
8
10
Daily Ration - kcal/fish

ration size. In general mean lipid content exceeded that of the initial population for groups fed ration levels above maintenance and were equivalent or slightly below initial means for reduced rations. Energy content followed a similar trend as body lipids. The pattern was reversed for body water in relation to ration and initial means. There was little evidence to indicate that the relative protein content varied consistently with ration and mean values at the completion of experiments were comparable with initial values.

(iv) Influence of Fish Size on Food Intake

Mean daily food intake over three biweekly periods for four sizes of dogfish supplied with excess food are given in Table 4.3. As noted in growth experiments there was considerable variation in the mean amount of food eaten per fish per feeding, with variation also reflected in mean daily intake for each biweekly period. This experiment was further complicated by loss in body weight that occurred in some of the samples, clearly suggesting that dogfish were feeding below their maximum level. Despite these problems daily intake, in terms of weight and energy increased with dogfish size. The quantitative relationship between body weight and food intake can be described by the allometric formula:

$I = a'W^{b'}$, where I = food intake, W = body weight, a' and b' are constants.

For energy intake (k cals) the equation becomes:

$$I = 0.125\ W^{0.623 \pm 0.213} \quad (r = 0.900)$$

On the other hand feeding rate, expressed as percentage of body weight, declined from 1.12 - 0.77% for small dogfish, to 0.56 - 0.36% for the largest size group.

Table 4.3 Food intake over a biweekly period, expressed as food consumed per dogfish per day, by different sized dogfish.

Mean body		Mean food intake per fish per day			
weight(g)*	n	Wet wt.(g)	FR (%)	Dry wt.(g)	Energy(kcals)
145.6	6	1.348	0.93	0.442	3.080
158.2	4	‡1.232	0.77	0.370	2.576
160.2	4	1.786	1.12	0.537	3.739
408.7	9	‡2.213	0.54	0.664	4.623
421.2	9	‡1.745	0.41	0.525	3.653
426.3	9	2.808	0.65	0.922	6.419
737.7	4	‡4.480	0.60	1.346	9.369
748.3	4	‡3.267	0.43	0.982	6.839
759.5	4	‡2.675	0.35	0.878	6.112
1013.8	5	5.560	0.56	1.825	12.704
1025.7	5	‡3.777	0.36	1.135	7.899
1033.9	5	5.562	0.54	1.672	11.644

* Defined as $\frac{W_T - W_t}{2}$ where W_T and W_t are the mean body weights at the commencement and finish of each period.

‡ Weight loss occurred over the biweekly period.

DISCUSSION

It was evident that food intake per individual on satiation rations showed considerable variability at each feeding session. Similar findings have been reported for other elasmobranchs (Clark, 1963; Graeber, 1974; Jones and Geen, 1977) as well as teleosts (Dawes, 1930; Brown, 1946b; Pandian, 1970; Brett, 1971a; de Silva and Balbontin, 1974). Work on teleosts has demonstrated that the quantity of undigested food in the gut exerts a considerable influence on the amount of food consumed at subsequent feedings (Brett, 1971a; Elliott, 1975b; Grove *et al*, 1978). Gastric evacuation estimates for *Scyliorhinus* (Chapter 2) indicate that the interval between each feeding, 48 h, would be insufficient to allow for complete gastric emptying at any of the experimental temperatures. It is conceivable therefore, that variations observed in the present study were due to changes in appetite, itself at least partly determined by the mass of food previously ingested and the rate of gastric evacuation. Heavy feeding (over compensation) followed deprivation for weighing, which in turn was followed by a period of reduced feeding (under compensation) and then heavy feeding. There was some evidence to suggest that the intervals between feeding peaks were shorter at higher temperatures, which conforms to the relationship between gastric evacuation rate and temperature (Chapter 2). Graeber (1974) reported similar cyclic patterns of feeding in another elasmobranch, *Negaprion*, but was unable to provide an adequate explanation for his results. Without knowledge of gastric evacuation rates Graeber (op cit.) discounted the possible effect that undigested food in the gut might have on appetite.

In the present study, growth responses of individuals exhibited a high degree of variation at all ration levels and temperatures. Similar findings have been noted in other growth studies (Dawes, 1930; Brown, 1946a, b, c; Edwards et al, 1972; de Silva and Balbontin, 1974; Jones and Hislop, 1978). According to Brown (1957) 'size heirarchy' can influence feeding such that certain individuals tend to grow faster than others (growth depensation); such a heirarchy based on size was not apparent for Scyliorhinus. Differences in feeding success and quantity of food remaining in the gut as well as genetic factors and physiological state no doubt accounted for much of the variance.

The relationship between specific growth rate and ration exhibited some differences in form at different temperatures (Figure 4.3). The large standard errors would justify the fitting of a straight line or sigmoid curve to data at 14.1°C while at 16.6°C specific growth rate could reach a plateau rather than a down-turn at a ration of 15.82 k cal/fish. The difference in form may be due to the fact that the maximum ration (in terms of energy) was considerably lower at 14.1°C than at 16.6°C. Lower intake would be partly due to the influence of temperature on consumption (see Brett et al, 1969; Niimi and Beamish, 1974; Elliott, 1975a), difference in dogfish size and to the lower energy content of the diet used at 14.1°C. Details of published GR curves indicate variability in form between species as well as for the same species under different experimental conditions. A straight line has been used to depict the relation for Pseudopleuronectes (Tyler and Dunn, 1976), Salmo gairdneri (Staples and Nomura, 1976), various gadoids (Jones and

Hislop, 1972, 1978); while a curve decelerating towards a plateau at high rations (i.e. maximum growth rates) is characteristic for other species; *Oncorhynchus* (Brett *et al*, 1969), *Gadus* (Edwards *et al*, 1972), *Salmo gairdneri* (Huisman, 1976; Wurtsbaugh and Davies, 1977a) and *S. trutta* (Elliott, 1975d). An exception to the general case has been given by Huisman (1976) for *Cyprinus*, who reported a GR relationship similar to that found for *Scyliorhinus* at 16.6°C with an apparent decline in growth rate at high ration levels.

Gross conversion efficiences were found to be dependent on ration level. Comparison between experiments was complicated because different batches of sprat and different sizes of dogfish were used in each experiment. Previous work on teleosts has shown that conversion efficiency is affected by the protein : energy ratio in the diet (Lee and Putnam, 1973) as well as by both temperature and fish size (Brett *et al*, 1969; Elliott, 1975d; Wurtsbaugh and Davies, 1977a, b, etc.). At 16.6°C conversion efficiency increased with ration size to a maximum level of 24% at a daily ration equivalent to 0.98% b.w. then decreased at higher levels of intake, while at 14.1°C maximum conversion of 14% was achieved on satiation rations. Relationships similar to that determined at 16.6°C with an optimum ration level for conversion have been reported in various other studies (Brett *et al*, 1969; Elliott, 1975d; Huisman, 1976), though in some cases conversion efficiences increased towards an asymptote at maximum rations (Staples and Nomura, 1976).

Conversion efficiency in *Scyliorhinus* of 13 - 24% for rations well in excess of maintenance compare with a figure of 12% for *Squalus* during the first year of life (Jones and Geen, 1977).

Brett and Groves (1979) noted that gross efficiences mainly range between 10 and 25% for juvenile fish up to maturity but values in excess of 30% have been reported for young fish (Pandian, 1967; Brett, 1971b; Flowerdew and Grove, 1980). The results of different studies are not, however, strictly comparable because of differences in diet, ration level, fish size and experimental conditions; factors which are known to affect conversion efficiencies (Brett and Groves, 1979). Comparison is further complicated by different expressions of growth used throughout the literature, i.e. increase in weight, protein or energy content.

Difficulties involved in determination of maintenance ration levels have been reviewed by Brown (1957) and Paloheimo and Dickie (1966). Many workers have estimated maintenance energy requirements by interpolation or extrapolation of GR curves (Brett *et al*, 1969; Elliott, 1975d; Huisman, 1976; Staples and Nomura, 1976; Tyler and Dunn, 1976; Wurtsbaugh and Davies, 1977 a, b; Jones and Hislop, 1972, 1978; Flowerdew and Grove, 1980).

Data from experiments on growth and feeding can yield estimates of metabolism which may usefully be related to estimates derived from studies of oxygen consumption rates. Studies of metabolic rates in elasmobranchs are relatively few (Brett and Blackburn, 1978) though several workers have determined respiration rates for *Scyliorhinus* at rest (Hughes and Umezawa, 1968; Butler and Taylor, 1971, 1975). Metabolism can be related to fish weight (W) by the allometric relationship:

$$Q = aW^b$$

where Q is metabolic rate (or rate of oxygen consumption) and a and b are constants characteristic for a given species.

A general figure for b of 0.8 seems applicable for many teleost species (Winberg, 1956; Paloheimo and Dickie, 1966) and preliminary results for Scyllium cassicula (or canicula?) (Buytendijk, 1910; cited by Winberg, 1956) gave a similar exponent. For the purposes of this comparison b was taken to be 0.8. By expressing resting respiratory rates (standard metabolism) determined by Butler and Taylor (1975) (Table 4.4) for a common dogfish weight, the effect of temperature on respiration gave a Q_{10} at 2.1. On the basis of this information it is possible to compare standard metabolism with maintenance energy requirements. Oxygen consumption for 450 g dogfish at 16.6°C and 335 g dogfish at 14.1°C would be 28.15 mg O_2/h and 18.47 mg O_2/ h respectively. Since the oxycalorific equivalent for respired oxygen in fish is considered to be 3.25 cal/mg O_2 (Elliott and Davidson, 1975) standard metabolic expenditure would be 91.50 cal/h or 2.01 k cal/day at 16.6°C and 60.03 cal/h or 1.44 k cal/day at 14.1°C. Dogfish fed a diet of sprat have been shown to defaecate about 10% of the ingested energy (Chapter 3). Fish on average excrete a further 7% of the dietary energy as nonfaecal matter, principally nitrogenous

TABLE 4.4 Resting or standard respiration rates for Scyliorhinus canicula : based on data of Butler and Taylor (1975)

Mean Wt (g)	n	Temperature (°C)	Oxygen consumption* mg O_2/kg/h
857 ± 46	7	7	29.7 ± 8.7
788 ± 27	8	12	39.9 ± 10.2
712 ± 37	7	17	64.3 ± 12.7

*Original data expressed as ml O_2 kg^{-1} min^{-1}

metabolites excreted via the kidney and gills (Brett and Groves, 1979). Because the physiologically useful portion of the ration is approximately 83% of the total ingested energy, maintenance energy requirements were 4.95 k cal/day at 16.6°C and 3.73 k cal/day at 14.1°C. Maintenance metabolism is thus between 2.46 and 2.59 times the standard metabolism. These figures compare favourably with Winberg's (1956) prediction of twice standard metabolism, Kerr's (1971) prediction of 1.5 - 2.5 times standard respiration rates and Flowerdew and Grove's (1980) calculated values of 2.0 - 2.4 times standard rates. A recent review of available literature by Brett and Groves (1979) gave the mean ratio of metabolic rate of a feeding fish to standard rate as 2.68 ± 1.18 (SD) (range, 1.0 - 5.8), though this comparison was complicated by the fact that metabolic expenditure is highly ration dependent. By extrapolation the predicted maintenance ration at 9.8°C of 335 g dogfish would be 3.19 **k** cal/day. Since daily consumption exceeded this value and no growth occurred the possibility that the dogfish were under physiological stress must be considered.

The weight exponent relating food intake (energy) with body weight was 0.62 ± 0.21. The predictive value of such a relationship must be treated with reservation as weight loss occurred in seven of the twelve biweekly periods used in the calculations. In a normal growing situation the exponent would be expected to be higher than 0.62.

Biochemical composition and energy content of fish do not remain static but are in a dynamic state, affected by interactions between the quality and quantity of ration, temperature and body size (Brett et al, 1969; Niimi and Beamish, 1974; Elliott, 1976a;

Staples and Nomura, 1976). Studies on teleosts have indicated that body lipid and moisture content are responsive to changes in ration level, the percentage fat (and energy) increases, while water content decreases, with increasing ration (Gerking, 1955; Brett _et al_, 1969; Niimi and Beamish 1974; Elliott, 1976a; Staples and Nomura, 1976; Flowerdew and Grove, 1980). Preliminary results for _Scyliorhinus_ in the present study indicate similar trends. Increased fat content was primarily attributable to enlargement of the liver. Body protein has been found to increase with ration level (Brett _et al_, 1969; Elliott, 1976a) though the current findings support those of Gerking (1955), Niimi and Beamish (1974) and Staples and Nomura (1976) which demonstrated that protein content remains relatively stable. Gadoids are apparently exceptional as proportions of protein and lipid in the body remain relatively constant over a wide range of rations (Edwards _et al_, 1972; Jones and Hislop, 1972).

In the light of the above it would have been preferable to depict growth in terms other than change in live weight. Dry weight determinations would remove error introduced by the influence of feeding level on body moisture content but fail to register changes in body biochemistry and energy content. As recognised by several workers (Gerking, 1954, 1962; Pandian, 1967; Birkett, 1969) the essential aspect of growth is protein elaboration, the basis of cellular increase. The efficiency of nitrogen retention has thus been used as the fundamental unit for growth efficiency calculations. This approach does have limitations since protein retention is influenced by the sparing action of carbohydrates and lipids on the utilization of protein as an energy source (Phillips, 1969). Other authors have described growth in terms of energy accumulation (Pandian, 1967; Huisman, 1976; Flowerdew and Grove, 1980) though a better understanding of growth processes may be provided by consideration of several growth parameters (Menzel, 1960; Staples and Nomura, 1976).

The extent of variation of individual responses in terms of growth, body biochemistry and energy content within each treatment suggest that with existing facilities increased precision, even using other growth parameters, would be difficult to attain. By the nature of the results obtained in the present study conclusions are preliminary, but it is thought that they do shed some light in understanding food intake, energy requirements, growth and conversion in Scyliorhinus and provide a basis for comparison with work on teleosts.

CHAPTER 5

Estimation of Food Consumption Rates in the Wild

INTRODUCTION

Knowledge of the rate of food consumption in fish is of fundamental importance in the assessment of production and impact on food resources. For these reasons considerable attention has been paid to the estimation of food intake of fishes in the wild. Basically there are two main approaches to the problem, by direct or by indirect methods, and these have been reviewed recently by Elliott and Persson (1978) and Mann (1978).

Direct methods utilize analyses of stomach contents and rates of gastric evacuation. In addition to yielding estimates of daily feeding rates they can be used in the study of feeding chronology. A variety of models have been proposed, one of the earliest being that of Bajkov (1935). Daily food consumption D is given by:

$$D = \frac{24\overline{A}}{n} \qquad (1)$$

where $\overline{A}$ is the average amount of food in the stomachs at the time of sampling and n the number of hours necessary for complete gastric emptying. The value of n is determined by keeping a sample of fish in a food-free container and killing subsamples at regular intervals until the stomachs are emptied. This model assumes that fish feed continuously, that the rate of gastric evacuation is constant and that the evacuation rate is independent of the quantity and type of food in the stomach and unaffected by capture and confinement. Even though these assumptions are basically unrealistic a number of workers have adopted Bajkov's formula either in its original or modified form (Darnell and Meierotto, 1962; Backiel, 1971; Noble, 1972; Doble and Eggers, 1978).

Seaburg and Moyle (1964) calculated daily intake as the product of the mean stomach volume, the percentage of food determined experimentally to be evacuated from the stomach in a 4-h period, and the number of 4-h periods in a day. Refinements of this basic approach have been proposed by several workers (e.g. Healey, 1971; Staples, 1975; Thorpe, 1977), the primary difference being that stomach content weights are sampled at regular times over a 24-h period. Thorpe (1977) suggested that the amount of food consumed over each sampling interval of t (h) could be given by the general expression:

$$C_t = S_t - S_o + A \qquad (2)$$

where S_t is the amount of food in the stomach at time t, S_o the amount of food in the stomach at time 0 and A the amount of food evacuated from the stomach during that interval. Daily food consumption is calculated by summing values of C_t for the various sampling periods. Accurate estimation of A is complicated because some of the food ingested between sampling periods may be evacuated. Thorpe (1977) attempted to account for this by assuming that the amount eliminated from the stomach during the interval between samples (A) was equivalent to the amount evacuated from a stomach containing the mean stomach content, $\frac{1}{2}(S_o + S_t)$, at the start of the interval. At the end of time t the stomach would contain the amount Sr, and thus the amount of food evacuated would be:

$$A = \tfrac{1}{2}(S_t + S_o) - Sr \qquad (3)$$

Jobling (1981b) has recognised that such an approach is an oversimplification and would underestimate A and thus daily food consumption. Jobling (op cit.) argues that since the instantaneous rate of evacuation is dependent on the amount of food in the stomach, the actual amount of food evacuated from the stomach (g/h) would increase as the stomach fills such that the degree of stomach filling (S) would approach S_t as an asymptotic curve. A better estimate of A would, therefore, be provided by assuming that the amount of food evacuated from the stomach during the sampling interval was equivalent to the amount eliminated from a stomach of fullness equivalent to one at time $t/_2$ on this stomach filling curve. Stomach fullness at time $t/_2$ is given by:

$$S_{t/2} = S_t \ (1 - e^{-Dt/2}) \qquad (4)$$

where D is dependent upon the rates of feeding and evacuation during each sampling period. The amount evacuated can be calculated as:

$$A = S_{t/2} - Sr \qquad (5)$$

Derivation of these models has been given because of their relevance in estimating food consumption in the present study.

Another important contribution has been made by Elliott and Persson (1978) who proposed two methods for estimating daily consumption rates, both assuming that gastric evacuation is exponential. The first is based on a constant feeding rate and the second assumes that the feeding rate decreases with time such that the amount of food consumed approaches an asymptote. While the models of Thorpe (1977), Elliott and Persson (1978) and Jobling (1981b) respresent considerable improvement over Bajkov's method they all assume that evacuation rates determined in the laboratory or with confined fish are comparable to those in the field.

Various other simpler models have been used to estimate daily food consumption. For example, Jones and Geen (1977) and Diana (1979) calculated food intake for predators which feed infrequently, Squalus and Esox respectively, by dividing meal size by feeding frequency. Daan (1973) proposed that intake in Gadus could be calculated as twice mean stomach content weight divided by the digestion time in days. Keast and Welsh (1968) summed differences between mean stomach content weights for peaks and values for succeeding troughs. For details of other models see Swenson and Smith (1973); Moriarty and Moriarty (1973); Kuipers (1975); Jones (1978); Nakashima and Leggett (1978); etc.

Indirect methods for the estimation of food consumption require information on metabolism and growth of fish, coupled with a knowledge of how these relationships are influenced by temperature, ration level and fish size. Food consumption may be estimated from the energetic requirements (Winberg, 1956; Mann, 1965; Backiel, 1971; Healey, 1972; Solomon and Brafield, 1972; Elliott, 1976c; Jones, 1978) or nitrogen requirements of fish (Gerking, 1954, 1962; Birkett, 1969). Alternatively, the relationship between growth and food intake (i.e. GR curve) measured in the laboratory can be used to estimate food consumption from growth rates in the wild (Brocksen et al, 1968; Carline and Hall, 1973; Wurtsbaugh and Davis, 1977a). Indirect methods generally include several assumptions regarding applicability of laboratory work to the field situation.

Radioisotopic methods have also been used to estimate consumption rates in the wild (Kevern, 1966; Kolehmainen, 1974) though this approach is of restricted usage. Examples of consumption estimates for several fish species determined by direct, indirect and radioisotopic methods are shown in Table 5.1

Previous interest in food consumption rates of elasmobranchs has been extremely limited. Information on the quantity of food eaten in the wild could be located for only two elasmobranchs, Squalus acanthias (Holden, 1966; Jones and Geen, 1977) and Raja clavata (de Souza, 1978). There is an obvious need for further research to be directed into this area of elasmobranch biology. As an attempt to rectify some of this neglect, daily rates of food consumption for a population of Scyliorhinus canicula from east of the Isle of Man were estimated. A direct method was adopted utilizing information derived from stomach content analysis (Chapter 1) and gastric evacuation rates (Chapter 2).

MATERIALS AND METHODS

Most previous methods for estimating food consumption have been based on the assumption that the pattern of gastric evacuation is either linear or exponential. Since evidence suggests that the square root model of gastric emptying (see Chapter 2) appears to be appropriate for many fish species (Jobling, 1981b) including Scyliorhinus, then mathematical description of gastric evacuation based on this model should be incorporated into methods for the estimation of daily rates of food consumption. From Chapter 2 the amount of food remaining in the stomach Sr, after time t will be:

$$Sr = (S_o^{0.5} - Rt)^2 \qquad (6)$$

where S_o is the initial meal size and R the instantaneous rate of gastric evacuation. Substitution into Thorpe's (1977) model

TABLE 5.1 Estimated food intake in fishes.

Species	Method	Estimated intake	Conditions (size, temp., season etc.)	Reference
Perca flavescens	Direct	0.02g/g fish/day	90-130mm, 18-22°C	Keast & Welsh (1968)
Ambloplites rupestris	"	0.04 "	100-170mm, "	"
Lepomis gibbosus	"	0.026 "	100-140mm, "	"
L. macrochirus	"	0.025 "	90-140mm, "	"
Fundulus diaphanus	"	0.014 "	65-85 mm, "	"
Stizostedion vitreum	"	1% b.w./day	June	Swenson & Smith (1973)
	"	2% b.w./day	July	
	"	3% b.w./day	Aug/Sept	
Perca fluviatilis	"	6.5% b.w./day	June, adults	Thorpe (1977)
	"	3.2% b.w./day	Sept, "	
Oncorhynchus nerca	"	4.41-1.35% b.w./day	Aug; juveniles	Doble & Eggers (1978)
	"	3.68-0.62% b.w./day	Oct; "	
	"	0.29-0.01 "	Dec; "	
	"	1.53-0.09 "	Feb; "	
Gobius minutus	"	2.2; 14.1% b.w./day	0-group, Dec; Aug	Healey (1971)
	"	1.4; 2.8 "	I-group, " ; "	
	"	1.9; 2.7 "	II-group, " ; "	
Esox lucius	"	14.4 kcal/kg fish/day	Summer	Diana (1979)
		0.7 "	Winter	
Rutilus rutilus	Indirect	161.4 kcal/m^2/yr		Mann (1965)
Alburnus alburnus	"	430.9 "		"
Leusiscus leusiscus	"	31.5 "		"
Perca fluviatilis	"	31.2 "		"
Gobio gobio	"	49.2		"
Aspius aspius	"	5582 kcal/recruit/yr		Backiel (1971)
Esox lucius	"	4038-6152 "		"
Stizostedion lucioperca	"	4032-6538 "		"
Silurus glanis	"	34274 "		"
Leusiscus cephalus	"	2094 "		"
Perca fluviatilis	"	2527-2995 "		"
Lepomis macrochirus	"	137.9 kcal (May-Sept)	20g fish, 20°C	Gerking (1962)
	"	371.8 "	61g fish, 20°C	
Cyprinus carpio	Radioisotopic	3.9% b.w./day	yearling; 16°C	Kevern (1966)
Lepomis macrochirus	"	0.8% b.w./day	Feb	Kolehmainen (1974)
	"	3.2% b.w./day	June	

(equations (2) and (3)) gives:

$$C_t = S_t - S_o + \frac{(S_t + S_o)}{2} - \left[\left(\frac{S_t + S_o}{2}\right)^{0.5} - Rt\right]^2 \qquad (7)$$

Similarly Jobling's (1981b) modification (equations (2) and (5)) can be written as:

$$C_t = S_t - S_o + S_{t/_2} - (S_{t/_2}{}^{0.5} - Rt)^2 \qquad (8)$$

Unfortunately full derivation of the factor D in equation (4) is not clear, and in any case the interrelationship between feeding rate and evacuation rate was not investigated in the present study. Thus even though Jobling (1981b) demonstrated that his modification was more accurate in predicting food consumption than Thorpe's (1977) model, the latter requires less information and consequently was adopted to estimate daily food consumption for Scyliorhinus.

As reported in Chapter 1 no diel periodicity of feeding was observed in Scyliorhinus; over a 24-h period the weight of stomach contents oscillated about a mean value. If the population rather than individual is considered, then on average the rate of feeding is equal to the rate of gastric emptying with the stomach content weight remaining more or less constant throughout a 24-h period. Thus $S_t \approx S_o$ which simplifies equation (7) to:

$$C_t = S - (S^{0.5} - Rt)^2 \qquad (9)$$

where S is the mean dry weight of stomach contents. Equation (9) estimates food intake for a sampling period t (h). Elliott and Persson (1978) and Jobling (1981b) stress that to obtain reliable estimates of food consumption the length of each interval must be short in relation to gastric evacuation time and subsequent return of appetite. Daily food consumption was therefore taken as the amount of food evacuated in a 4-h period multiplied by six.

In Chapter 2 (page 50) it was shown that gastric evacuation rate can be described as a function of fish size W (g), temperature T (°C), and the amount of food in the stomach S (mg), such that:

$$R = 0.0087\ e^{0.0910T}\ W^{0.2552}\ S^{0.1392} \tag{10}$$

In order to solve equations (9) and (10) data given in Chapter 1 were used. Four size classes of dogfish were considered in stomach content analysis, namely $\leqslant 39$ cm (mean 36.6 cm); 40 - 52 cm (mean 47.1 cm); 53 - 62 cm (mean 57.0 cm); and $\geqslant 63$ cm (mean 65.6 cm)[1]. Applying length-weight relationship for Scyliorhinus (Figure 1.2) these give mean live weights of 153.4 g, 332.8 g, 597.7g and 920.0 g respectively. Mean seasonal temperatures were determined from bottom water temperatures sampled throughout the study (Figure 1.8) and were 13.6°C for summer, 10.9°C for autumn, 7.9°C for winter and 10.2°C for spring. Values for S were based on mean dry weight of the solid component of the stomach contents (expressed in milligrams) given in Table 1.4. For conversion of dry weight of food consumed to wet weight, values were multiplied by the wet weight : dry weight ratio determined from stomach content analysis for each sample (Table 1.4). A constant factor was not adopted because the composition of the diet changed with time of year and dogfish size (Chapter 1).

Caloric content of selected prey species was determined by oxygen bomb calorimetry. Several individuals of each prey species, within the size range normally observed in stomach contents, were dried and ground into a fine powder for analysis.

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[1] Mean lengths calculated from length-frequencies over the entire study period (Figure 1.3).

RESULTS

Daily rates of food consumption on a seasonal basis and for each size group of dogfish are presented in Table 5.2 and energy values for representative prey species are given in Table 5.3. Based on the proportions by weight that (a) reptant crustacea (excluding pagurids), (b) natant crustacea and (c) pagurids and other crustacea contributed to the total crustacean element in the diet of each dogfish size class (Table 1.3) multiplied respectively by the energy content for Macropipus, Palaemon and Eupagurus, energy equivalents for crustacean food consumed by each size class were calculated. Mean values for molluscan prey were similarly determined. Caloric contents of pectinids and other mollusca, excluding Buccinum (and Neptunea) and Glycymeris, were assumed to be similar to that for Chlamys. Clupea was assumed to be identical to Sprattus and remaining taxa similar to Nereis in terms of energy content.

In calculating the dry weight of the solid component of stomach contents (Chapter 1), the major prey groups; crustacea, mollusca, herring, and all other prey; were dried separately. The relative composition of the daily food intake was taken to be in direct proportion to the composition of the stomach contents. It was possible thus to express daily consumption in k cals per day (Table 5.2).

The semi-fluid component of the stomach contents contained, in addition to gastric juices, food particles exceeding 280µ. Since gastric evacuation rates were based on residuum particle size greater than 280µ, values of S based on the solid component

Table 5.2 Estimation of daily food intake for different sized *Scyliorhinus canicula* on a seasonal basis.*

		1979			1980		
Size class		Summer	Autumn	Winter	Spring	Summer	Autumn
≤39cm	Dry wt.(g)	0.465	0.156	0.180	0.173	0.270	0.117
(153.4g)	Wet wt.(g)	2.170	0.795	0.799	0.973	1.285	0.579
	% b.w.	1.41	0.52	0.52	0.63	0.84	0.38
	kcals	1.437	0.497	0.605	0.558	0.922	0.441
40-52cm	Dry wt.(g)	0.637	0.340	0.318	0.417	0.617	0.368
(332.8g)	Wet wt.(g)	3.071	1.669	1.572	2.063	2.811	1.798
	% b.w.	0.92	0.50	0.47	0.62	0.84	0.54
	kcals	2.679	1.049	1.177	1.449	2.479	1.342
53-62cm	Dry wt.(g)	1.057	0.598	0.671	0.675	1.068	0.739
(597.7g)	Wet wt.(g)	4.245	2.799	2.882	3.105	4.517	3.173
	% b.w.	0.71	0.47	0.48	0.52	0.76	0.53
	kcals	5.054	2.036	2.448	2.460	4.524	2.723
≥63cm	Dry wt.(g)	1.651	0.900	0.804	0.934	1.298	0.716
(920.0g)	Wet wt.(g)	6.155	3.604	3.408	3.904	5.251	2.912
	% b.w.	0.67	0.39	0.37	0.42	0.57	0.32
	kcals	8.120	3.671	3.244	3.510	5.378	2.669

(*Calculation excludes semifluid component of stomach contents)

Table 5.3 Energy content of representative prey species.

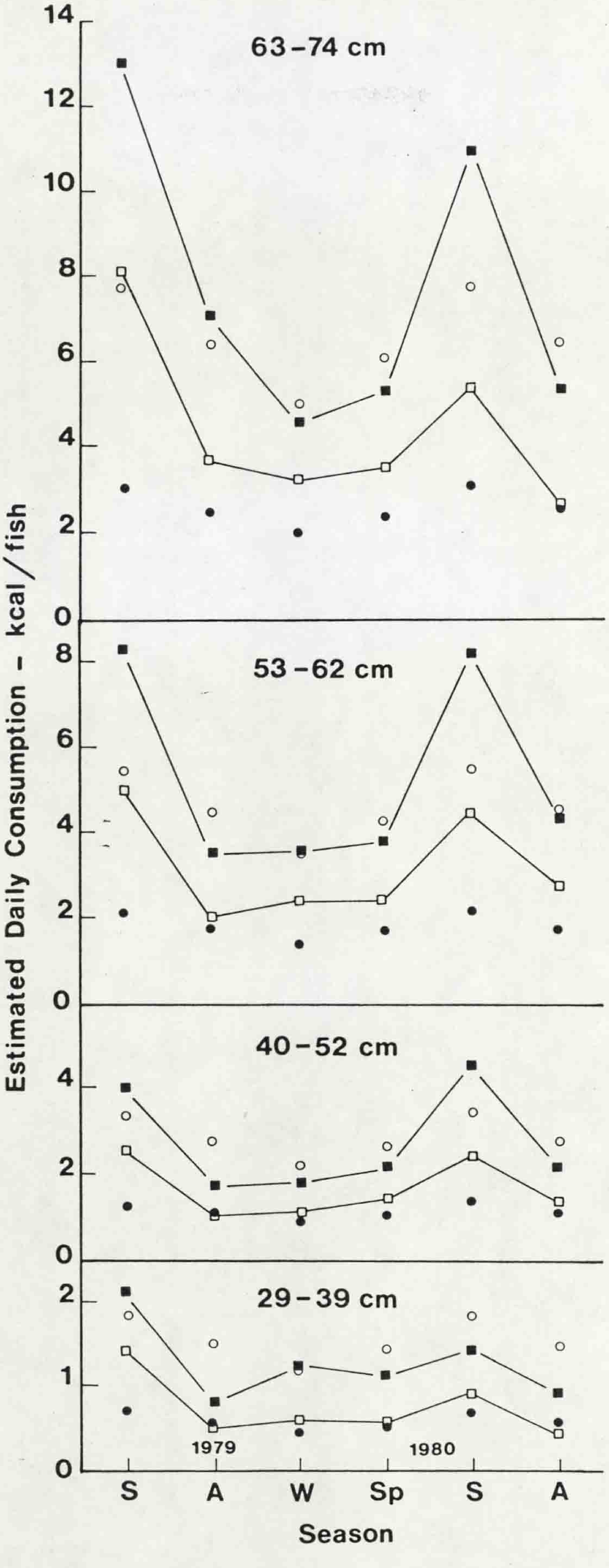
	kcal/g dry wt. (±SD)
CRUSTACEA	
Eupagurus bernhardus	2.905 ± 0.094
Macropipus depurator	2.448 ± 0.022
Palaemon elegans	4.332 ± 0.139
MOLLUSCA	
Buccinum undatum (head and foot)	4.907 ± 0.135
Glycymeris glycymeris	4.969 ± 0.043
Chlamys opercularis (adductor)	4.700 ± 0.071
TELEOSTEI	
Sprattus sprattus	7.143 ± 0.178
POLYCHAETA	
Nereis virens	3.582 ± 0.132

Table 5.4 Estimation of daily food intake for different sized <u>Scyliorhinus</u> <u>canicula</u> on a seasonal basis. Calculations include semifluid component of stomach contents.

		1979			1980		
Size class		Summer	Autumn	Winter	Spring	Summer	Autumn
≤39cm	Dry wt.(g)	0.680	0.256	0.376	0.356	0.425	0.236
(153.4g)	Wet wt.(g)	3.173	1.305	1.669	2.000	2.020	1.168
	% b.w.	2.07	0.85	1.09	1.31	1.32	0.76
	kcals	2.101	0.816	1.264	1.148	1.451	0.889
40-52cm	Dry wt.(g)	0.967	0.570	0.492	0.612	1.153	0.618
(332.8g)	Wet wt.(g)	4.662	2.798	2.432	3.028	5.253	3.019
	% b.w.	1.40	0.84	0.73	0.91	1.58	0.91
	kcals	4.067	1.758	1.821	2.126	4.632	2.254
53-62cm	Dry wt.(g)	1.741	1.035	0.983	1.040	1.942	1.183
(597.7g)	Wet wt.(g)	6.992	4.844	4.222	4.784	8.213	5.079
	% b.w.	1.17	0.81	0.71	0.80	1.37	0.85
	kcals	8.324	3.524	3.586	3.790	8.226	4.359
≥63cm	Dry wt.(g)	2.658	1.744	1.141	1.409	2.881	1.409
(920.0g)	Wet wt.(g)	9.909	6.984	4.836	5.889	11.655	5.730
	% b.w.	1.08	0.76	0.53	0.64	1.27	0.62
	kcals	13.073	7.113	4.604	5.295	11.937	5.252

Figure 5.1 Seasonal variation in estimated daily consumption for different size classes of *Scyliorhinus canicula*. Estimates derived from solid component of stomach contents , □—□, and total stomach contents ; ■—■, and compared with standard metabolism (●) and predicted maintenance metabolism (○).

(See text for explanation)



Estimated Daily Consumption - kcal / fish
63-74 cm
53-62 cm
40-52 cm
29-39 cm
0
2
4
6
8
10
12
14
1
1979
1980
S
A
W
Sp
S
A
Season

would be underestimates and daily food consumption estimates minimal. Daily intake was recalculated for total dry weight of stomach contents and converted to wet weight and energy with the same conversion factors used in the preceding analysis (Table 5.4). Daily energy intake given by each analysis is compared in Figure 5.1.

DISCUSSION

Calculation of food intake based on the solid component of stomach contents will produce minimum estimates while that based on total contents will be too high because gastric juices as well as comminuted food are included (Tables 5.2, 5.4). The best available estimate therefore lies between these two values; for the purposes of further discussion the best estimate was assumed to be the mean of the two values. Daily consumption rates for Scyliorhinus fell between 0.5 and 1.4% b.w./day depending on season and size of dogfish (Table 5.5). These figures compare favourably with a general value for sharks feeding in captivity of 0.4 - 2% b.w./day proposed by Clark (1963) and comparison with findings reported for other elasmobranchs (Table 5.5) gave rates of food intake of similar order to those for Scyliorhinus. In general feeding rates for elasmobranchs are lower than those reported for teleosts (see Table 5.1), largely related to their comparatively low level of metabolism (Brett and Blackburn, 1978).

On a seasonal basis there was marked variation in daily food intake for Scyliorhinus. Consumption was greatest during summer; daily intake was between 1.4 and 2.3 times higher than in autumn and winter. Comparatively rapid rates of gastric evacuation coupled

TABLE 5.5 Food intake for some elasmobranchs.

Species	Size	Estimated Intake	Conditions	References
Squalus acanthias	1 kg	1.8 times b.w./year		Holden (1966)
	< 46 cm	5.0 times b.w./year		Jones & Geen (1977)
	46-78 cm	3.2 " "		
	> 78 cm	2.5-2.7 " "		
Negaprion brevirostris	1.6 kg	0.8-1.5% b.w./day	Aug (30.2°C); laboratory	Graeber (1974)
		1.4-1.7% " "	Sept-Oct (28.8°C); "	
	approx. 136 kg	1.0% b.w./day	Sept; 21-30°C; laboratory	Clark (1963)
		0.7% " "	Oct; " ; "	
		0.6% " "	Nov; " ; "	
Ginglymostoma cirratum	approx. 136 kg	0.5% b.w./day	Sept; 21-30°C; "	"
		0.4% " "	Oct; " ; "	
		0.3% " "	Nov; " ; "	
Raja clavata	158 g	1.6% b.w./day	Summer	de Souza (1978)
		1.3% " "	Autumn	
		1.1% " "	Winter	
		1.0% " "	Spring	
	528 g	0.9% b.w./day	Summer	
		1.0% " "	Autumn	
		0.8% " "	Winter	
		0.7% " "	Spring	
Scyliorhinus canicula	153 g	1.4% b.w./day	Summer	This study
		0.6% " "	Autumn	
		0.8% " "	Winter	
		1.0% " "	Spring	
	333 g	1.2% b.w./day	Summer	
		0.7% " "	Autumn	
		0.6% " "	Winter	
		0.8% " "	Spring	
	598 g	1.0% b.w./day	Summer	
		0.7% " "	Autumn	
		0.6% " "	Winter	
		0.7% " "	Spring	
	920 g	0.9% b.w./day	Summer	
		0.5% " "	Autumn	
		0.5% " "	Winter	
		0.5% " "	Spring	

with increased food availability during summer (Chapter 1) contributed to the maxima. The inclusion of high energy foods such as herring in the diet of dogfish larger than 40 cm had a very significant effect on the caloric intake during summer.

Annual consumption by 153 g dogfish was estimated to be 3.5 times the body weight, 333 g dogfish 3.0 times b.w., 598 g dogfish 2.7 times b.w., and 920 g dogfish 2.2 times b.w. These values are comparable to Jones and Geen's (1977) estimates of annual consumption of 5 times biomass for small Squalus to 2.5 times for larger animals and de Souza's (1978) estimates that Raja of 158 g consume 4.6 times b.w. and 528 g rays consume 3.2 times b.w. in a year.

Calculation of daily food intake relies heavily on two assumptions. The first is that gastric evacuation rates are similar for dogfish in the wild and under laboratory conditions. Dogfish in nature feed before the completion of gastric evacuation and consume a wide variety of prey taxa such that at any instant in time a stomach may contain several items at various stages of digestion (Chapter 1). Gastric evacuation studies on the other hand were based largely on the removal of single meals. Even though consistent differences in evacuation rates for different prey and multiple meals were not evident these aspects were only superficially investigated (Chapter 2). In fact Healey (1971) and Kuipers (1975) have found that gastric evacuation rates obtained from laboratory studies were slower than those that would occur in the wild. Retardation may arise from stress due to handling and confinement and from the type of feeding technique (refer to Chapter 2, page 36 - 37). The second assumption is that the stomach contents of captured dogfish are representative of the population in general. 'Standing crop' of stomach contents on a seasonal basis were based on the means of comparatively large samples, except for 29 - 39 cm size group, and thus are likely to be representative. The possibility that estimates of consumption for the smallest size group may be biased because of small sample sizes must be considered. For instance the high value for standing crop and consequent rate of consumption during summer 1979 was influenced markedly by the occurrence of two large hermit crabs in the stomach contents.

Although the adequacy of the estimates of daily food intake cannot be assessed directly, comparison on theoretical grounds with minimum energy requirements and predicted growth rates may provide a useful check. From Chapter 4 standard metabolism was assumed to be related to dogfish size to the exponent 0.8, and to temperature with a Q_{10} of 2.1. On the basis of Butler and Taylor's (1975) respiration data and these relationships, daily energy requirements for standard metabolism, Q_s (k cal/day), can be described mathematically as a function of dogfish weight W (g), and temperature T (°C):

$$Q_s = 0.0048\ W^{0.8}\ e^{0.075T} \tag{11}$$

Since maintenance metabolism, Q_m was approximately 2.5 times standard metabolism (Chapter 4):

$$Q_m = 0.012\ W^{0.8}\ e^{0.075T} \tag{12}$$

By substituting in equations (11) and (12), estimates of standard and maintenance metabolism may be compared with daily food consumption (energy) (Figure 5.1). Energy intake was consistently higher than standard metabolism, as expected, but with the exception of summer did not exceed maintenance requirements.

Further, only about 80-85% of the ingested energy would be available for metabolism and growth (see Chapter 3 and 4) because of faecal and non-faecal losses. The most obvious explanation for these discrepancies, for it is unlikely that dogfish subsist on sub-maintenance rations throughout most the year, is that estimates of daily consumption are low. However, because Butler and Taylor (1975) restrained and surgically cannulated their dogfish observed respiratory rates may be higher than expected. In addition maintenance metabolism was determined for dogfish under laboratory conditions, feeding on a high energy diet (sprat) and at comparatively high temperatures. It is conceivable that these factors may have contributed to produce overestimates of maintenance requirements in the wild.

Knowledge of growth rates and food consumption enable gross conversion efficiency to be computed. Holden (1974) has recognised the difficulties in estimating growth rates in elasmobranchs and has proposed that 'von Bertalanffy growth curves' could be constructed on the basis of embryonic growth rates. Since no published accounts of growth rates for Scyliorhinus could be located Holden's (1974) procedure was adopted[2]. The von Bertalanffy growth equation is usually expressed in the form:

$$l_t = L\infty\,(1 - e^{-K\,(t - t_o)}) \qquad (13)$$

where l_t is length at time t, $L\infty$ maximum theoretical length, K growth constant and t_o theoretical age at zero length. Holden (op cit.) modified equation (13):

$$l_{t + T} = L\infty\,(1 - e^{-Kt'}) \qquad (14)$$

[2] In the present study attempts to estimate growth of wild dogfish were undertaken but without significant success. Over 200 dogfish were tagged with Petersen tags and released on the studied ground. There were no recaptures. Vertebrae of approximately 80 dogfish were examined for growth rings under oblique incident light. Rings were visible in some instances but they were deceptive and appearance changed under different lighting conditions. Dehydration and clearing in xylene proved the best method of vertebral preparation attempted, though results were on the whole disappointing.

where $l_{t + T}$ is length at birth and t' the gestation period or hatching period (= $-t_o$). The method assumes that the growth rate, either in utero or in the egg, is the same as that for post-natal growth. Holden (op cit.) does acknowledge that this assumption does not hold for all elasmobranchs; growth rate before birth tending to be faster than afterwards. According to Wheeler (1978) maximum length for Scyliorhinus is approximately 100 cm, the hatching period between 5 - 11 months (t' was taken to be 0.7 year) and length at birth 10 cm. By solving equation (14) K was found to be 0.151. On this basis a growth curve was constructed and predicted annual growth increments for each size of dogfish calculated (Table 5.6). Annual gross conversion efficiencies were relatively high, between 26.5 and 11.2%, and although similar to conversion efficiencies determined under laboratory conditions (Chapter 4) comparison is not strictly valid. Since predicted metabolic requirements suggest that the growing season would be limited to summer then actual conversion

TABLE 5.6 Predicted age, annual growth and gross conversion efficiency for four size groups of Scyliorhinus canicula; based on Holden's (1974) procedure.

Size Group (cm)	Mean length (cm)	Age from equation (11) t(yr.)	Length at t + 1 (yr)	Annual weight increment* (g)	Gross conversion effficiency (%)
39	36.6	2.3	45.3	141.4	25.6
40 - 52	47.1	3.5	54.4	184.3	18.6
53 - 62	57.0	4.9	63.1	217.5	13.6
63	65.6	6.4	70.5	225.7	11.2

* Based on length-weight relationship, Figure 1.2

efficiencies would be unrealistically high. Despite the fact that the energetic and growth rate approaches are largely theoretical and subject to untested assumptions they do support the likelihood that consumption estimates are low.

Underestimation of food intake of fish in the wild probably applies to most previous studies (see Elliott and Persson, 1978; Jobling, 1981b), the result of simplifying and often erroneous assumptions. Nonetheless, daily food consumption rates for *Scyliorhinus* presented in this study represent preliminary estimates which should provide useful comparison with future research into aspects of feeding, energetics and growth of this species and of other elasmobranchs.

SUMMARY

1. Feeding of a population of *Scyliorhinus canicula* from a coarse ground east of the Isle of Man was investigated. Numerical and gravimetric methods of analysis were used.

2. Stomach contents include a component of partially digested food remains, "solid component", and a quantity of semifluid chyme - comminuted food and gastric juices. For stomach content analysis, these components were considered separately.

3. Dogfish consume a wide variety of macrobenthic fauna; important prey include *Eupagurus bernhardus*, *Macropipus* spp., *Upogebia* spp., *Buccinum undatum*, *Glycymeris glycymeris*, *Chlamys opercularis* and *Thyone* sp. Pelagic fish such as *Clupea harengus* are also consumed when they are locally abundant. Within limits, dogfish feed indiscriminately, consuming those species that are most readily available.

4. Molluscs became increasingly important to the diet of larger dogfish while concurrently crustaceans (other than *Eupagurus*) became less important.

5. Seasonal variation in the composition of the diet occurred, reflecting variation in availability of certain prey species. Most conspicuous variation was for *Glycymeris* which was consumed heavily during summer. Occurrence of *Clupea* in the diet was almost exclusively restricted to summer.

6. 'Standing crop' of stomach contents was highest during summer, which could in part be accounted for by increased food supply (herring). Standing crop was least during autumn.

7. Weight of stomach contents did not correlate regularly with time of day or state of tide. Dogfish feed at any time of the day.

8. Gastric emptying was studied in the laboratory for dogfish force-fed and voluntary-fed natural foods. Relationship between weight of food remaining in the stomach, 'residuum', and time after feeding was curvilinear, but could be linearised by applying square root transformation to the residuum weight.

9. Instantaneous rate of gastric emptying 'R' increased exponentially with rising temperature, while the time to complete gastric evacuation 'GET' decreased exponentially with rising temperature.

10. Meal size did not significantly affect R, thus a single curve adequately describes the removal of a meal for dogfish of a given weight and at a stated temperature. GET increased with meal size to the exponent of 0.35 at 7.7°C and 0.46 at 13.5°C.

11. Relationship between dogfish size and gastric emptying was variable. Small dogfish generally eliminated a meal based on a known proportion of the body weight quicker than larger individuals. There was some compensation through increased evacuation rate with increasing dogfish size. Larger dogfish empty a meal of a given weight more quickly than small dogfish.

12. R did not differ significantly for the removal of several prey species.

13. Force-feeding was found to suppress the evacuation rate when compared to dogfish allowed to feed voluntarily. A correction factor to account for the bias due to force-feeding was applied where relevant.

14. Multiple non-linear regression analysis was used to describe R and GET (h) as functions of water temperature 'T' (°C), dogfish size 'W' (g) and meal size 'S' (mg):

$$R = 0.0087\, e^{0.091T}\, W^{0.2552}\, S^{0.1392}$$

and $$GET = 100.595\, e^{-0.0862T}\, W^{0.2005}\, S^{0.3132}$$

15. Mean assimilation efficiency was 94.9 ± 0.36% for protein and 91.0 ± 0.49% for calories for a diet of <u>Buccinum</u> muscle. Assimilation efficiency was not influenced by temperature or dogfish size.

16. Meal type exerted some influence on assimilation efficiency, though values for both protein and calories remained consistently high ($>80\%$). Assimilation was highest for molluscs, intermediate for teleosts and lowest for crustacean foods.

17. Laboratory studies of food intake and growth were subject to considerable variation of response. Food intake suggested a pattern of overfeeding followed by a period of reduced consumption. Growth rate was highly dependent on ration level and tended to increase with

increased ration. At 16.6°C growth rate on satiation rations was lower than for an intermediate ration level. No sustained growth occurred at temperatures below 10.9°C.

18. By interpolation to zero growth on growth-ration curves, maintenance energy requirements were calculated. Maintenance energy requirements for 450g dogfish at 16.6°C is 4.95 kcal/day, while a 335g dogfish requires 3.73 kcal/day at 14.1°C (values based on physiological useful portion of the ration). Maintenance metabolism is between 2.46-2.59 times standard metabolism.

19. Study of the influence of temperature on growth was complicated because of differences in the size of dogfish and biochemical composition of the diets used in each experiment.

20. Preliminary study of the relationship between biochemical composition of the body and ration level revealed that body moisture decreased while lipids (and energy) increased with increasing ration level. Protein and ash content remained stable.

21. Food consumption rates in the wild were estimated using data from stomach content analysis and gastric evacuation studies. It was assumed that on average the rate of feeding equals the rate of gastric emptying, with the stomach content weight remaining more or less constant throughout the 24 h period.

22. Consumption estimates were determined from the solid component of the stomach contents and from the total weight of stomach contents. It is argued that the best available estimate lies between these, and was therefore taken to be the mean of the two values. Daily

food intake was greatest during summer, between 1.4 and 2.3 times that in autumn and winter.

23. Annual consumption varied between 3.5 times body weight for 153g dogfish to 2.2 times body weight for 920g dogfish.

24. The adequacy of the food consumption estimates was tested by comparison with predicted metabolic requirements and predicted growth in the wild. Though theoretical, these comparisons support the possiblity that consumption estimates were minimal.

REFERENCES

Allen, J.A. (1967) Crustacea : Euphausiacea and Decapoda. In : The fauna of the Clyde Sea area. Publ. Scott. mar. biol. Ass., Millport 116p.

Allen, K.R. (1941) Studies on the biology of the early stages of the salmon (Salmo salar) : 2 Feeding habits. J. anim. Ecol., 10 : 47-76.

Alliot, E. (1967) Absorption intestinal de l'N-acetyl-glucosamine chez la petite Roussette : Scylliorhinus canicula. C.r. Séanc. Soc. Biol., 161 : 2544-2546.

Alliot, E., and Bocquet, J. (1967) Présence d'un système enzymatique chitinolytique dans le tube digestif d'un Sélacien : Scylliorhinus canicula. C.r. Séanc. Soc. Biol., 161 : 840-845.

Andrews, J.W., and Page, J.W. (1975) The effects of frequency of feeding on the culture of catfish. Trans. Am. Fish. Soc., 104 : 317-321.

Ansell, A.D., and Trueman, E.R. (1967) Observations on burrowing in Glycymeris glycymeris (L.) (Bivalvia, Arcacea). J. exp. mar. Biol. Ecol., 1 : 65-75.

Armstrong, M.J. (1980) The feeding ecology of a demersal fish community over a muddy substrate of the West coast of the Isle of Man. Ph.D. Thesis, Univ. of Liverpool, 182p.

Armstrong, R.H., and Blackett, R.F. (1966) Digestion rate of the dolly varden. Trans. Am. Fish. Soc., 95 : 429-430.

Arthur, D.R. (1950) Abnormalities in the sexual apparatus of the common dogfish (Scyliorhinus caniculus). Proc. Linn. Soc. Lond., 162 : 52-56.

Azouz, A., and Capapé, C. (1971) Les relations alimentaires entre les sélaciens et le zoobenthos des côtes nord de la Tunisie. Bull. Inst. natn. Sci. Techn., Océanogr. Pêche, 2 : 121-130.

Backiel, T. (1971) Production and food consumption of predatory fish in the Vistual River. J. Fish Biol., 3 : 369-405.

Bagge, O. (1977) Meal size and digestion in cod (Gadus morrhua L.) and sea scorpion (Myoxocephalus scorpius L.). Meddr. Danm. Fisk.-og Havunders, N.S. 7 : 437-446.

Bajkov, A.D. (1935) How to estimate the daily food consumption of a fish under natural conditions. Trans. Am. Fish. Soc., 65 : 288-289.

Bateson, W. (1890a) Notes on the senses and habits of some crustacea. J. mar. biol. Ass. Lond., N.S.1 : 211-217.

Bateson, W. (1980b) The sense organs and perceptions of fishes, with remarks on the supply of bait. J. mar. biol. Ass. Lond., N.S.1 : 225-256.

Beamish, F.W.H. (1972) Ration size and digestion in largemouth bass, Micropterus salmoides Lacépède. Can. J. Zool., 50 : 153-164.

Beamish, F.W.H. (1974) Apparent specific dynamic action of largemouth bass, Micropterus salmoides. J. Fish. Res. Bd Can., 31 : 1763-1769

Birkett, L. (1969) The nitrogen balance in plaice, sole and perch. J. exp. Biol., 50 : 375-386.

Blaxter, J.H.S. (1968) Light intensity, vision and feeding in young plaice. J. exp. Biol. Ecol., 2 : 293-307.

Boord, R.D., and Campbell, C.B.G. (1977) Structural and functional organization of the lateral-line system of sharks. Am. Zool., 17 : 431-444.

Bowen, S.H. (1978) Ghromic acid in assimilation studies - a caution. Trans. Am. Fish. Soc., 107 : 755-756.

Bowers, A.B. (1969) Spawning beds of Manx autumn herrings. J. Fish Biol., 1 : 355-359.

Brett, J.R. (1971a) Satiation time, appetite and maximum food intake of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd Can., 28 : 409-415.

Brett, J.R. (1971b) Growth responses of young sockeye salmon (Oncorhynchus nerka) to different diets and planes of nutrition. J. Fish. Res. Bd Can., 28 : 1635-1643.

Brett, J.R. (1979) Environmental factors and growth. In : Fish Physiology, Vol. VIII. (W.S. Hoar, D.J. Randall and J.R. Brett, eds) pp. 599-675. Academic Press, N.Y. and London.

Brett, J.R., and Blackburn, J.M. (1978) Metabolic rate and energy expenditure of the spiny dogfish, Squalus acanthias. J. Fish. Res. Bd Can., 35 : 816-821.

Brett, J.R., and Groves, T.D.D. (1979) Physiological energetics. In : Fish Physiology, Vol. VIII. (W.S. Hoar, D.J. Randall and J.R. Brett, eds.) pp. 280-352. Academic Press, N.Y. and London.

Brett, J.R., and Higgs, D.A. (1970) Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, Oncorhynchus nerka. J. Fish. Res. Bd Can., 27 : 1767-1779.

Brett, J.R., Shelbourn, J.E., and Shoop, C.T. (1969) Growth rate and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Bd Can., 26 : 2363-2394.

Brightwell, L.R. (1953) Further notes on the hermit crab, Eupagurus bernhardus and associated animals. Proc. zool. Soc. Lond., 123 : 61-64.

Brocksen, R.W., and Bugge, J.P. (1974) Preliminary investigations on the influence of temperature on food assimilation by rainbow trout Salmo gairdneri Richardson. J. Fish Biol., 6 : 93-97.

Brocksen, R.W., Davis, G.E., and Warren, C.E. (1968) Competition, food consumption, and production of sculpins and trout in laboratory stream communities. J. Wildl. Mgnt., 32 : 51-75.

Brody, S. (1945) Bioenergetics and Growth. Reinhold Publ. Corp., N.Y. 1023p.

Brown, M.E. (1946a) The growth of brown trout (Salmo trutta Linn.) I Factors influencing the growth of trout fry. J. exp. Biol., 22 : 118-129.

Brown, M.E. (1946b) The growth of brown trout (Salmo trutta Linn.) II The growth of two-year-old trout at a constant temperature of 11.5°C. J. exp. Biol., 22 : 130-144.

Brown, M.E. (1946c) The growth of brown trout (Salmo trutta Linn.) III The effect of temperature on the growth of two-year-old trout. J. exp. Biol., 22 : 145-155.

Brown, M.E. (1957) Experimental studies on growth. In : Physiology of Fishes Vol. I (ed M.E. Brown) Academic Press Inc., N.Y. 447p.

Bruce, J.R., Colman, J.S., and Jones, N.S. (eds.) (1963) Marine fauna of the Isle of Man and its surrounding seas. Liverpool Univ. Press, Liverpool. 307p.

Butler, P.J., and Taylor, E.W. (1971) Response of the dogfish (Scyliorhinus canicula) to slowly induced and rapidly induced hypoxia. Comp. Biochem. Physiol., 39A : 307-323.

Butler, P.J., and Taylor, E.W. (1975) The effect of progressive hypoxia on respiration in the dogfish (Scyliorhinus canicula) at different seasonal temperatures. J. exp. Biol., 63 : 117-130.

Canadjija, S. (1961) Analiza sadržaja želudaca mačke bljedice (Scyllium canicula Cuv.). Biol. glasnik, 14 : 217-228.

Capapé, E.C.(1974) Contribution à la biologie des Scyliorhinidae des côtes tunisiennes. 2. Scyliorhinus canicula Linné 1758 : Régime alimentaire. Ann. Inst. Michel. Pacha, 1974(7) : 13-29.

Capapé, C. (1977) Contribution à la biologie des Scyliorhinidae des côtes tunisiennes I Scyliorhinus canicula (Linné, 1758) Répartition géographique et bathymétrique, sexualité, reproduction, fécondité. Bull. Off. natn. Pêch. Tunisie, 1 : 83-101.

Carline, R.F., and Hall, J.D. (1973) Evaluation of a method for estimating food consumption rates of fish. J. Fish. Res. Bd Can., 30 : 623-629.

Clark, E. (1963) The maintenance of sharks in captivity with a report on their instrumental conditioning. In : Sharks and Survival (P.W. Gilbert, ed) pp. 115-149. D.C. Heath and Co., Boston.

Clarke, M.R., and Stevens, J.D. (1974) Cephalopods, blue sharks and migration. J. mar. biol. Ass. U.K., 54 : 949-957.

Clark, R.S. (1922) Rays and skates (Raiae) No. 1. Egg capsules and young. J. mar. biol. Ass. U.K., 12 : 577-643.

Cowey, C.B., Adron, J., Blair, A., and Shanks, A.M. (1974) Studies on the nutrition of marine flatfish. Utilization of various dietary proteins by plaice (Pleuronectes platessa). Br. J. Nutr., 31 : 297-306.

Craik, J.C.A. (1978) An annual cycle of vitellogenesis in the elasmobranch Scyliorhinus canicula. J. mar. biol. Ass. U.K., 58 : 719-726.

Daan, N. (1973) A quantitative analysis of the food intake of North Sea cod, Gadus morhua L. Neth. J. Sea Res., 6 : 479-517.

Dansky, L.M., and Hill, F.W. (1952) Application of the chromic oxide indicator method to balance studies with growing chickens. J. Nutr., 47 : 449-459.

Darnell, R.M., and Meierotto, R.R. (1962) Determination of feeding chronology in fishes. Trans. Am. Fish. Soc., 91 : 313-320.

Davies, P.M.C. (1964) The energy relations of Carassius auratus L. - 1. Food input and energy extraction efficiency at two experimental temperatures. Comp. Biochem. Physiol., 17 : 67-79.

Dawes, B. (1930) Growth and maintenance in the plaice (Pleuronectes platessa L.) Part I. J. mar. biol. Ass. U.K., 17 : 103-174.

De Silva, S.S., and Balbontin, F. (1973) Laboratory studies on food intake, growth and food conversion of young herring, Clupea harengus (L.). J. Fish Biol., 6 : 645-658.

De Souza, T.F. (1978) Feeding and digestion in the Raiidae. M.Sc. Thesis, Univ. College of North Wales 126p.

Diana, J.S. (1979) The feeding pattern and daily ration of a top carnivore, the northern pike (Esox lucius). Can. J. Zool., 57 : 2121-2127.

Dijkgraaf, S. (1975) Zur Sinnesphysiologie der Beutewahrnehmung beim Hundshai, Scyliorhinus canicula. Rev. Suisse Zool., 82 : 41-46.

Doble, B.D., and Eggers, D.M. (1978) Diel feeding chronology, rate of gastric evacuation, daily ration, and prey selectivity in Lake Washington juvenile sockeye salmon (Oncorhynchus nerka). Trans. Am. Fish. Soc., 107 : 36-45.

Dodd, J.M., Dodd, M.H.I., and Goddard, C.K. (1959) Force-feeding fish under experimental conditions. Nature, Lond., 184 : 1660-1661.

Eales, N.B. (1949) The food of the dogfish, Scyliorhinus canicula L. J. mar. biol. Ass. U.K., 28 : 791-793.

Edwards, D.J. (1971) Effect of temperature on rate of passage of food through the alimentary canal of the plaice, Pleuronectes platessa L. J. Fish Biol., 3 433-439.

Edwards, D.J. (1973) The effects of drugs and nerve-section on the rate of passage of food through the gut of the plaice, Pleuronectes platessa (L.). J. Fish Biol., 5 : 441-446.

Edwards, R.R.C., Finlayson, D.M., and Steele, J.H. (1969) The ecology of O-group plaice and common dabs in Loch Ewe. II Experimental studies of metabolism. J. exp. mar. Biol. Ecol., 3 : 1-17.

Edwards, R.R.C., Finlayson, D.M., and Steele, J.H. (1972) An experimental study of the oxygen consumption, growth and metabolism of the cod (Gadus morhua L.). J. exp. mar. Biol. Ecol., 8 : 299-309.

Elliott, J.M. (1972) Rates of gastric evacuation in brown trout, Salmo trutta L. Freshwat. Biol., 2 : 1-18.

Elliott, J.M. (1975a) Weight of food and time required to satiate brown trout, Salmo trutta L. Freshwat. Biol., 5 : 51-64.

Elliott, J.M. (1975b) Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, Salmo trutta L. Freshwat. Biol., 5 : 287-303.

Elliott, J.M. (1975c) The growth rate of brown trout (Salmo trutta L.) fed on maximum rations. J. anim. Ecol., 44 : 805-821.

Elliott, J.M. (1975d) The growth rate of brown trout (Salmo trutta L.) fed on reduced rations. J. anim. Ecol., 44 : 823-842.

Elliott, J.M. (1976a) Body composition of brown trout (Salmo trutta L.) in relation to temperature and ration size. J. anim. Ecol., 45 : 273-289.

Elliott, J.M. (1976b) Energy losses in the waste products of brown trout (Salmo trutta L.). J. anim. Ecol., 45 : 561-580.

Elliott, J.M. (1976c) The energetics of feeding, metabolism and growth of brown trout (Salmo trutta L.). J. anim. Ecol., 45 : 923-948.

Elliott, J.M., and Davidson, W. (1975) Energy equivalents of oxygen consumption in animal energetics. Oecologia, 19 : 195-201.

Elliott, J.M., and Persson, L. (1978) The estimation of daily rates of food consumption for fish. J. anim. Ecol., 47 : 977-991.

Fābian, Gy., Molnār, Gy., and Tölg, I. (1963) Comparative data and enzyme calculations on changes caused by temperature in the duration of gastric evacuation of some predatory fishes. Acta biol. hung., 14 : 123-129.

Fänge, R., and Grove, D.J. (1979) Digestion. In : Fish Physiology Vol. VIII (W.S. Hoar, D.J. Randall, and J.R. Brett, eds). pp 161-278. Academic Press, N.Y. and London.

Flowerdew, M.W., and Grove, D.J. (1979) Some observations of the effects of body weight, temperature, meal size and quality on gastric emptying time in the turbot, Scophthalmus maximus (L.) using radiography. J. Fish Biol., 14 : 229-238.

Flowerdew, M.W., and Grove, D.J. (1980) An energy budget for juvenile thick-lipped mullet, Crenimugil labrosus (Risso). J. Fish Biol., 17 : 395-410.

Fonds, M. (1978) A seasonal fluctuation in growth rate of young plaice (Pleuronectes platessa) and sole (Solea solea) in the laboratory at constant temperatures and natural daylight cycle. Proc. 13th Europ. mar. biol. Symp. : 151-156.

Ford, E. (1921) Contribution to our knowledge of the life-history of the dog-fishes landed at Plymouth. J. mar. biol. Ass. U.K., 12 : 468-505.

Forster, J.R.M., and Gabbott, P.A. (1971) The assimilation of nutrients from compounded diets by the prawns Palaemon serratus and Pandalus platyceros. J. mar. biol. Ass. U.K., 51 : 943-961.

Gerald, V.M. (1973) Rate of digestion Ophiocephalus punctatus Bloch. Comp. Biochem. Physiol., 46A : 195-205.

Gerking, S.D. (1952) The protein metabolism of sunfishes of different ages. Physiol. Zool., 25 : 358-372.

Gerking, S.D. (1954) The food turnover of a bluegill population. Ecology, 35 : 490-498.

Gerking, S.D. (1955) Influence of rate of feeding on body composition and protein metabolism of bluegill sunfish. Physiol. Zool., 28 : 267-282.

Gerking, S.D. (1962) Production and food utilization in a population of bluegill sunfishes. Ecol. Monogr., 32 : 31-78

Gilbert, P.W. (1963) The visual apparatus of sharks. In : Sharks and Survival (P.W. Gilbert, ed.). pp. 283-326. D.C. Heath and Co., Boston.

Goddard, J.S. (1974) An x-ray investigation of the effects of starvation and drugs on intestinal motility in the plaice, Pleuronectes platessa L. Ichthyologia, 6 : 49-58.

Graeber, R.C. (1974) Food intake patterns in captive juvenile lemon sharks, Negaprion brevirostris. Copeia, 2 : 554-556.

Greer Walker, M., Riley, J.D., and Emerson, L. (1980) On the movements of sole (Solea solea) and dogfish (Scyliorhinus canicula) tracked off the east Anglian coast. Neth. J. Sea Res., 14 : 66-77.

Griffiths, W.E. (1976) Feeding and gastric evacuation in perch (Perca fluviatilis L.). Mauri Ora, 4 : 19-34.

Gross, W.L., Roelofs, E.W., and Fromm, P.O. (1965) Influence of photoperiod on growth of green sunfish, Lepomis cyanellus. J. Fish. Res. Bd Can., 22 : 1379-1386.

Grove, D.J., and Crawford, C. (1980) Correlation between digestion rate and feeding frequency in the stomachless teleost, Blennius pholis L. J. Fish Biol., 16 : 235-247.

Grove, D.J., Liozides, L.G., and Nott, J. (1978) Satiation amount, frequency of feeding and gastric emptying rate in Salmo gairdneri. J. Fish Biol., 12 : 507-516.

Gudger, E.W. (1949) Natural history notes on tiger sharks, Galeocardo tigrinus, caught at Key West, Florida, with emphasis on food and feeding habits. Copeia, 1 : 39-47.

Gwyther, D. (1978) The control of appetite in the dab Limanda limanda (L.). Ph.D. thesis, Univ. College of North Wales 154p.

Gwyther, D., and Grove, D.J. (1981) Gastric emptying in Limanda limanda (L.) and the return of appetite. J. Fish Biol., 18 : 245-259.

Harris, J.E. (1952) A note on the breeding season, sex ratio and embryonic development of the dogfish Scyliorhinus canicula L. J. mar. biol. Ass. U.K., 31 : 269-274.

Hastings, W.H. (1969) Nutritional score. In : Fish in Research (O.W. Neuhaus and J.E. Halver, eds) pp. 263-292. Academic Press, N.Y. and London.

Healey, M.C. (1971) Distribution and abundance of sand gobies, Gobius minutus, in the Ythan estuary. J. Zool., Lond., 163 : 177-229.

Healey, M.C. (1972) Bioenergetics of a sand goby (Gobius minutus) population. J. Fish. Res. Bd Can., 29 : 187-194.

Hermann, R.B., Warren, C.E., and Doudoroff, P. (1962) Influence of oxygen concentration on the growth of juvenile coho salmon. Trans. Am. Fish. Soc., 91 : 155-167.

Herting, G.E., and Witt, A.Jr. (1968) Rate of digestion of the bowfin. Progve Fish-Cult., 30 : 26-28.

Hoar, W.S. (1966) General and Comparative Physiology. Prentice-Hall, Inc., New Jersey. 815p.

Hogben, C.A.M. (1967) Secretion of acid by the dogfish Squalus acanthias. In : Sharks, Skates and Rays. (P.W. Gilbert, R.F. Mathewson and D.P. Rall, eds). pp. 299-315. Johns Hopkins, Baltimore.

Holden, M.J. (1966) The food of the spurdog, Squalus acanthias (L.). J. Cons. perm. int. Explor. Mer, 30 : 255-266.

Holden, M.J. (1974) Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In : Sea Fisheries Research (F.R. Harden-Jones, ed) pp 117-138. Logos Press, London.

Holden, M.J. (1977) Elasmobranchs. In : Fish Population Dynamics (J.A. Gulland, ed). pp 187-214. Wiley, London,

Holden, M.J., and Tucker, R.N. (1974) The food of Raja clavata Linnaeus 1758, Raja montagui Fowler 1910, Raja naevus Muller and Henle 1841, and Raja brachyura Lafont 1873 in British waters. J. Cons. perm. int. Explor. Mer, 35 : 189-193.

Homans, R.E.S., and Vladykov, V.D. (1954) Relation between feeding and the sexual cycle of the haddock. J. Fish. Res. Bd Can., 11 : 535-542.

Hopkins, A. (1966) The pattern of gastric emptying : a new view of old results. J. Physiol., 182 : 144-149.

Hughes, G.M., and Umezawa, S.-I. (1968) Oxygen consumption and gill water flow in the dogfish Scyliorhinus canicula L. J. exp. Biol., 49 : 557-564.

Huisman, E.A. (1976) Food conversion efficiencies at maintenance and production levels for carp, Cyprinus carpio L., and rainbow trout, Salmo gairdneri Richardson. Aquaculture, 9 : 259-273.

Hynes, H.B.N. (1950) The food of fresh-water sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius), with a review of methods used in studies of the food of fishes. J. anim. Ecol., 19 : 36-58.

Hyslop, E.J. (1980) Stomach content analysis - a review of methods and their application. J. Fish Biol., 17 : 411-429.

Inaba, D., Ogino, C., Takamatsu, C., Sugano, S., and Hata, H. (1962) Digestibility of dietary components in fishes. I. Digestibility of dietary proteins in rainbow trout. Bull. Jap. Soc. scient. Fish., 28 : 367-371.

Jardas, I. (1972) Supplement to the knowledge of ecology of some Adriatic cartilaginous fishes (Chondrichthyes) with special reference to their nutrition. Acta adriat., 14 (7) : 60p

Jardas, I. (1979) Morphological, biological and ecological characteristics of the lesser spotted dogfish, Scyliorhinus canicula (Linnaeus, 1758), population in the Adriatic Sea. Izv-Rep. Inst. Oceanogr. Ribar. Split, 4 (2-3) 104p.

Jobling, M. (1980a) Gastric evacuation in plaice, Pleuronectes platessa L. : effects of dietary energy level and food consumption. J. Fish Biol., 17 : 187-196.

Jobling, M. (1980b) Effects of starvation on proximate chemical composition and energy utilization of plaice, Pleuronectes platessa L. J. Fish Biol., 17 : 325-334.

Jobling, M. (1980c) Gastric evacuation in plaice, Pleuronectes platessa L. : effects of temperature and fish size. J. Fish Biol., 17 : 547-551.

Jobling, M. (1981a) Dietary digestibility and the influence of food components on gastric evacuation inplaice, Pleuronectes platessa L. J. Fish Biol., 19 : 26-36.

Jobling, M. (1981b) Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish Biol., 19 : 245-257.

Jobling, M., and Davies, P.S. (1979) Gastric evacuation in plaice, Pleuronectes platessa L. : effects of temperature and meal size. J. Fish Biol., 14 : 539-546.

Jobling, M., and Davies, P.S. (1980) Effects of feeding on metabolic rate, and the specific dynamic action in plaice, Pleuronectes platessa L. J. Fish Biol., 16 : 629-638.

Jobling, M., Gwyther, D., and Grove, D.J. (1977) Some effects of temperature, meal size and body weight on gastric evacuation time in the dab Limanda limanda (L.). J. Fish Biol., 10 : 291-298.

Jones, A. (1973) The ecology of young turbot, Scophthalmus maximus (L.), at Borth, Cardiganshire, Wales. J. Fish Biol., 5 : 367-383.

Jones, B.C., and Geen, G.H. (1977) Food and feeding of spiny dogfish (Squalus acanthias) in British Columbia waters. J. Fish. Res. Bd Can., 34 : 2067-2078.

Jones, N.S. (1951) The bottom fauna off the south of the Isle of Man. J. anim. Ecol., 20 : 132-144.

Jones, R. (1974) The rate of elimination of food from the stomachs of haddock Melanogrammus aeglefinus, cod Gadus morhua and whiting Merlangius merlangus. J. Cons. perm. int. Explor. Mer, 35 : 225-243.

Jones, R. (1978) Estimates of the food consumption of haddock (Melanogrammus aeglefinus) and cod (Gadus morhua). J. Cons. perm. int. Explor. Mer, 38 : 18-27.

Jones, R., and Hislop, J.R.G. (1972) Investigations into the growth of haddock Melanogrammus aeglefinus (L.) and whiting Merlangius merlangus (L.) in aquaria. J. Cons. perm. int. Explor. Mer, 34 : 174-189.

Jones, R., and Hislop, J.R.G. (1978) Further investigations on the relation between food intake and growth of gadoids in captivity. J. Cons. perm. int. Explor. Mer, 38 : 244-251.

Kalmijn, A.J. (1971) The electric sense of sharks and rays. J. exp. Biol., 55 : 371-383.

Kalmijn, A.J. (1977) The electric and magnetic sense of sharks, skates and rays. Oceanus, 20 : 45-52.

Kapoor, B.G., Smit, H., and Verighina, I.A. (1975) The alimentary canal and digestion in teleosts. Adv. mar. Biol., 13 : 109-239.

Karpevitch, A.F., and Bokova, E.N. (1937) The rate of digestion in marine fishes. Part 2. Zool. Zh., 16 : 21-44.

Katre, S., and Reddy, S.R. (1977) Environmental restraints. on the food intake, growth and conversion efficiency of Gambusia affinis : influence of living space. Proc. Indian Acad. Sci., Sect. B, 85 (6) : 407-411.

Katsuki, Y., Yanagisawa, K., Tester, A.L., and Kendall, J.I. (1969) Shark pit organs : response to chemicals. Science, 163 : 405-407.

Keast, A., and Welsh, L. (1968) Daily feeding periodicities, food uptake rates and dietary changes with hour of day in some lake fishes. J. Fish. Res. Bd Can., 25 : 1133-1144.

Kelso, J.R.M. (1972) Conversion, maintenance and assimilation for walleye, Stizostedion vitreum vitreum, as affected by size, diet and temperature. J. Fish. Res. Bd. Can., 29 : 1181-1192.

Kerr, S.R. (1971) Prediction of fish growth efficiency in nature. J. Fish. Res. Bd Can., 28 : 809-814.

Kevern, N.R. (1966) Feeding rate of carp estimated by a radioisotopic method. Trans. Am. Fish. Soc., 95 : 363-371.

Kinne, O. (1960) Growth, food intake and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zool., 33 : 288-317.

Kionka, B.C., and Windell, J.T. (1972) Differential movement of digestible and indigestible food fractions in rainbow trout Salmo gairdneri. Trans. Am. Fish. Soc., 101 : 112-115.

Kitamikado, M., Morishita, T., and Tachino, S. (1964) Digestibility of dietary protein in rainbow trout - II Effect of starch and oil contents in diets and size of fish. Bull. Jap. Soc. scient. Fish., 30 : 50-54.

Kitchell, J.F., and Windell, J.T. (1968) Rate of gastric digestion in pumpkinseed fish Lepomis gibbosus. Trans. Am. Fish. Soc., 97 : 489-492.

Kolehmainen, S.E. (1974) Daily feeding rates of bluegill (Lepomis macrohirus) determined by a refined radioisotope method. J. Fish. Res. Bd Can., 31 : 67-74.

Kuchnow, K.P. (1971) The elasmobranch pupillary response. Vision Res., 11 : 1395-1406.

Kuipers, B. (1975) Experimental and field observations on the daily food intake of juvenile plaice, Pleuronectes platessa L. Proc. 9th Europ. mar. biol. Symp., : 1-12.

Kwain, W.-H. (1975) Embryonic development, early growth, and meristic variation in rainbow trout (Salmo gairdneri) exposed to combinations of light intensity and temperature. J. Fish. Res. Bd Can., 32 : 397-402.

Laurence, G.C. (1971) Digestion rate of larval largemouth bass. N.Y. Fish Game J., 18 : 52-56.

Leake, L.D. (1975) Comparative Histology. An introduction to the microscopic structure of animals. Academic Press, London, New York and San Francisco. 738p.

Lee, D.J., and Putnam, G.B. (1973) The response of rainbow trout to varying protein/energy ratios in a test diet. J. Nutr., 103 : 916-922.

Leloup, J., and Olivereau, M. (1951) Données biométriques comparatives sur la roussette (Scyllium canicula L.) de la Manche et de la Méditerranée. Vie Milieu, 2 : 182-209.

Magnuson, J.J. (1969) Digestion and food consumption by skipjack tuna (Katsuwonus pelamis). Trans. Am. Fish. Soc., 98 : 379-392.

Maliyenko, A.V. (1975) Rate of passage of food through the alimentary canal in juveniles of some fish species from the Kremenchug Reservoir. Hydrobiol. J., 11 : 65-68.

Mann, H. (1969) Difference in the digestibility of plant and animal protein by various kinds of fish. Tech. Pap. Europ. Inld. Fish. Adv. Comm. No. 9 : 194-196.

Mann, K.H. (1965) Energy transformation by a population of fish in the River Thames. J. anim. Ecol., 34 : 253-275.

Mann, K.H. (1978) Estimating the food consumption of fish in nature In : Ecology of Freshwater Fish Production (S.D. Gerking, ed) pp 250-273. Blackwell Scientific Publs., Oxford.

Markus, H.C. (1932) The extent to which temperature changes influence food consumption in the largemouth bass, Huro floridana. Trans. Am. Fish. Soc., 62 : 202-210.

Mathewson, R.F., and Hodgson, E.S. (1972) Klinotaxis and rheotaxis in orientation of sharks toward chemical stimuli. Comp. Biochem. Physiol., 42A : 79-84.

McEachran, J.D., Boesch, D.F., and Musick, J.A. (1976) Food division within two sympatric species-pairs of skates (Pisces : Rajidae). Mar. Biol., 35 : 301-317.

McGinnis, A.J., and Kasting, R. (1964) Colorimetric analysis of chromic acid used to study food utilization by phytophagous insects. J. Agric. Food Chem., 12 : 259-262.

McKone, D. (1971) Rate at which sockeye salmon alevins are evacuated from the stomach of mountain whitefish (Prosopium williamsoni). J. Fish. Res. Bd Can., 28 : 110-111.

Menzel, D.W. (1958) Utilization of algae for growth by the angelfish Holacanthus bermudensis. J. Cons. perm. int. Explor. Mer, 24 : 308-313.

Menzel, D.W. (1960) Utilization of food by a Bermuda reef fish, *Epinephelus guttatus*. J. Cons. perm. int. Explor. Mer, *25* : 216-222.

Metten, H. (1941) Studies on the reproduction of the dogfish. Phil. Trans. R. Soc., B *230* : 217-238.

Mitchell, K.A. (1974) Activities of 2 British species of *Pagurus* Mar. Behav. Physiol., *2* : 229-236.

Molnár, Gy., Tamássy, E., and Tölg, I. (1967) The gastric digestion of living predatory fish. *In* : The Biological Basis of Freshwater Fish Production (S.D. Gerking, ed) pp 135-149. Blackwell Scientific Publs. Oxford.

Molnár, G., and Tölg, I. (1962) Relation between water temperature and gastric digestion of largemouth bass (*Micropterus salmoides* Lacépède) J. Fish. Res. Bd Can., *19* : 1005-1012.

Moriarty, C.M., and Moriarty, D.J.W. (1973) Quantitative estimation of the daily ingestion of phytoplankton by *Tilapia nilotica* and *Haplochromis nigripinnis* in Lake George, Uganda. J. Zool. Lond., *171* : 15-23.

Morris, D.J. (1978) The respiratory physiology of the subtidal bivalves *Glycymeris glycymeris* (L.), *Anomia ephippium* L. and *Modiolus modiolus* L. Ph.D. Thesis, Univ. of Liverpool 121p

Moss, S.A. (1977) Feeding mechanisms in sharks. Am. Zool., *17* : 355-364.

Muir, B.S., and Niimi, A.J. (1972) Oxygen consumption of the euryhaline fish aholehole (*Kuhlia sandvicensis*) with reference to salinity, swimming and food consumption. J. Fish. Res. Bd Can., *29* : 67-77.

Nakashima, B.S., and Leggett, W.C. (1978) Daily ration of yellow perch (*Perca flavescens*) from Lake Memphremagog, Quebec-Vermont, with a comparison of methods for in situ determinations. J. Fish. Res. Bd Can., *35* : 1597-1603.

Nicholls, J.V.V. (1933) The effect of temperature variations and of certain drugs upon the gastric mobility of elasmobranch fishes. Contr. Can. Biol. Fish., *7* : 447-463.

Niimi, A.J., and Beamish, F.W.H. (1974) Bioenergetics and the growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. Can. J. Zool., *52* : 447-456.

Nikolsky, G.V. (1969) The theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver and Boyd, Edinburgh. 323p.

Nobel, R.L. (1972) A method of direct estimation of total food consumption with application to young yellow perch. Progve Fish-Cult., 34 : 191-204.

Nobel, R.L. (1973) Evacuation rates of young yellow perch, *Perca flavescens* (Mitchell). Trans. Am. Fish. Soc., 102 : 759-763.

Nose, T. (1964) Protein digestibility of several test diets in cray and prawn fish. Bull. Freshwat. Fish. Res. Lab. Tokyo, 14 : 23-28.

Nose, T. (1967) On the metabolic fecal nitrogen in young rainbow trout. Bull. Freshwat. Fish. Res. Lab. Tokyo, 17 : 97-105.

Nose, T., and Mamiya, H. (1963) Protein digestibility of flatfish meal in rainbow trout. Bull. Freshwat. Fish. Res. Lab. Tokyo, 12 : 1-4.

Nose, T., and Toyama, K. (1966) Protein digestibility of brown fish meal in rainbow trout. Bull. Freshwat. Fish. Res. Lab. Tokyo, 15 : 213-224.

Nottage, A.S., and Perkins, E.J. (1980) Observations on the general biology of the thornback ray (*Raja clavata* L.) in the Solway Firth. 2. Cumbria Sea Fish. Comm., Sci. Rept. 80/4 12pp.

Owen, T.G., and Wiggs, A.J. (1971) Thermal compensation in the stomach of the brook trout. Comp. Biochem. Physiol., B40 : 465-473.

Page, J.W., and Andrews, J.W. (1973) Interactions of dietary levels of protein and energy on channel catfish (*Ictalurus punctatus*). J. Nutr., 103 : 1339-1346.

Paloheimo, J.E., and Dickie, L.M. (1966) Food and growth of fishes. II Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Bd Can., 23 : 869-908.

Pandian, T.J. (1967) Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. Mar. Biol., 1 : 16-32.

Pandian, T.J. (1970) Intake and conversion of food in the fish *Limanda limanda* exposed to different temperatures. Mar. Biol., 5 : 1-17.

Parker, G.H. (1914) The directive influence of the sense of smell in the dogfish. Bull. U.S. Bur. Fish., 33 : 61-68.

Pearson, D. (1976) The Chemical Analysis of Foods, 7th Edition. Churchill Livingston, Edinburgh, London and New York, 575p.

Pearson, D., and Muslemuddin, M. (1969) The accurate determination of total volatile nitrogen in meat and fish. Part III Application to elasmobranch fish. J. Ass. public Analysts, 7 : 73-82.

Pérès, G., and Rigal, A. (1970) Étude comparative de la consommation d'oxygène par le tissue intestinal chez différentes espèces de poissons. C.R. Soc. Biol. Fil., 164 : 1510-1512.

Persson, L. (1979) The effects of temperature and different food organisms on the rate of gastric evacuation in perch *Perca fluviatilis*. Freshwat. Biol., 9 : 99-104.

Persson, L. (1981) The effects of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) fed on fish larvae. Freshwat. Biol., 11 : 131-138.

Peters, D.S., and Hoss, D.E. (1974) A radioisotopic method of measuring food evacuation time in fish. Trans. Am. Fish Soc., 103 : 626-629.

Phillips, A.M. (1969) Nutrition, digestion, and energy utilization *In* : Fish Physiology Vol. I (W.S. Hoar, and D.J. Randall, eds) pp 391-432. Academic Press, N.Y.

Pierce, E.L. (1936) Rates of digestion in the yellowtail (*Ocyurus chrysurus*) and the white grunt (*Haemulon plumieri*). Copeia, 2 : 123-124.

Pillay, T.V.R. (1952) A critique of the methods of study of food of fishes. J. zool. Soc. India, 4 : 185-200.

Quigley, J.P., and Meschan, I. (1941) Inhibition of the pyloric sphincter region by the digestion products of fat. Am. J. Physiol., 134 : 803-808.

Rae, B.B. (1967a) The food of cod in the North Sea and on West of Scotland grounds. Mar. Res. 1967, No. 1 : 68p.

Rae, B.B. (1967b) The food of the dogfish, *Squalus acanthias* L. Mar. Res. 1967, No. 3 : 19p.

Raymont, J.E.G. (1947) An experiment in marine fish cultivation : IV The bottom fauna and the food of flatfishes in a fertilized sea-loch (Loch Craiglin). Proc. R. Soc. Edinb., B 63 : 34-55.

Reshetnikov, Yu.S., Claro, R., and Silva, A. (1972) The pattern of feeding and the rate of digestion in some tropical predatory fish. J. Ichthyol. (Vopr. Ikhtiol (Eng Ed)), 12 : 818-824.

Richard, J.D. (1968) Fish attraction with pulsed low-frequency sound. J. Fish. Res. Bd Can., 25 : 1441-1452.

Richards, A.G. (1951) The Integument of Arthropods. Univ. of Minnesota Press, Minneapolis.

Rosenthal, H., and Hempel, G. (1970) Experimental studies in feeding and food requirements of herring larvae (Clupea harengus L.) In : Marine Food Chains (J.H. Steele, ed) pp344-364. Oliver and Boyd, Edinburgh.

Rosenthal, H., and Paffenhöfer, G.A. (1972) On the digestion rate and calorific content of food and feces in young fish. Naturwissenschaften, 59 : 274-275.

Ross, B., and Jauncey, K. (1981) A radiographic estimation of the effect of temperature on gastric emptying time in Sarotherodon niloticus (L.) x S. aureus (Steindachner) hybrids. J. Fish Biol., 19 : 333-344.

Rozin, P., and Mayer, J. (1964) Some factors influencing short-term food intake of the goldfish. Am. J. Physiol., 206 : 1430-1436.

Rychly, J., and Spannhof, L. (1979) Nitrogen balance in trout. I Digestibility of diets containing varying levels of protein and carbohydrate. Aquaculture, 16 : 39-46.

Schürch, A.F., Lloyd, L.E., and Crampton, E.W. (1950) The use of chromic oxide as an index for determining the digestibility of a diet. J. Nutr., 41 : 629-636.

Seaburg, K.G. (1957) A stomach sampler for live fish. Progve Fish-Cult., 19 : 137-139.

Seaburg, K.G., and Moyle, J.B. (1964) Feeding habits, digestive rates, and growth of some Minnesota warm water fishes. Trans. Am. Fish. Soc., 93 : 269-285.

Shelbourn, J.E., Brett, J.R., and Shirahata, S. (1973) Effect of temperature and feeding regime on the specific growth rate of sockeye salmon fry (Oncorhynchus nerka) with a consideration of size effect. J. Fish. Res. Bd Can., 30 : 1191-1194.

Sheldon, R.E. (1911) The sense of smell in selachians. Exp. Zool., 10 : 51-62.

Shrable, J.B., Tiemeier, O.W.., and Deyoe, C.W. (1969) Effects of temperature on rate of digestion by channel catfish. Progve Fish-Cult., 31 : 131-138.

Smit, H. (1967) Influence of temperature on the rate of gastric juice secretion in the brown bullhead, Ictalurus nebulosus. Comp. Biochem. Physiol., 21 : 125-132.

Smith, K.L. Jr. (1973) Energy transformations by the sargassum fish, Histrio histrio (L.). J. exp. mar. Biol. Ecol., 12 : 219-227.

Smith, R.R. (1971) A method of measuring digestibility and metabolizable energy of fish feeds. Progve Fish-Cult., 33 : 132-134.

Solomon, D.J., and Brafield, A.E. (1972) The energetics of feeding, metabolism and growth of perch (Perca fluviatilis L.). J. anim. Ecol., 41 : 699-718.

Staples, D.J. (1975) Production biology of the upland bully Philypnodon breviceps Stokell in a small New Zealand lake. III Production, food consumption and efficiency of food utilization. J. Fish Biol., 7 : 47-69.

Staples, D.J., and Nomura, M. (1976) Influence of body size and food ration on the energy budget of rainbow trout Salmo gairdneri Richardson. J. Fish Biol., 9 : 29-43.

Steigenberger, L.W., and Larkin, P.A. (1974) Feeding activity and rates of digestion of northern squawfish (Ptychocheilus oregonensis). J. Fish. Res. Bd Can., 31 : 411-420.

Steven, G.A. (1930) Bottom fauna and the food of fishes. J. mar. biol. Ass. U.K., 16 : 677-706.

Sumpter, J.P., and Dodd, J.M. (1979) The annual reproductive cycle of the female lesser spotted dogfish, Scyliorhinus canicula L., and its endocrine control. J. Fish Biol., 15 : 687-695.

Swenson, W.A., and Smith, L.L. Jr. (1973) Gastric digestion, food consumption, feeding periodicity and food conversion efficiency in walleye (Stizostedion vitreum vitreum). J. Fish. Res. Bd Can., 30 : 1327-1336.

Teichmann, H., and Teichmann, R. (1959) Untersuchungen über den Geruchssinn der Haifische. Pubbl. Stazione Zool. Napoli, 31 : 76-81.

Tester, A.L. (1963) Olfaction, gustation, and the common chemical sense in sharks. In : Sharks and Survival (P.W. Gilbert, ed.) pp 255-282. D.C. Heath and Co., Boston.

Thorpe, J.E. (1977) Daily ration of adult perch, Perca fluviatilis L. during summer in Loch Leven, Scotland. J. Fish Biol., 11 : 55-68.

Tyler, A.V. (1970) Rates of gastric emptying in young cod. J. Fish. Res. Bd Can., 27 : 1177-1189.

Tyler, A.V. (1972) Food resource division among northern, marine demersal fishes. J. Fish. Res. Bd Can., 29 : 997-1003.

Tyler, A.V., and Dunn, R.S. (1976) Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, Pseudopleuronectes americanus, with hypotheses regarding population homeostasis. J. Fish. Res. Bd Can., 33 : 63-75.

Vahl, O. (1979) A hypothesis on the control of food intake in fish. Aquaculture, 17 : 221-229.

Van Slyke, D.D., and White, G.F. (1911) Digestion of protein in the stomach and in intestine of the dogfish. J. biol. Chem., 9 : 209-217.

Ware, D.M. (1972) Predation by rainbow trout (Salmo gairdneri) : the influence of hunger, prey density, and prey size. J. Fish. Res. Bd Can., 29 : 1193-1201.

Warren, C.E., and Davis, G.E. (1967) Laboratory studies on the feeding, bioenergetics, and growth of fish. In : The Biological Basis of Freshwater Fish Production (S.D. Gerking, ed.) pp 175-214. Blackwell Scientific Publs., Oxford and Edinburgh.

Western, J.R.H. (1971) Feeding and digestion in two cottid fishes, the freshwater Cottus gobio L. and the marine Enophrus bubalis (Euphrasen). J. Fish Biol., 3 : 225-246.

Wheeler, A. (1978) Key to the fishes of Northern Europe. Fredrick Warne (Publ.) Ltd, London, 380p.

Winberg, G.G. (1956) Rate of metabolism and food requirements of fishes. Fish. Res. Bd Can. Transl. Series No. 194 (1960)

Windell, J.T. (1966) Rates of digestion in the bluegill sunfish. Invest. Indiana Lakes and Streams, 7 : 185-214.

Windell, J.T. (1978) Digestion and the daily ration of fishes. In : Ecology of Freshwater Fish Production (S.D. Gerking, ed) pp 159-183. Blackwell Scientific Publications, Oxford, London, Edinburgh, Melbourne.

Windell, J.T., Kitchell, J.F., Norris, D.O., Norris, J.S., and Foltz, J.W. (1976) Temperature and rate of gastric evacuation by rainbow trout, Salmo gairdneri. Trans. Am. Fish. Soc., 105 : 712-717.

Windell, J.T., and Norris, D.O. (1969) Gastric digestion and evacuation in rainbow trout. Progve Fish-Cult., 31 : 20-26.

Windell, J.T., Norris, D.O., Kitchell, J.F., and Norris, J.S. (1969) Digestive response of rainbow trout, Salmo gairdneri, to pellet diets. J. Fish. Res. Bd Can., 26 : 1801-1812.

Wurtsbaugh, W.A., and Davis, G.E. (1977a) Effects of temperature and ration level on the growth and food conversion efficiency of rainbow trout Salmo gairdneri Richardson. J. Fish Biol., 11 : 87-98.

Wurtsbaugh, W.A., and Davis, G.E. (1977b) Effects of fish size and ration level on the growth and food conversion efficiency of rainbow trout Salmo gairdneri Richardson. J. Fish Biol., 11 : 99-104.

Young, J.Z. (1962) The Life of Vertebrates, Second Edition. Oxford Univ. Press, Oxford and New York 820p.

Young, J.Z. (1980) Nervous control of stomach movements in dogfishes and rays. J. mar. biol. Ass. U.K., 60 : 1-17.

APPENDIX 1 Scyliorhinus canicula: composition of the diet based on sex, size and season, expressed as percentage digested weight.

Diet comparison using Spearman rank correlation coefficient (r_s) to examine the influence of sex $^+$

Size group: 40 - 52 cm	1979								1980			
Prey category	Summer		Autumn		Winter		Spring		Summer		Autumn	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Eupagurus bernhardus	11.06	9.39	46.76	22.58	22.69	24.46	28.00	38.03	28.12	15.10	30.72	25.22
Other Paguridae	4.93	6.76	1.63	1.67	1.67	0.41	6.31	3.12	0.52	1.75	0.42	2.52
Upogebia spp.	8.10	8.72	26.68	32.10	2.78	0.45	4.39	1.92	4.19	16.62	3.56	12.82
Macropipus spp.	2.73	5.64	2.10	2.50	3.43	4.30	6.33	4.53	3.68	1.75	5.68	5.71
Other Crustacea	10.42	7.29	6.53	14.40	11.79	11.76	12.15	10.53	14.58	9.33	12.43	10.86
Buccinum undatum	7.08	14.78	1.50	3.12	2.18	5.97	4.63	5.06	2.00	3.08	23.02	8.47
Glycymeris glycymeris	25.58	25.10	3.30	7.89	6.55	12.75	17.35	16.47	39.05	31.71	8.25	5.35
Pectinidae	2.95	12.66	0.83	5.32	26.37	15.38	5.32	5.42	0.27	2.04	4.75	10.11
Other Mollusca	2.01	3.02	1.13	0.06	8.96	6.88	1.97	3.09	2.94	0	8.46	10.76
Polychaeta	4.20	2.67	5.67	2.12	5.91	5.23	3.54	3.45	1.16	1.21	2.06	5.97
Clupea harengus	15.81	0	2.38	1.69	0	0	0	0	2.58	16.54	0	0
Other Pisces	0	0.07	0.23	0	0.30	1.00	0.29	0.26	0.15	0.01	0.62	1.02
Holothuroidea	0.94	2.76	1.06	0.74	4.44	11.09	9.70	6.96	0.01	0.09	0	1.13
Other	4.18	1.11	0.18	5.87	0.76	0.32	0.03	1.11	0.74	0.76	0.13	0.03
Sample size	32	35	46	40	50	50	79	81	31	26	27	38
r_s	0.429		0.59•		0.864••		0.930••		0.680••		0.797••	

n.s., $P > 0.05$

+ For comparison purposes, prey categories were determined such that each category contributed a minimum of 5% to the diet in at least one sample.

• $P < 0.05$

•• $P < 0.01$

APPENDIX 1 (continued)

Size group:53 - 62 cm

Prey category	1979				1980								63 - 74 cm ‡	
	Summer		Autumn		Winter		Spring		Summer		Autumn		Entire Study Period	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Eupagurus bernhardus	19.92	13.60	40.20	33.51	42.57	34.14	43.49	26.03	25.53	16.36	39.74	37.58	18.66	31.10
Other Paguridae	3.16	0.34	0	7.63	1.20	1.31	0.67	0.82	0.93	0.39	1.16	0.06	3.13	2.15
Upogebia spp.	4.61	5.18	9.96	18.65	0.17	0.07	3.25	3.30	5.52	4.60	3.97	4.79	2.30	2.24
Macropipus spp.	1.74	1.31	0.66	0.94	1.96	1.89	1.76	1.33	8.56	2.28	3.63	0.77	0.66	1.05
Other Crustacea	3.40	3.67	14.52	11.33	5.57	2.84	9.48	7.40	8.68	4.20	7.50	5.40	5.97	5.75
Buccinum undatum	19.36	12.16	12.42	7.54	18.07	21.11	9.00	20.31	9.82	6.49	14.70	14.02	26.16	21.65
Glycymeris glycymeris	23.55	16.15	10.48	4.36	8.68	8.47	14.50	12.54	28.82	34.49	16.36	9.36	18.39	6.04
Pectinidae	3.94	0.86	4.50	4.70	7.87	8.57	4.91	15.79	0.34	4.36	1.55	7.26	5.51	9.74
Other Mollusca	3.40	3.84	2.11	3.64	2.93	4.40	2.19	1.99	1.85	0.67	5.72	8.22	2.21	5.11
Polychaeta	4.52	3.92	2.12	2.91	1.61	1.44	2.86	3.32	0.98	1.14	2.04	0.96	1.77	1.82
Clupea harengus	9.10	35.78	0	0	0	0	0	0	8.54	15.57	0	0	10.93	0.29
Other Pisces	0.65	0.02	0.86	3.68	2.22	12.13	0.29	0.21	0.29	6.11	0	11.33	0.35	8.83
Holothuroidea	2.53	2.57	0.45	0	6.45	3.48	6.43	6.67	0.05	2.89	3.40	0.16	3.33	3.92
Other	0.18	0.46	1.33	1.10	0.66	0.19	1.18	0.26	0.09	0.46	0.15	0.03	0.68	0.42
Sample size	45	31	60	33	45	53	76	68	36	27	31	35	203	43
r_s	0.885••		0.704••		0.917••		0.943••		0.609•		0.638•		0.490•	

Statistical analyses indicate that with a single exception the diets for male and female dogfish are similar. Data given by Canadjija (1961), Jardas (1972) and Capapé (1974) for Scyliorhinus were also tested using Spearman rank correlation (for 8 prey categories) and in accordance with the present findings, sex had no significant influence on the relative composition of the diet.

‡ Only hauls in which male and female individuals occurred together were used in the analysis.

• $P < 0.05$ •• $P < 0.01$

APPENDIX IIa *Scyliorhinus canicula*: composition of the diet by percentage digested weight and percentage numbers.

	Size Class							
	29 - 39 cm		40 - 52 cm		53 - 62 cm		63 - 74 cm	
PREY	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
CRUSTACEA								
Eupagurus bernhardus	30.39	4.26	25.04	7.43	32.77	9.65	27.92	10.82
E. prideauxi	0.92	0.22	1.95	0.74	0.79	0.43	0.88	0.72
E. pubescens	0.11	0.33	0.08	0.25	0.24	0.15	0.02	0.13
E. cuanensis	0.09	0.44	0.23	0.70	0.10	0.74	0.05	0.42
Paguridae	0.55	0.44	1.23	0.74	0.01	0.37	0.92	0.25
Upogebia spp.	9.92	3.28	7.27	4.45	3.87	4.20	1.85	3.04
Macropipus spp.	5.08	6.23	4.59	6.91	2.53	5.82	1.51	4.61
Galathea spp.	2.21	18.25	0.50	8.72	0.26	3.46	0.08	2.37
Porcellana longicornis	0.81	3.39	0.18	2.09	0.03	0.89	+	0.21
Atelecyclus rotundatus	–	–	0.18	0.03	–	–	0.20	0.08
Pinnotheres pisum	–	–	0.05	0.37	0.01	0.12	+	0.04
Maiidae	0.26	0.44	0.33	0.52	0.35	0.52	0.16	0.38
Hyas araneus	2.90	1.31	0.48	0.58	0.44	0.46	0.76	1.23
Ebalia tumefacta	0.09	0.44	+	0.06	+	0.03	–	–
Xanthidae	–	–	–	–	0.02	0.03	–	–
Other Reptantia	0.58	0.98	0.18	0.43	0.20	0.55	0.21	0.38
Eualus pusiolus	1.16	13.88	0.05	1.44	+	0.21	+	0.17
Pandalina brevirostris	0.12	0.66	0.06	1.04	0.01	0.37	0.02	0.85
Dichelopandalus bonnieri	0.10	0.66	0.02	0.24	0.02	0.37	0.02	0.42
Pandalus montagui	0.41	1.31	0.08	0.43	0.05	0.58	0.01	0.30
Crangon allmani	0.62	0.87	0.26	0.86	0.01	0.31	0.04	0.38
Other Natantia	0.13	1.86	0.17	2.49	0.03	0.95	0.02	0.51
Gammaridae	0.27	3.28	0.06	1.41	0.02	0.52	+	0.38
Isopoda	0.48	1.75	0.17	1.87	0.04	0.70	+	0.17
Mysidacea	+	0.11	+	0.12	–	–	–	–
Euphausiacea	–	–	+	0.06	–	–	–	–
Unident. remains	11.09		7.99		5.66		4.64	
MOLLUSCA								
Buccinum undatum	4.01	0.77	6.02	1.72	14.21	4.57	25.59	8.11
Neptunea antiqua	0.49	0.33	0.27	0.09	0.40	0.18	1.58	0.34
Glycymeris glycymeris	11.75	6.45	16.22	18.91	14.10	26.14	14.00	33.47
Chlamys sp.	2.23	1.09	8.36	3.38	5.49	3.95	4.73	3.89
Pecten maximus	–	–	1.75	0.06	0.98	0.09	0.31	0.04
Ensis sp.	–	–	1.93	0.86	1.51	1.13	0.96	0.97
Cardium sp.	–	–	0.21	0.15	0.23	0.12	0.16	0.13
Mya sp.	–	–	0.38	0.06	0.22	0.09	0.89	0.55
Lutraria lutraria	0.04	0.11	0.16	0.06	0.22	0.24	0.16	0.13
Sepiola atlantica	0.01	0.22	0.06	0.12	0.28	0.31	0.24	0.21
Other Mollusca	2.05	0.87	0.70	0.46	0.80	0.31	0.21	0.30

APPENDIX II a (continued)

	Size Class							
	29 - 39 cm		40 - 52 cm		53 - 62 cm		63 - 74 cm	
PREY	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
POLYCHAETA								
Ammotrypane aulogaster	0.60	11.91	0.13	6.41	0.04	3.28	0.01	1.14
Nereis spp.	0.45	1.42	0.33	1.75	0.21	1.84	0.16	2.07
Harmothöe spp.	0.52	2.95	0.37	5.46	0.22	5.39	0.09	3.25
Aphrodite aculeata	–	–	–	–	0.08	0.12	0.08	0.04
Aphroditidae	0.32	1.31	0.16	1.87	0.23	3.16	0.10	1.90
Nephthys spp.	–	–	0.39	0.55	0.17	0.52	0.06	0.42
Glycera spp.	0.67	0.55	0.16	0.95	0.22	1.47	0.08	0.72
Eunicidae	0.69	0.98	0.63	1.50	0.48	1.93	0.48	2.07
Unident. Polychaeta	3.86	3.28	1.34	3.22	0.84	3.46	0.40	3.08
PISCES								
Fish post-larvae	0.02	0.22	0.01	0.18	+	0.15	0.02	0.04
Clupea harengus	–	–	1.97	0.21	3.78	0.28	4.97	0.59
Sprattus sprattus	0.71	0.11	0.02	0.12	–	–	–	–
Callionymus lyra	–	–	–	–	0.44	0.06	0.09	0.04
Glyptocephalus cynoglossus	–	–	–	–	0.51	0.06	–	–
Pleuronectidae	–	–	–	–	–	–	0.44	0.13
Diplecogaster bimaculata	0.03	0.11	0.02	0.15	0.01	0.15	0.01	0.13
Pholis gunnellus	0.01	0.11	–	–	–	–	–	–
Ammodytes spp.	–	–	0.01	0.09	+	0.09	–	–
Trisopterus luscus	–	–	–	–	0.55	0.03	–	–
Agonus cataphractus	–	–	–	–	–	–	0.12	0.04
Cottidae	–	–	+	0.03	–	–	–	–
Gobius microps	–	–	0.03	0.03	–	–	–	–
Gobidae	–	–	0.01	0.03	–	–	–	–
Scyliorhinus canicula	0.81	0.11	–	–	–	–	–	–
Lumpenus lampetraeformis	–	–	0.02	0.03	–	–	–	–
Unident. Teleostei	1.25	1.31	0.53	0.70	1.27	0.98	0.62	0.93
OTHER								
Hydroids	+	0.11	0.07	0.55	0.03	0.80	0.05	1.10
Thyone spp.	1.07	0.87	5.24	4.76	4.50	5.46	3.67	4.61
Ophiura sp.	–	–	–	–	0.07	0.15	–	–
Asterias rubens	–	–	0.24	0.03	0.02	0.06	0.04	0.04
Branchiostoma lanceolatum	–	–	+	0.03	–	–	–	–
Goldfingia sp.	0.12	0.44	0.98	1.38	0.34	1.84	0.26	1.39
Other	–	–	0.12	0.09	0.05	0.12	0.06	0.25
No. examined	175		686		642		500	
No. empty	1		4		5		5	

+ indicates values less than 0.01%

APPENDIX IIb *Scyliorhinus canicula*: diet composition by mean digested weight (g.) and mean number per feeding fish.

	Size Class							
	29 - 39 cm		40 - 52 cm		53 - 62 cm		63 - 74 cm	
PREY	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
CRUSTACEA								
Eupagurus bernhardus	0.66	0.22	1.34	0.35	3.16	0.49	3.22	0.52
E. prideauxi	0.02	0.01	0.10	0.04	0.08	0.02	0.10	0.03
E. pubescens	+	0.02	+	0.01	0.02	0.01	+	0.01
E. cuanensis	+	0.02	0.01	0.03	0.01	0.04	+	0.02
Paguridae	0.01	0.02	0.07	0.04	+	0.02	0.11	0.01
Upogebia spp.	0.22	0.17	0.39	0.21	0.37	0.22	0.21	0.15
Macropipus spp.	0.11	0.33	0.24	0.33	0.24	0.30	0.17	0.22
Galathea spp.	0.05	0.96	0.03	0.42	0.02	0.18	0.01	0.11
Porcellana longicornis	0.02	0.18	0.01	0.10	+	0.05	+	0.01
Atelecyclus rotundatus	–	–	0.01	+	–	–	0.02	+
Pinnotheres pisum	–	–	+	0.02	+	0.01	+	+
Maiidae	+	0.02	0.02	0.02	0.03	0.03	0.02	0.02
Hyas araneus	0.06	0.07	0.02	0.03	0.04	0.02	0.09	0.06
Ebalia tumefacta	+	0.02	+	+	+	+	–	–
Xanthidae	–	–	–	–	+	+	–	–
Other Reptantia	0.01	0.05	0.01	0.02	0.02	0.03	0.02	0.02
Eualus pusiolus	0.02	0.73	+	0.07	+	0.01	+	0.01
Pandalina brevirostris	+	0.03	+	0.05	+	0.02	+	0.04
Dichelopandalus bonnieri	+	0.03	+	0.01	+	0.02	+	0.02
Pandalus montagui	0.01	0.07	+	0.02	+	0.03	+	0.01
Crangon allmani	0.01	0.05	0.01	0.04	+	0.02	+	0.02
Other Natantia	+	0.10	0.01	0.12	+	0.05	+	0.02
Gammaridae	+	0.17	+	0.07	+	0.03	+	0.02
Isopoda	0.01	0.09	0.01	0.09	+	0.04	+	0.01
Mysidacea	+	+	+	+	–	–	–	–
Euphausiacea	–	–	+	+	–	–	–	–
Unident. remains	0.24		0.43		0.54		0.53	
MOLLUSCA								
Buccinum undatum	0.09	0.04	0.32	0.08	1.37	0.23	2.95	0.39
Neptunea antiqua	0.01	0.02	0.01	+	0.04	0.01	0.18	0.02
Glycymeris glycymeris	0.26	0.34	0.87	0.90	1.36	1.34	1.61	1.60
Chlamys sp.	0.05	0.06	0.45	0.16	0.53	0.20	0.54	0.19
Pecten maximus	–	–	0.09	+	0.09	+	0.03	+
Ensis sp.	–	–	0.10	0.04	0.14	0.06	0.11	0.05
Cardium sp.	–	–	0.01	0.01	0.02	+	0.02	0.01
Mya sp.	–	–	0.02	+	0.02	+	0.10	0.03
Lutraria lutraria	+	+	0.01	+	0.02	0.01	0.02	0.01
Sepiola atlantica	+	0.01	+	+	0.02	0.02	0.03	0.01
Other Mollusca	0.04	0.05	0.04	0.02	0.08	0.02	0.02	0.01

APPENDIX IIb (continued)

	Size Class							
	29 – 39 cm		40 – 52 cm		53 – 62 cm		63 – 74 cm	
PREY	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
POLYCHAETA								
Ammotrypane aulogaster	0.01	0.63	0.01	0.31	+	0.17	+	0.05
Nereis spp.	0.01	0.07	0.02	0.08	0.02	0.09	0.02	0.10
Harmothöe spp.	0.01	0.16	0.02	0.26	0.02	0.28	0.01	0.16
Aphrodite aculeata	–	–	–	–	0.01	+	0.01	+
Aphroditidae	0.01	0.07	0.01	0.09	0.02	0.16	0.01	0.09
Nephthys spp.	–	–	0.02	0.03	0.02	0.03	0.01	0.02
Glycera spp.	0.01	0.03	0.01	0.04	0.02	0.08	0.01	0.03
Eunicidae	0.01	0.05	0.03	0.07	0.05	0.10	0.06	0.10
Unident. Polychaeta	0.08	0.17	0.07	0.15	0.08	0.18	0.04	0.15
PISCES								
Fish post-larvae	+	0.01	+	0.01	+	0.01	+	+
Clupea harengus	–	–	0.10	0.01	0.36	0.01	0.57	0.03
Sprattus sprattus	0.01	+	+	+	–	–	–	–
Callionymus lyra	–	–	–	–	0.04	+	0.01	+
Glyptocephalus cynoglossus	–	–	–	–	0.05	+	–	–
Pleuronectidae	–	–	–	–	–	–	0.05	0.01
Diplecogaster bimaculata	+	+	+	0.01	+	0.01	+	0.01
Pholis gunnellus	+	+	–	–	–	–	–	–
Ammodytes spp.	–	–	+	+	+	+	–	–
Trisopterus luscus	–	–	–	–	0.05	+	–	–
Agonus cataphractus	–	–	–	–	–	–	0.02	+
Cottidae	–	–	+	+	–	–	–	–
Gobius microps	–	–	+	+	–	–	–	–
Gobidae	–	–	+	+	–	–	–	–
Scyliorhinus canicula	0.02	+	–	–	–	–	–	–
Lumpenus lampetraeformis	–	–	+	+	–	–	–	–
Unident. Teleostei	0.03	0.07	0.03	0.03	0.12	0.05	0.07	0.04
OTHER								
Hydroids	+	+	+	0.03	+	0.04	+	0.05
Thyone spp.	0.02	0.05	0.28	0.23	0.43	0.28	0.42	0.22
Ophiura sp.	–	–	–	–	0.01	0.01	–	–
Asterias rubens	–	–	0.01	+	+	+	+	+
Branchiostoma lanceolatum	–	–	+	+	–	–	–	–
Goldfingia sp.	+	0.04	0.05	0.07	0.03	0.09	0.03	0.07
Other	–	–	+	+	+	0.01	0.01	0.01
No. examined	175		686		642		500	
No. empty	1		4		5		5	

APPENDIX IIIa Seasonal variation in the composition of the diet of 29-39 cm size class <u>Scyliorhinus canicula</u>, by percentage digested weight and percentage numbers.

PREY	1979				1980							
	Summer		Autumn		Winter		Spring		Summer		Autumn	
	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
CRUSTACEA												
Eupagurus bernhardus	67.79	11.54	20.78	3.85	18.07	3.26	34.02	4.44	6.24	2.27	6.68	3.45
Paguridae	–	–	5.46	3.85	0.36	1.08	2.59	1.12	0.61	2.27	0.18	0.69
Upogebia spp.	4.47	5.77	37.72	10.00	8.44	2.17	3.29	1.11	22.18	6.82	9.33	2.07
Macropipus spp.	1.60	5.77	1.66	3.85	6.13	8.70	5.58	5.83	16.12	6.82	3.64	6.21
Galathea spp.	–	–	0.02	0.77	2.01	21.20	4.48	31.94	0.42	6.82	0.83	6.21
Maiidae	–	–	–	–	4.26	2.71	5.80	2.78	–	–	0.60	0.69
Other Reptantia	2.37	15.39	0.19	1.54	1.58	3.26	1.37	4.44	3.92	20.45	0.30	2.07
Natantia	0.59	11.54	6.97	46.16	3.65	11.41	1.47	12.79	0.19	4.54	4.06	28.28
Other Crustacea	0.33	11.54	0.17	3.85	0.68	3.80	1.08	6.39	2.24	11.40	0.06	0.69
Unident. remains	3.44		6.68		10.00		13.09		15.61		21.50	
MOLLUSCA												
Buccinum undatum	2.97	1.92	13.67	1.54	1.34	1.09	1.15	0.56	–	–	–	–
Neptunea antiqua	–	–	–	–	0.80	1.09	0.83	0.28	–	–	–	–
Glycymeris glycymeris	5.22	5.77	2.85	1.54	12.25	5.98	11.94	8.61	25.35	15.91	15.35	3.45
Chlamys sp.	0.59	3.85	0.32	0.77	1.15	0.54	4.99	1.39	–	–	23.46	0.69
Pecten maximus	–	–	–	–	–	–	–	–	–	–	–	–
Ensis sp.	–	–	–	–	–	–	–	–	–	–	–	–
Mya sp.	–	–	–	–	–	–	–	–	–	–	–	–
Other mollusca	2.96	3.85	1.46	1.54	6.00	2.17	0.43	0.56	–	–	–	–
POLYCHAETA												
Ammotrypane aulogaster	–	–	1.32	16.15	0.19	4.89	0.19	5.56	0.19	4.54	3.76	39.31
Harmothöe spp.	0.32	5.77	–	–	0.32	4.35	0.67	2.50	2.42	11.36	0.12	1.38
Other Polychaeta	4.21	13.46	0.29	2.31	15.04	18.47	4.26	5.00	4.52	6.81	1.94	2.76
PISCES												
Clupea harengus	–	–	–	–	–	–	–	–	–	–	–	–
Other	3.16	1.92	0.43	2.31	6.40	1.63	0.43	2.23	–	–	8.20	2.07
OTHER												
Goldfingia sp.	0.03	1.92	–	–	0.43	1.09	0.05	0.28	–	–	–	–
Thyone sp.	–	–	–	–	0.85	0.54	2.37	1.94	–	–	–	–
Other	–	–	–	–	0.01	0.54	+	0.28	–	–	–	–
No. examined	11		26		32		63		9		34	
No. empty	0		1		0		0		0		0	

APPENDIX IIIb Seasonal variation in the composition of the diet of 40–52 cm size class *Scyliorhinus canicula*, by percentage digested weight and percentage numbers.

PREY	1979				1980							
	Summer		Autumn		Winter		Spring		Summer		Autumn	
	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
CRUSTACEA												
Eupagurus bernhardus	9.46	4.60	37.35	11.42	21.87	5.66	31.92	8.91	22.52	7.05	27.40	7.46
Paguridae	9.07	5.12	1.65	1.95	1.98	1.62	4.35	2.12	1.05	2.56	1.68	2.09
Upogebia spp.	9.62	6.40	28.78	14.49	2.57	1.96	3.49	2.33	9.54	3.85	9.14	4.78
Macropipus spp.	4.01	5.63	2.20	4.46	5.27	9.15	5.16	7.85	2.85	3.85	5.70	5.07
Galathea spp.	0.36	3.84	0.05	1.95	0.46	7.63	0.68	11.66	0.30	6.41	1.01	18.51
Maiidae	0.33	0.77	–	–	1.19	1.63	1.22	1.59	0.23	0.32	0.06	0.60
Other Reptantia	2.02	5.64	0.01	0.28	0.46	1.85	0.48	4.99	0.28	1.92	0.09	1.19
Natantia	0.94	7.68	0.81	15.32	0.89	4.78	0.24	3.29	0.13	2.88	1.09	12.84
Other Crustacea	0.47	7.42	0.44	6.13	0.08	1.86	0.23	3.17	0.18	2.24	0.38	3.28
Unident. remains	4.16		8.35		7.27		9.14		11.21		8.81	
MOLLUSCA												
Buccinum undatum	10.14	2.04	2.13	1.95	5.66	1.74	4.73	1.27	2.47	1.92	14.24	2.09
Neptunea antiqua	–	–	–	–	0.13	0.11	0.74	0.21	0.07	–	0.02	–
Glycymeris glycymeris	24.36	31.46	5.09	4.74	11.86	14.60	16.71	19.19	35.89	44.87	6.50	6.27
Chlamys sp.	1.62	1.53	1.97	1.95	17.25	6.43	6.37	2.86	1.03	1.28	7.98	2.09
Pecten maximus	5.86	0.26	–	–	3.10	0.11	–	–	–	–	–	–
Ensis sp.	1.00	0.26	0.85	0.28	4.09	2.18	–	–	0.50	0.32	5.27	1.79
Mya sp.	–	–	–	–	0.56	0.11	–	–	–	–	1.66	0.30
Other mollusca	1.39	0.51	0.48	0.84	0.72	0.55	1.51	1.17	1.11	0.32	2.90	1.50
POLYCHAETA												
Ammotrypane aulogaster	0.01	0.77	0.46	16.99	0.06	3.92	0.06	4.45	0.12	4.81	0.49	15.52
Harmothöe spp.	0.29	3.84	0.46	6.41	0.56	8.60	0.15	2.86	0.27	4.81	0.58	5.67
Other Polychaeta	3.30	6.91	3.35	6.14	3.52	13.94	2.85	11.35	0.79	5.76	3.36	5.67
PISCES												
Clupea harengus	7.29	0.51	–	–	–	–	–	–	8.59	1.60	–	–
Other	0.03	0.26	2.25	2.51	1.47	2.08	0.35	1.07	0.09	0.64	0.86	1.49
OTHER												
Goldfingia sp.	0.61	1.28	2.38	1.39	1.96	2.18	0.11	0.85	0.34	1.60	0.06	0.60
Thyone sp.	1.87	2.56	0.94	0.56	6.87	6.54	9.19	8.27	0.05	0.64	0.68	0.90
Other	1.78	0.77	0.01	0.28	0.10	0.76	0.42	0.64	0.41	0.32	0.01	0.60
No. examined	72		86		219		187		57		65	
No. empty	3		1		0		0		0		0	

APPENDIX IIIc Seasonal variation in the composition of the diet of 53-62 cm size class <u>Scyliorhinus canicula</u>, by percentage digested weight and percentage numbers.

PREY	1979				1980							
	Summer		Autumn		Winter		Spring		Summer		Autumn	
	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
CRUSTACEA												
Eupagurus bernhardus	17.91	6.12	37.73	13.03	34.34	8.27	39.38	11.19	21.36	8.23	38.61	12.77
Paguridae	1.83	3.79	2.81	1.60	0.77	0.82	0.97	1.96	0.69	0.72	0.59	1.45
Upogebia spp.	4.51	3.80	13.17	14.90	0.88	1.98	2.65	2.08	5.10	3.39	4.43	5.11
Macropipus spp.	2.02	4.85	0.76	2.39	2.99	8.73	1.73	4.73	5.70	5.81	2.15	6.57
Galathea spp.	0.08	1.90	0.04	1.33	0.19	4.89	0.66	4.15	0.09	1.94	0.08	4.75
Maiidae	0.32	0.42	-	-	1.13	1.74	0.98	1.50	1.34	6.24	0.01	0.36
Other Reptantia	0.56	2.95	0.03	0.53	0.39	0.82	0.12	2.31	0.26	1.93	0.06	0.72
Natantia	0.26	5.91	0.27	4.52	0.12	2.09	0.03	0.92	0.02	1.21	0.31	5.47
Other Crustacea	0.13	2.32	0.05	1.07	0.05	1.05	0.03	0.92	0.08	1.21	0.02	1.09
Unident. remains	2.37		12.95		4.15		6.49		4.87		5.93	
MOLLUSCA												
Buccinum undatum	15.57	3.80	10.62	3.99	17.44	6.05	13.43	4.73	8.31	2.91	14.39	4.01
Neptunea antiqua	-	-	-	-	0.62	0.23	0.46	0.12	0.34	0.24	0.56	0.73
Glycymeris glycymeris	19.99	32.07	8.45	16.49	8.63	17.69	13.21	21.69	31.40	55.45	12.72	25.55
Chlamys sp.	2.45	2.32	4.58	4.52	9.56	6.87	4.14	3.00	2.17	1.45	4.52	4.01
Pecten maximus	-	-	-	-	-	-	3.95	0.23	-	-	-	-
Ensis sp.	-	-	0.91	0.80	2.75	2.21	0.14	0.23	0.34	0.24	5.14	4.38
Mya sp.	-	-	0.50	0.53	-	-	0.43	0.12	0.05	+	0.63	+
Other mollusca	4.40	1.89	1.28	0.54	1.19	0.47	1.23	1.39	0.59	0.48	0.69	1.09
POLYCHAETA												
Ammotrypane aulogaster	0.01	0.42	0.17	11.70	0.01	1.40	0.02	3.23	0.02	1.69	0.07	5.11
Harmothöe spp.	0.30	4.85	0.20	5.59	0.20	6.75	0.25	5.77	0.17	3.15	0.11	4.01
Other Polychaeta	4.22	13.71	2.06	10.91	1.78	11.87	2.84	18.46	0.84	4.82	1.29	7.28
PISCES												
Clupea harengus	18.95	0.84	-	-	-	-	-	-	11.74	1.21	-	-
Other	0.63	1.69	1.90	1.60	5.13	2.57	0.22	1.05	2.94	0.73	5.88	0.72
OTHER												
Goldfingia sp.	0.26	1.90	0.66	2.13	0.42	2.33	0.30	1.61	0.24	0.97	0.09	1.82
Thyone sp.	3.24	3.80	0.29	0.53	7.17	10.01	6.01	6.92	1.34	0.97	1.72	2.92
Other	0.02	0.63	0.59	1.36	0.07	1.17	0.34	1.74	0.01	0.97	-	-
No. examined	83		93		167		170		63		66	
No. empty	1		1		2		1		0		0	

APPENDIX IIId Seasonal variation in the composition of the diet of 63-74 cm size class *Scyliorhinus canicula*, by percentage digested weight and percentage numbers.

PREY	1979				1980							
	Summer		Autumn		Winter		Spring		Summer		Autumn	
	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
CRUSTACEA												
Eupagurus bernhardus	15.21	8.62	22.87	10.70	26.89	9.56	37.66	12.93	27.49	9.70	34.51	12.62
Paguridae	5.21	1.04	0.17	1.12	2.14	2.08	1.00	1.64	0.21	1.12	1.08	1.94
Upogebia spp.	2.49	3.13	4.91	7.61	0.58	1.66	0.98	1.93	3.24	2.61	1.62	2.43
Macropipus spp.	2.22	3.66	0.40	2.25	1.78	8.32	1.11	4.31	2.42	4.10	1.19	3.40
Galathea spp.	0.03	1.57	0.01	0.05	0.06	2.91	0.14	2.38	0.09	2.61	0.14	6.31
Maiidae	0.26	0.78	-	-	1.48	3.12	1.65	2.97	-	-	-	-
Other Reptantia	1.37	2.35	-	-	0.62	0.63	0.01	0.45	0.02	0.75	-	-
Natantia	0.09	3.39	0.09	1.12	0.12	2.29	0.04	0.60	0.05	1.87	0.57	12.62
Other Crustacea	+	0.26	0.02	1.12	+	0.21	0.02	0.60	+	0.37	0.09	1.95
Unident. remains	2.26		8.08		2.43		6.36		5.00		5.80	
MOLLUSCA												
Buccinum undatum	22.19	7.31	29.49	7.32	34.57	12.27	21.63	7.58	20.45	5.97	14.03	5.83
Neptunea antiqua	-	-	-	-	2.21	0.42	1.43	0.30	4.87	1.12	2.83	0.49
Glycymeris glycymeris	17.77	45.43	16.31	41.69	6.07	15.38	13.29	29.12	29.13	52.24	16.18	29.13
Chlamys sp.	3.02	3.66	8.05	5.35	7.82	7.28	2.36	2.23	1.07	1.12	5.61	2.91
Pecten maximus	-	-	-	-	-	-	1.08	0.15	-	-	-	-
Ensis sp.	-	-	0.47	0.28	1.51	1.87	0.87	1.04	0.15	0.37	3.77	2.34
Mya sp.	0.03	0.26	3.03	1.13	0.51	0.62	0.60	0.30	1.27	0.75	1.58	0.49
Other mollusca	0.30	0.78	1.29	0.84	0.62	0.63	0.72	0.80	0.19	0.37	2.58	0.98
POLYCHAETA												
Ammotrypane aulogaster	-	-	0.02	1.97	+	0.62	0.01	1.49	0.02	1.12	0.02	1.94
Harmothöe spp.	0.07	2.61	0.05	1.97	0.09	4.99	0.13	4.01	0.06	1.87	0.12	1.94
Other Polychaeta	1.14	7.83	2.63	10.13	1.12	11.22	1.57	14.27	0.64	5.97	0.67	5.83
PISCES												
Clupea harengus	23.67	2.61	-	-	1.70	0.21	0.55	0.15	1.79	0.75	-	-
Other	0.27	0.52	0.14	0.56	2.03	2.29	1.67	1.34	0.33	1.12	3.07	0.97
OTHER												
Goldfingia sp.	0.11	0.78	0.22	1.13	0.20	1.66	0.50	1.49	0.07	1.49	0.08	1.94
Thyone sp.	2.01	2.61	1.65	3.10	5.37	7.28	4.47	6.24	1.43	1.87	4.36	2.91
Other	0.36	0.78	0.06	0.56	0.09	1.66	0.17	1.64	0.03	0.75	0.07	0.97
No. examined	66		74		121		144		42		53	
No. empty	0		1		1		1		0		2	

APPENDIX IV <u>Scyliorhinus canicula</u>: seasonal importance of selected prey species, expressed as mean digested weight (g) and mean numbers per feeding fish.

PREY	1979				1980							
	Summer		Autumn		Winter		Spring		Summer		Autumn	
	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.
	29-39 cm length size class											
Eupagurus bernhardus	3.76	0.54	0.34	0.19	0.47	0.19	0.77	0.25	0.15	0.11	0.07	0.15
Upogebia spp.	0.24	0.27	0.62	0.50	0.22	0.12	0.07	0.06	0.52	0.33	0.09	0.09
Buccinum undatum	0.16	0.09	0.22	0.08	0.04	0.06	0.03	0.03	-	-	-	-
Glycymeris glycymeris	0.28	0.27	0.05	0.08	0.32	0.34	0.27	0.49	0.60	0.78	0.15	0.15
Chlamys sp.	0.03	0.18	0.01	0.04	0.03	0.03	0.11	0.08	-	-	0.23	0.03
Clupea harengus	-	-	-	-	-	-	-	-	-	-	-	-
Thyone spp.	-	-	-	-	0.02	0.03	0.05	0.11	-	-	-	-
	40-52 cm length size class											
Eupagurus bernhardus	0.67	0.26	1.43	0.48	1.14	0.28	1.83	0.45	1.36	0.39	1.16	0.38
Upogebia spp.	0.67	0.36	1.10	0.61	0.13	0.08	0.20	0.12	0.58	0.21	0.38	0.23
Buccinum undatum	0.71	0.12	0.08	0.08	0.29	0.07	0.27	0.06	0.15	0.11	0.61	0.11
Glycymeris glycymeris	1.71	1.78	0.19	0.20	0.62	0.61	0.96	0.97	2.17	2.46	0.28	0.32
Chlamys sp.	0.11	0.09	0.08	0.08	0.90	0.27	0.37	0.14	0.06	0.07	0.34	0.11
Clupea harengus	0.51	0.03	0.08	0.01	-	-	-	-	0.52	0.09	-	-
Thyone spp.	0.13	0.14	0.04	0.02	0.36	0.28	0.53	0.42	+	0.04	0.03	0.05
	53-62 cm length size class											
Eupagurus bernhardus	1.78	0.35	2.62	0.53	3.99	0.43	3.56	0.57	2.24	0.54	3.38	0.53
Upogebia spp.	0.45	0.21	0.91	0.61	0.10	0.10	0.24	0.11	0.53	0.22	0.38	0.21
Buccinum undatum	1.54	0.22	0.74	0.16	2.02	0.32	1.21	0.24	0.87	0.19	1.26	0.17
Glycymeris glycymeris	1.98	1.85	0.59	0.67	1.00	0.92	1.19	1.11	3.29	3.63	1.11	1.06
Chlamys sp.	0.24	0.13	0.32	0.18	1.11	0.35	0.37	0.16	0.23	0.10	0.40	0.17
Clupea harengus	1.88	0.05	-	-	-	-	-	-	1.23	0.08	-	-
Thyone spp.	0.32	0.22	0.02	0.02	0.83	0.52	0.54	0.36	0.14	0.06	0.15	0.12
	63-74 cm length size class											
Eupagurus bernhardus	2.34	0.50	2.17	0.52	3.43	0.38	4.33	0.61	3.08	0.46	2.39	0.40
Upogebia spp.	0.38	0.18	0.47	0.37	0.07	0.07	0.11	0.09	0.36	0.17	0.11	0.09
Buccinum undatum	3.41	0.42	2.80	0.36	4.40	0.49	2.49	0.36	2.29	0.38	0.97	0.23
Glycymeris glycymeris	2.73	2.64	1.55	2.03	0.77	0.62	1.53	1.37	3.26	3.33	1.12	1.13
Chlamys sp.	0.46	0.21	0.76	0.26	1.00	0.29	0.40	0.10	0.12	0.07	0.39	0.11
Clupea harengus	3.64	0.15	-	-	0.22	0.01	0.06	0.01	0.20	0.04	-	-
Thyone spp.	0.31	0.15	0.16	0.15	0.68	0.29	0.51	0.29	0.16	0.12	0.30	0.11

APPENDIX V : *Scyliorhinus canicula*: mean weight of stomach contents (g) over three 24-hr sampling periods. Solid, partially digested remains considered separately from the semifluid digested component.

TIME OF DAY (hr) - G.M.T.

(A) NOVEMBER 1979

Date:		7/11/79		19-20/11/79			
29-39 cm size class		1100-1310	1525-1615	1915-2045	2305-0045	0315-0445	0715-0845 •
	n	15	0	2	6	0	0
Solid	Wet wt.	1.37	–	1.40	1.50	–	–
component	Dry wt.	0.26	–	0.30	0.24	–	–
Semifluid	Wet wt.	2.77	–	2.47	3.46	–	–
component	Dry wt.	0.37	–	0.38	0.44	–	–
40-52 cm size class							
	n	20	3	20	20	3	0
Solid	Wet wt.	6.52	1.87	2.96	3.08	3.21	–
component	Dry wt.	1.45	0.53	0.57	0.58	0.57	–
Semifluid	Wet wt.	6.97	6.59	8.16	8.08	6.55	–
component	Dry wt.	0.90	0.90	0.96	0.95	0.86	–
53-62 cm size class							
	n	19	11	14	20	9	7
Solid	Wet wt.	7.82	7.66	6.14	5.34	7.91	7.48
component	Dry wt.	1.65	1.57	1.29	1.20	1.65	1.45
Semifluid	Wet wt.	16.33	13.42	15.55	14.36	14.06	11.10
component	Dry wt.	2.05	2.32	2.16	1.96	1.80	1.09
63-74 cm size class							
	n	13	21	11	10	3	5
Solid	Wet wt.	12.85	10.26	5.11	7.00	12.16	6.54
component	Dry wt.	3.46	2.53	1.22	1.86	2.85	1.37
Semifluid	Wet wt.	21.94	20.82	17.92	16.34	16.18	14.03
component	Dry wt.	6.85	4.37	2.48	2.37	2.33	1.96

• Net torn

(B) FEBRUARY 1980

Date:		19-20/2/80				27/2/80	
29-39 cm size class		1130-1330	1600-1730	1930-2100	2300-0030	0530-0700	0830-1000
	n	6	2	2	1	1	6
Solid	Wet wt.	1.63	1.10	6.70	5.21	0.21	2.80
component	Dry wt.	0.24	0.21	1.27	1.02	0.04	0.57
Semifluid	Wet wt.	4.43	3.59	6.46	2.94	1.84	4.72
component	Dry wt.	0.58	0.65	2.04	0.95	0.37	0.76
40-52 cm size class							
	n	19	20	20	20	20	20
Solid	Wet wt.	4.42	7.48	5.28	5.29	5.87	5.32
component	Dry wt.	0.89	1.64	1.10	0.96	1.29	1.08
Semifluid	Wet wt.	10.07	10.36	8.44	9.11	8.26	8.50
component	Dry wt.	1.23	1.29	0.98	0.99	0.86	1.06
53-62 cm size class							
	n	17	15	17	10	20	20
Solid	Wet wt.	8.69	6.96	7.04	7.73	7.58	11.61
component	Dry wt.	1.73	1.38	1.59	1.56	1.71	2.74
Semifluid	Wet wt.	16.78	12.77	12.30	13.58	16.10	16.68
component	Dry wt.	2.09	1.47	1.52	1.50	2.10	1.83
63-74 cm size class							
	n	8	8	6	3	17	20
Solid	Wet wt.	13.46	14.38	15.44	7.19	10.19	11.42
component	Dry wt.	3.26	2.94	3.93	1.68	2.58	2.70
Semifluid	Wet wt.	16.67	15.95	17.63	12.36	19.91	18.52
component	Dry wt.	2.18	2.06	2.81	1.77	2.25	2.33

APPENDIX V (cont.)

TIME OF DAY (hr) - G.M.T.

(C) JUNE 1980

Date: 24-25/6/80

		1015-1215	1415-1615	1815-2000	2215-2400	0145-0330	0515-0645
29-39 cm size class							
	n	9	15	8	5	11	5
Solid component	Wet wt.	2.29	2.56	2.68	1.80	2.03	2.37
	Dry wt.	0.46	0.50	0.46	0.06	0.39	0.42
Semifluid component	Wet wt.	3.90	4.06	3.14	1.72	3.56	3.97
	Dry wt.	0.46	0.46	0.35	0.31	0.43	0.52
40-52 cm size class							
	n	20	22	22	20	20	16
Solid component	Wet wt.	6.95	5.19	4.48	5.69	4.88	4.04
	Dry wt.	1.48	1.15	0.90	1.18	0.95	0.78
Semifluid component	Wet wt.	8.87	10.60	8.71	8.60	7.54	8.74
	Dry wt.	0.92	1.34	0.95	0.96	0.84	1.05
53-62 cm size class							
	n	14	22	22	20	20	2
Solid component	Wet wt.	10.73	9.50	7.17	8.58	11.60	10.57
	Dry wt.	2.55	2.15	1.61	1.88	2.66	2.01
Semifluid component	Wet wt.	18.75	18.93	16.56	17.31	12.18	14.63
	Dry wt.	2.20	2.27	1.92	2.05	1.38	1.97
63-74 cm size class							
	n	15	19	20	20	17	6
Solid component	Wet wt.	8.95	11.22	13.00	11.20	12.45	15.21
	Dry wt.	2.20	2.79	3.28	2.79	3.19	3.39
Semifluid component	Wet wt.	14.16	20.76	18.92	20.15	16.47	20.88
	Dry wt.	1.76	2.91	2.06	2.63	2.01	2.53

APPENDIX VI

The possible causes of ulceration observed in growth experiments (Chapter 4) were investigated in collaboration with Professor R.J. Roberts and Dr M. Horne, University of Stirling.

Pathology Report (Dr M. Horne)

1. A. Lesions were sampled at two 'depths'; viz.
   (a) normal subcutaneous postion away from centre of necrosis,
   (b) from area of fresh necrosis deep in musculature; onto marine, blood agar

   B. Numerous strains were obtained but those which were considered the most likely pathogens were subcultured

   C. Six likely isolates were studied in depth; four were generally of the marine vibrio-aeromonas group and the other two were the same as each other and close to *Vibrio anguillarum*.

2. A. Dogfish at 9°C in recirculating sea water were challenged by intramuscular injection of 10^7 viable cells in 0.1 ml saline. A group of fish were maintained as controls in separate tanks. Fifteen days post challenge one experimental fish was moribund with subcutaneous haemorrhage on ventral surface - not typical of the diseased dogfish.

   B. Two of the challenged fish were sacrificed and all lymphoid organs sampled for bacteria. Bacteria were obtained in small numbers from the spleen of the 'healthy' fish; all other samples were negative.

3. Water temperature was increased to 15°C and a further batch challenged IP. Scarifications were made on the dorsal surface and bacteria infiltrated into these areas. Five weeks post challenge all fish were healthy and scarifications healed. During week six one dogfish died with lesions typical of those of the condition. Unfortunately this fish was frozen and no bacteria could be isolated.

4. In conclusion:

   The work is far too incomplete to make any sound conclusion. The pathogen may be bacterial, Gram negative infection, though it has not been shown that it is not a viral condition and its infectious nature has not been proven.

APPENDIX VII Scyliorhinus canicula: details of growth and food consumption at different temperatures and varying ration levels for each biweekly period.

A. Experimental Temperature: 16.6°C (16.0–17.0°C)

			Mean weight (g)		Daily food intake per dogfish			Growth (± SD)	
	Week ending	No. of dogfish	Initial	Final	FR	Dry wt. (g)	Energy (kcal)	Increment (g)	Cumulative % initial b.w.
TI	2	11	452.82	483.02	1.53	2.784	19.886	30.20 ± 26.77	6.55 ± 5.90
	4	11	483.02	476.30	0.96	1.813	12.947	-6.72 ± 16.41	4.69 ± 7.12
	6	11	476.30	484.77	1.02	1.833	13.095	8.47 ± 27.94	6.89 ± 7.66
	8	11	484.77	507.10	1.10	2.127	15.196	22.20 ± 19.22	11.71 ± 7.95
TII	2	11	444.01	459.84	0.98	1.722	12.301	15.83 ± 23.26	3.44 ± 5.27
	4	11	459.84	473.21	0.98	1.809	12.919	13.37 ± 16.85	6.55 ± 3.27
	6	11	473.21	489.95	0.98	1.773	12.664	16.74 ± 21.98	10.39 ± 4.39
	8	11	489.95	506.56	0.98	1.919	13.705	16.61 ± 5.02	14.16 ± 4.80
TIII	2	12	412.06	418.72	0.70	1.121	8.009	6.66 ± 13.58	1.68 ± 3.30
	4	12	418.72	420.61	0.70	1.150	8.213	1.88 ± 18.36	2.22 ± 4.97
	6	12	420.61	436.87	0.68	1.104	7.887	16.26 ± 20.27	5.82 ± 3.33
	8	12	436.87	433.07	0.70	1.220	8.716	-3.8 ± 35.87	5.30 ± 7.25
TIV	2	12	426.25	421.49	0.40	0.661	4.722	-4.76 ± 8.41	-1.07 ± 1.99
	4	12	416.72	416.72	0.40	0.662	4.726	-4.77 ± 8.25	-2.32 ± 2.56
	6	12	416.37	416.37	0.40	0.624	4.758	-0.35 ± 11.56	-2.50 ± 3.83
	8	12	414.21	414.21	0.40	0.652	4.656	-2.16 ± 5.50	-2.93 ± 3.82

B. Experimental Temperature: 14.1°C (13.0–15.5°C)

TI	2	10	344.59	354.35	1.04	1.187	8.064	9.76 ± 13.76	3.10 ± 3.92
	4	10	354.35	360.58	1.07	1.138	7.726	6.23 ± 12.65	4.60 ± 4.68
	6	10	360.58	367.43	1.10	1.315	8.932	6.85 ± 12.78	6.21 ± 5.62
	8	10	367.43	375.62	1.29	1.557	10.579	8.19 ± 14.80	8.44 ± 8.25
TII	2	10	347.96	352.28	0.70	0.794	5.392	4.32 ± 14.40	0.79 ± 4.09
	4	9	346.29	345.89	0.70	0.718	4.878	-0.37 ± 11.13	0.47 ± 5.67
	6	9	345.89	348.42	0.70	0.796	5.408	2.53 ± 9.29	1.34 ± 5.61
	8	9	348.42	347.79	0.70	0.790	5.365	-0.63 ± 11.22	1.01 ± 8.04
TIII	2	9	344.20	340.29	0.40	0.449	3.049	-3.91 ± 9.60	-1.48 ± 2.57
	4	9	340.29	334.06	0.40	0.405	2.753	-6.23 ± 8.73	-3.52 ± 4.51
	6	9	334.06	330.58	0.40	0.440	2.986	-3.43 ± 6.68	-4.49 ± 6.11
	8	9	330.58	321.42	0.41	0.429	2.915	-9.16 ± 9.79	-7.45 ± 5.41
TIV	2	11	319.57	311.69	0.20	0.210	1.426	-7.88 ± 5.59	-2.42 ± 1.81
	4	11	311.69	302.23	0.20	0.186	1.266	-9.46 ± 7.32	-5.21 ± 2.98
	6	11	302.23	295.41	0.20	0.199	1.354	-6.82 ± 7.51	-7.21 ± 3.90
	8	11	295.41	283.62	0.20	0.192	1.306	-11.79 ± 7.02	-10.77 ± 4.47

C. Experimental Temperature: 10.9°C (10.0–11.6°C)

TI	2	9	422.50	430.12	0.65	0.922	6.419	7.62 ± 26.75	2.34 ± 7.26
	4	9	430.12	412.18	0.41	0.525	3.653	-17.94 ± 13.01	-1.73 ± 7.03
	6	9	412.18	405.59	0.54	0.664	4.623	-6.59 ± 16.01	-3.62 ± 6.03

D. Experimental Temperature: 9.8°C (8.5–10.5°C)

TI	2	9	337.69	332.67	0.48	0.622	4.441	-5.02 ± 11.58	-1.86 ± 3.83
	4	8	348.25	344.86	0.29	0.398	2.846	-3.39 ± 12.29	-2.31 ± 4.97
	6	8	344.86	347.78	0.45	0.589	4.212	2.92 ± 14.11	-1.68 ± 5.66
	8	8	347.78	345.21	0.56	0.778	5.559	-2.57 ± 8.81	-2.08 ± 4.04
TII	2	8	348.79	348.29	0.33	0.447	3.197	-0.50 ± 15.15	-0.26 ± 4.69
	4	8	348.29	346.69	0.39	0.530	3.786	-1.60 ± 9.73	-0.64 ± 6.76
	6	8	346.69	344.75	0.38	0.493	3.523	-1.94 ± 13.48	-1.29 ± 7.70
	8	7	348.54	340.74	0.37	0.513	3.666	-7.80 ± 7.90	-2.20 ± 5.34
TIII	2	8	372.15	371.08	0.43	0.621	4.438	-1.07 ± 12.91	-0.09 ± 2.99
	4	8	371.08	364.46	0.33	0.481	3.433	-6.62 ± 14.17	-1.63 ± 3.67
	6	8	364.46	353.18	0.34	0.467	3.338	-11.28 ± 12.48	-4.55 ± 5.19
	8	7	351.34	329.53	0.28	0.385	2.754	-21.81 ± 14.21	-8.83 ± 4.96
TIV	2	9	311.44	302.21	0.19	0.227	1.619	-9.23 ± 12.39	-3.03 ± 4.04
	4	8	315.79	310.91	0.20	0.251	1.796	-4.88 ± 9.50	-4.06 ± 5.04
	6	8	310.91	304.86	0.20	0.233	1.667	-6.05 ± 7.34	-5.88 ± 5.60
	8	8	304.86	296.22	0.20	0.242	1.730	-8.64 ± 4.60	-10.03 ± 8.30

T = tank number

APPENDIX VIII *Scyliorhinus canicula*: results of analyses of body constituents at the start and end of growth experiments. Values are means with ranges in brackets, except the start, mean ± standard deviation.

Temp. (°C)	Ration Level kcal/fish/day	Water Content (%)	Protein Content (% wet wt.)	Lipid Content (% wet wt.)	Ash (% dry wt.)	Energy Content (kcal/g dry wt.)
16.6	Start	71.46 ± 2.37	22.20 ± 1.40	7.46 ± 3.14	4.49 ± 0.66	6.002 ± 0.295
	15.281	66.87 (65.42-69.71)	20.97 (19.44-23.30)	12.61 (8.40-15.96)	2.95 (1.45-3.99)	6.349 (6.109-6.525)
	12.897	69.37 (67.32-71.25)	22.18 (21.28-23.25)	9.41 (7.60-10.40)	4.06 (3.70-4.35)	6.295 (6.102-6.623)
	8.206	71.70 (71.33-72.42)	19.40 (18.70-19.83)	7.08 (6.52-6.98)	4.14 (4.05-4.22)	5.963 (5.891-6.037)
	4.64	71.15 (64.81-73.45)	21.35 (18.22-23.01)	9.78 (5.97-18.18)	3.75 (2.98-4.50)	6.085 (5.794-6.413)
14.1	Start	72.28 ± 2.72	22.18 ± 1.60	6.66 ± 2.96	4.35 ± 0.57	5.881 ± 0.377
	8.825	71.49 (69.27-73.39)	22.41 (22.17-22.75)	7.17 (5.90-9.11)	4.69 (3.95-5.67)	5.922 (5.677-6.091)
	5.261	70.13 (68.82-71.33)	22.18 (21.93-22.46)	9.43 (8.57-10.17)	3.82 (3.51-4.16)	6.052 (5.917-6.237)
	2.915	73.57 (70.55-76.03)	22.25 (21.72-22.98)	5.26 (1.87-8.86)	4.80 (4.33-5.11)	5.544 (5.101-6.090)
	1.338	74.33 (72.99-76.89)	22.27 (21.55-23.00)	4.94 (2.08-6.85)	5.58 (4.39-7.60)	5.582 (5.153-5.876)
9.8	Start	71.28 ± 3.77	21.25 ± 1.34	7.39 ± 4.17	4.23 ± 0.88	5.973 ± 0.558
	4.264	71.08 (69.67-72.99)	21.88 (21.10-22.35)	7.92 (6.15-9.36)	4.62 (4.45-4.79)	5.952 (5.802-6.099)
	3.543	71.58 (67.33-73.71)	21.95 (21.58-22.49)	7.63 (4.65-12.70)	4.07 (2.91-4.65)	5.914 (5.621-6.451)
	3.491	70.24 (68.41-71.36)	21.94 (20.97-22.77)	8.17 (6.68-10.38)	3.98 (3.58-4.28)	6.152 (5.958-6.496)
	1.703	72.03 (68.68-74.21)	22.36 (21.91-22.64)	5.86 (4.11-8.56)	4.77 (4.61-4.88)	5.913 (5.635-6.352)