The feeding ecology of the European otter (lutra lutra l.) in a marine environment

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ABSTRACT

THE FEEDING ECOLOGY OF THE EUROPEAN OTTER (LUTRA LUTRA L.) IN A MARINE ENVIRONMENT

HUGH CHRISTOPHER WATSON

The bulk of the research took place on the coast of Fetlar, Shetland, in 1976-78. Otters were studied by direct observation of individuals recognised by variations in natural markings on the lips and throat, and in addition their diet was studied by means of spraint (faecal) analysis. Most foraging occurred in the sea within 150 m of the shore, a wide variety of fish species being eaten, the majority demersal, as well as some crabs. The pronounced seasonal variation in dietary composition is considered in the light of available information on the behaviour of the prey species. Detailed observations of an adult female and her cub revealed a significant difference in the composition of their diets, the cub taking a lower proportion of the faster prey species as well as a significant number of crabs which were not predated at all by the adult. Most feeding was localised in bouts in relatively restricted areas. There was no clear correlation between otter activity and the diel or tidal cycles. The adult female and her cub had a home range consisting of 2.5km of coastline with a maximum foraging area of 42.6ha, and their pattern of use of this home range is described. Evidence suggests that for the effective exploitation of foraging areas, breeding females require holt sites (resting places) close by. In 1977 the minimum population density along 11km of coast was 1 otter : 1.2km of coast; and in 1978 along 16km of coast was 1 otter : 0.9km of coast. A positive correlation between dive duration and water depth was noted and it is hypothesised that this is a causal relationship determined by the necessity for minimising the upthrust produced by the air in the lungs during diving. The implications of this for otter foraging behaviour and population distribution are discussed.

THE FEEDING ECOLOGY OF THE EUROPEAN OTTER (LUTRA LUTRA L.) IN A MARINE ENVIRONMENT

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Master of Science

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I declare that all the material contained in this thesis is my own and has not previously been submitted for a degree in this or any other university.

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CHAPTER 1

INTRODUCTION

1.1 The European Otter

The European Otter Lutra lutra L. (Mammalia, Order Carnivora, family Mustelidae, sub-family Lutrinae) is an amphibious carnivore, widely distributed in the Palaearctic. It is found right across Eurasia from Ireland and the Iberian Peninsula in the west to Japan in the east, and from sub-arctic Scandinavia and Siberia in the north to North Africa, India and the Great Sunda Islands in the south. Over most of this range it is the sole representative of the Lutrinae, but in southern Asia it is sympatric with three other species of otter. It occurs in and around a wide range of freshwater habitats : rivers, streams, estuaries, lakes and marshes, and in certain parts of Northern Europe along the sea-coast.

The European Otter is long-bodied and short-legged. The tail is long and tapering, quite thick towards the base, and is slightly flattened dorso-ventrally; the feet are webbed and each has five toes; the neck is thick and not much less in circumference than the head; the eyes are situated quite high and quite well forward; the muzzle is fleshy and well-endowed with stout vibrissae; vibrissae are also present on the cheeks, throat, above the eyes, and on the elbows; the pelage consists of a dense, short underfur with longer, glossy guard hairs; the colour is generally some shade of brown above, becoming paler below, and the chin and throat are usually white to off-white. Males are generally larger and heavier than females, the mean total length of a sample of males measured by Stephens (1957) being 119 cm, compared with 104 cm for females. Males had a mean weight of 10.3 kg, and females one of 7.4 kg.

Table 1: Synonyms used in the literature for otter faeces and resting places

Faeces	Resting Places
excrements	dens
faeces	holes
stools	hovers (if used only for short periods)
scats	holts (if more-or-less permanent)
spraints	lie-ups (if used only for short periods)
	resting places

The terms used in this thesis are underlined

1.2 Previous studies

Otters have featured in European stories and legends for centuries, and in Britain were until recently hunted with dogs for sport, and shot or trapped for their pelts or as vermin. Consequently a specific otter terminology has developed (Table 1), and a considerable body of popular lore and dogma, much of it conflicting, has accumulated. The memoirs of sportsmen and naturalists are full of anecdotes which, while often interesting and indicative of the otter's behavioural plasticity, contribute only marginally to an understanding of its ecology. The general consensus of this popular body of knowledge was, however, reasonable, and suggested that the otter lives primarily along rivers, eats mostly fish, is largely nocturnal and that it is unpredictable in its movements.

The first attempt at scientific study was that of Stephens (1957), who examined data and corpses received from the masters of the various Otter Hunts (packs of otter hounds) in order to determine the relative abundance of otters in different parts of Britain, and to investigate the breeding cycle. She also examined the distribution of otter spraints along a stretch of the River Clettwr in Wales, and analysed a small sample (178) of spraints, in order to study the diet.

Between 1958 and 1966, Sam Erlinge carried out detailed studies of otter ecology in a lake and river system in Southern Sweden. These studies covered most aspects of otter ecology: diet in relation to habitat, season and prey availability (Erlinge,1967a); home range size and usage in relation to sex and reproductive status (Erlinge, 1967b); territoriality (Erlinge, 1968a); foraging behaviour of captive animals (Erlinge,1968b); and the comparative feeding ecology of the otter and the mink (Mustela vison) (Erlinge, 1969). His principal techniques were spraint analysis (14,615 spraints examined) and tracking.

Erlinge defined the otter's ecological niche as that of "a predator feeding on animals of suitable size, which are more or less associated with aquatic habitats". He noted that while a wide range of animals occurred in the diet, comparatively few species, most of them fish, made up the bulk of it. He showed convincingly that local and seasonal variations in dietary composition could be correlated with variations in the availability and vulnerability of the different prey species (Erlinge, 1967a), and concluded that there was a preference for more motile prey, i.e. fish, rather than frogs and crayfish (Erlinge, 1968b).

His tracking study, carried out between 1958 and 1966 was outstandingly successful. From measurements, and by making plaster casts for reference, he was able to identify the tracks of individual otters, and thus to trace their movements. This was most readily done in winter when there was a cover of snow on the ground, but could also be accomplished in the summer months when tracks were to be found in sand or mud. One of his principal discoveries (Erlinge, 1967b and 1968a) was that females with cubs (family groups) occupied discrete home ranges and that there was apparently little territorial conflict between these groups. Adult males had larger territories which usually included the home range of a family group and sometimes also the ranges of non-breeding females. Boundaries between male territories were overlapping zones where conflict occurred continually, mostly in the form of intense olfactory signalling, using spraints deposited at prominent and regularly-frequented spots.

Territorial behaviour was manifested only between individuals of the same sex, and he concluded that whereas the territoriality of family groups was primarily concerned with ensuring an adequate supply of food for the young, that of males was primarily of sexual significance. He estimated that during winter approximately two thirds of the population was in established territories, while the remaining third (consisting of non-breeding females, immature animals and males without territories) behaved as temporary residents or transients. The overall population density was 1 otter per 0.7-1.0 km^2 of water, equivalent on the lakes to 1 otter per 2-3 km length of lake shore and on the streams to 1 otter per 5 km length of stream.

Erlinge's work remains the most comprehensive study on the ecology of the European Otter to date, and all subsequent research has served primarily to corroborate or modify his findings.

In Britain a widespread decline in otter numbers and distribution, particularly in England and Wales, started in the late 1950's. Its causes have been analysed and attributed primarily to ingestion of organochlorine pesticide residues (Chanin and Jefferies, 1978), and its extent is now well documented (e.g. Lenton et al., 1980). It was gradually realised that greater knowledge about the behaviour and ecology of the otter in Britain would be helpful in devising conservation measures. However, studying otters in Britain has proved to be difficult. No tracking studies along the lines of Erlinge's have been carried out successfully, probably because the population densities of otters along British rivers are relatively low, and it is therefore physically difficult to cover a large enough area in a short enough period to build up a reasonably unambiguous body of evidence on individual movements (Watson, unpublished data). Nor, at the time when the present study was being planned (1975) had anyone managed to gather much information by direct observation. A few useful observations had been published, most notably those of Bates (1960), but it seemed that the problems of locating, watching and following otters in Britain were so great that they precluded systematic observation.

It is, however, relatively easy to locate, map and analyse spraints, and almost all studies of otters have relied largely on this faecal evidence. The various surveys of otter distribution in Britain and Europe have relied entirely on the presence or absence of spraints (e.g. Green and Green, 1980), and dietary studies have also relied primarily on spraint analysis. At the time when the present study was started (1976), published dietary studies had been carried out exclusively in freshwater and estuarine habitats, e.g. Fairley, 1972; Fairley and Wilson, 1972; Hewson, 1973; Ommen and Santen, 1970; Veen, 1975; Webb, 1975; Weir and Banister, 1973 and 1975. In so far as information was available on the potential prey, all these studies tended to confirm Erlinge's view of the otter being a facultative amphibious carnivore.

An attempt to study the movements of otters using activity recorders placed at sprainting points was made by Graham Moysey and E. & H. Hurrell, but insufficient data were collected to build up an acceptable picture of local movements (Hurrell, 1963). Initial attempts to study otter behaviour and ecology using radio-telemetry and the injection of radio-active isotopes met with limited success (Jenkins, 1980 and pers.comm.), but current studies are beginning to produce valuable data (Green, Green and Jefferies, 1984; Kruuk, Conroy, Glimmerveen and Ouwekerk, 1986).

1.3 Background to the present study

The author's interest in otters started in 1968, and by 1975 he had firsthand knowledge of the problems associated with carrying out and interpreting tracking and spraint distribution studies, and of the extreme difficulty of actually watching otters on British rivers. Having been alerted to the possibility of watching otters on the west coast of Scotland by an article written by Rowbottom (1969), he first tried it himself on the island of Rum (or Rhum) in 1974. The results were encouraging in that the otters were partially diurnal and could be watched without causing disturbance. However the nature of Rum's coastline (mostly high cliffs) made it very difficult to follow them and keep them under observation.

To carry out a study based on the direct observation of wild otters, it therefore seemed necessary to find an area with both diurnal otters and a generally low coastline which would enable an observer to follow them. Further enquiries suggested that such an area might be found in the Shetlands, and subsequently the present study was started there, on the island of Fetlar, in July 1976.

It would not have been possible to continue the project in 1977 and 1978 without the financial support of the Vincent Wildlife Trust, and Professor George Dunnett permitted the use of the facilities of the Zoology Department, University of Aberdeen, in between periods of fieldwork, but otherwise the study was undertaken independently, without formal affiliation to any institution or organisation, until 1980.

1.4 Aims of the present study

The aims of the study were broad: it was not intended to test any particular hypotheses, but rather to explore the possibilities offered by a partially diurnal population of otters, and to discover which aspects of their ecology could usefully be studied by direct observation. It was hoped that it would be possible to estimate the population density of otters in the coastal environment, and after it was found that they could be identified individually, the main aim of the study became the establishment of the home ranges of as many individuals as possible. However the problems of reliably and regularly locating particular individuals necessitated an opportunistic approach to data collection, and throughout the study the weather and sea conditions played a large part in determining and modifying its course. It should also be mentioned that during each season's fieldwork there was never any guarantee that financial support would be forthcoming for the next one, and this dictated that the project could only be planned in the short-term.

This thesis is concerned with those aspects of the study most directly relevant to feeding ecology. Most of the information gathered on social behaviour, breeding behaviour and ontogeny will be presented elsewhere.

CHAPTER 2

STUDY AREA

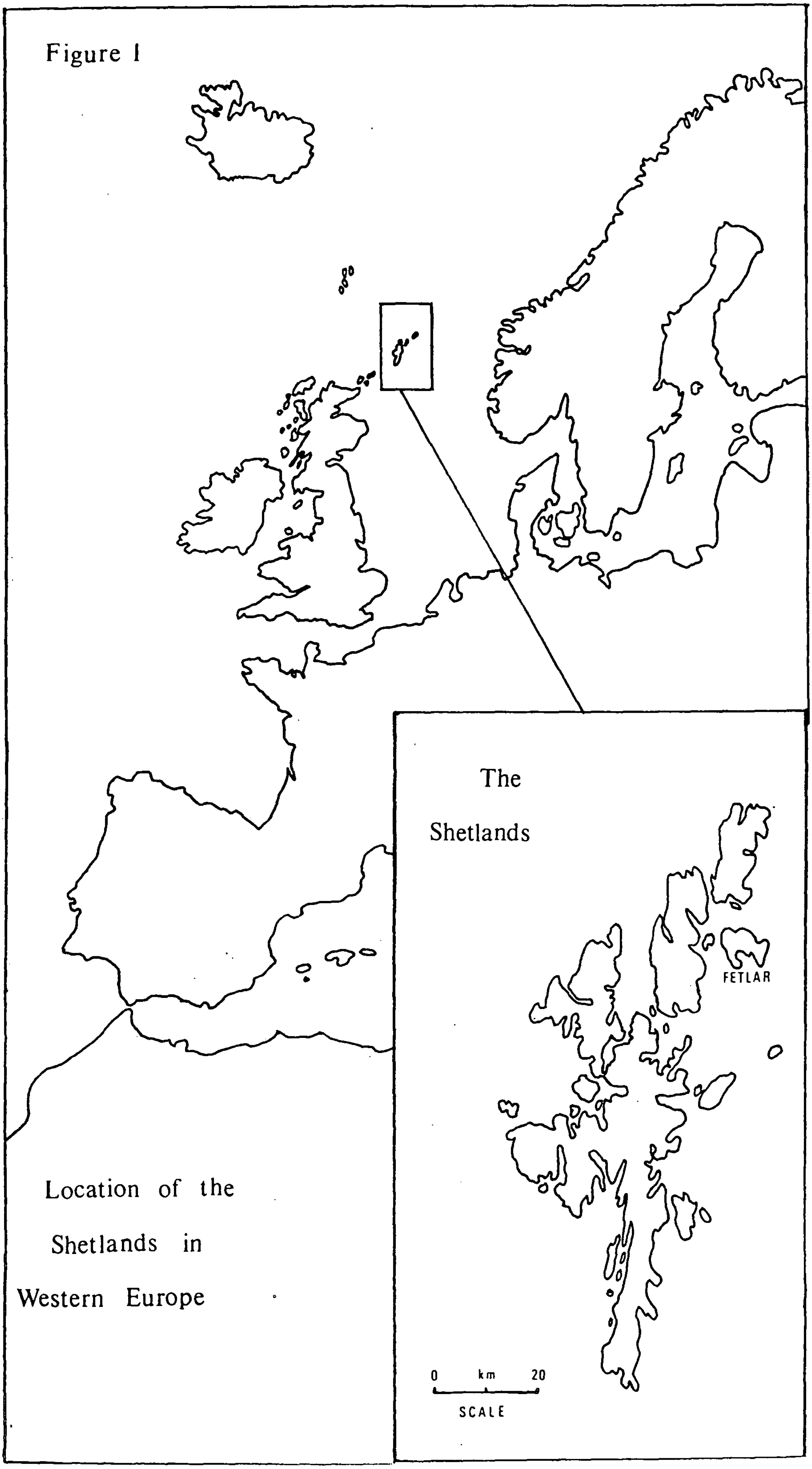
2.1 Location and coastal geomorphology

The Shetlands are a group of islands lying some 200 km north-east of mainland Britain and 350 km west of Norway, at the latitude of 60°N and the longitude of 1°W (Figure 1). There are three main islands and many smaller ones, separated by narrow sea channels. The islands, which extend for 160 km north to south and for 70 km west to east (excluding the outliers Foula and Fair Isle), have a total land area of about 1,440 km^2, but the coastline is so involuted that no part of the islands is more than five kilometres from the sea.

Structurally they are a range of partially submerged hills rising above the plains of the North Sea floor. They consist of Pre-Cambrian metamorphic rocks with younger plutonic intrusions, and some Old Red Sandstone (Devonian) in the west and south-east (Mykura, 1974). The hills are generally smooth, rounded and low (maximum height of 450 m), with a superficial cover of peat or boulder clay.

The coastline can be divided into two geomorphological categories (Flinn, 1974). The <u>Outer Coast</u> consists largely of cliffs, some very high, which face the open sea and plunge without interruption beneath the water. It is considered to have resulted from marine erosion with varying sea levels, both above and below the present level, for many millions of years, and forms rather less than a third of the present Shetland coastline.

Figure I



Location of the Shetlands in Western Europe

The more sheltered coastline in inlets and between the islands forms the Inner Coast. It has resulted from the rapid relative rise in sea level during post-glacial times, and the consequent submergence of the hillsides. This has resulted in a shoreline of low cliffs with numerous small indentations (known locally as geos), and with beaches at the heads of the larger inlets and in the more sheltered bays. Beach deposits, ranging from boulders to mud and peat, occur below tide level around much of the Inner Coast, even where the shoreline itself consists of cliffs.

Both types of coastline are to be found on Fetlar (Figure 2), most of the fieldwork being carried out on the inner coast between Tressa Ness and Corbie Head (Figure 3). Sub-littoral beach deposits are found around most of this stretch of coastline, locally extending up to high tide level, and at one locality, Sand of Sand, above it. Most of these beach deposits are in the form of boulders with localised patches of sand.

2.2 Climate

Shetland's climate has been classified as sub-montane oceanic (Spence, 1960) or as hyperoceanic humid northern temperate (Birse, 1971). The average annual rainfall at Lerwick, on Mainland, is about 1000 mm, and at Baltasound, on Unst, is about 1125 mm. The wettest months are November to January, and the driest are May and June. The average annual mean temperature is 7.1°C at Lerwick, the average January mean being 3.4°C, and the average July mean being 11.9°C. The islands are extremely exposed and windy (the average wind speed at Lerwick is 7.3 ms^{-1}), and gales are frequent. Indeed, with the exception of parts of the Outer Hebrides, Shetland is the windiest part of the British Isles.

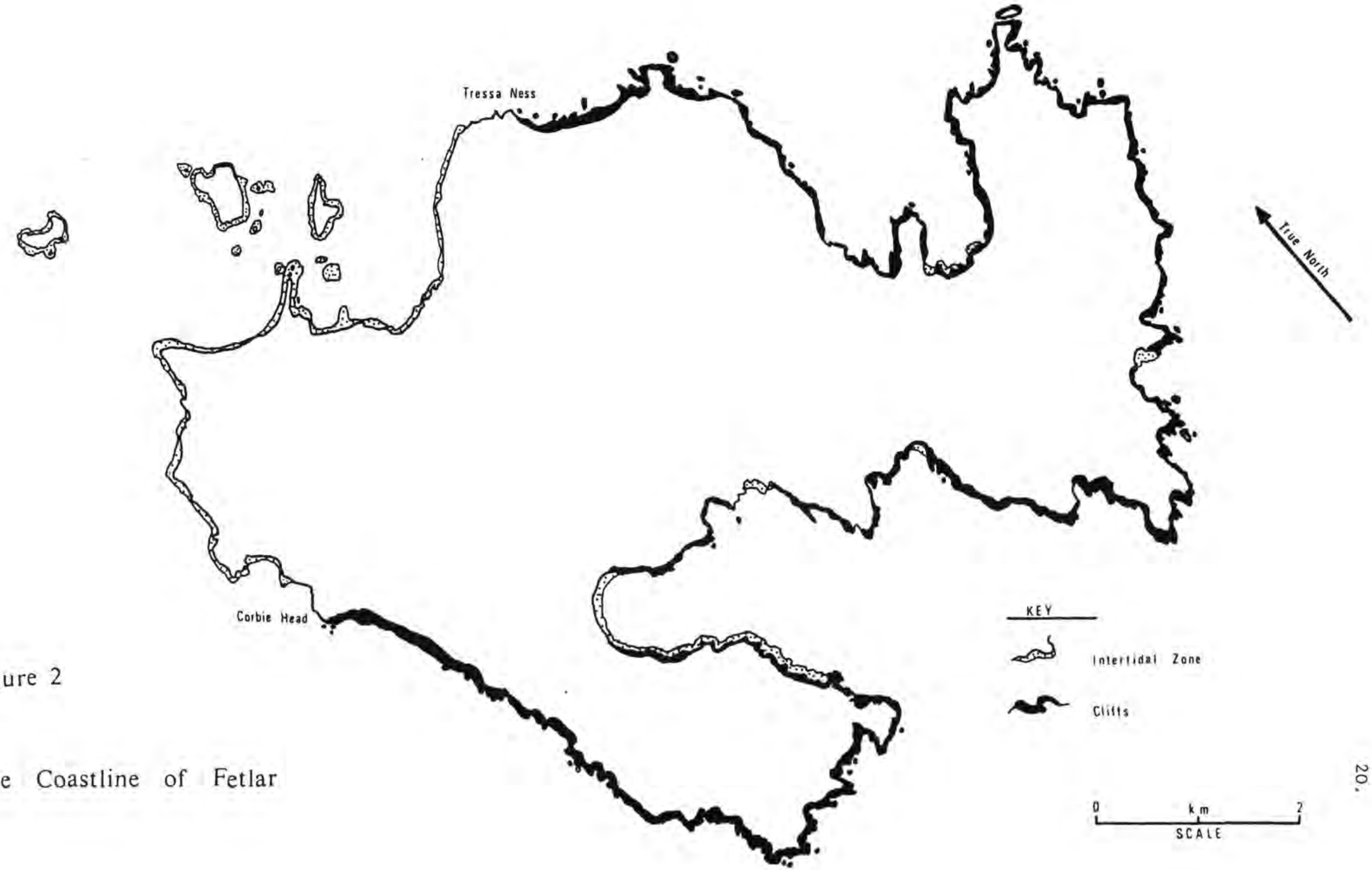


Figure 2

The Coastline of Fetlar

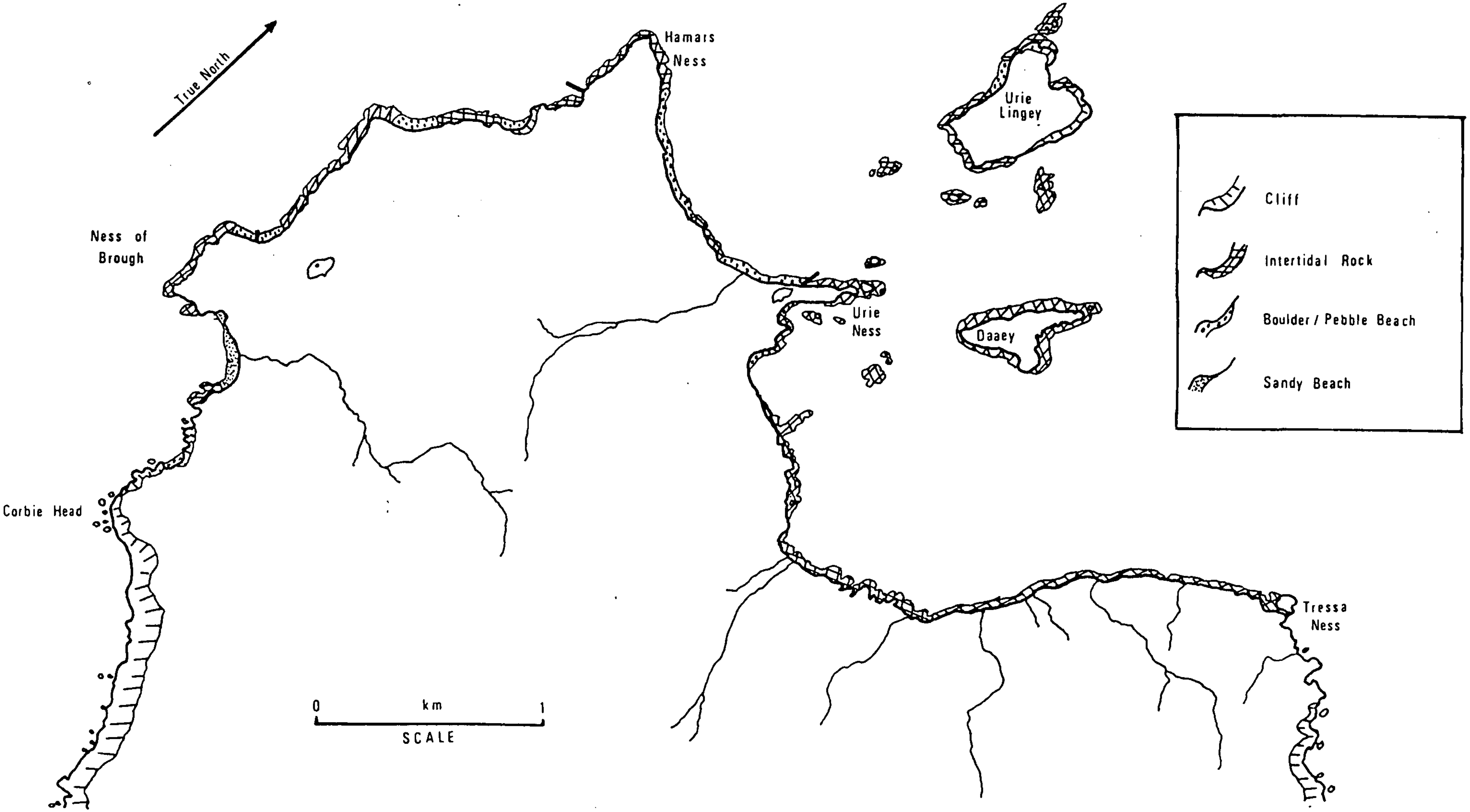


Figure 3. The Main Study Area, North-West Fetlar.

Being at 60°N, winter daylength is very short, and summer daylength is correspondingly long. On clear nights in June it was occasionally possible to continue to follow otters throughout the night.

2.3 Terrestrial vegetation

Throughout the Shetlands the severity of the wind and the high concentrations of wind blown salt result in very difficult growing conditions for trees. On Fetlar, as in most other parts of the islands, trees are found only in sheltered gardens. Most of Fetlar is covered with sedge-grass heath, locally herb-rich, with little or no peat development. However on the more acidic rocks of the long Lamb Hoga ridge in the west of the island there is wet Calluna moorland with extensive peat development. For a detailed description of vegetation types in Shetland, see Johnston (1974).

2.4 Tidal range and marine vegetation

The tidal range in Shetland is low in comparison with the rest of the British Isles. At Basta Voe, on Yell, some 5 km away from the main study area on Fetlar, on the other side of Colgrave Sound, the difference between mean high water level and mean low water level is 2.0 m at springs and 1.0 m at neaps. Since the coastline is mostly steep, the eulittoral zone is mostly narrow. Rock-pools are few, and small in size. Along the main study area this zone is for the most part moderately exposed and dominated by barnacles (Balanus balanoides). Appreciable fucoid growth occurs only at the heads of sheltered inlets and where the rocky shore levels out. Below the barnacle zone there is a narrow zone of red algae mixed with the kelp

Laminaria digitata. In the sub-littoral zone rock and boulder substrates are dominated by the kelp Laminaria hyperborea, while sandy substrates are devoid of vegetation. Where there are extensive sub-littoral boulder deposits, large areas of kelp are visible not far below the sea surface.

2.5 Human settlement and land-use

During the study period there were approximately 100 people living on the island of Fetlar, almost all engaged in crofting. Although settlement was more extensive in the past, all the occupied dwellings are now concentrated in a belt across the south-central part of the island (Figure 4). West of the settlement area a road leads to the inter-island ferry terminal at Oddsta, where thrice-daily ferries link the island with the rest of Shetland. A branch of this road leads past the deserted house at Brough to a rarely-used slipway. Away from the immediate vicinity of the occupied crofts, the land is used solely as rough pasture for sheep, ponies and cattle. Sheep are also grazed on the small offshore islands of Daaey, Urie Lingey and Sound Gruney.

There is no commercial fishing, but fishing for home consumption is occasionally carried out from the shore at various points along the south coast, and at Oddsta. The most commonly caught fish is the saithe (Pollachius virens). Thus the only part of the main study area that was frequently visited by people was the Oddsta Ferry Terminal.

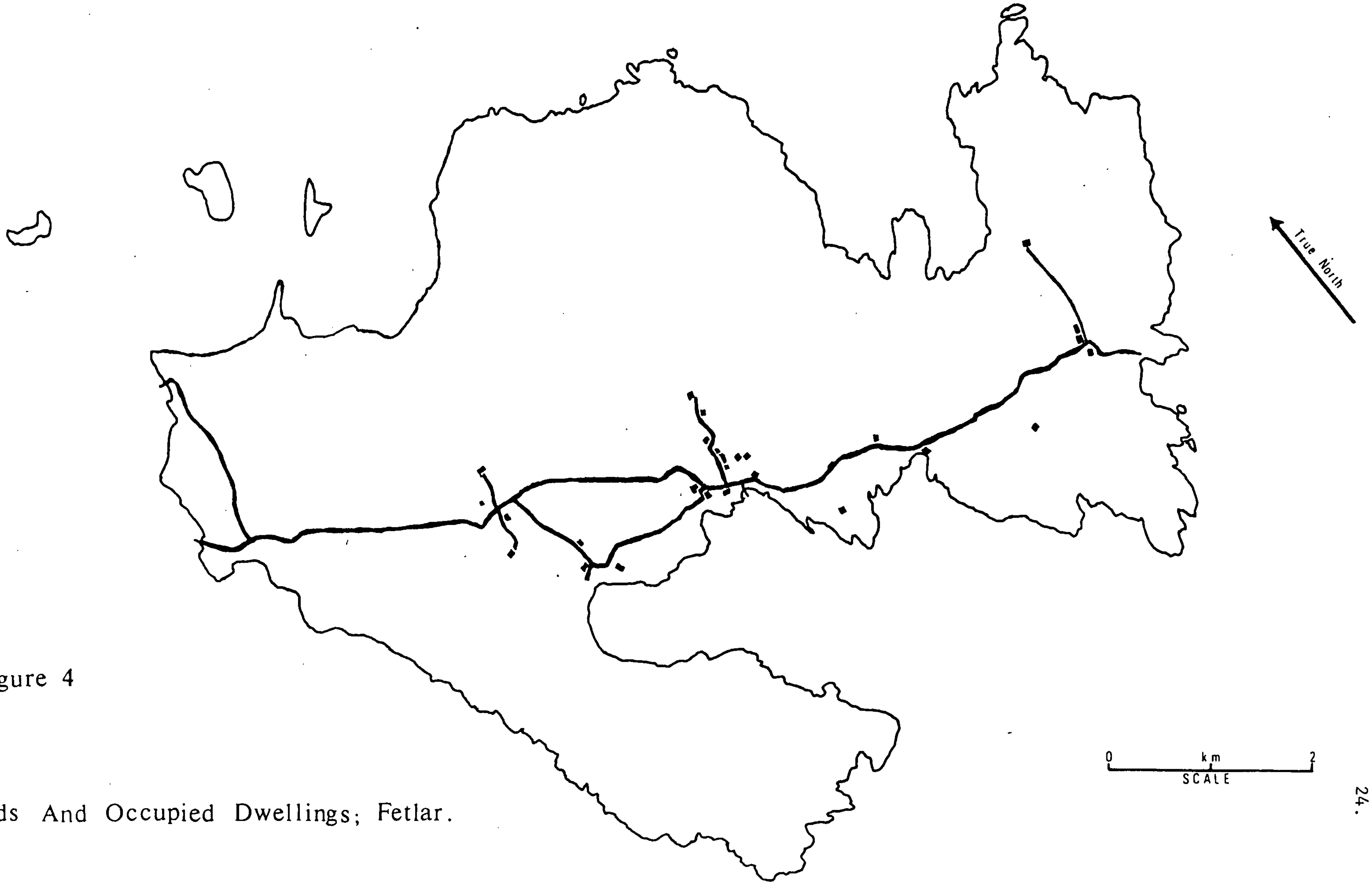


Figure 4

Roads And Occupied Dwellings; Fetlar.

CHAPTER 3

METHODS

3.1 Fieldwork: periods and personnel

Periods of fieldwork and hours of direct observation of otters are shown in Table 2.

Additional fieldwork was undertaken over a three month period at various localities in the Outer Hebrides, Orkney and Shetland in 1980, and over a three week period on the Erradale Peninsula, Wester Ross, in August 1981.

Fieldwork was carried out unassisted in 1976, 1977, 1980 and 1981, and with the assistance of Tessa Jones and Andrew Savage in 1978.

3.2 Direct observation methods

Otters were rarely located during early attempts at systematic coverage of the coast, so decisions on which stretch of the coast to search for otters at any particular time were based on cumulative experience of the behaviour of the individuals, on apparent levels of activity as indicated by the quantities and distribution of fresh spraints, and on the weather and sea conditions. Attention was focussed on any otters that were behaving fairly predictably.

Table 2: Duration of fieldwork on Fetlar and time spent observing otters

		Duration (weeks)	No. of hours direct observation of otters
July - September	1976	6	26.8
January	1977	1	0.1
April - August	1977	18	102.6
May - September	1978	19	39.9
	TOTAL	44	169.4

In areas where it was anticipated, or hoped, that otters would be active, searching was carried out by a combination of waiting at suitable vantage points and by slowly walking along the coast. Most otters were first located in the water. Once located, they were followed and kept under observation for as long as possible. For prolonged periods of observation it was necessary to keep downwind of the otter as much as possible, and to try not to get into a position where the otter was likely to come close enough to notice a stationary observer (5-10 m). Most observations were made at distances of 10-100 m, using 10x50 binoculars. Observations were generally written directly into a notebook, but in 1978 a cassette-recorder was used on occasions and the data transcribed later. By moving only when the otter was underwater, it was usually fairly easy to keep pace with it. Most watches were continued until contact with the otter was lost and it could not be re-located. This occurred due to difficult sea conditions (breaking waves, strong swell or reflected light); to failing light in the evening; to the onset of heavy rain plus wind (the observer wears spectacles); to the otter entering a lie-up or holt; or to the otter becoming alarmed at the observer's presence. Occasionally, since the Shetland climate is frequently not conducive to prolonged periods of immobility in exposed places, watches were terminated due to observer discomfort.

The durations of dives and of periods spent on the surface between dives were measured by timing continuously-recorded field observations on a casette-recorder.

Distances were estimated by eye relative to landmarks or to the size of the otter.

3.3 Spraint analysis

Samples of spraints were collected throughout the main study area in 1976 and 1977. Only recently-deposited spraints that could reliably be collected intact were chosen (at well-used sites, spraints tend to accumulate into a homogenous mass). They were stored separately in plastic bags for later analysis. The method of analysis used was basically that of Erlinge (1967a). Spraints consist of undigested food remains loosely bound together in a matrix of mucus. This mucus, whether wet or dry, can be removed by soaking in any kind of detergent. Following Webb (1976) spraints were soaked overnight in a solution of the denture-cleaner "Steradent", then washed in a 0.5 mm mesh sieve, left to dry, then examined with the aid of a binocular microscope.

Since the bulk of the prey remains consisted of fish bones, it was necessary to build up a reference collection of the hard parts of littoral and inshore fish. Vertebrae, being both numerous and readily classifiable, were the most useful remains for the present purpose, so a key to, primarily, the antero-caudal vertebrae, which generally showed the specific identification features most clearly, was prepared. Obtaining fresh specimens of some of the less commonly caught non-commercial fish species was not easy, and the final key was prepared in 1981, although a prelininary key had been prepared in 1978 which proved adequate for the majority of fish vertebrae (Appendix 1). As it was not always possible to identify vertebrae to the species level, broader taxa had to suffice for some types of vertebrae.

Other remains, e.g. scales, skin tubercles and jaw-bones, were found to be diagnostic for particular taxa, but they were discounted for the purposes of analysis since in the absence of vertebrae in a particular spraint, their inclusion would lead to a bias in favour of these particular taxa.

In the case of the Gadidae, it was possible to separate its members into two taxa (Rocklings, e.g. Ciliata and Gaidropsarus, and Non-Rockling Gadoids, e.g. Pollachius and Gadus, but only if postero-caudal vertebrae were present (postero-caudal vertebrae of rocklings have prominent anterior metapophyses and zygapophyses, those of non-rockling Gadoids have minute anterior metapophyses and zygapophyses). If antero-caudal vertebrae only were present, they could be classified only as "Unattributed Gadoid".

Crabs (Brachyrhyncha) and Squat Lobsters (Galatheidae), the two main categories of crustaceans taken, were identified from the pattern and texture of carapace and leg fragments. Bird feathers were recorded, but no attempt was made to identify them further. The only mammalian remains found were otter hairs, presumably ingested during grooming. Small amphipod and isopod crustaceans, and small molluscs, all of which were frequent in spraints, were not recorded, since direct observation of the foraging otters suggested that they did not take such small prey: it was considered that these derived entirely from the alimentary tracts of prey fish, most of which do feed on small invertebrates.

CHAPTER 4

RESULTS

4.1 Individual identification

4.1.1 Sex and age differences

Although sexual dimorphism is not as pronounced in the otter as it is in some other Mustelids, e.g. the mink (Mustela vison) and stoat (Mustela erminea), males are on average considerably larger and heavier than females. Thus adult males, when compared with adult females, have a markedly heavy-bodied appearance, and it is particularly striking that the neck is thicker and the head broader. However in respect of smaller otters not accompanied by cubs, the author considered that it was unsafe to ascribe a sex to any individual solely on the grounds of size and build. The apparent build of an individual depends on whether its fur is still sleek and wet from the water, spiky and half-dry after shaking, or fluffy and fully-dry after grooming. Young cubs are easily distinguished by their small size and fluffy coats, and older cubs, even when they are similar in length to their mothers, are notably thin-necked and generally skinnier. Solitary, lightly-built, rather small otters were presumed to be immature, probably between 1 and 2 years old. However there remained a heterogeneous category of medium-sized, moderately built otters which was presumed to consist of sub-adults of both sexes and non-breeding adult females.

Towards the end of the study it was noticed that males and females could be distinguished by the angle of urination. When seen from the side it is apparent that in the case of females the urine splashes down between the hind-legs, while in males it is directed forwards in a stream to land under the belly. These observations were, unfortunately, made too late to be of much value in the present study.

4.1.2 Differences in coat markings

As was the case with body build, the general colour of the coat appeared to vary with the otter's wetness and with light conditions. On all the otters seen the general body colour was brown, becoming paler and off-white on the chin and throat. However it was discovered that superimposed on this off-white pelage were brighter white or yellowish markings which varied in shape and extent between individuals. There was also a variable extent of white on the upper lips. Thus it was possible to recognise individuals if a clear view of the throat was obtained during a watch (Figure 5). Provided that the observer was close enough and that there was sufficient light, a clear view of the throat could usually be obtained while the otter was eating or grooming, but inevitably this was not always possible, and on many occasions the identity of the individual under observation remained uncertain or unknown.

Two of the individuals studied (Buda and Norma-Jean) were located and watched in three successive seasons (1975-78). Their throat and lip markings remained the same throughout this period, so this seems to be a useful long-term means of individual recognition.

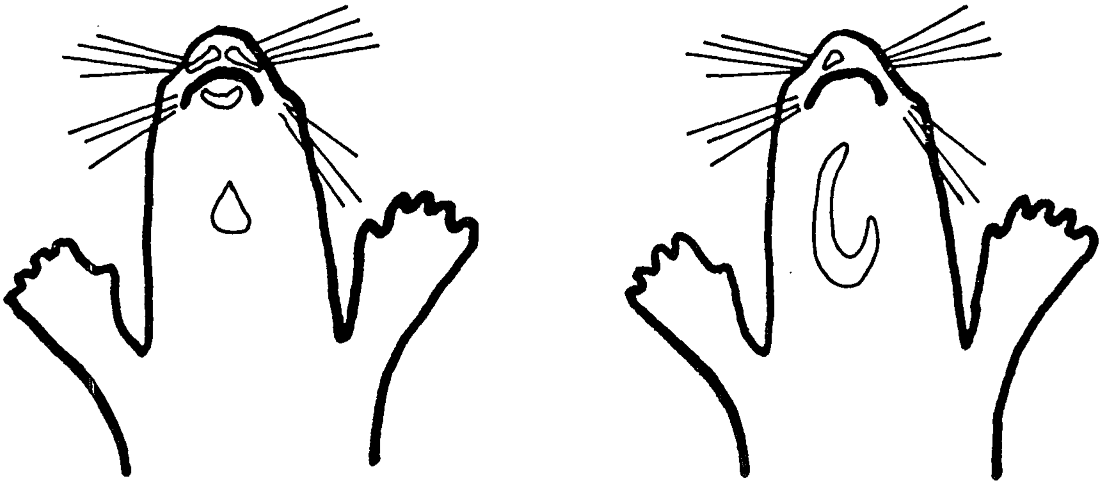
4.2 Foraging behaviour

4.2.1 Diving

Foraging otters spent most of their time in the sea between 10 m and 100 m offshore. No accurate bathymetric data were available for the entire

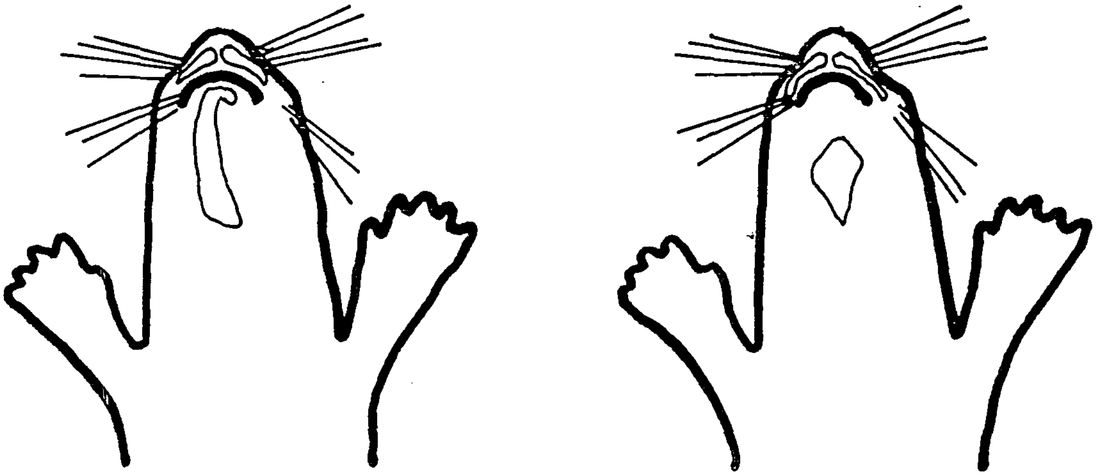
Figure 5

The Lip and Throat Markings of some Otters on Fetlar



Adult male
‘Scooby’

Adult female
‘Buda’



Juvenile
‘Harald’

Adult female
‘Norma-Jean’

study area, but observations and spot soundings indicated that the water they were diving in was generally between 2 m and 5 m deep. From a good vantage point in calm conditions it was possible to watch otters swimming underwater. On such occasions they invariably dived down almost vertically into the dense growth of Laminaria hyperborea. Their subsequent progress could only be followed by the trail of air bubbles rising behind them, and an otter was actually seen in pursuit of prey on only one occasion. In this instance the quarry was a butterfish (Pholis gunnellus) which was chased into the open water above the Laminaria. It then doubled back down in amongst the fronds with the otter still in pursuit. The trail of bursting air bubbles (which originate from both air squeezed out of the fur and from air exhaled out of the corners of the mouth (Wayre, 1977)), generally proceeded in an interrupted wavering line across the surface, frequently culminating in a localised turmoil of many large bubbles, shortly after the appearance of which the otter would surface, with or without prey. Otters occasionally floated on the surface with their heads underwater, but for the most part there was no visual reconnaissance before diving.

The duration of dives and inter-dive periods on the surface which were timed are given in Table 3. The data were gathered from at least 9 individuals on a total of 15 separate occasions. The mean duration of a successful dive (25.4 ± 10.2s) was significantly shorter than that of an unsuccessful dive (32.7 ± 8.5s) ($t = 3.76$; $df = 138$; $p < 0.001$), being on average 7.3s shorter. Surface periods following successful dives were longer (mean = 23.3s) than those following unsuccessful dives (mean = 11.0s), presumably because of the extra time required for eating the prey. Instances where prey were brought ashore to be eaten are excluded from this analysis.

Table 3: Duration of dives and inter-dive surface periods during foraging by otters

	No of Dives		No of Surface Periods	
Time (s)	Successful	Unsuccessful	With Food	Without Food
0 - 5	-	-	-	13
6 - 10	-	-	4	41
11 - 15	5	2	6	37
16 - 20	9	8	5	13
21 - 25	3	12	2	3
26 - 30	5	27	1	-
31 - 35	5	24	-	1
36 - 40	2	14	2	-
41 - 45	3	8	-	-
46 - 50	-	10	2	-
51 - 55	-	1	1	-
56 - 60	-	1	1	-
61 - 65	-	1	-	-
TOTAL	32	108	24	108
Mean sd	25.4 ±10.2	32.7 ± 9.5	23.3 ± 15.2	11.0 ± 5.0

The durations of unsuccessful dives and subsequent surface periods were positively correlated ($r = 0.55$, df = 96, $p < 0.001$) (Figure 6). The distribution of points suggests that the relationship between these two variables may not have been one simply of direct proportionality, but the sample size was too small to determine any pattern with confidence.

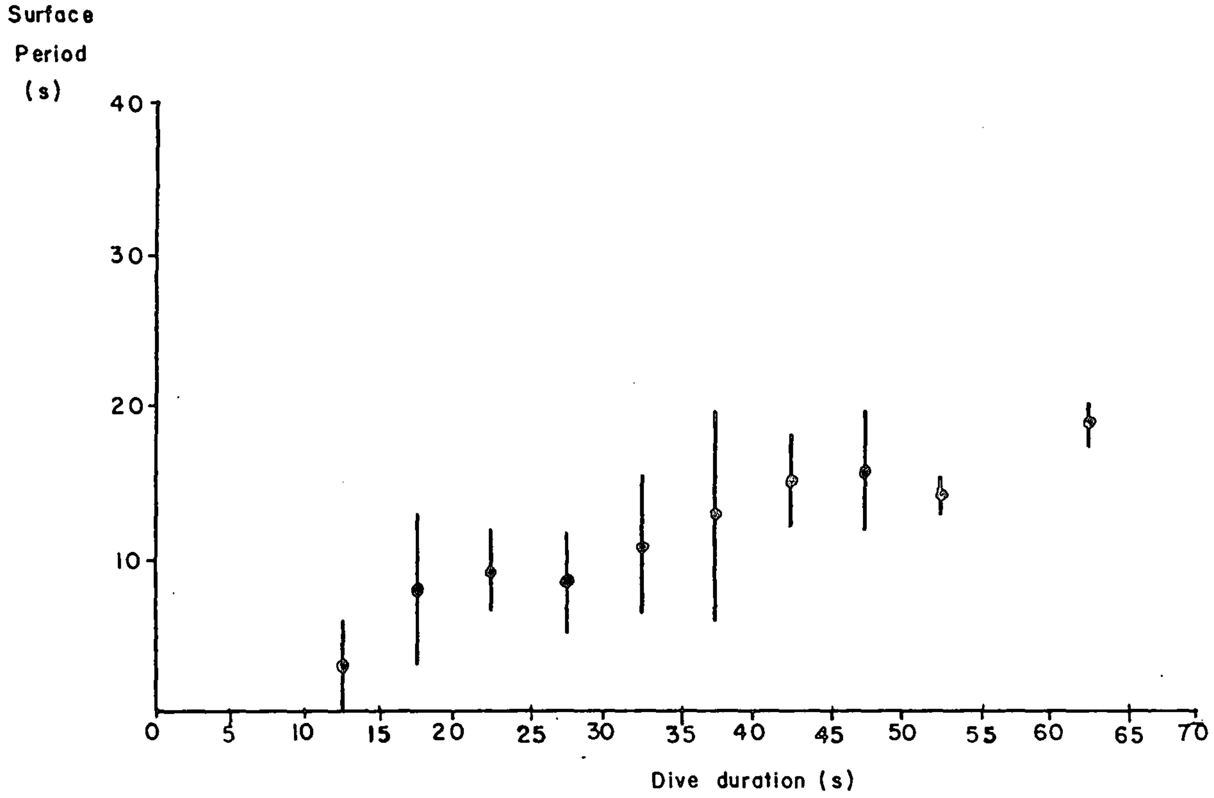
4.2.2. Surface-pushing

The only other method of foraging that was seen took place at the water's edge. At low tide otters would frequently push and search their way through the partially exposed Laminaria, half-swimming and half-walking, with their heads below the surface. This method of foraging was also used by otters hunting for Common Eels (Anguilla anguilla) in the fringe of green filamentous algae around the edge of a brackish pool.

4.2.3 Prey size and eating methods

Most of the fish seen to be caught were between 10 and 20 cm long (length estimated by comparison with the otter's head), but occasionally much longer specimens were taken: the largest was a Conger Eel, Conger conger, estimated to be 115 cm in length. Fish greater than about 15 cm in length, and crabs, were always brought ashore, but smaller fish caught more than about 10 m offshore were eaten in the water.

All the fish caught were consumed entirely, with the exceptions of the above-mentioned Conger Eel, which was too big, and of Lumpsuckers, Cyclopterus lumpus, which have a thick sub-dermal layer of connective tissue, a broad band of which, from around the middle of the body, was left.



n	2	5	8	24	26	11	7	10	3	0	2
dive duration / surface period	4·17	2·19	2·43	3·19	2·95	2·88	2·81	3·08	3·67		3·29

FIGURE 6 : MEAN SURFACE PERIOD DURATION PLOTTED AGAINST DURATION OF UNSUCCESSFUL DIVES (5s Units)

Vertical lines show standard deviation of mean.

Crabs (all of which were estimated to be between 8 and 12 cm across the carapace) were held down, ventral side uppermost. The chelae were pulled off and discarded, then the thorax and abdomen was removed as a unit, chewed up and eaten, and the legs discarded (the very tips of the legs were, however, frequently found in spraints, having presumably been eaten accidentally, or derived secondarily from prey fish). Finally the carapace was held down with the forepaws and the remaining adherent tissue scraped out with the incisors. It was noticeable that those otters which took crabs frequently (there were considerable individual differences in the proportions of crabs in the diet - see Chapter 4.6) usually had all or part of the rhinarium (the hairless tip of the nose) a pink colour, as opposed to the usual blackish-brown. This was ascribed to superficial injuries inflicted with their chelae by crabs.

4.3 Composition of the diet deduced from spraint analysis

A total of 437 spraints were collected, in 4 seasonal samples : 146 in September 1976; 95 in January 1977; 112 in May-June 1977 and 84 in July-August 1977. The prey taxa present in each spraint were recorded, and the proportion of spraints in which each taxon occurred (the frequency of the taxon) calculated. Since spraints usually contain the remains of more than one prey taxon (mean 3.0 taxa/spraint) the relative frequency (the frequency of a taxon as a percentage of the sum of the frequencies of all the taxa) was also used to facilitate the comparison of the seasonal samples (Erlinge, 1967a).

The results of the analyses of seasonal samples are presented in Table 4 and in Figure 7. These reveal that :

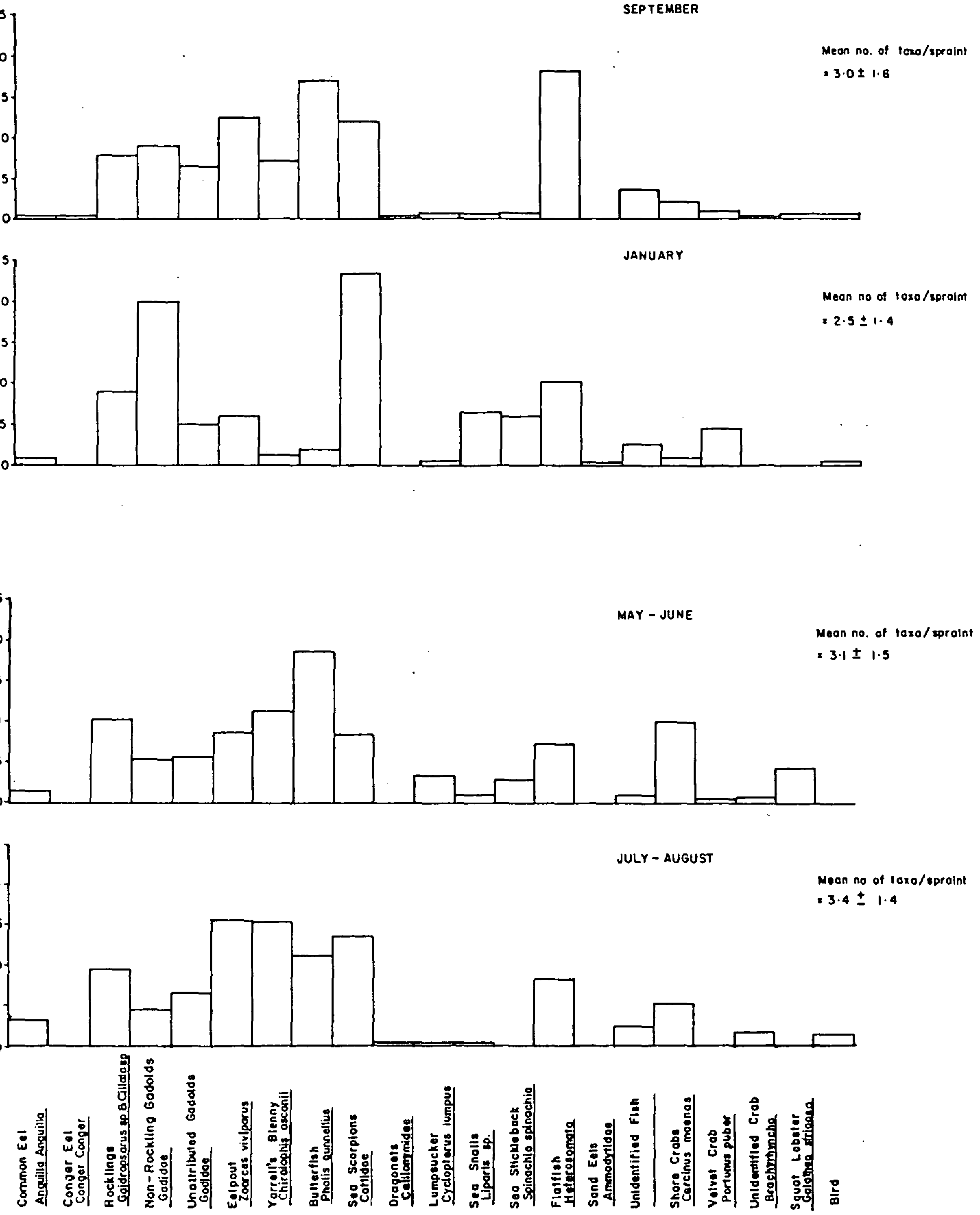
Table 4: Seasonal variation in the composition of spraints

Taxon	SEPTEMBER n = 142			JANUARY n = 95			MAY-JUNE n = 112			JULY-AUGUST n = 84		
	Frequency		Relative Frequency	Frequency		Relative Frequency	Frequency		Relative Frequency	Frequency		Relative Frequency
	No.	%	%	No.	%	%	No.	%	%	No.	%	%
* Common Eel *Anguilla anguilla*	2	1.4	0.5	2	2.1	0.9	5	4.5	1.4	9	10.7	3.1
* Conger Eel *Conger conger*	2	1.4	0.5	0	0	0	0	0	0	0	0	0
* Rocklings (*Ciliata sp.* and *Gaidropsarus sp.*)	34	23.3	7.9	21	22.1	9.0	36	32.1	10.3	27	32.1	9.4
Non-Rockling Gadoids (Gadidae, but not a Rockling)	38	26.0	8.8	47	49.5	20.1	18	16.1	5.2	13	15.5	4.5
Unattributed Gadoid (Gadidae)	26	17.8	6.0	12	12.6	5.1	20	17.9	5.7	19	22.6	6.6
* Eelpout *Zoarces viviparus*	54	37.0	12.5	14	14.7	6.0	30	26.8	8.6	45	53.6	15.7
* Yarrell's Blenny *Chirolophis ascanii*	31	21.2	7.2	3	3.2	1.3	39	34.8	11.2	44	52.4	15.4
* Butterfish *Pholis gunnellus*	73	50.0	16.9	5	5.3	2.1	65	58.0	18.6	32	38.1	11.2
* Sea Scorpions (Cottidae)	51	34.9	11.8	55	57.9	23.5	29	25.9	8.3	39	46.4	13.6
* Dragonets (Callionymidae)	1	0.7	0.2	0	0	0	0	0	0	1	1.2	0.3
* Lumpsucker *Cyclopterus lumpus*	3	2.1	0.7	1	1.1	0.4	12	10.7	3.4	1	1.2	0.3
* Sea Snails *Liparis sp.*	2	1.4	0.5	15	15.8	6.4	3	2.7	0.9	1	1.2	0.3
Sea Stickleback *Spinachia spinachia*	3	2.1	0.7	14	14.7	6.0	10	8.9	2.9	0	0	0
* Flatfish (Heterosomata)	78	53.4	18.1	24	25.3	10.3	26	23.2	7.4	24	28.6	8.4
Sand Eels (Ammodytidae)	0	0	0	1	1.1	0.4	0	0	0	0	0	0
Unidentified Fish	15	10.3	3.5	6	6.3	2.6	3	2.7	0.9	7	8.3	2.4
* Shore Crab *Carcinus maenas*	9	6.2	2.1	2	2.1	0.9	35	31.3	10.0	15	17.9	5.2
* Velvet Crab *Portunus puber*	4	2.7	0.9	11	11.6	4.7	1	0.9	0.3	0	0	0
* Unidentified Crab	1	0.7	0.2	0	0	0	2	1.8	0.6	5	6.0	1.7
* Squat Lobster *Galathea strigosa*	2	1.4	0.5	0	0	0	15	13.4	4.3	0	0	0
Birds	2	1.4	0.5	2	1.1	0.4	0	0	0	4	4.8	1.4
TOTAL	431	295.4	100.0	235	246.5	100.1	349	301.7	100.0	286	340.6	99.5

* demersal species

n = number of spraints in the sample

FIGURE 7. RELATIVE FREQUENCIES OF OCCURRENCE OF PREY TAXA IN SPRAINTS COLLECTED AT DIFFERENT TIMES OF YEAR.



(a) *the prey taken were almost entirely aquatic*: (Table 5). The sum of the relative frequencies of aquatic taxa varied from 98.1 to 100%. The only prey that were not necessarily aquatic were birds, but since many of the birds on and around Fetlar are maritime species, and since the only dead bird fou that had been partially eaten by otters was a seabird (a Fulmar *Fulmarus glacialis*), it is quite likely that any birds caught and eaten were in fact captured in the sea. Certainly there was no evidence to suggest any but very occasional predation of terrestrial species. In north-western Fetlar the potential terrestrial prey were various species of ground-nesting birds (locally numerous), Wood Mice (*Apodemus sylvaticus*) and Rabbits (*Oryctolagus cuniculus*). Although rabbits were abundant in part of the study area in 1976, only one corpse that had been partially eaten by otters was ever found, and since this was at a time when myxomatosis was rampant (reducing the rabbit population to a low level in 1977 and 1978), it may even have been taken as carrion.

(b) *the prey taken were almost entirely marine*: The sum of the relative frequencies of undoubted marine prey taxa ranged between 95.0 and 98.8%. Only one prey species, the Common Eel (*Anguilla anguilla*), was to be found in the streams draining the main study area. However this species is also found in salt water, and was sometimes captured by otters in a large brackish pool on Urie Ness, and since both direct observations and the pattern of distribution of sprainting points indicated that the otters made little use of the stream system, it is probable that most Common Eels were not caught in freshwaters. Two other fish species, the Trout (*Salmo trutta*) and the Three-Spined Stickleback (*Gasterosteus aculeatus*), are to be found in lakes on the island (as well as in the sea), but neither occurred in spraints in the main study area.

Table 5: Some general data on prey taxa extracted from the results of the spraint analyses

	Months when sample was collected:	September	January	May-June	July-August
(1)	Sum of Relative Frequencies (%) of aquatic taxa	99.5	99.7	100	98.1
(2)	Sum of Relative Frequencies (%) of aquatic/terrestrial taxa (birds)	0.5	0.4	0	1.4
(3)	Sum of Relative Frequencies (%) of marine taxa	98.0	98.8	98.6	95.0
(4)	Sum of Relative Frequencies (%) of marine/freshwater taxa	0.5	0.9	1.4	3.1
(5)	Sum of Relative Frequencies (%) of demersal taxa	80.5	65.5	85.3	84.6
(6)	Sum of Relative Frequencies (%) demersal fish	76.8	60.9	70.1	77.7
(7)	Sum of Relative Frequencies (%) of crustaceans	3.7	4.6	15.2	6.9
(8)	Ratio of (6) : (7)	21:1	13:1	5:1	11:1
(9)	Maximum Relative Frequency (%) of any single prey taxon	18.1	23.5	18.6	15.7
(10)	Mean number of prey taxa per spraint	3.0	2.5	3.1	3.4

(c) the prey taken were mostly demersal (living on the sea-bed): Prey were classified as demersal or pelagic from information presented in Jenkins (1936) and Wheeler (1969). The sum of the relative frequencies of completely demersal taxa (those marked with an asterisk in Table 4) ranged from 65.5% to 85.3%. Of the 20 fish and crustacean taxa identified in the spraint samples, 15 were completely demersal. Of the remainder, Sea Sticklebacks (Spinachia spinachia), while not demersal, do generally live close to the bottom amongst the fronds of seaweed; Sand Eels (Ammodytidae) are demersal when dormant and pelagic (open water) when feeding; Non-Rockling Gadoids are pelagic, but Unattributed Gadoids are a mixture of demersal and pelagic species; Unidentified Fish probably includes both demersal and pelagic species.

The commonest Non-Rockling Gadoid in the area, and the one seen to be taken by otters most frequently, was the Saithe (Pollachius virens), which occurs at all depths and is common close to the shore. It was concluded that the bulk of Non-Rockling Gadoid vertebrae in the spraints were probably those of Saithe.

(d) fish formed a larger component of the demersal prey than crustaceans: the ratios of the relative frequency of demersal fish: relative frequency of crustaceans (all of which were demersal) ranged from 5:1 in the May-June sample to 21:1 in the January sample.

(e) a wide range of prey species was taken, none of which formed a dominant component of the diet: no single taxon had a relative frequency greater than 23.5% in any of the samples (Table 5). Furthermore the taxon with the highest relative frequency was different in each of the 4 seasonal samples.

Table 6: Significance of seasonal variations in frequency (No) of prey taxa in spraint samples (chi-squared test, 95% confidence limits)

	January	May-June	July-August	January	May-June	July-August	January	May-June	July-August
		Common Eel			Rocklings			Non-Rockling Gadoids	
May-June	-			NS			*		
July-August	NS	NS		NS	NS		*	NS	
September	-	-	-	NS	NS	NS	*	NS	NS
		Unattributed Gadoids			Eelpout			Yarrell's Blenny	
May-June	NS			NS			*		
July-August	NS	NS		*	*		*	NS	
September	NS	NS	NS	*	NS	NS	*	NS	*
		Butterfish			Sea Scorpions			Lumpsucker	
May-June	*			*			NS		
July-August	*	NS		NS	NS		-	NS	
September	*	NS	NS	*	NS	NS	-	*	-
		Sea Snails			Sea Stickleback			Flatfish	
May-June	*			NS			NS		
July-August	*	-		*	NS		NS	NS	
September	*	-	-	*	NS	-	*	*	*
		Shore Crab			Velvet Crab			Squat Lobster	
May-June	*			*			*		
July-August	*	NS		*	-		-	*	
Septebmer	NS	*	NS	NS	-	-	-	*	-

* $p < 0.05$ significant
NS $p < 0.05$ not significant
\- insufficient data

(f) *although the same range of species was taken throughout the year, there were marked seasonal differences in their relative contributions to the diet*: this is clear from Figure 7 which shows how the relative frequencies of the prey taxa were in constant flux. The seasonal changes in each taxon's contribution is more clearly seen by examining the changes in its frequency of occurrence (Figure 8). Most taxa showed marked variations in frequency. Where there was sufficient data the significance of these seasonal differences was tested using chi-squared tests on all the possible pairs of seasonal samples (Table 6). Significant differences were found in the seasonal frequencies of occurrence of 12 taxa. Yarrell's Blenny (*Chirolophis ascanii*) showed the greatest inter-sample variation (4 significant differences in 6 sample pairs), with Non-Rockling Gadoids (Gadidae), Eelpout (*Zoarces viviparus*) Butterfish (*Pholis gunnellus*), Sea Snails (*Liparis sp.*), Flatfish (*Heterosomata*), Shore Crab (*Carcinus maenas*) and Squat Lobster (*Galathea strigosa*) all having 3 sample pairs significantly different. Only 2 taxa - Rocklings (*Ciliata sp.* and *Gaidropsarus* sp.) and Unattributed Gadoids (Gadidae) showed no significant seasonal differences.

(g) *the composition of the winter (January) diet shows the most differences from the other seasonal samples*: the greatest number of significant differences in the frequency of prey taxa was between the January sample and the other seasonal samples (24, as compared with 14 for May-June, 12 for July-August and 14 for September). Figure 8 shows how some taxa which were important spraint constituents in May-September were very scarce in January, most notably Yarrell's Blenny (*Chirolophis ascanii*) and Butterfish (*Pholis gunnellus*), while others were then more abundant, most notably Non-Rockling Gadoids and Sea Snails (*Liparis sp.*).

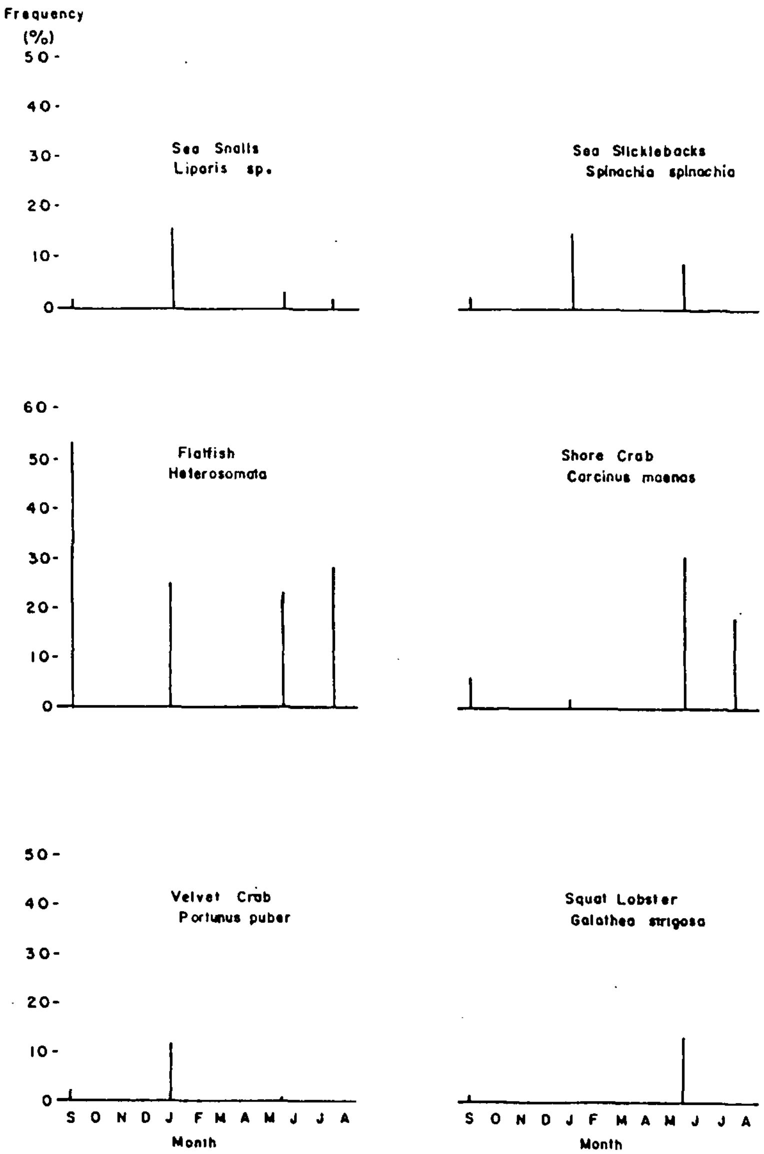
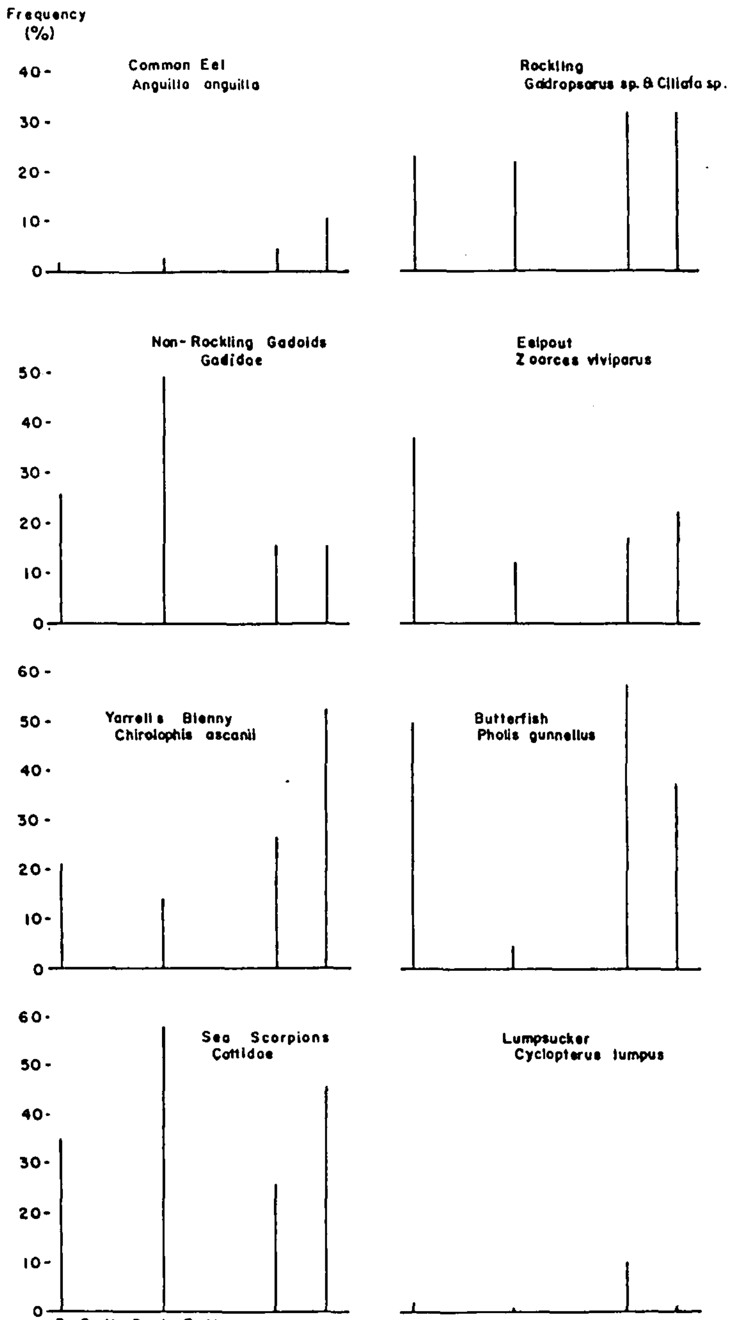


FIGURE 8. FREQUENCIES OF OCCURRENCE OF PREY TAXA IN SPRAINT SAMPLES COLLECTED AT DIFFERENT TIMES OF YEAR.



4.4 Temporal and spatial pattern of foraging

The mean prey capture rate (calculated from 29.4 hrs of discontinuous observations of a minimum of 10 individuals, excluding the adult female, Buda, and her cub, Harald, examined in more detail in section 4.6) was 1 prey item/ 7.8 min of observed foraging time. Capture of prey was not spread randomly throughout the foraging periods, the majority of prey items being caught within a relatively short time of each other (Figure 9). With the data from Buda and Harold also included, the mean prey capture interval was 8.1 ± 10.6 min; median prey capture interval was 5.1 min; and modal class was 0.5 - 1.5 min.

The mean rate of travel of a foraging otter along the coast was 9m/min (based on estimates made during 16.2 hrs of discontinuous observation), so if prey capture was randomly distributed in space, a modal inter-catch distance of around 72.9 m (mean prey-capture interval multiplied by mean rate of travel) would be anticipated. In fact the modal class of estimated inter-catch distance was 50 m (Table 7), so it is apparent that prey capture was aggregated spatially as well as temporally. It is typical to see a foraging otter proceed gradually through the sea, catching an occasional fish, with periodic intervals of persistent diving in relatively restricted areas where several prey are caught in a relatively short period. Individual otters were seen to capture prey on each of up to five consecutive dives, and on one occasion an otter caught 12 butterfish, each about 15 cm long, during a 41 minute period in an area of about 50 m^2.

Otters spent up to 88 mins in the sea without coming onto land other than to consume prey, the mean duration of foraging periods being (30.7 ± 18.6 mins, n = 34). The effort being put into foraging appeared to vary considerably and sometimes it was apparent that otters were primarily travelling or prospecting rather than actively searching for food. Since, however, it was not possible to differentiate these activities reliably, all time spent in

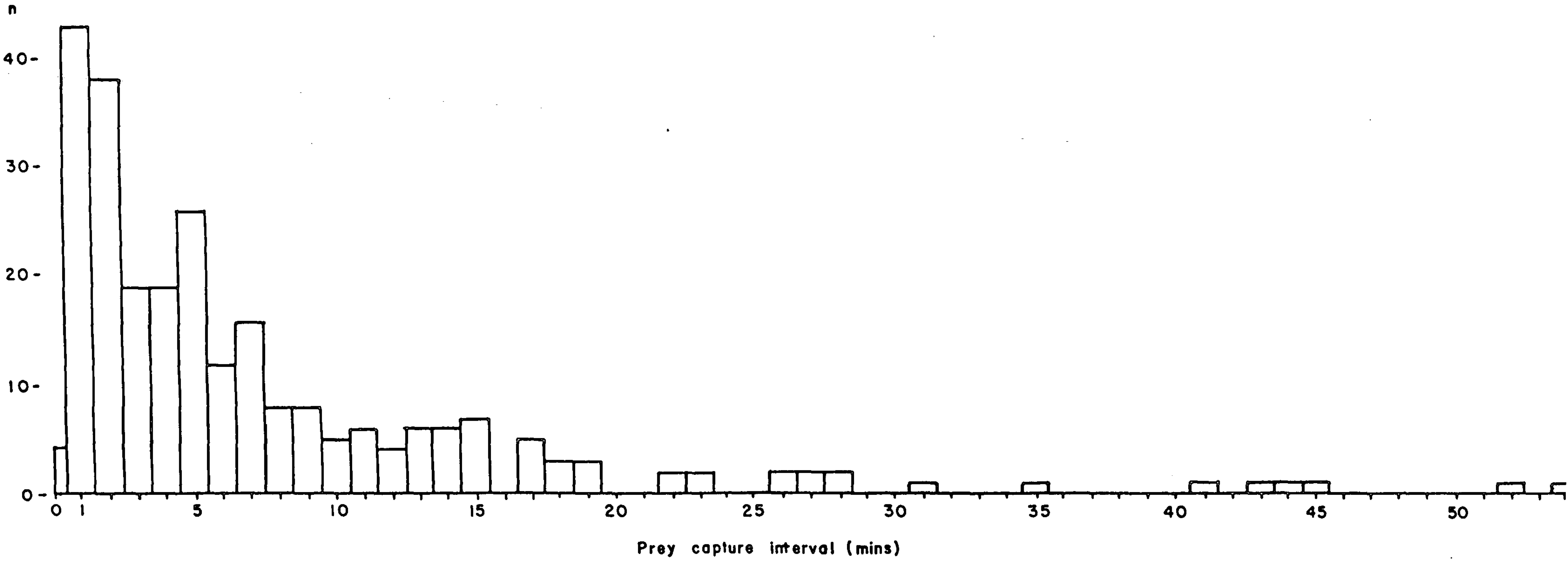


FIGURE 9 FREQUENCY DISTRIBUTION OF TIME INTERVALS BETWEEN SUCCESSIVE PREY CAPTURES (n = 258)

Table 7: Estimated distance travelled between successive prey captures

Inter-catch Distance (m)	No of occasions	%
50	188	79
51 - 150	30	13
151 - 250	10	4
251 - 350	8	3
351 - 450	3	1
Total	239	100

the sea was for the purposes of this analysis, assumed to be time spent foraging. Between these foraging periods, otters landed to defaecate, dry their fur, roll, groom and, frequently, to sleep. These periods on land were very variable in duration (mean value of 16.7 ± 17.0 mins; n = 51). Longer periods of sleep were presumed to occur inside the holts. The adult female, Buda, and her cub, Harold, spent 63.6% of the time they were under observation in the sea, and 36.4% on land (total time spent watching = 92.6 hrs). It was not possible to make a reliable estimate of the proportion of time spent in the holt, nor, due to the problem of observing at night, to collect data on time-budgetting throughout the complete diel cycle.

4.5 Behaviour in relation to the time of day and state of the tide

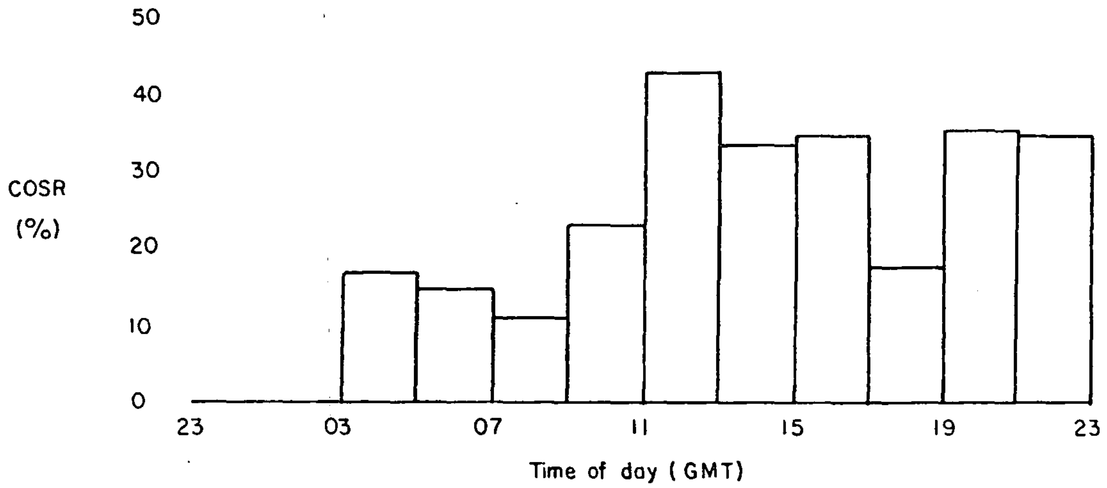
Lacking the means of studying otters within their holts, only behaviour taking place outside could be studied. Continuous watching of holts throughout complete twenty-four hour periods was not attempted, since during the only field season when sufficient manpower was available (1978) no readily accessible holts with single entrances were under continuous occupation by otters. For the same reason, use of the activity-recorder was not viable on Fetlar in 1978. An attempt to use this devise at a single-entranced holt on the coast of the Erradale Peninsula, Wester Ross, in 1981 failed to produce useful results due to the impossibility of determining whether it was an otter, a rabbit (of which there were many in the area),or some other animal which had triggered the recorder. Thus it has not been possible to estimate the relative proportions of time spent inside and outside the holt.

Individual otters showed considerable variability in the timing of their activity outside their holts. Indeed the difficulty of predicting when otters would be active proved to be a major problem in this study. Individuals could sometimes be found on the same stretch of coast at approximately the same time of day for up to five days in succession, but they would then change their routine in an unpredictable manner. Although most otters, particularly adult males, were apparently primarily nocturnal, certain individuals were also frequently active during the day. The adult female, Buda, and her cub Harald, were particularly diurnal, although in other respects they were no more predictable. A measure of the variation in their activity in relation to the diel cycle was obtained by calculating the Cumulative Observation Success Rate (hereafter referred to as COSR), which is the cumulative proportion of time spent by the observer on the stretch of coast which constituted their home range during which the otters were under observation, expressed as a percentage (see Figure 10a). There is a suggestion of a bimodal activity pattern, with COSRs of 30 to 40% between 1100 and 2300 GMT being interrupted by a short period with a low COSR between 1700 and 1900, and the COSR was generally lower prior to 1100. The absence of records between 2300 and 0300 GMT was due to the impossibility of reliable observation during the darkest hours of the night, and, in view of occasional observations of other individuals during this period, is unlikely to reflect a genuine cessation of activity.

Plotting the COSR for all other otters in the main study area gives somewhat different results (Figure 10b). The highest COSR was for the two-hour period 0900-1100 (14%). Again there is a suggestion of bimodality but with an earlier morning activity peak. Interpreting these data is difficult since there are several potential sources of bias in the method. These will be discussed later.

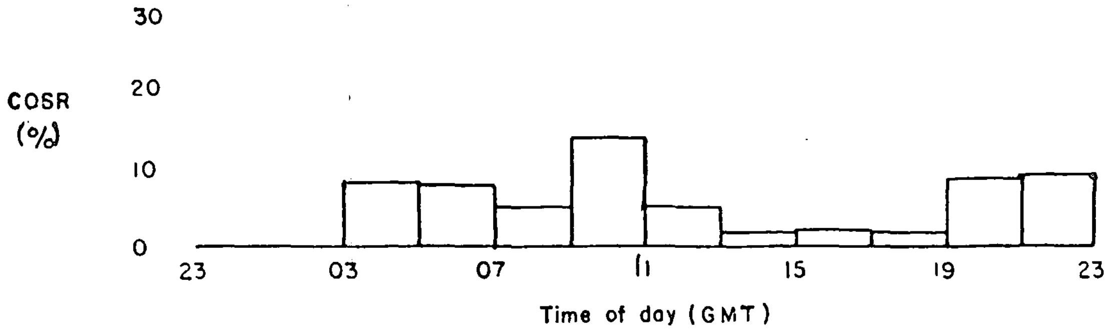
Prey-capture rate (number of prey items caught per minute of activity in the sea) varied considerably through the day (Figure 11). In the case of Buda and Harald the pattern was clearly bimodal, with the highest rates between 0700 and 0900 GMT, and between 1900 and 2300. Only the later peak coincides

FIGURE 10: DIEL VARIATION IN ACTIVITY: CUMULATIVE OBSERVATION SUCCESS RATE (COSR) THROUGH THE DAY. COSR IS THE PROPORTION OF TIME SPENT BY THE OBSERVER ON THE COAST DURING WHICH OTTERS WERE UNDER OBSERVATION.



Time spent by observer in the home range (hrs) 6·1 7·3 18·9 37·6 46·9 33·0 31·9 33·5 33·8 10·6

(a) BUDA and HARALD : April–August, 1977



(b) All other Otters: April – August, 1977.

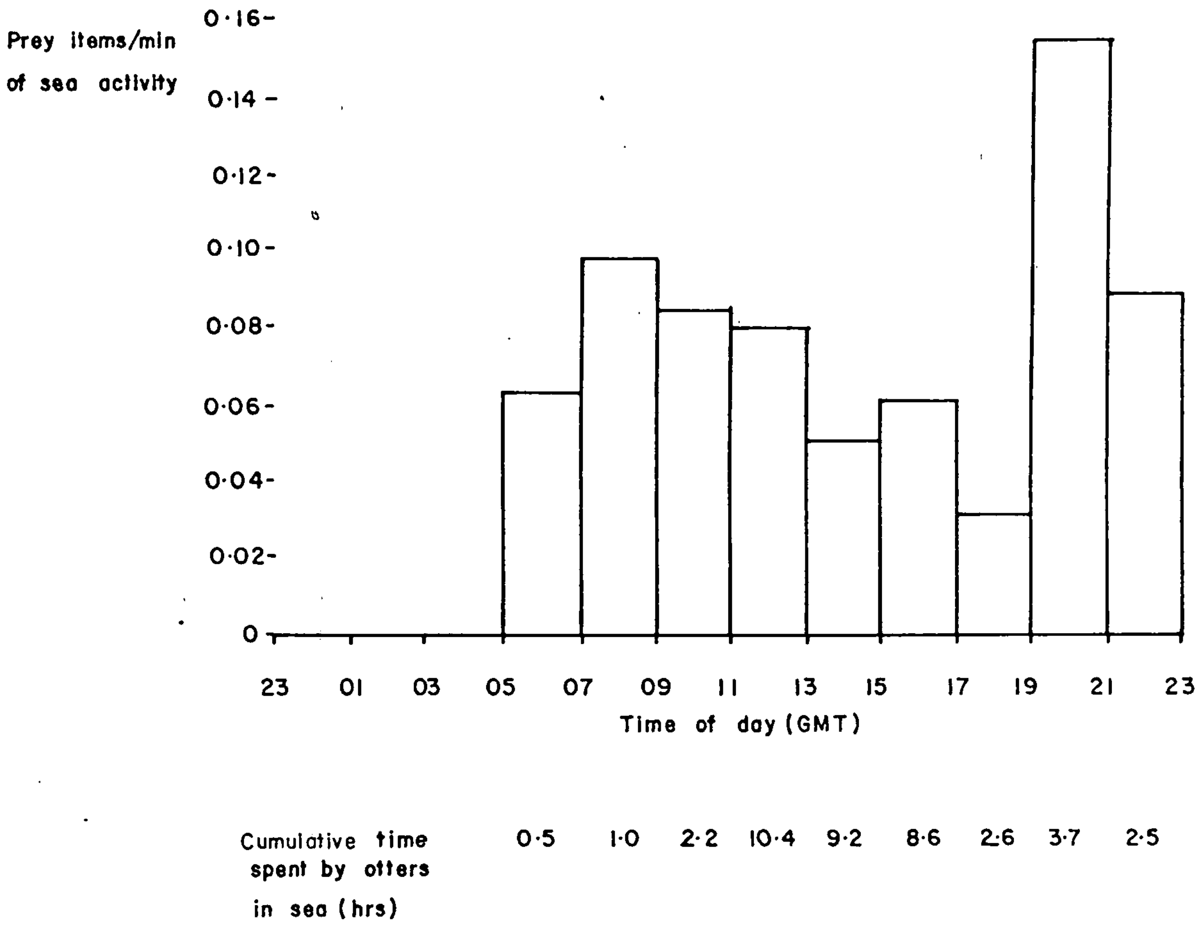


FIGURE 11.

DIEL VARIATION IN PREY CAPTURE RATES: ADULT FEMALE (BUDA) AND HER CUB (HARALD). CUMULATIVE OBSERVATIONS DURING PERIOD APRIL – AUGUST 1977.

with a period of high COSR. The prey-capture rates calculated from the cumulative observations of other otters can also be interpreted as showing a bimodal pattern through the diel cycle (Figure 12), but in view of the methodological problems, little weight should be attached to this.

For purposes of analysis the tidal cycle was divided into four states:

a) High : 1½ hours on either side of High Water, totalling three hours;
b) Low : 1½ hours on either side of Low Water, totalling three hours;
c) Falling : } the periods between High and Low Tide states; variable in
d) Rising : } duration, but approximately three hours each.

The variable duration of Falling and Rising Tide states is due to variations in the length of the tidal cycle correlated with the state of the Moon.

The COSR for Buda and Harald was least during Low Tide (Figure 13a) whereas their prey-capture rate was highest during this tide state, lowest during High Tide, and intermediate during Falling and Rising Tides (Figure 14a). The COSR for the cumulative observations of all other otters was least during High Tide (Figure 13b), but cumulative prey-capture rate was similar during all tide states (Figure 14b).

The numbers of identifiable fish taken by the otters were too low in most cases to provide useful information on predation of particular prey taxa in relation to tide state. However it is perhaps worth noting that only one out of a total of twenty-two Sea Scorpions (Cottidae) seen to be captured was taken during High Tide.

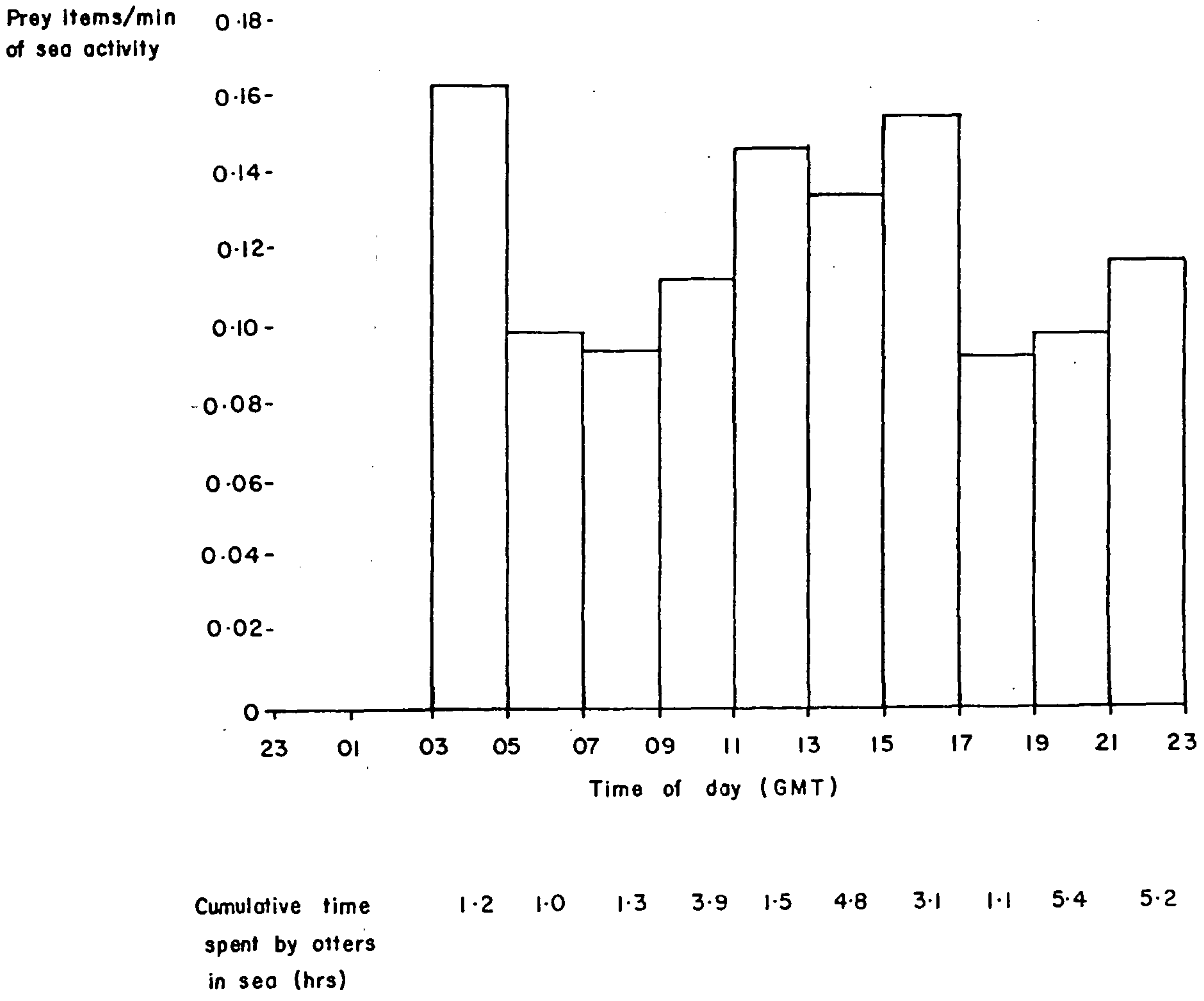


FIGURE 12.

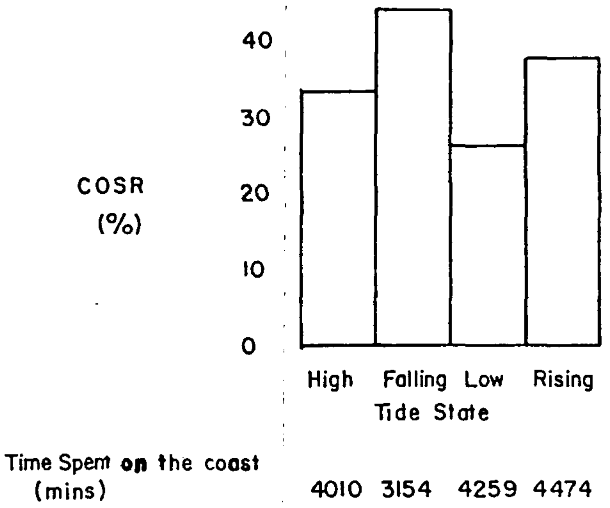
DIEL VARIATIONS IN PREY CAPTURE RATES:

OTHER OTTERS. CUMULATIVE OBSERVATIONS DURING 1977–78.

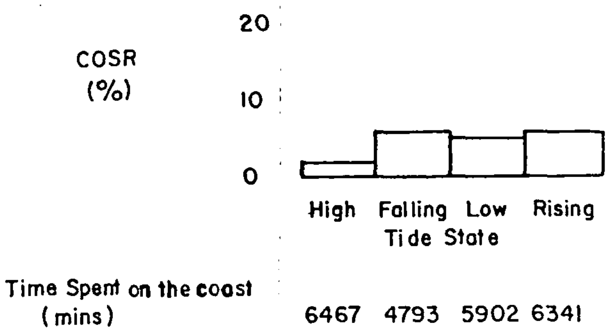
AT LEAST 10 INDIVIDUALS INVOLVED.

FIGURE 13. VARIATION IN ACTIVITY IN RELATION TO THE TIDAL CYCLE:

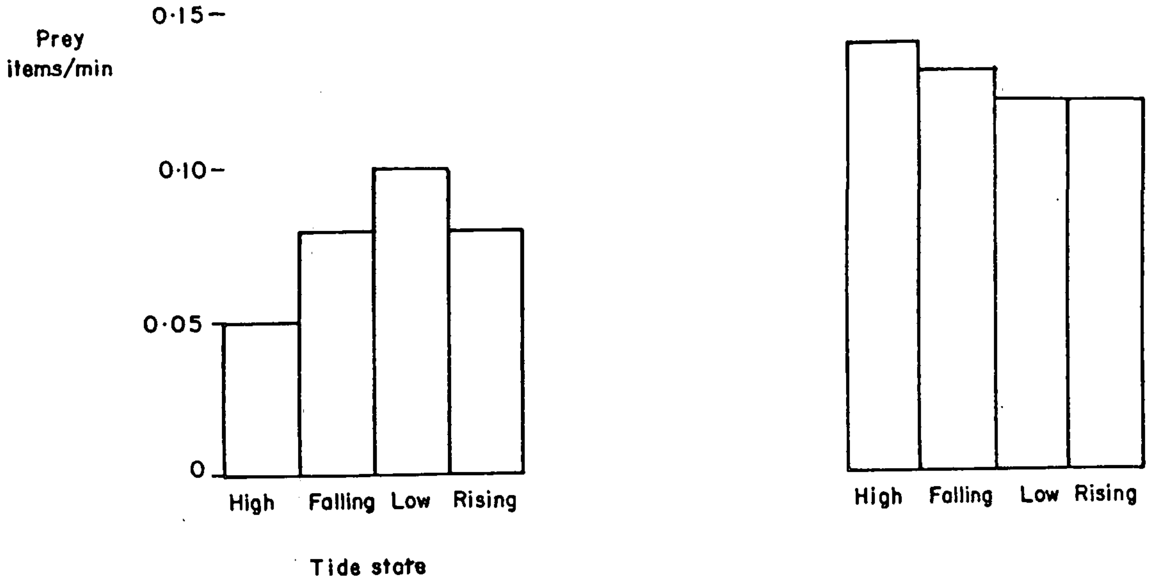
CUMULATIVE OBSERVATION SUCCESS RATE (COSR) IS THE PROPORTION OF TIME SPENT BY THE OBSERVER ON THE COAST DURING WHICH OTTERS WERE UNDER OBSERVATION.



(a) Buda and Harold: April-August, 1977.



(b) All Other Otters : April-August, 1977



Total duration of observed foraging 506 839 454 633 311 437 482 531

(a)
Adult female (Buda) and her cub (Harold), April- August 1977 .

(b)
Other otters, cumulative observations during 1977 - 78, at least 10 individuals involvec

FIGURE 14.

VARIATION IN PREY CAPTURE RATE IN RELATION TO THE TIDAL CYCLE.

4.6 Comparison of the foraging behaviour and diet of an adult female with that of her cub

Between April and August 1977, sufficient observations were made of the foraging behaviour of two individual otters, an adult female (Buda) and her cub (Harald), to allow a comparison of their diets. Harald first began to accompany Buda on foraging trips at the beginning of September 1976. Since according to Wayre (1976) cubs reach this stage of development at an age of about three months,Harald would have been about 10 months old in April 1977. At this time he was still noticeably smaller than Buda, but by August 1977 there was little difference in their lengths, although his build was still lighter. Prey was identified to species or to some broader taxon. Given that prey items could only be identified in good light and often only at a fairly short distance, only observations made under good lighting conditions have been included in this analysis.

During the period April-July, Harald was almost invariably accompanied by Buda (98% of 56.4 hours that he was under observation), but she sometimes foraged on her own. When together their activites were synchronous, foraging, sleeping and grooming as a pair, and leaving and entering the water together at the end and beginning of foraging periods. There was, however, no apparent co-operation during hunting, and Buda's prey-capture rate (1 item/11.8 mins, in a total foraging time of 16.6 hrs) was more than twice that of Harald (1 item/25.6 mins, in a total foraging time of 12.1 hrs). There is a significant difference in these prey capture rates ($\chi^2 = 15.0$; df = 1; $p < 0.001$). Harald often attempted to take captured prey from Buda, and she was seen to relinquish 6% of her prey (5 out of 85 items) to him.

From the beginning of August, Harald became more independent, and spent progressively less time with Buda (he was solitary for 42% of the 16.6 hrs that he was under observation that month). Whereas Buda's prey capture rate at 1 item/10.0 mins in a total foraging time of 4.4 hrs) was not significantly different from before ($\chi^2 = 0.55$; df = 1; NS), Harald's prey capture rate at 1 item/10.6 mins in a total foraging time of 7.5 hrs was now much greater than before ($\chi^2 = 9.9$; df = 1; $p < 0.01$), and was no longer significantly different from Buda's ($\chi^2 = 0.05$; df = 1; NS). In view of this marked increase in Harald's foraging success, the data on his prey composition has been split into two periods: April-July and August.

There were considerable differences in the observed diets of these two otters (Table 8). In comparison with Buda, Harald took a lower proportion of butterfish, unidentified anguilliforms and flatfish, and a higher proportion of sea scorpions and lumpsuckers. The most obvious difference was that whereas Buda took no crabs at all, they formed a significant part of Harald's diet.

The prey taxa were divided into groups on the basis of their morphology and behaviour :

(1) Pelagic : contains only saithe (_Pollachius virens_)

(2) Flatfish (Heterosomata)

(3) Anguilliforms : consists of those demersal fish with long, slender eel-like bodies, namely eelpout (_Zoarces viviparus_), butterfish (_Pholis gunnellus_), Yarrell's blenny (_Chirolophis ascanii_), five-bearded rockling (_Ciliata mustela_) and unidentified fish of this morphological type

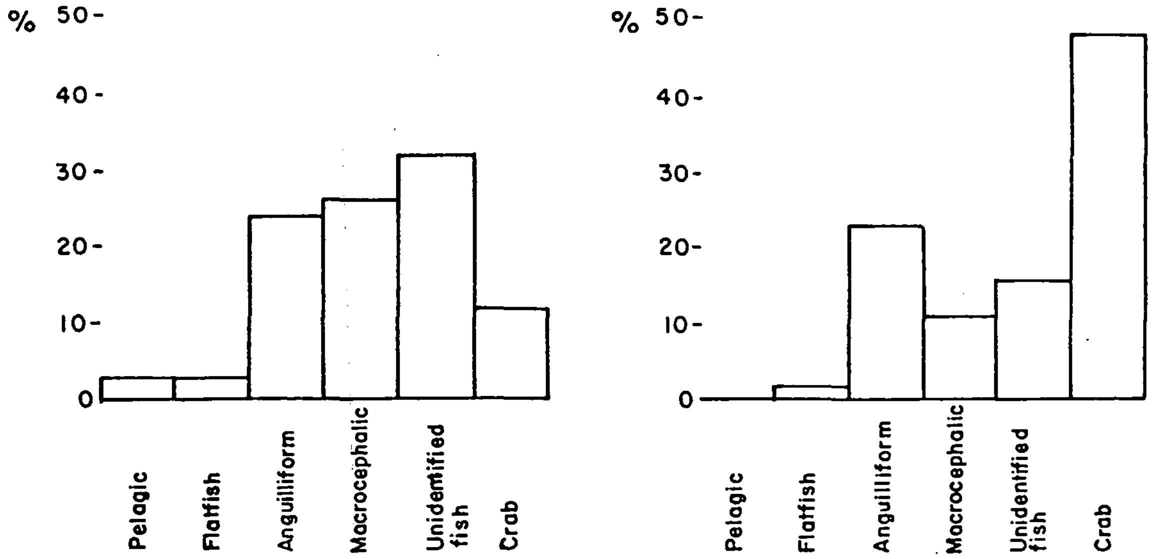
(4) Macrocephalic : consists of stout demersal species, namely the sea scorpions (_Cottidae_), pogge (_Agonus cataphractus_) and lumpsucker (_Cyclopterus lumpus_)

(5) Unidentified Fish : consists of all those fish, most of them small, which could not be ascribed to any taxon.

(6) Crabs

Table 8 : Prey taken by an adult female otter (Buda) and her cub (Harald)

	Estimated Size (cm)	Buda April-August		Harald April-July		Harald August	
		no.	%	no.	%	no.	%
VIVIPAROUS BLENNY Zoarces viviparus	15	2	2.1	0	0	0	0
BUTTERFISH Pholis gunnellus	10-25	30	30.9	6	17.6	8	18.2
YARRELL'S BLENNY Chirolophis ascanii	10-15	5	5.2	1	2.9	0	0
5-BEARDED ROCKLING Ciliata mustela	10-15	2	2.1	1	2.9	0	0
UNIDENTIFIED ANGUILLIFORM	10-25	12	12.4	0	0	2	4.5
FLATFISH Heterosomata	10-30	9	9.3	1	2.9	1	2.3
SEA SCORPIONS Myoxocephalus scorpius & Taurulus bubalis	10-15 & 30-35	6	6.2	5	14.7	5	11.4
POGGE Agonus cataphractus	10-15	2	2.1	0	0	0	0
LUMPSUCKER Cyclopterus lumpus	20-35	4	4.1	4	11.8	0	0
SAITHE Pollachius virens	15-20	1	1.0	1	2.9	0	0
UNIDENTIFIED FISH	10-15	13	13.4	7	20.6	2	4.5
UNIDENTIFIED ITEM	<10	11	11.3	4	11.8	5	11.4
SHORE CRAB Carcinus maenas	8-12	0	0	1	2.9	3	6.8
VELVET CRAB Portunus puber	8-12	0	0	3	8.8	10	22.7
UNIDENTIFIED CRAB	8-12	0	0	0	0	8	18.2
TOTALS		97	100.1	34	99.8	44	100.0


(b) Cub (Harold) April-July. n = 34

(c) Cub (Harold) August. n= 44

(a) Adult female (Buda) April-August
n = 97

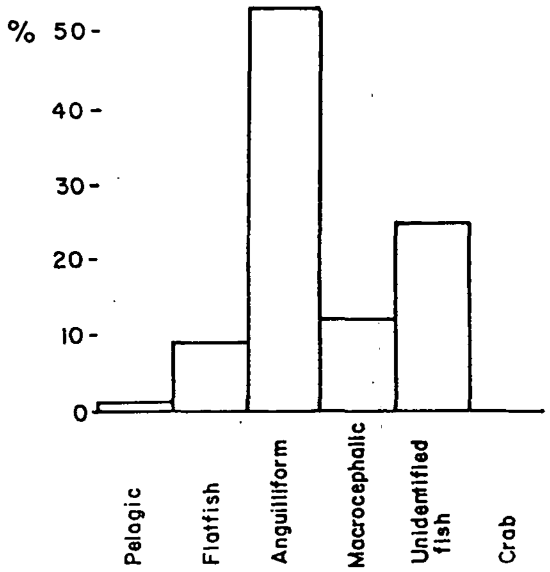


FIGURE 15

INDIVIDUAL DIFFERENCES IN DIETARY COMPOSITION; PREY DIVIDED INTO GROUPS ON THE BASIS OF THEIR MORPHOLOGY AND BEHAVIOUR.

Species in groups (1) to (3) are capable of rapid evasive action when disturbed, whereas those in groups (4) and (6) are not. It is apparent that the potentially less-easily caught prey, notably the anguilliforms, comprised a greater part of Buda's diet (63%) than of Harald's (30% in April-July; 24% in August) (Figure 15). In a comparison of Harald's prey composition in August with that in April-July, it is striking that the proportion of crabs, which in view of their slowness and abundance must be the most easily captured prey, increased substantially, from 12% to 48%, a significant difference ($\chi^2 = 7.8$; df = 1; $p < 0.01$).

4.7 Home range use by an adult female and her cub

The home range of the adult female, Buda, and her cub, Harald (Figure 16), extended along approximately 2.5 km of coast (owing to the irregularity of the coastline, it was impossible to measure exactly). Buda was never seen outside this range, and Harald only once, in August 1977 by which time he had become largely independent of Buda. When attempting to locate these two otters, the whole of their home range was walked, as well as stretches beyond the observed limits, so the data on their movements should reflect actual use of the range, at least during daylight hours. The seaward limit of the coastal strip in which they foraged varied between 100 and 150 m from the shore, and if a line 150 m from the nearest point on shore is taken as the seaward limit of the home range, then the maximum foraging area was 42.6 ha (making no allowance for irregularity in the topography of the seabed).

For recording purposes the home range was divided into eleven sections, defined by approximate bearings from convenient landmarks along the coast.

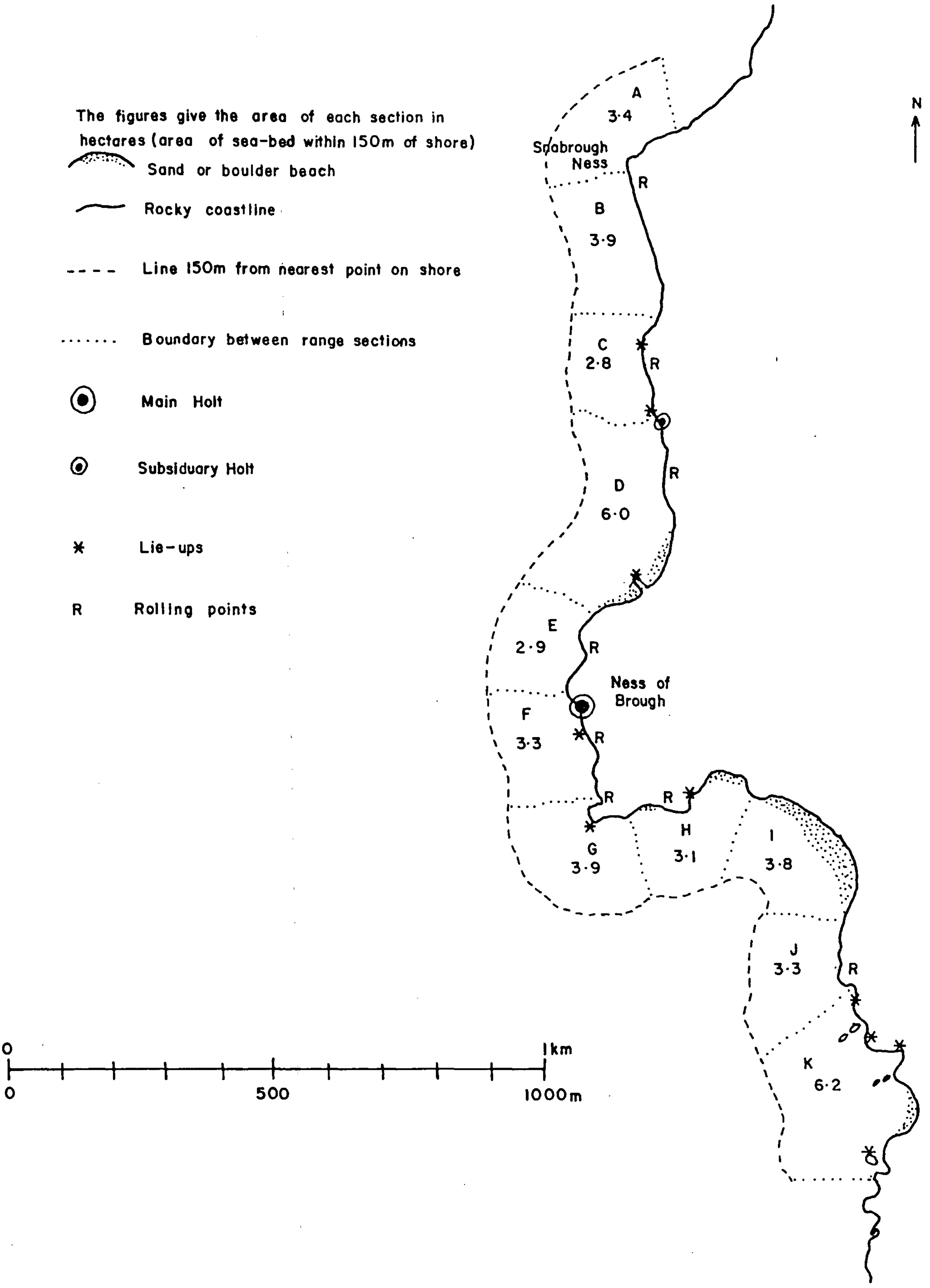


FIGURE 16.

THE HOME RANGE OF AN ADULT FEMALE (BUDA) AND HER CUB (HARALD).

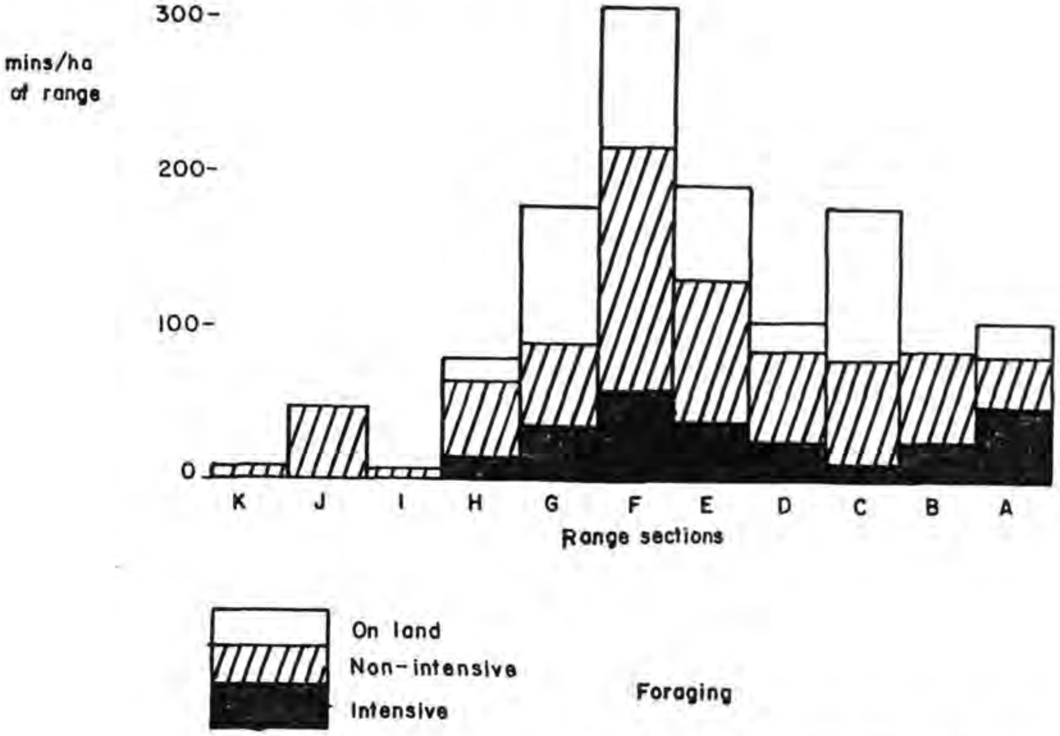
The main holt, a single-entranced tunnel about 4 m above high tide level, formed by a fault in the bedrock, was in Section F. A second holt, used less often and also in a fault, was closer to sea level in Section D. Lie-ups were present in Sections C, D, F, G, H and K. All of these were in rock faults or amongst boulders in sites which were occasionally or regularly submerged at high tide. One, a cavity in a crumbling slipway in Section D, was well below high tide level and could only be used for fairly short periods when the tide was low. In addition to these there were eight principal "rolling points", where the otters frequently landed to dry themselves, to groom, and to sleep for short periods. These activities were not however restricted to these eight points, and could take place anywhere - on seaweed, bare rock or grass. At six of these rolling points there were well developed depressions in the turf above the rocky shore. Much of the otters' time on land, other than that passed in holts, was spent at the rolling points.

The otters spent more time in the vicinity of the main holt, in Section F, than towards the extremities of their home range, and more foraging was seen here than in any other section (Figure 17a). Most time was spent on land in Sections C, E, F and G.

The relative importance of each section for foraging was assessed in two ways: (a) from the amount of time spent in foraging (all time spent in the sea) and in intensive feeding (defined as periods when the prey capture rate was at least 1 item/10 mins of foraging) (Figure 17a); (b) from the number of prey items seen caught per unit area (Figure 17b).

A similar general trend of decreasing use away from the main holt was shown, with no intensive feeding being recorded in the three least-frequented sections at the southern end of the range. The trend was broken at the northern

(a) Time spent in different sections of the home range



(Intensive foraging defined as capture rate of 1 prey/10 mins or greater)

(b) Number of prey taken per unit area in each section of the home range.

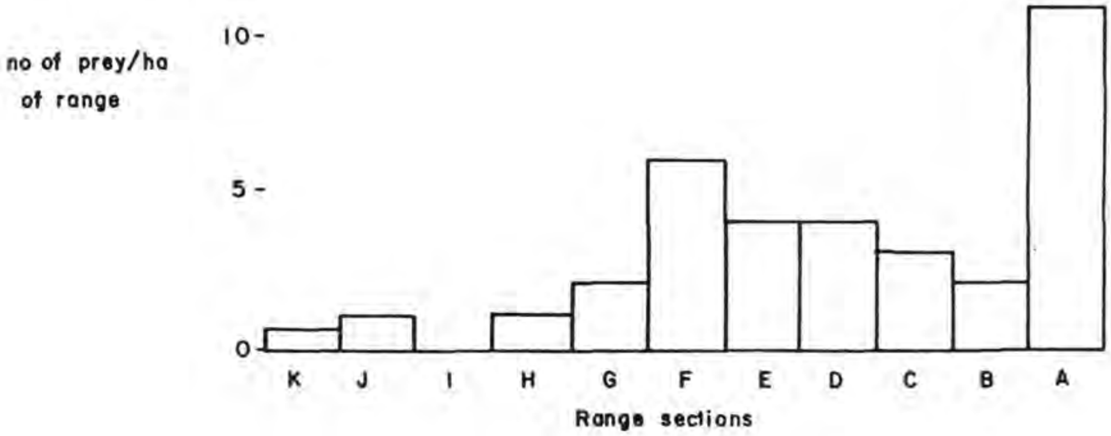


FIGURE 17.

HOME RANGE USE: ADULT FEMALE (BUDA) AND HER CUB (HARALD),

APRIL – JULY 1977.

end of the range in Section A, where the proportionof foraging time spent in intensive feeding was greatest (43%), and where the greatest number of prey items per unit area was captured. The only part of the range where no prey was ever captured was Section I, which was the only one where the seabed consisted almost entirely of bare sand, rather than kelp-covered rocks with occasional sand patches as was the case in all the other sections. The otters generally swam directly across Section I without pausing to dive.

A significant southward shift in Buda's home range occurred between August 1977 and May 1978. Between May and October 1978 she ranged between Ness of Brough and Corbie Head, and mainly used a small holt in Section K which she had used in 1977 only as a lie-up. No otters were resident at her former main holt in Section F, and otters were only very occasionally seen at all along the entire Ness of Brough to Snabrough Ness stretch of coastline. The apparent abandonment of this stretch followed on the destruction by winter storm action of the holt in Section D. This change in home range use is illustrated in Figure 18.

4.8 Population density and distribution

There were insufficent observations of individuals other than Buda and Harald to establish the limits of their home ranges, though for some it was possible to determine their centres of activity.

In 1977, on the approximately 11 km of coastline between Corbie Head and Tressa Ness, excluding the islands of Urie Lingey and Daaey, a minimum of nine otters was present. These were: two adult females one with a single cub (Harald) and the other with at least two very young cubs which were still in the holt; two adult males which appeared to have ranges which overlapped in

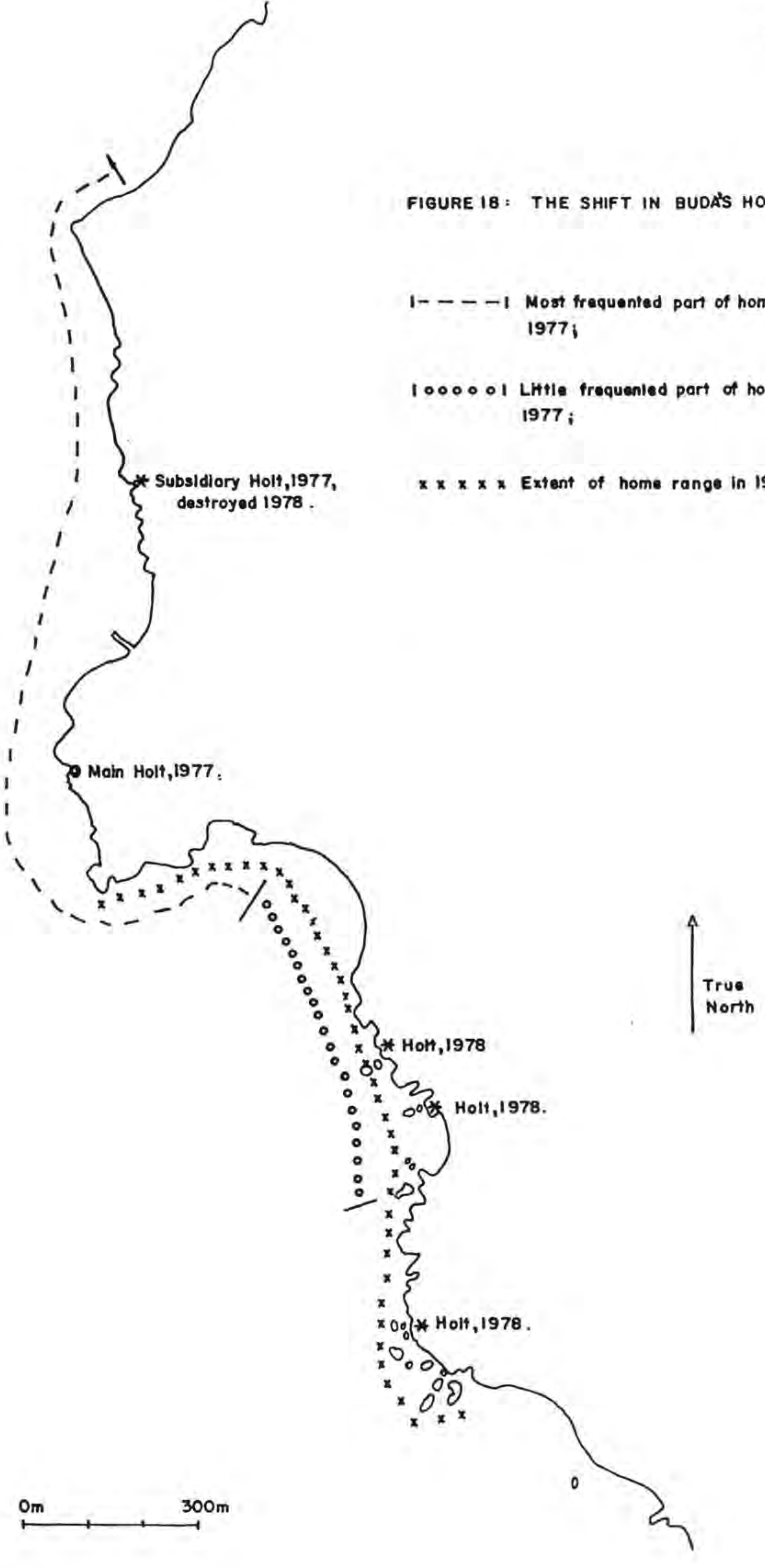


FIGURE 18: THE SHIFT IN BUDA'S HOME RANGE:

the Hamars Ness area; one independent immature temporarily resident; and one immature/small adult temporarily resident (Figure 19). This gives a minimum population density of 1 otter : 1.2 km of coast. In addition it was thought that there was one more adult female with a single cub on the island of Urie Lingey (it was not possible to visit the island during the summer, but in January these two animals had been present), and two more transient medium-sized otters seen only once each, one of which may have been resident at Russetter. This would give a population density of thirteen otters on 14 km of coast equivalent to 1 otter : 1.1 km of coast. Thus the population composition on this 14 km of coast was thought to be 2 adult males; 3 adult females; 4 dependent cubs; 4 transient adults/sub-adults.

In 1978 the length of coastline covered stretched from Corbie Head to Il Holm (16 km). The three adult females present in 1977 were still resident (although Buda had shifted her range southwards), and in addition there were two adult females between Tressa Ness and Il Holm (Figure 20). Proceeding clockwise from Corbie Head these females had 2, 1, 1, 2 and minimum 1 cubs.

There was still two adult males present, but the one most often seen in the Hamars Ness - Urie Ness section had not been present the previous year, and appeared to have replaced the previous year's occupant. The adult male to the east was never seen clearly enough to establish its identity with certainty, but it was thought to be the same animal as in the previous year. There was a zone of intense sprainting and marking activity at the landward end of Urie Ness in the area where these males' ranges apparently overlapped.

In addition, at various times, three transient sub-adults/adults were seen on different stretches of the coast.

FIGURE 19 : THE DISTRIBUTION OF OTTERS IN NORTH-WEST FETLAR, SUMMER 1977.

SQUARE BRACKETS INDICATE EXTENT OF MAIN STUDY AREA. OFFSHORE ISLANDS NOT INCLUDED.

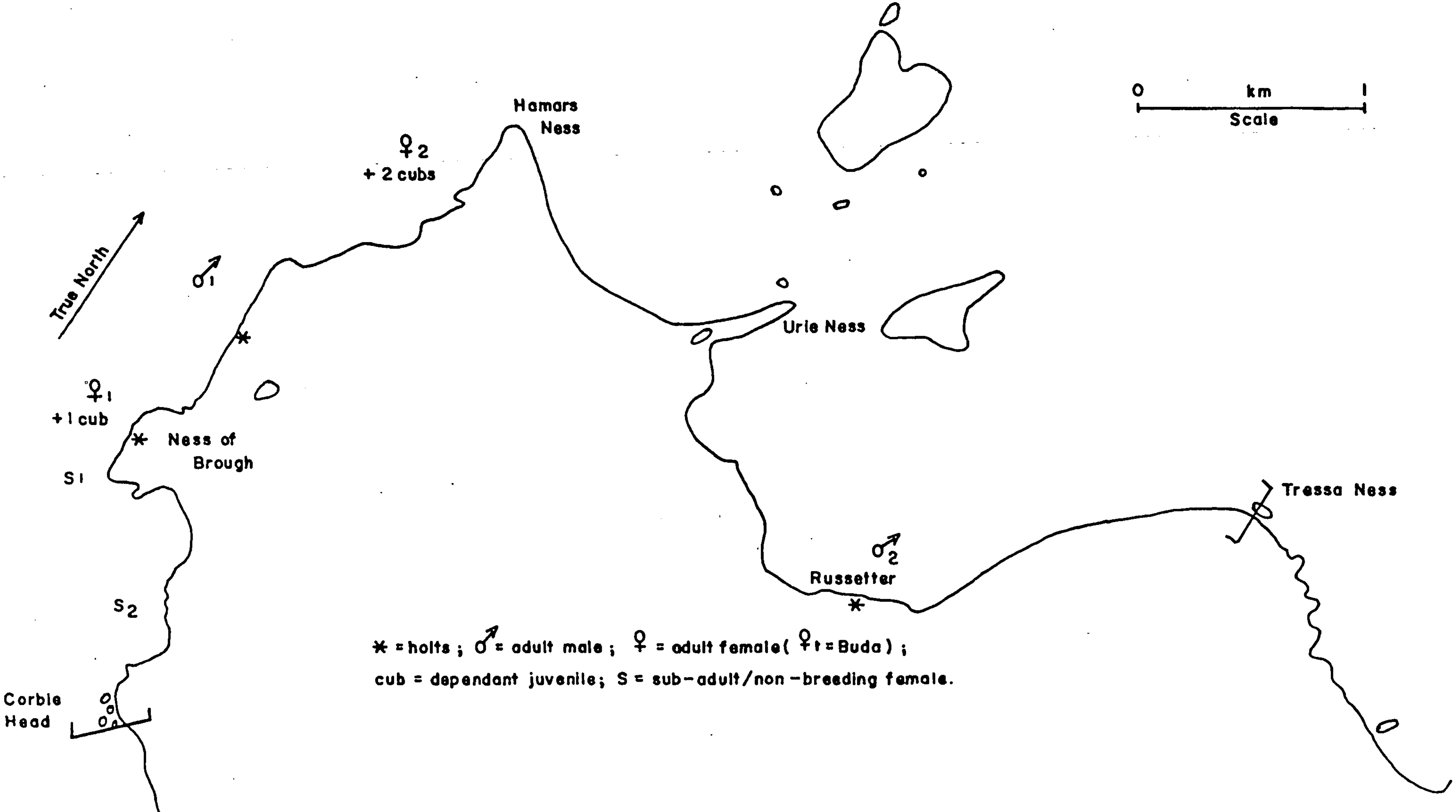
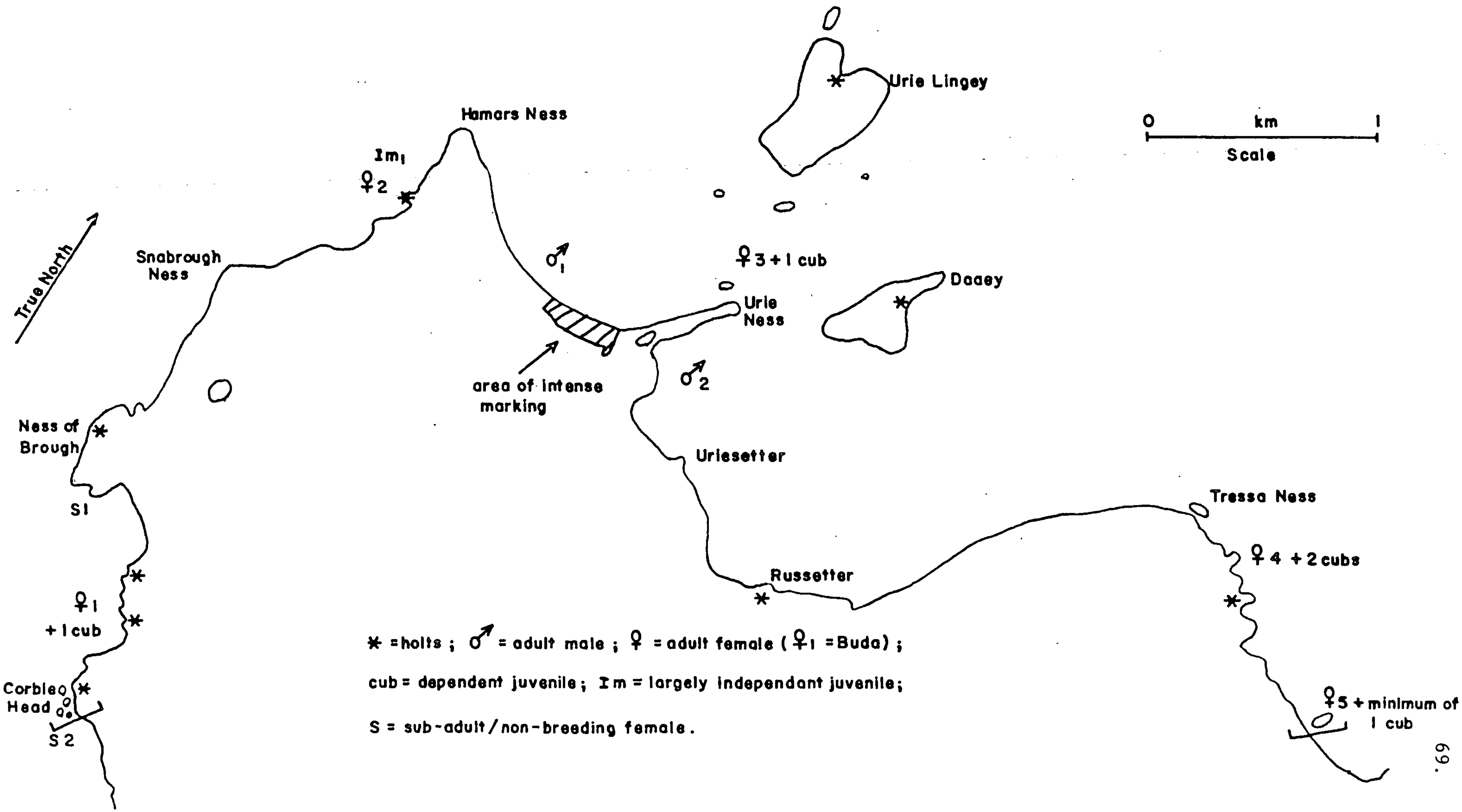


FIGURE 20: THE DISTRIBUTION OF OTTERS IN NORTH-WEST FETLAR, SUMMER 1978. SQUARE BRACKETS INDICATE EXTENT OF MAIN STUDY AREA, OFFSHORE ISLANDS INCLUDED.



This gives a population density of 17 otters on 16 km of coast equivalent to 1 otter : 0.9 km of coast, and a population composition of 2 adult males; 5 adult females; 7 dependent cubs; 3 transient adults/sub-adults.

There was no evidence for regular spacing of holts such as was found by Kruuk and Hewson (1978) around the coast of the Ardnish peninsula on the Scottish coast.

CHAPTER 5

DISCUSSION

5.1 Foraging behaviour

The dives and surface periods of otters foraging in the sea were first timed by Kruuk and Hewson (1978) on the west coast of Scotland. They proposed that it is possible from these data to calculate the amount of time that an otter, during an average dive, spends in travelling between the surface and the sea bed (the otters in their study area were also foraging demersally), and the amount of time left for actual foraging. Their schematic representation of an otter dive is reproduced in Figure 21. They reasoned that assuming an otter has an equal likelihood of encountering a prey item at any time during its foraging on the bottom, and assuming that the time taken to return to the surface from the seabed is unaffected by whether or not the otter has a prey item, then F_+ (the time spent on the bottom during the average successful dive) must equal $\frac{1}{2} F_-$ (time spent on the bottom during the average unsuccessful dive), and that these must both be equal to the difference between mean unsuccessful and mean successful dive durations.

This they expressed algebraically as follows (refer to Figure 21):

$$S_- = D + F_- + U \qquad (1)$$

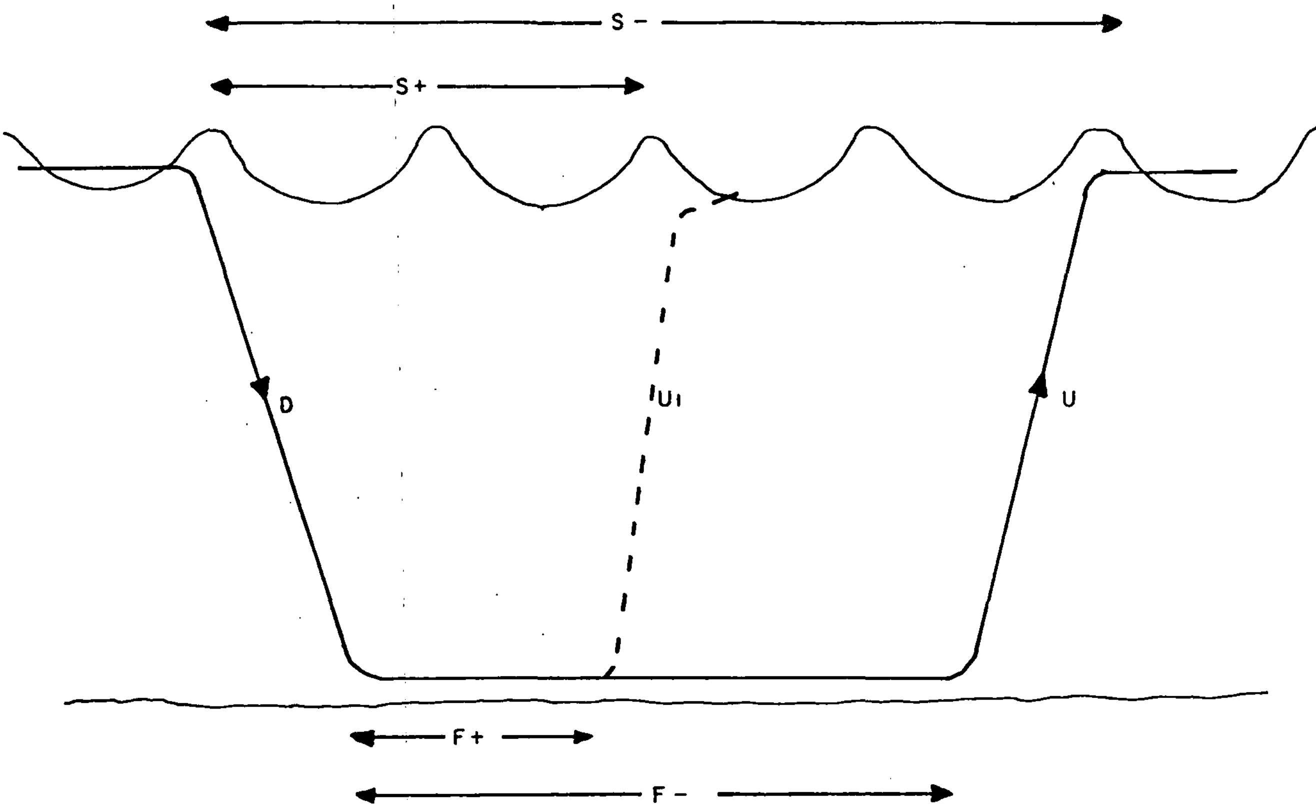
$$S_+ \doteq D + F_+ + U^1 \qquad (2)$$

Assuming that $F_+ = \frac{1}{2}F_-$, and that $U^1 \doteq U$

$$\text{then} \quad S_+ = D + \tfrac{1}{2}F_- + U \qquad (3)$$

Subtracting (3) from (1) :

$$S_- - S_+ = \tfrac{1}{2} F_- \qquad (4)$$



S−, total time under water, unsuccessful.

S+, total time under water, successful.

D, time spent travelling down, for unsuccessful and successful dives.

U, time spent travelling up, for unsuccessful dives.

U1, time spent travelling up, for successful dives.

F+, time spent foraging on bottom, with success.

F−, time spent foraging on bottom, without success.

It is assumed that on average $F+ = 1/2 \times F-$

$U = U1$

Figure 21. Schematic representation of an otter dive.
(After Kruuk and Hewson, 1978.)

Using their observed values of S_- (24.8s) and S_+ (15.9s) in equation (4), the time spent foraging on the seabed during an average unsuccessful dive was 2(24.8 - 15.9) = 17.8s, and the time spent in travelling between the surface and the bottom was 24.8 - 17.8 = 7.0s i.e. 28% of an unsuccessful dive is "travel time", and 72% is available for foraging on the bottom.

Applying this equation to the Fetlar results, then $S_- - S_+ = 7.3$s. Hence time available for foraging is 14.6s, and travel time is 32.7 - 14.6 = 18.1s, i.e. 55% of an unsuccessful dive is travel time and 45% is foraging time.

Now, while it is to be anticipated that travel time will be greater in the deeper water used by otters on Fetlar (estimated to be 2-5 m, as opposed to 2-3 m at Ardnish (Kruuk and Hewson, 1978)), and while none of the dives where otters were watched swimming underwater was timed, it was clear from these direct observations that descent to and ascent from the canopy of the kelp were relatively rapid, and that most of the otters' time underwater was in fact spent amongst the kelp, either at or close to the bottom. It is therefore necessary to look for possible faults with Kruuk's and Hewson's equation.

Accepting that the otter has an equal likelihood of encountering prey at any time during its foraging on the bottom, then it does not necessarily follow that $F_+ = \frac{1}{2} F_-$. For one thing, unless the prey is totally passive there will be a period of pursuit, after detection has taken place, before the prey is captured and brought to the surface. The demersal fish that make up most of the otters' diet are active, and although they probably cannot swim fast for any great distance, they are living in a habitat which offers many refuges into which they can escape, even if only temporarily. If this is the case then $F_+ > \frac{1}{2} F_-$, and what can be concluded is only that F_- must be at least $2(S_- - S_+)$ i.e. Kruuk's and Hewson's model will underestimate the time available for foraging on the seabed.

Secondly, accepting that the otter has an equal likelihood of encountering prey at any time during its foraging on the seabed, only implies accepting that the prey are randomly distributed within the otter's foraging area. The relationship between F_+ and F_- will also be determined by prey abundance: in areas of high prey density F_+ will be shorter than in areas of low prey density. In deducing that $F_+ = \frac{1}{2} F_-$ Kruuk and Hewson are therefore making the implicit assumption that dive duration is related to prey density i.e. that the otter is adjusting the duration of its dives to the rate at which it encounters prey, presumably in an attempt to optimise foraging efficiency.

In order to determine whether this is a valid assumption, it is first necessary to consider some of the physical and physiological problems confronting a diving air-breathing animal.

Normally an air-breathing animal meets its oxygen requirement by regular breathing at short intervals, but while it is underwater it cannot, of course, do this, and so must ensure that it takes sufficient oxygen with it to meet its requirements until it next surfaces. The most highly specialised air-breathing divers, the seals (Pinnipedia) and whales (Cetacea) can stay submerged for many minutes (up to an hour or more in the case of the Sperm Whale <u>Physeter catodon</u>) and are known to have a range of physiological adaptations, e.g. high oxygen-carrying capacity in the muscles or blood and high tolerance of lactic acid accumulation, which enable them both to take more oxygen with them and to function with lower oxygen supplies (Bonner, 1980). However the less specialised divers, e.g. diving ducks (Anatidae), auks (Alcidae), cormorants (Phalacrocoracidae), mink (<u>Mustela vison</u>) and otters, normally stay submerged for less than a minute, and will drown if forced to stay underwater for more than a few minutes (no more than 3-4 minutes for an otter, according to Harris, 1968). This is no longer than many terrestrial mammals, e.g. Man, can remain submerged, and in the absence of any evidence to the contrary, it seems reasonable to assume that such "short time divers" have only limited physiological adaptations for submergence, and that their principal oxygen reserve is the air taken down in the lungs and trachea. It is therefore to be anticipated that there will be a positive correlation between dive duration and the amount of air taken down in the lungs.

Taking air into the lungs however decreases the density of an animal, and thus may pose problems in an aquatic environment because of its effect on buoyancy. According to Archimedes' Principle a body immersed in a fluid experiences an upthrust equal in magnitude to the weight of fluid displaced. This means that if an animal is more dense than water it will have to use energy to prevent itself from sinking, while if it is less dense than water it will have to use energy to prevent itself from rising to the surface. Therefore to minimise energetic loss, an animal must try to have a body density of $1 \mathrm{g\ cm}^{-3}$ (the density of water) in order to achieve neutral buoyancy. This poses a considerable dilemma to a diving animal since air, being a gas, displaces a large quantity of water for its mass, and so the more air that the animal takes down in order to meet its oxygen requirements while submerged, the more energy it will use in counteracting the upthrust on its body.

There are several ways in which an animal can reduce or counter this dilemma. One is to have a very dense body and so reduce the effect of air in the lungs. This would appear to be the case with the otter: no figures on their body density are available, but anyone who has ever picked up an otter will be aware of how surprisingly heavy they are for their size. Another way is to dive to a greater depth. In fluids pressure increases with depth. Now liquids are virtually incompressible, but the volume of a gas varies inversely with its pressure (Boyle's Law: $V \alpha \frac{1}{p}$). In water pressure increases by 10 kN m^{-2} for each metre of depth. Since atmospheric pressure at sea level is 102 kN m^{-2}, at 10 m depth pressure is about twice this, at 202 kN m^{-2}. Doubling the pressure halves the volume of a gas, and thus, provided that the increased pressure can be transmitted fully through the animal's body (via its abdomen and thorax) then its lungs will contain only half the volume of air that they did at the surface, and the upthrust on that air will now be halved. Thus an animal with a given initial volume of air in its lungs will use only half as much energy in countering the upthrust on that air at a depth of 10 m as it would if it were just below the surface. This also means that any animal following a strategy of achieving neutral buyoyancy can do so with correspondingly more air in its lungs the deeper it is. The state of neutral buoyancy is a highly desirable one for an aquatic animal since it not only prevents energetic loss through countering upthrust or tendency to sink, but because it makes precise accurate control of movements underwater easier and allows the animal to remain motionless, suspended in the water. The evolutionary success of the Teleost fishes has been attributed in large part to their possession of a swim bladder - an organ containing gas, the volume of which can be controlled by excretion or absorption of gas so that the fish can achieve a state of neutral buoyancy over a wide depth range.

The only way of controlling buoyancy available to an otter is to control the volume of air in its lungs, and since buoyancy is directly proportional to the volume of the air in its lungs, and since air volume decreases with depth, it is to be expected that the quantity of air that it can afford to submerge with will be directly proportional to the depth of the water in which it is foraging. Hence, in view of the importance of the air in the lungs as an oxygen supply, the otter's dive duration will be directly proportional to water depth.

An examination of the available data on dive duration and water depth confirms that this is indeed the case (Figure 22). In all five of these studies it was known or believed that the otters were feeding on demersal prey, and thus the depth at which foraging was taking place could be estimated quite accurately. The point that shows the poorest fit (Hewson, 1973) is based on the smallest sample - only 2 series of dives timed which, as Hewson pointed out, had very different means and could have taken place in different depths.

Moreover a positive correlation between dive duration and water depth was long ago noted in diving birds (Gätke, 1891, quoted in Dewar, 1924), and thoroughly established by Dewar (1924) for 21 species of diving birds in five families : ducks (Anatidae), divers (Gaviidae), grebes (Podicipitidae), auks (Alcidae) and cormorants (Phalacrocoracidae). He formulated an empirical rule to relate dive duration and water depth (the "20 + 10" rule), which says that a diving bird behaves as if it spends 20s for the first fathom of water it dives in, plus 10s for each succeeding fathom, but he was unable to explain the relationship, hypothesising that it was due to similar morphological and anatomical constraints acting upon all diving birds, and to energetic contraints which were not, as yet, understood.

More recently a tendency has also been noted in mink (Mustela vison) to increase dive duration with depth (Dunstone, 1983). Dunstone hypothesised that the mink could be prolonging its dive in order to compensate for the extra effort required to reach the bottom. However unless correspondingly increased nutritional returns are available with greater depth, this would appear to be an energetically uneconomic strategy to pursue.

The most reasonable hypothesis to explain this relationship detween water depth and dive duration in otters, mink and birds is that it results from all of them minimising the energy required to control buoyancy (both

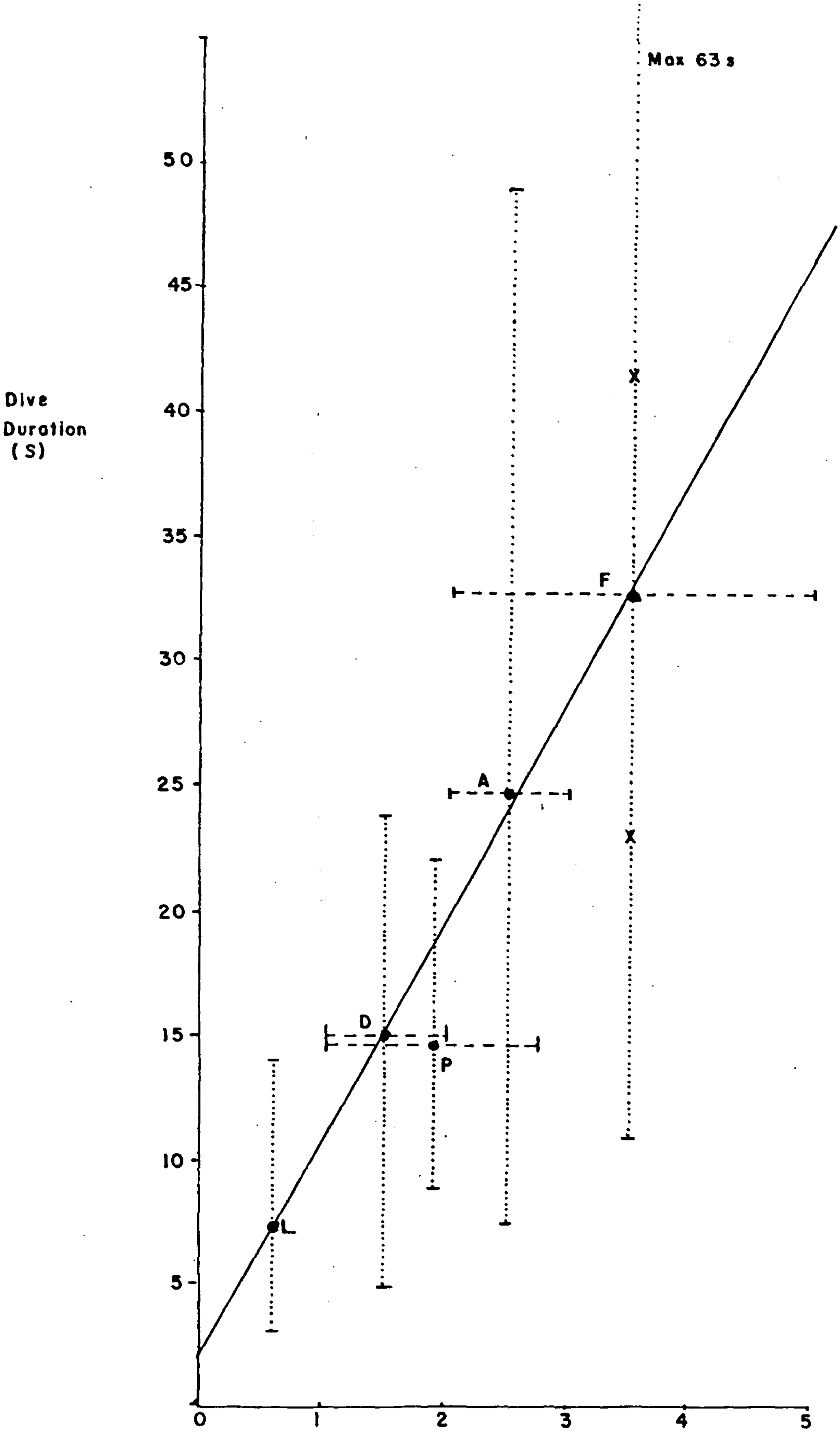


FIGURE 22: WATER DEPTH AND MEAN DURATION OF UNSUCCESSFUL OTTER DIVES IN FIVE STUDY AREAS. F=FETLAR; A=ARDNISH (KRUUK AND HEWSON 1978); P=LOCH PARK (HEWSON, 1973); D=DINNET LOCHS (JENKINS, 1980); L=LEIGHTON MOSS (J. GREEN, PERS. COMM.). DASHED LINES INDICATE FORAGING DEPTH RANGE IN EACH AREA. DOTTED LINES INDICATE RANGE OF UNSUCCESSFUL DIVE DURATIONS. X MARKS STANDARD DEVIATION OF MEAN OF UNSUCCESSFUL DIVE DURATIONS.

Solid line: line of best fit, by eye.

positive and negative). Thus it is not a case of the otter, mink or bird being forced to stay submerged for longer where the depth is greater, but rather a case of it being forced to stay submerged for less time where the water is shallower. Provided that the energetic cost of taking a given mass of air down deep is not too great, and can be done quickly enough, then it will be more economical to forage in deeper water than in shallow water.

Since the upthrust on a given mass of air decreases as its volume decreases with depth, the key to diving with an excess of air in the lungs is the initial acceleration at the start of a dive. Once an otter has exerted sufficient force to overcome upthrust and drag forces, it will accelerate downwards if it continues to exert the same force, or it can continue downwards at a steady velocity with the exertion of progressively less force.

On the recommendation of the examiners, the latter part of Section 5.1 has been excised.

5.2 Composition of the diet

The accuracy of frequency analysis of prey occurrence in spraints as a measure of the relative importance of the prey taxa in the diet has been discussed by Erlinge (1967a), who used this method, and by Jenkins, Walker and MacCowan (1979) who, in addition, estimated the bulk of the remains of each taxa occurring in a spraint (bulk analysis). Stephens (1957) pointed out that prey items with a large proportion of indigestible parts tend to be over-represented in spraints. Thus bulk analysis will tend to lead to an over-estimate of the relative contribution of small bony fish to the diet, and to and under-estimate of the relative contribution of large fleshy fish, unless correction factors relating bulk of remains to the size or numbers of each prey taxon have been derived and are used in the analysis.

The otter's food is evidently well mixed in its stomach (the stomach in one corpse examined contained the remains of 14 fish of 5 species, in various stages of digestion, from almost intact to completely disarticulated bones), and the average spraint contained 3.0 taxa. It was noticeable that the mean number of taxa per spraint varied seasonally, from 3.4 in the July-August sample to 2.5 in the January sample. Since there was no perceptible seasonal variation in spraint size this was evidence of less diversity in the winter diet, which is supported by the increased relative abundance of a few taxa in the January sample, and the corresponding relative rarity of the others. This does, however, draw attention to a possible source of bias in frequency analysis: the presence of the remnants of a single individual of a rare prey taxon is likely, since one vertebra is scored the same as fifty would be, to lead to an over-estimate of such a taxon's contribution to the diet. The lower the mean number of taxa per spraint, the greater the bias towards rarer taxa will be, so that the frequency analysis results for the January sample are more likely to give such an inflated estimate of the true contribution of the rarer taxa to the diet than are those for the other seasonal samples where the mean number of taxa per spraint was higher. However the generally high diversity of prey in the diet of this coastal otter population will reduce this problem in comparison with those results from study areas where prey diversity was lower, and in view of both the practical difficulties of obtaining correction factors (a captive otter is necessary) and Erlinge's conclusion (from an empirical test on captive otters) that relative frequency was proportional to the relative proportions by weight of prey taxa (Erlinge, 1968), it was concluded that frequency analysis was an adequate technique for this study.

One factor which could cause problems in using spraint analysis to examine diet would be if otters were eating prey which had no or few indigestible remains. The only species observed to be eaten by otters on Fetlar that might have caused this problem was the Northern Octopus (Eledone cirrhosa). This however was only taken very occasionally. When present it gave a distinctive purple colour to the spraints, and in some cases fragments of the tentacular suckers were present. This problem is therefore unlikely to affect the results significantly.

If the Fetlar results are compared with those from various studies in freshwater habitats, it is apparent that the Fetlar otters were taking a lower proportion of prey that was not entirely aquatic. For example Erlinge (1967a) found the overall relative frequency of birds and mammals combined to be 9.8% on a Swedish lake and river system and on a Welsh river the figure was 21% (Stephens, 1957). In Fetlar, however, the corresponding relative frequency was only 0.6%. In the only other analysis of coastal spraints, the relative frequency of non-aquatic prey (only birds in this instance) was again low, at 2.1% (Mason and MacDonald, 1980). It would appear then, that the availability of fish and crustacean prey in the sea is sufficient for there to be little inducement for the otters to diversify their diet with birds and mammals. The alternative explanation that birds and mammals were either insufficiently abundant or too difficult to capture, is unlikely to be even a partial explanation, given that rabbits, breeding waders and seabirds were present in the area in some numbers, and that otters were on several occasions seen to pass close by, and to ignore, immature fulmars (<u>Fulmarus glacialis</u>) and gulls (<u>Laridae</u>) that would have been easy prey. Freshwater streams and lakes on Fetlar could potentiall provide otters with foraging areas, (common eels, trout and three-spined sticklebacks are present) but the low density of spraints found along these freshwaters indicated that they were little used even in comparison with the least frequented parts of the coast. This was presumably because prey are either less numerous or harder to catch in these freshwaters.

The discussion of buoyancy constraints in Chapter 5.1 has pointed out some of the potential advantages of demersal foraging to otters.

However it is likely to be more significant that most species of demersal fish are slow-moving in comparison with open-water species. In other words, there is a greater effective density of available prey on the seabed and among the kelp than there is in open-water. While it was never possible to see otters foraging on the sea-bed it is known, from observations of tame otters, e.g. Wayre (1977), that they are able and prepared to investigate and enter holes and tunnels on the bottom. Twelves (1983) records that otters drowned in lobster creels had to pass through entrances only 12 cm in diameter, and her observation that males (which are larger than females) were rarely drowned in this manner indicates that it is its own body size which determines how small a hole an otter will enter. Studies on captive American Mink (_Mustela_ _vison_), another species of amphibious mustelid, suggest that the presence of fixed points of reference makes systematic searching for prey on the bottom easier than searching homogenous open water (Dunstone, 1978; Dunstone and O'Connor, 1979). This too is likely to lead to a preference for demersal foraging.

In Loch Broom, Mason and MacDonald (1980) found that demersal species made up 76% of the taxa in spraints collected in the winter, a value similar to the 80.5% in the January sample from Fetlar.

Perhaps the most striking feature of the diet of coastal otters as revealed by spraint analysis is the much wider array of fish and crustacean species taken than is the case in freshwaters that have been studied. This can be explained simply by the much greater species diversity of fish and crustaceans in the sea.

In considering the reasons for seasonal variations in spraint composition, the main problem is the lack of information on seasonal variations in the numbers and distribution of prey taxa. Perhaps the most extreme case is that regarding published information on Yarrell's Blenny (Chirolophis ascanii). According to Wheeler (1969) all that is known of its distribution is that it is usually found at depths of 40-50 m, and occasionally down to 400 m; and that its distribution around Britain is very patchy. The two reference specimens from which the vertebrae were obtained during the present study were collected at the low-water mark, during spring tides, in rock crevices. Vertebrae of this species were present in all the spraint samples, and during the summer months it was evidently one of the most frequently captured prey species (highest frequency was 52.4%, relative frequency 15.4%, in the July-August sample). It was also a significant component of winter sample of spraints in Loch Broom, with a frequency of 30% (Mason and MacDonald, 1980). Thus it is apparent that not only is Yarrell's Blenny found in much shallower water than previous thought, but it would appear to be a common and perhaps significant component of the sub-littoral fish fauna on northern and western Scottish coasts. There is as yet no information available to explain why Yarrell's Blenny occurred in 42.4% of spraints in July-August, and only 3.2% in January. The information available for the the other prey species suggests that the changes in representation of most taxa in spraints are due largely to their migrations and annual population rhythms. Two of the most important summer prey species, butterfish (Pholis gunnellus) and eelpout (Zoarces viviparus), are known to migrate into deeper water offshore in winter (Gibson, 1969). One species, the Lumpsucker (Cyclopterus lumpus) migrates inshore to breed in spring (Gibson, 1969). In this species the eggs are laid in clusters and then guarded by the male until hatching, and in respect of this behaviour it is interesting that not only does this species show a spring peak in its frequency in spraints, but that of 21 lumpsuckers seen to be captured in April-August 1977, 20 (95%) were males (easily distinguished by their red bellies). Squat lobsters (Galatheidae) also appear to migrate inshore in spring (pers.observation). Other taxa that are reputed to spawn inshore, in this case in the winter, are the sea scorpions (Myoxocephelus scorpius) and (Taurulus bubalis) and sea snails (Liparis sp.) (Jenkins, 1936). R.Gibson suggests (pers.comm.) that the high frequency of flatfish (Heterosomata) in the September spraint sample is a consequence of the growth of the young flatfish, which migrate inshore in May/June, to a size where they have become economically worthwhile prey for an otter. The higher levels of sea sticklebacks (Spinachia spinachia) in winter and spring are also consistent with the idea that some fish are only taken when they reach a suitable size. This species is annual, the adults dying after breeding during the summer, and would therefore only be available as small juveniles in late summer and autumn.

Given that some otters do not appear to take crabs (Brachyrhyncha) at all (see Chapter 3.6), whereas they form a considerable proportion of the diet of others, any seasonal variations in crab frequency are likely to be obscured by the differences in foraging habits of the otters producing the assortment of spraints analysed.

The most striking annual variation in diet is the low frequencies of three eel-like fish (Eelpout, butterfish and Yarrell's Blenny) in winter, and the correspondingly high frequencies of sea scorpions and non-rockling gadoids at that time. The disappearance of eelpout and butterfish can be ascribed to their migration offshore in winter, the increase in sea scorpions to their migrating onshore in winter. Yarrell's Blenny may also be an offshore winter migrant. It is the high relative frequency of the non-rockling gadoids in winter that is hardest to account for. As was mentioned in Chapter 3.4, non-rockling gadoids were believed to be pelagic species, probably largely comprised of saithe (Pollachius virens). Smaller size classes of this species are present inshore at all times of year, and are abundant in many localities, but being pelagic are probably much more difficult prey for otters to catch. It would seem most likely that faced with a relative shortage of demersal fish in winter, the otters are forced to pursue the more difficult open-water non-rockling gadoids. Alternatively, or in combination with this explanation, it may be that with the lower sea temperature in winter, fish, being poikilothermic, have a lower metabolic rate, as Gerell (1967) has suggested, and thus species which are relatively difficult to catch at other times of year fall prey to the otter more easily in winter.

5.3 Temporal and spatial pattern of foraging

The tendency for the majority of prey captures to be aggregated in space and time is almost certainly a reflection of prey distribution, which in turn is probably determined primarily by environmental factors such as sea-bed topography and structure, vegetation and currents, and which may be influenced by prey behaviour in relation to such variable factors as time of day and the state of the tide. Localisation of foraging is demonstrated for Buda and Harald in Chapter 3.7 and is discussed in Chapter 4.5, while environmental factors are referred to in several parts of the text including Chapter 4.8.

The assumption that all time spent in the sea is time spent foraging was only made in order to find a way of calculating comparative prey-capture rates (see also Chapter 3.6). This procedure was considered valid, despite the readily apparent, but unquantifiable, variation in foraging effort in the short-term, since the comparisons are all based on a reasonable duration of cumulative observations (minimum of 4.4 hours).

The relatively high proportion of time spent on land reflects the importance of grooming and coat-care to otters. Lacking appreciable sub-dermal fat deposits they are reliant on the layer of air trapped in their underfur for insulation. Since some of this air is squeezed out by pressure each time they dive (see Chapter 3.2.1) it will be necessary to re-aerate the fur periodically, and the principal way of achieving this seems to be by grooming. There was no indication that the European Otter can aerate its fur by blowing bubbles into its fur underwater as has been reported for the Sea Otter (Enhydra lutris) by Kenyon (1969).

5.4 Behaviour in relation to the time of the day and state of the tide

In view of the many potential sources of bias in the use of such cumulative data based on discontinuous observations of several individuals, it is difficult to interpret these data with any degree of confidence. The correlations between activity, and time of day, and between activity and tide state that are suggested by the data, are ambiguous, suggesting that they are not strong correlations and that they may, given the potential sources of bias, be misleading. Unless the correlations are very strong they may well be atrributable to the interaction of the sources of bias. Potential sources of bias include : (1) the relative difficulty of seeing and watching otters during Low Tide due to the half-exposed kelp at the water surface; (2) the observer's tendency to concentrate his searching effort in Buda's home range during the periods when past experience suggested that she and Harald were most likely to be active; (3) conversely the observer's tendency to search other stretches of coast at times when it was anticipated that Buda and Harald would not be active, or when a search of their home range had failed to reveal them; (4) individual otters may behave differently in relation to time of day and tide state; (5) interaction of other potential environmental determinants of behaviour, e.g. aspect of the coast, weather and sea conditions, with time of day and tide state.

In view of the difficulty of assessing the impact of these potential sources of bias it is hard to draw firm conclusions about the influence of time of day and tide state on otter activity. It is, however, apparent that these were not the sole determinants of the timing of their activity.

It is interesting to compare the finding that individual otters on Fetlar varied in their propensity towards nocturnal or diurnal activity with the results from recent radio-tracking studies carried out elsewhere. In their coastal study area on the Mainland of Shetland, Kruuk et al. (1986) found that twelve radio-collared otters showed very little nocturnal activity. In contrast three radio-collared otters on a river system in Perthshire were predominantly nocturnal (Green et al., 1984). It is generally believed that preferential nocturnality is a consequence of the risk of human disturbance (e.g. Green et al., 1984), so it is not surprising to find a substantial proportion of otters showing a diurnal preference in areas like Shetland where the human population is low. It is probably also true to say that it is far easier for an otter to disappear and avoid the threat of being cornered or driven onto land along the sea-coast than it is on a restricted inland waterway.

The bimodal pattern of diel activity indicated by the Cumulative Observation Success Rates on Fetlar appears to be independent of the timing of activity. Bimodal activity patterns were clearly demonstrated by both the diurnal otters on Mainland Shetland, and by the nocturnal otters in Perthshire.

5.5 Comparison of the foraging behaviour and diet of an adult female with that of her cub

Since Buda and Harald almost always foraged together, differences in prey abundance and distribution could not be the cause of the dietary differences observed, but must be due to behavioural differences between the two otters, or to limitations imposed differentially by the environment.

There was no indication that the dive durations of Buda and Harald were significantly different: they often dived and surfaced in synchrony. The difference in prey capture rates indicates that Buda was a more successful hunter (prey capture rate = 1 item/11.8 mins) than Harald (prey capture rate = 1 item/25.6 mins). The difference is highly unlikely to have been due to a lower food requirement on his part, given his attempts to take prey from Buda. This attempted klepto-parasitism was accompanied by aggressive vocalisation from both otters, and was usually unsuccessful. In September 1976, when Harald had only recently emerged from the holt for the first time, Buda would bring prey to him, but this was never observed during April-July 1977.

During August, after their separation, Buda's prey capture rate remained much as before, so it is reasonable to suppose that without a cub to support she could meet her nutritional requirements in a shorter time. At this time Harald's prey capture rate more than doubled (to 1 item/10.6 mins), but it was evident that this was achieved only by greatly increasing his consumption of crabs; his fish capture rate remaining similar to that prior to separation.

The greater proportion of slow-moving fish in Harald's diet coupled with his low capture rate of fish clearly indicate that he was a less efficient hunter than his mother. While with her he was able to make good this deficit by taking prey from her, but after separation he was found to rely on crabs, which although they were likely, in view of their tough shells, low flesh:hard parts ratio, and long "handling time", to provide relatively low nutritional returns, were abundant and easily caught. His continued low rate of nutritional uptake would necessitate continued extended foraging periods. It is also apparent that with any additional cubs, Buda would have been obliged to spend even more time in foraging.

Foraging then, will require more time for adult females with cubs to support and for immature otters, than it will for adult males and adult females without dependent cubs.

5.6 Home range use by an adult female and her cub

The 2.5 km length of coast used by Buda and Harald, with its maximum foraging area of 42.6 ha, was evidently sufficiently extensive to provide enough food for an adult female and her cub. Indeed sections I, J and K were used so seldom that they can be considered as subsidiary parts of the home range. If they had not been available it seems likely that the remaining 1.7 km of coastline with a maximum foraging area of 29.3 ha would still have been sufficient to support these two otters.

It was apparent that the areas offshore from the two promontories Snabrough Ness (section A) and Ness of Brough (sections E, F and G) were those most important for feeding, given that 60% of all the prey items seen to be caught by Buda and Harald (n = 194) were taken in these 4 sections which constituted 32% of the total potential foraging area. It appears that for the successful exploitation of the Snabrough Ness area, which was about 1.0 km from the main holt at Ness of Brough, the availability of the secondary holt in section D, less than 500 m away, was useful if not essential. Evidence for this came in the following year, 1978. During the winter of 1977-78 the holt in section D was destroyed by marine erosion, and during the summer and autumn of 1978 Buda had her home range centred on a small holt in section K, and foraged south of here, beyond the limits of her 1977 home range, and north as far as section G. No otters were resident at the holt in section F, and the whole stretch of coastline from section C to H was very little used by otters. If it is assumed that the subsidiary holt was necessary for the successful exploitation of sections A, B and C, then it may be justifiable to infer that the maximum available foraging area of 19.2 ha in sections D to H is insufficient to support a breeding female. Although hardly conclusive this does suggest that the availability of suitably spaced holts may play a significant role in determining the distribution, the habitat use and ultimately the population density of otters.

Areas where the seabed is largely bare sand, e.g. section I,evidently have little foraging potential for otters. This is probably because they support few demersal fish of suitable size other than the relatively fast flatfish, which, while they are clearly feasible prey in areas where the sand is hemmed in by Laminaria beds, are probably very difficult to catch on a bare, flat open sandy bottom.

Until recently the only data available for comparison with the present study were those of Erlinge (1967b) who found that on a Swedish river and lake system the home ranges of breeding females were about 7 km in diameter. However he also pointed out that this was the total area covered during the course of the year, and that in summer the home range was very much more restricte he illustrates this for one family group, which was using a single eutrophic cove with a shoreline of about 2.5 km. In Erlinge's study area the lakes and slower reaches of the rivers were frozen in winter, so that the otters using their eutrophic cove in summer were forced to move from the lake to its outflow stream in winter, thus inevitably increasing the size of the home range as a whole. In Shetland however the sea rarely freezes, and there was no evidence of seasonal variation in home range size (although from the distribution of old spraints it did appear that in winter otters tended to use holts and lie-ups further away from the sea, presumably because holts and lie-ups close to sea-level were liable to inundation during storms).

The radio-tracking study on a river system in Perthshire (Green et al., 1984) has now revealed the home range sizes of two adult females. One (unaccompanied by cubs at the time of the study) used 13.45 km of lowland river and streams, four small lakes with a total area of 43 ha and 4.5 ha of "semi-aquatic" habitat (reedbed, marsh and alder carr). The total available foraging area was 66.5 ha. The second female, which was accompanied by one cub, used 22.4 km of river and streams (mostly upland) and 117.4 ha of upland marsh, the total available foraging area being 135.6 ha. While the second female exploited her range fairly evenly (with a tendency for decreasing use towards the edges, as in Buda's case), the first female concentrated her activity on the small lakes at either end of her home range, using the connecting river and streams primarily as a thoroughfare between these core areas. It is notable that the principal foraging area of this otter (43 ha) is almost the same extent as the maximum foraging area of Buda and Harald (42.6 ha).

Within their ranges each of these Perthshire females used several daytime resting sites (five in the case of the lowland female, fourteen in the case of the upland female) with an average distance between resting sites of 1040 m (lowland female) and 1600 m (upland female). Obviously it is to be expected that with much more extended and linear home ranges these freshwater otters will require a greater number of secure resting sites, and the relatively close spacing of these again suggests their importance to the otters.

Taken together these three studies suggest that the main factors determining the size and pattern of use of adult female otters' home ranges are the distribution of good foraging habitat and the availability of suitably placed holts.

5.7 Population distribution and density

Observations indicated that the pattern of distribution of breeding females was fairly conservative from year to year, with females staying where they were unless environmental changes necessitated a shift in home range. Spatially the pattern of distribution appears principally to reflect the distribution of suitable holt sites in conjunction with good feeding areas. For example the stretch of coast between Hamars Ness and Uriesetter was fringed by extensive shallow water suitable for foraging extending out towards the offshore islands of Daaey and Urie Lingey, but there were no suitable holt sites on the mainland. These shallow waters were, however, used constantly by otters based in holts at Oddsta and on the offshore islands (see Figure 20). Between Uriesetter and Tressa Ness there was only a narrow fringe of shallow water. Here there was one apparently suitable holt site (at Russetter), but this was used only occasionally, there being no otters resident there. In contrast, on the 1.5 km stretch of coast immediately east of Tressa Ness where the shallow water fringe was wider than between Uriesetter and Tressa Ness but not nearly as extensive as in the Urie Ness area, there were numerous potential holt sites in boulder screes, and here two breeding females were present. Erlinge (1967b) found the same pattern of breeding females dispersed in more or less discrete home ranges which were fairly conservative from year to year on Swedish freshwaters.

There was no evidence on Fetlar for regular spacing of occupied holts as was found to be the situation on the Ardnish peninsula (Kruuk and Hewson, 1978). Kruuk and Hewson interpreted this regular spacing as evidence of territoriality, and concluded that holt distribution was determined by social pressures. This may indeed be the case in areas like Ardnish where there is an abundance of holt sites (Kruuk and Hewson say that "There were many places along the coast which appeared to be as suitable for an otter holt as those actually used,....."), but is clearly not the primary determinant in areas where only a limited number of suitable holt sites are available. Workers in other areas have also shown that the distribution of occupied holts reflects the distribution of potential holt sites both on the sea-coast in Western Scotland (MacDonald and Mason, 1980) and in a lowland river system (MacDonald, Mason and Coghill, 1978).

The evidence suggests that the distribution pattern of adult males on Fetlar is, like that of adult females, similar to that obtaining in Swedish freshwaters. Erlinge (1967b) found that adult males had home ranges which were much larger than those of adult females; which tended to overlap with those of other males, and which included the range of at least one female. For comparison the adult male radio-tracked by Green et al. (1984) in Perthshire included 39.1 km of water ways in his home range, which included the ranges of three breeding females and additional non-breeding females. On Fetlar adult males could not be associated with particular holts or foraging areas in the way that females could, and they were seen too infrequently to establish the full extent of their home ranges. However, in 1978 the study area included one apparent male/male boundary.

Erlinge (1968a) described how intense olfactory signalling behaviour was evident in zones of overlap between adult male territories, and in 1978 just such a zone existed on Fetlar at the western end of Urie Ness where the ranges of the two adult males known to be present in the main study area overlapped. (Besides nightly deposition of spraints at traditional sprainting sites, this signalling behaviour consisted of frequent scratching at well-used rolling points on turf to the extent that all the grass was removed and shallow pits were excavated in the soil below).

Erlinge (1968a) recorded a population density on freshwaters of 1 otter/ 0.7-1.0 km^2 of water, equivalent to 1 otter /2-3 km of lakeshore or 1 otter/ 5 km length of stream. It would be tempting to conclude that the population density on the Fetlar coast was much higher (approximately 1 otter/1 km of coastline) because the sea offers a richer food supply with a higher density of available prey. However no comparable data on available prey density exists, and there are other probable explanations for the difference in otter population density which make such an explanation unnecessary and unlikely.

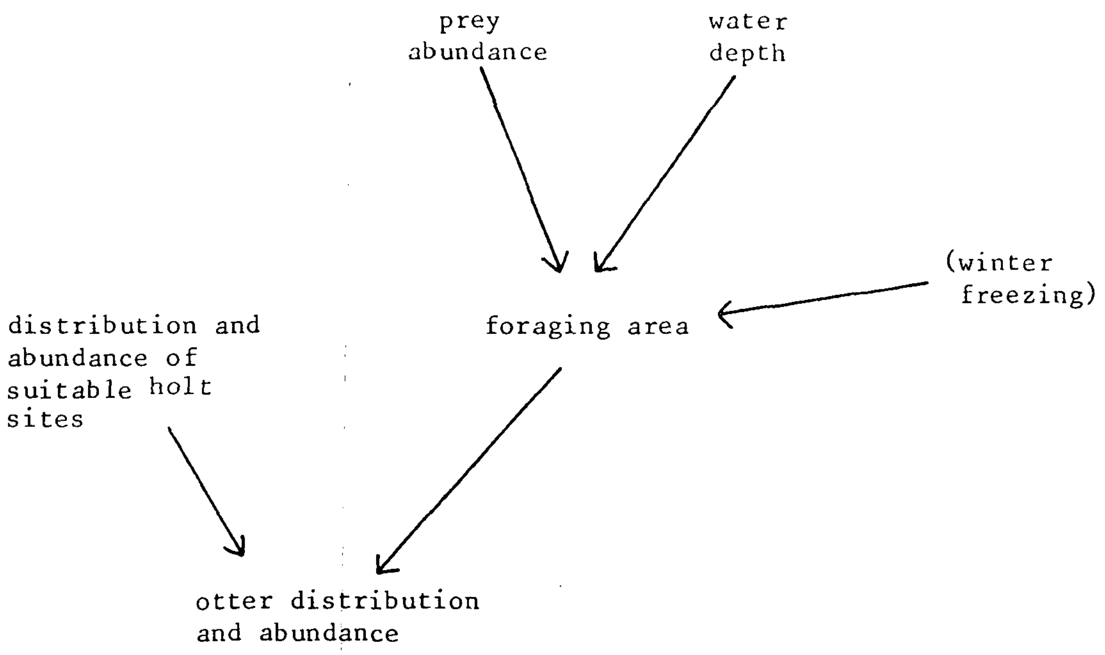
Firstly, as Chanin (1985) has pointed out, the seasonal temperature changes which have a profound effect on the freshwater environment in Sweden are likely to affect otter populations. In particular the freezing of much of the Swedish freshwaters for some three months severely limits the extent of foraging area available to that otter population in winter, leading to concentrations of up to seven to eight individuals on four to five kilometres of stream (approximately 1 otter /0.6 km of stream) (Erlinge, 1968a). Thus it is clear that over a limited part of the year otters in Swedish freshwaters can survive at population densities higher than those observed in the marine environment. In view of this it is likely that the Swedish freshwater otter population density is limited by the availability of winter foraging areas; unfortunately no comparable population density estimates are available for eutrophic freshwaters in an area which does not freeze annually, but a higher density would be predicted in such circumstances. In Shetland the sea never freezes so there is no seasonal reduction in the foraging area available to the otters, and although the relative scarcity of demersal fish remains in the January spraint sample suggests that winter may be the time of year when foraging is most difficult, there is no evidence to indicate that this is a major factor determining population density.

Secondly, as has been pointed out by Chanin (1985), the ratio of shoreline length to area of foraging habitat must be taken into consideration. For a given length of shoreline the otters living on the coast of Fetlar have a far greater foraging area available to them than do otters living in most freshwater environments. Although Buda's home range was only 2.5 km of coastline, she had an estimated foraging area of 42.6 ha (see Chapter 3.7). In order to have the same area of foraging habitat an otter living on a 10 m wide river would require a home range 42.6 km in length. If it is assumed, for the purposes of these calculations, that 150 m is the average seaward limit of foraging in the main study area on Fetlar, then given a population density of approximately 1 otter/1.0 km of coast, there is approximately 1 otter/15 ha of foraging habitat. A direct comparison of this result with Erlinge's (1968a) for Swedish freshwaters of 1 otter /70-100 ha of water would not be valid since Erlinge included the entire area of the lakes in his study area in his calculations. Since several of these lakes were large (up to 12 km^2) and the otters are likely to have exploited only their shallower parts, there was probably much less than 70-100 ha of actual foraging habitat per individual. In his papers Erlinge does not say how wide the streams in his study area were, but from his published photographs (Erlinge, 1967a) they appear to be less than 10 m across. This means therefore, that a population density of 1 otter/5 km of stream was equivalent to 1 otter /5 ha or less of foraging area. This implies that if prey density is the principal factor limiting otter population density, then eutrophic freshwater streams must be a better foraging habitat than are marine coastal waters.

In conclusion it appears that eutrophic freshwaters are capable of supporting a higher population density of otters in terms of numbers of otters per unit area of foraging habitat, and that the higher concentrations of otters along the Shetland sea coast are due to the more extensive areas of shallow water suitable for foraging that are available there. The optimal habitat for otters is therefore likely to be an extensive shallow lake and marsh system with numerous small islands in an area which does not freeze in winter.

5.8 Concluding remarks

Basically this study has elaborated Erlinge's interpretation of the ecology of the European Otter and has illustrated some of the responses of this species to life in a marine environment. The otter's preference for fish, especially demersal species, as prey is clear, and it is apparent that hunting on the sea-bed is the preferred foraging technique. The observations of Buda and Harald indicate why otter cubs are dependent on their mothers for so long, while the findings on home range use and size, population distribution and population density show that suitable holt sites in close proximity to foraging areas are a necessity for breeding females. The buoyancy hypothesis which seeks to explain why dive duration is proportional to water depth, if correct, leads to the prediction that water depth and prey density inter-relate to set limits to the foraging area available, which in turn will limit the distribution and density of otter populations.
The way in which it is predicted that these factors interact can be expressed diagrammatically :



The argument for the buoyancy hypothesis has been presented in some detail despite the limited quantity of data because of its far-reaching implications for the understanding of the ecology, not only of otters, but also of other air-breathing aquatic vertebrates. Since the hypothesis is predictive it should be relatively easy to test on various species of animals both experimentally and by making detailed observations in the field.

A full understanding of the ecology of otters in a marine environment requires better knowledge of the ecology of the sub-littoral environment: as yet there is no generally accepted system of classifying underwater habitat types at anything other than a very superficial level,and much remains to be learned about the ecology, behaviour and distribution of sub-littoral fish before the details of otter foraging behaviour and dietary composition can be interpreted with confidence.

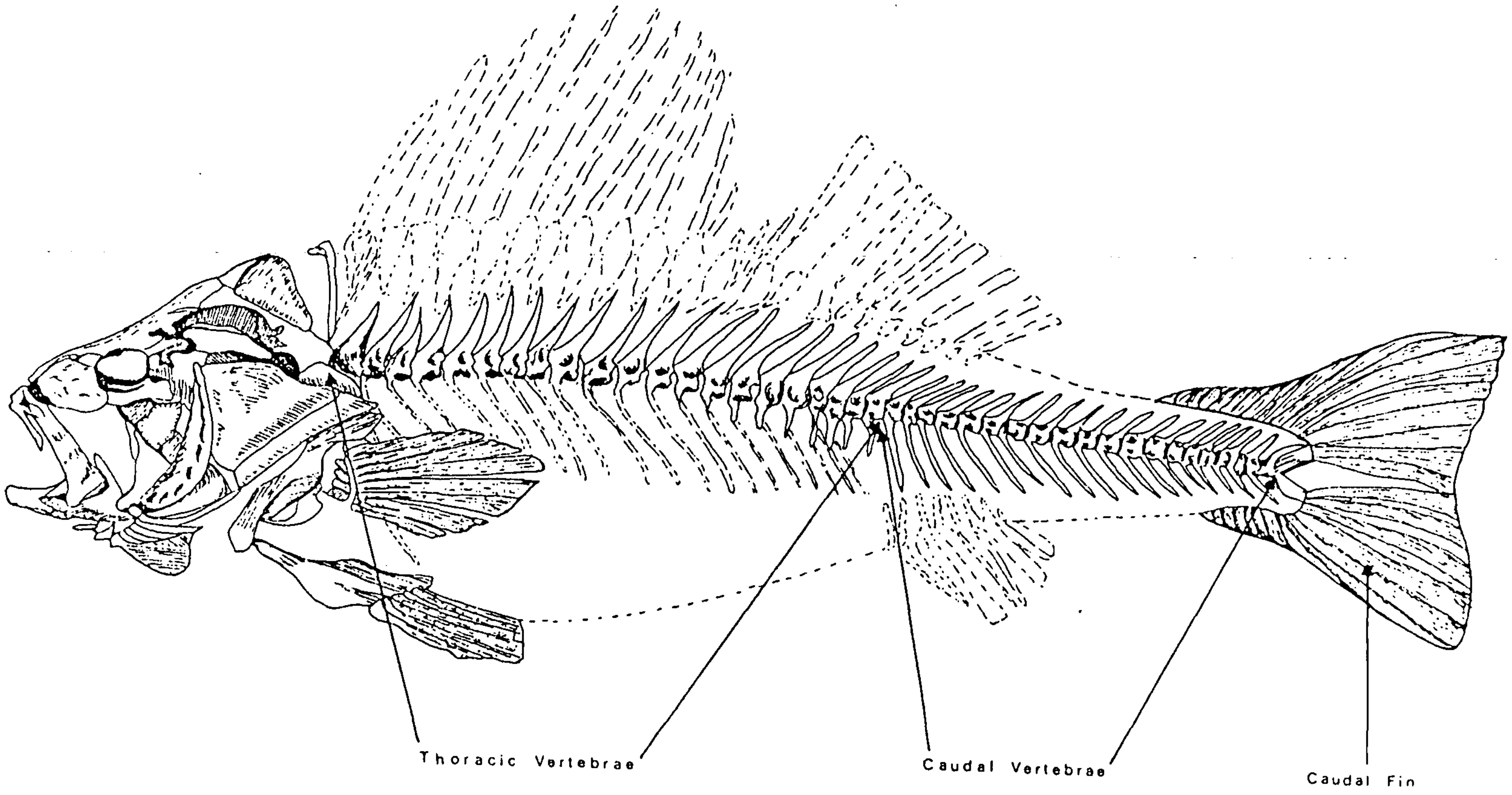
This study has demonstrated that much useful information can be gathered simply by watching otters in the wild, but it is worth drawing attention to the main drawbacks with this technique. The return, in terms of time spent watching otters, was low relative to the expenditure, in terms of time spent looking for them; and reliance on natural markings for individual identification meant that the value of many observations was reduced because it was not always possible to see these markings clearly enough for reliable identification of individuals. The use of radio-telemetry is overcoming these problems, but it should be borne in mind that unless the transmitters are implanted, foraging efficiency will probably be impaired, for the attachment of a harness is likely to affect an otter's underwater manoeuvrability and speed, with consequent effects on its behaviour.

APPENDIX : A guide to the identification of the vertebrae of inshore fish found in Shetland.

This guide is laid out in the form of a key, an earlier version of which has been found useful by other workers (e.g. Mason and MacDonald, 1980). It has been expanded and revised as specimens of additional species have become available for comparison, and now covers all the families of fish likely to occur in inshore waters around Shetland.

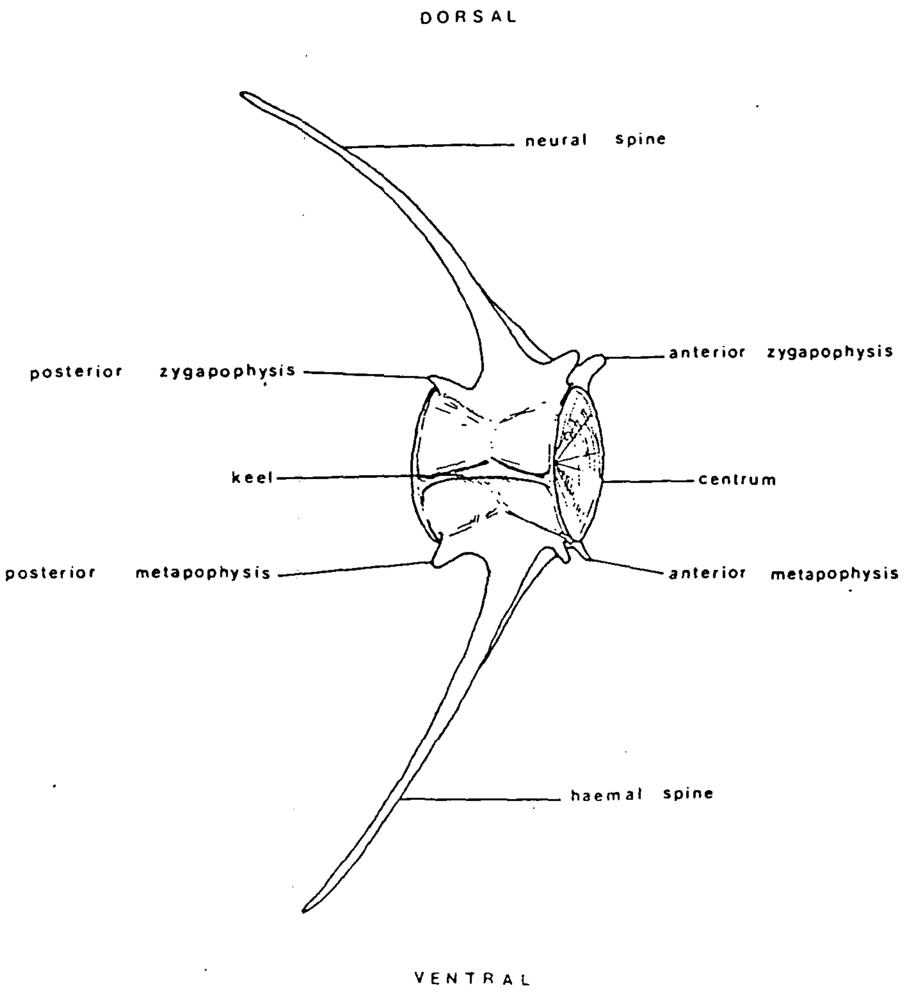
In most cases it was possible to determine vertebrae only to the taxonomic level of family. However in the case of the Gadidae consistent differences were noted in the vertebrae of the genera *Ciliata* and *Gaidropsarus* (the Rocklings) which enabled their differentiation from the rest of the family. Similarly in the family Cyclopteridae vertebrae of *Cyclopterus lumpus* could be readily distinguished from those of the genus *Liparis*. At the other extreme no reliable features could be found to enable the differentiation of the two flatfish families Scophthalmidae and Pleuronectidae. Several fish familes are represented in the inshore waters around Shetland by only a single species, e.g. the Pholidae by *Pholis gunnellus*, or have only a single common inshore representative at this latitude, e.g. *Chirolophis ascanii* in the Stichaeidae, so that a specific identity can be ascribed to many vertebrae with reasonable confidence.

Unless otherwise stated, the key refers to the *antero-caudal* vertebrae, which exhibit a set of features characteristic to each family. Towards the caudal fin the *postero-caudal* vertebrae become smaller and many of the distinguishing features are obscure, while the *thoracic* vertebrae of a single individual vary considerably in form depending upon their precise position. The more posterior thoracic vertebrae have two transverse processes which in the caudal vertebrae are fused to form the haemal spine (see Figures).



The Skeleton of a Bony Fish

The Caudal Vertebra of a Fish.



KEY

				Page
1.	Neural spine anterior	2		
	Neural spine posterior	6		
	Neural spine roughly central	10		
2.	Prominent anterior zygapophysis, and "plough-handle" posterior zygapophysis. Centrum with a pronounced waist	*Gadidae*		114
	Not with this combination of features	3		
3.	Centrum at least twice as long as it is high. Anterior zygapophysis very small or absent. Delicate	*Goby*	*Gobiidae*	115
	Centrum less than twice as long as it is high	4		
4.	Strong keel, honeycomb pattern on centrum, anterior zygapophysis rounded, sturdy	*Hake*	*Merluciidae*	115
	Delicate appearance. Haemal and neural spines long and thin	5		
5.	Prominent anterior metapophysis	*Herring*	Clupeidae	116
	Anterior metapophysis very small	*Sprat*	Clupeidae	117

KEY

			Page
6.	Haemal spine anterior	7	
	Haemal spine posterior	8	
7.	Prominent, downward-pointing anterior metapophysis	Common Eel Anguillidae	117
	Very small anterior metapophysis	Gurnard Triglidae	118
8.	Sturdy. Large, rounded anterior zygapophysis. Honeycomb surface on centrum	Angler Lophiidae	118
	Laterally flattened. Bone thin and papery. Neural and haemal spines nearly parallel	9	
9.	Upper and lower edges frilly. Thoracic vertebrae with prominent, dorso-ventrally flattened lateral processes. Delicate.	Sea Stickleback Gasterosteidae	118
	Neither frilly nor delicate	Dragonet Callionymiidae	119
10.	Neural and haemal spines very short, near-vertical and latterally flattened. Prominent, dorso-ventrally flattened lateral processes	Pipefish Syngnathidae	119

KEY

			Page
10.	con'd		
	Neural and haemal spines long and straight, often nearly vertical. With lateral processes - often asymmetrically developed	11	
	Not like either of above	12	
11.	Haemal spine anterior: base less than a third of centrum length	*Sole* Soleidae	120
	Harmal spine central, or if anterior, then base more than a third of centrum length	*Scophthalmidae*	121
		Pleuronectidae	122
12.	No anterior zygapophysis	13	
	Distinct anterior zygapophysis	14.	
13.	Large, translucent, papery	*Lumpsucker* Cyclopteridae	123
	Haemal spine broad-based, and considerably longer than neural spine. Delicate.	*Sea Snail* Cyclopteridae	123
	Single, strong keel. Prominent posterior metapophysis. Sturdy	*Wrasse* Labridae	124
14.	Centrum about twice as long as high	15	
	Centrum roughly square in profile, or taller than long	18	

KEY

				Page
15.	Haemal spine anterior	16		
	Haemal spine central	17		
16.	2 or 3 thin keels. Delicate	Sand Eel	Ammodytidae	125
	No keels. Anterior zygapophysis and metapophysis both long and slender	Red Mullet	Mullidae	125
17.	Prominent, right-angled anterior zygapophysis and metapophysis. No keel	Mackerel	Scombridae	126
	Anterior metapophysis club-ended. Centrum deeply hollowed	Scad	Carangidae	127
18.	Haemal spine central	19		
	Haemal spine anterior	20		
19.	Haemal and neural spines thin and recurved. Honeycomb pattern on centrum. No keel. Zygapophyses and metapophyses small	Trout	Salmonidae	128
	2 strong keels. Zygapophyses and metapophyses prominent	Ray's Bream	Bramidae	128
20.	Anterior xygaopophysis projects beyond front edge of centrum	21		

KEYS

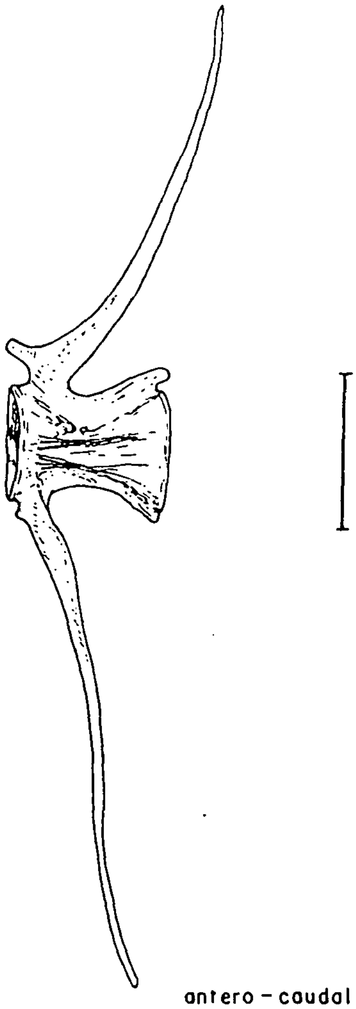
				Page
20.	con'd Anterior zygapophysis may reach to, but does not project beyond, front edge of centrum	23		
21.	Centrum much taller than long. Large, leaf-like anterior zygapophysis. No posterior metapophysis. Neural and haemal spines long.	John Dory	Zeidae	129
	Length of neural spine less than centrum length	Hook-Nose	Agonidae	130
	Length of neural spine greater than centrum length. Prominent posterior metapophysis	22		
22.	Anterior zygapophysis slender, inclined upwards. Single, prominent keel. Neural spine straight	Weever	Trachinidae	131
	Anterior zygapophysis broad and blunt, inclined upwards. Keel not prominent. Neural spine straight. Posterior metapophysis very long	Shanny	Blenniidae	132
	Anterior zygapophysis horizontal. Keel sometimes prominent (larger specimens). Neural spine usually curves upwards	Cottidae		130 & 131

K E Y

			Page
23.	Anterior zygapophysis horizontal. Single promient keel	Butterfish Pholidae	132
	Ornate. Anterior zygapophysis vertical. More anterior vertebrae have prominent lateral processes	Conger Eel Congridae	132
	Anterior zygapophysis inclined upwards, but not vertical. No lateral processes	24	
24.	Single keel. Usually pale turquoise in colour	Viviparous Blenny Zoarcidae	133
	2 or 3 thin keels (may be asymmetrical). Posterior zygapophysis horizontal, or inclined upwards slightly	Yarrell's Blenny Stichaeidae	133
	Prominent, honeycomb keel. Posterior zygapophysis inclined upwards	Catfish Anarhichidae	134

Throughout the following illustrations, the bars indicate the actual size of the vertebrae drawn

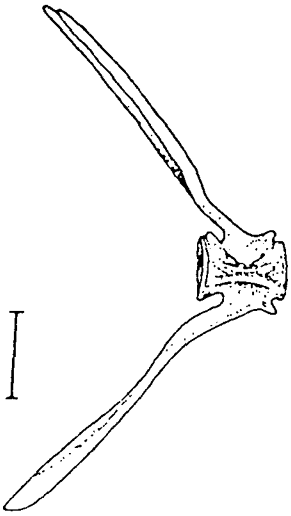
Gadidae

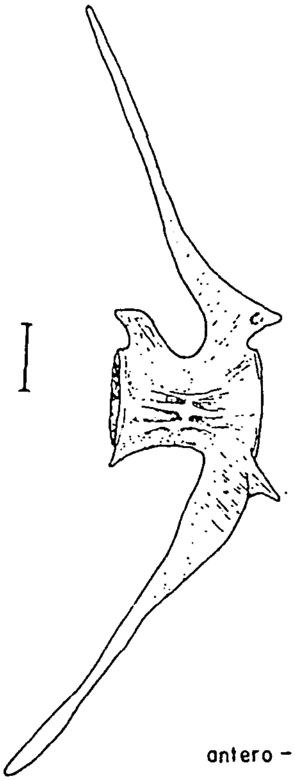


antero - caudal

SAITHE *Pollachius virens*

postero - caudal

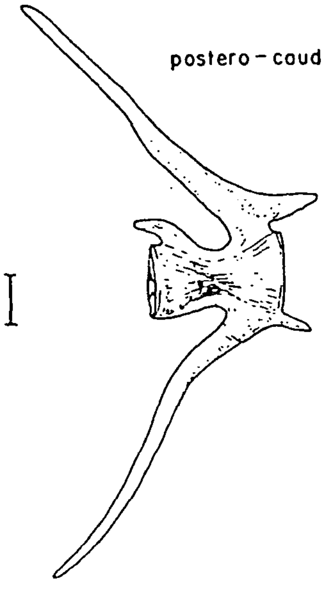




antero - caudal

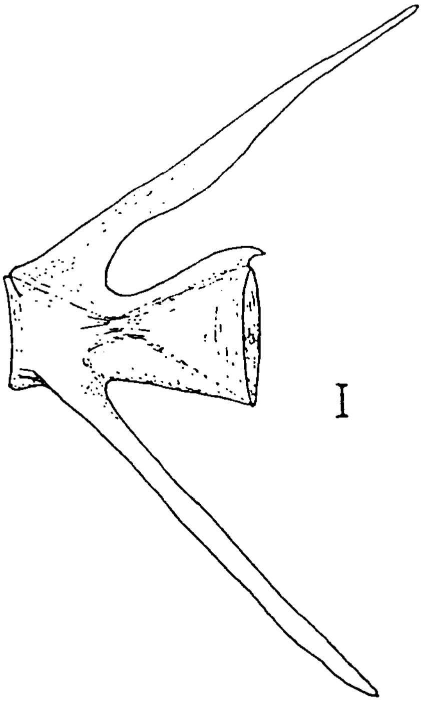
FIVE BEARDED ROCKLING *Ciliata mustela*

postero - caudal



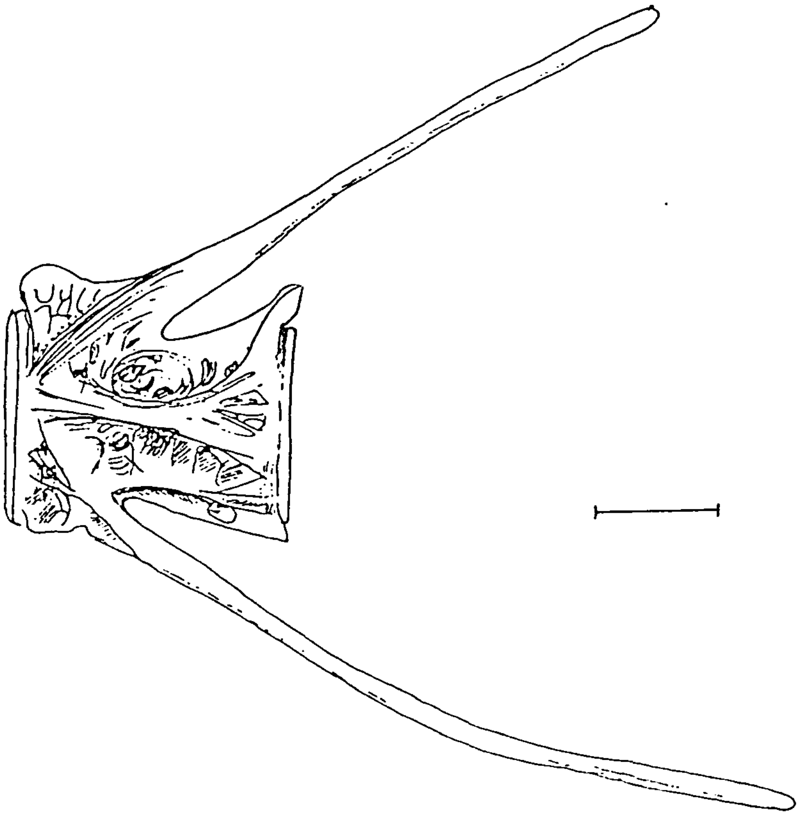
GOBIES Gobiidae

Pomatoschistus sp.

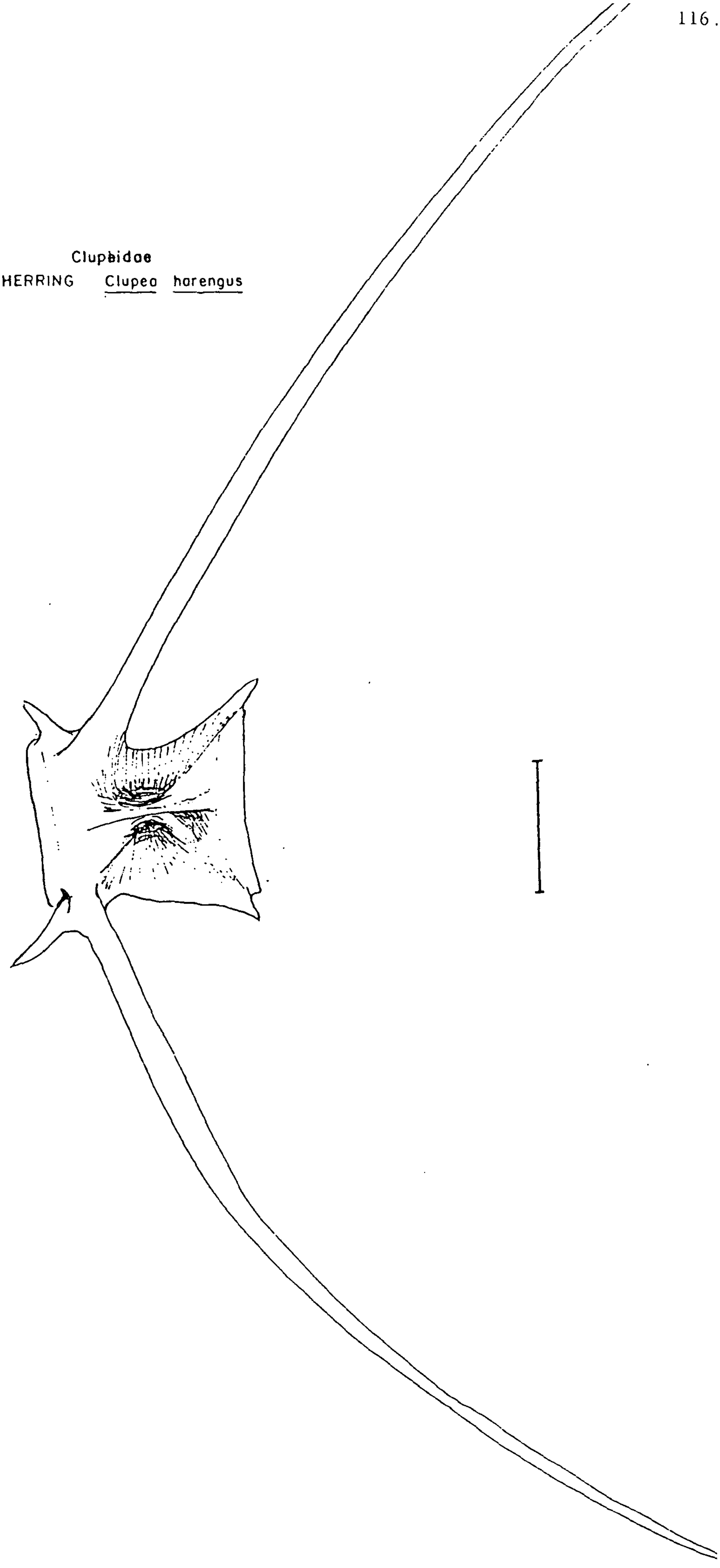


Merluciidae

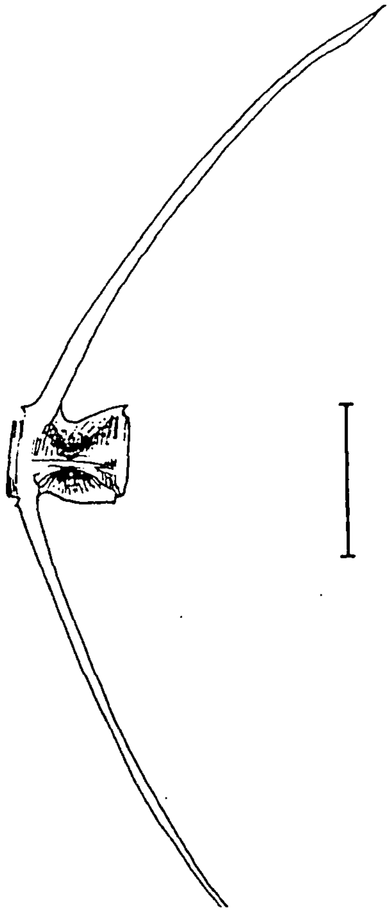
HAKE Merluccius merluccius



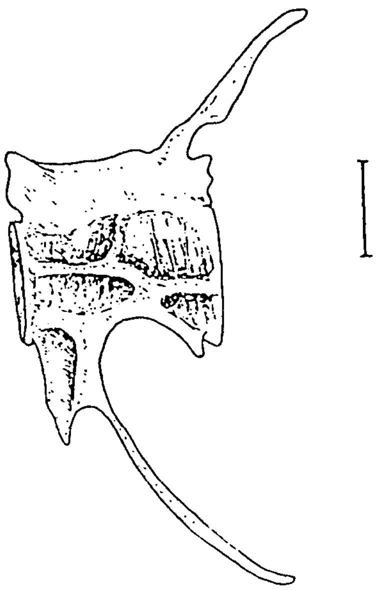
Clupeidae
HERRING *Clupea harengus*



Clupeidae
SPRAT *Sprattus sprattus*

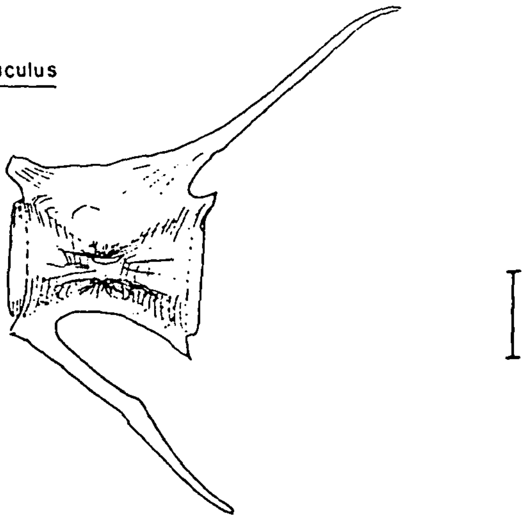


COMMON EEL Anguillidae
Anguilla anguilla



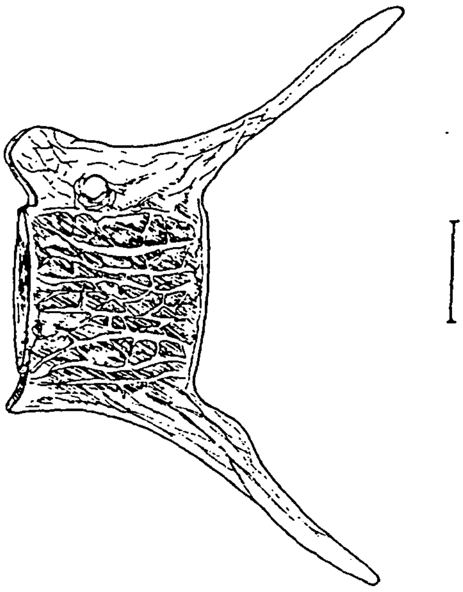
Triglidae

RED GURNARD *Aspitrigla cuculus*



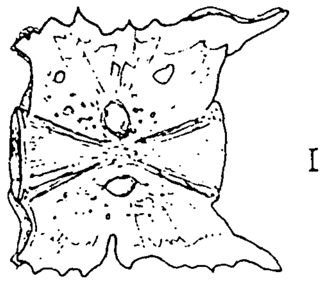
ANGLER Lophiidae

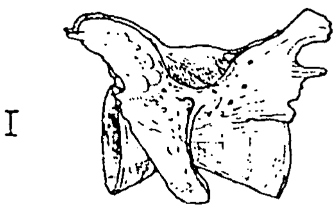
Lophius piscatorius



SEA STICKLEBACK Gasterosteidae

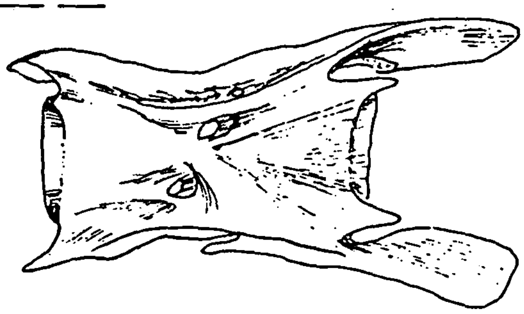
Spinachia spinachia





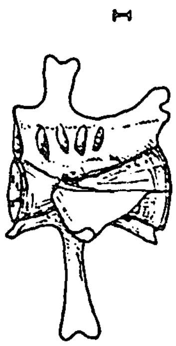
Callionymidae

DRAGONET <u>Callionymus lyra</u>

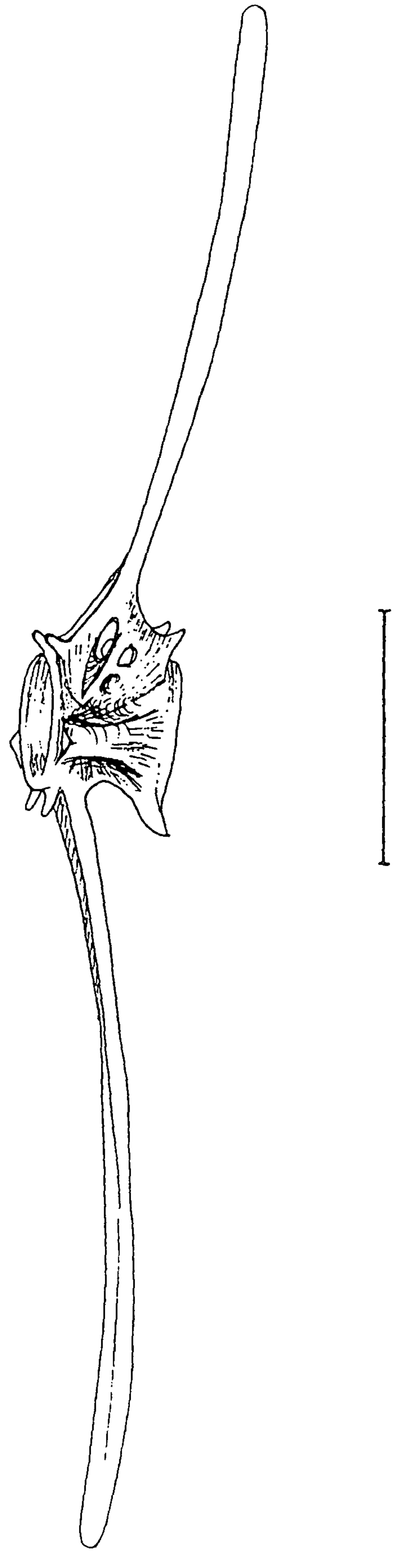


PIPEFISH Syngnathidae

<u>Nerophis lumbriciformis</u>

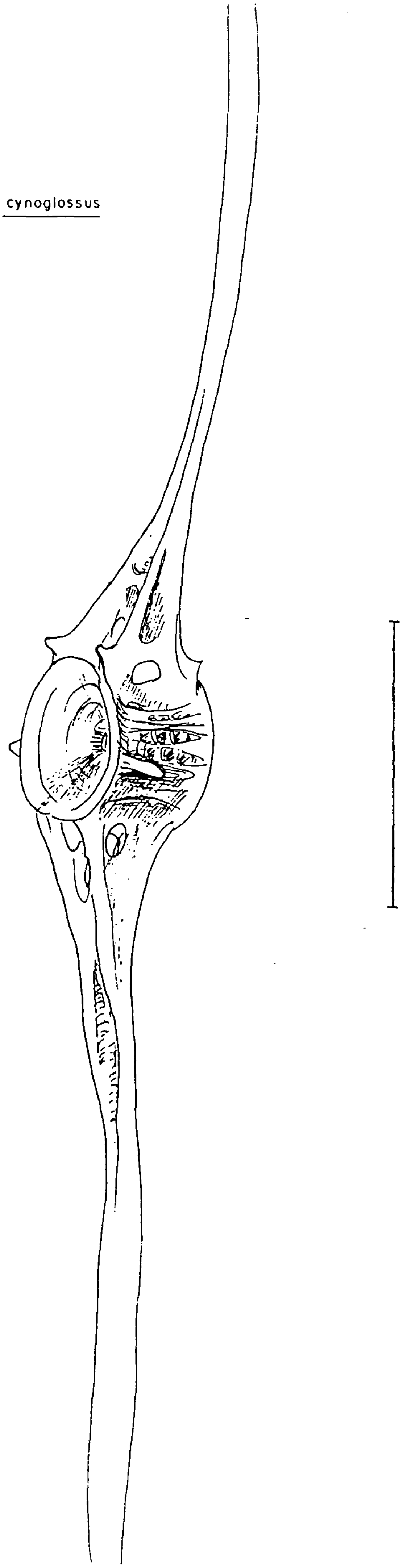


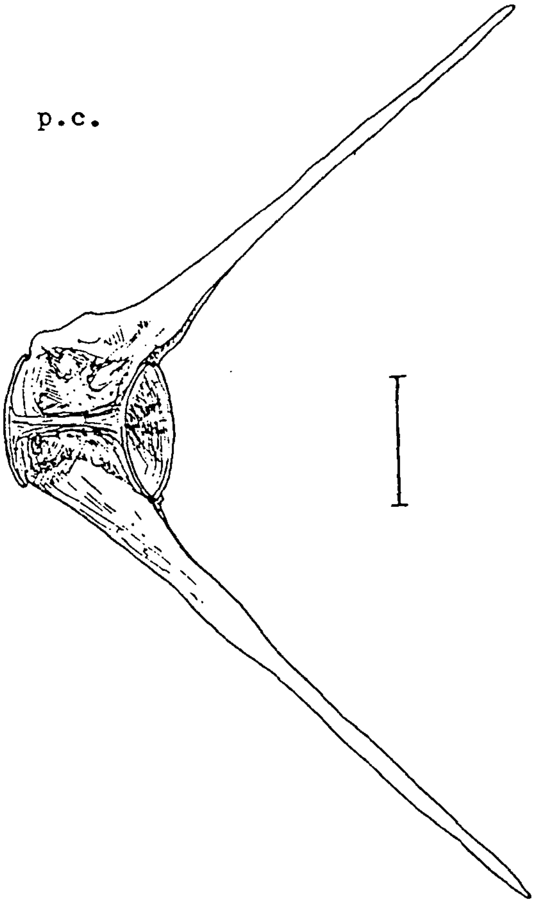
Soleidae
SOLE <u>Solea</u> <u>solea</u>

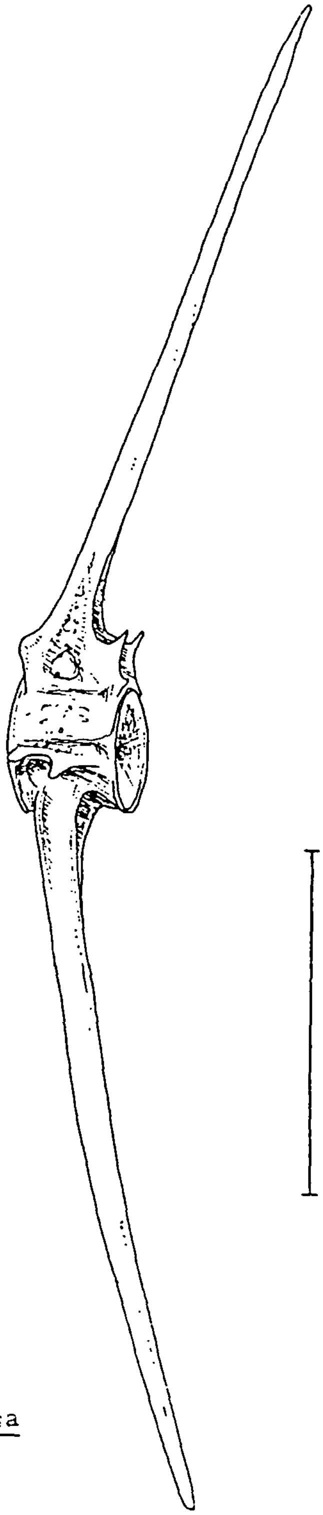


Scophthalmidae

WITCH *Glyptocephalus* *cynoglossus*





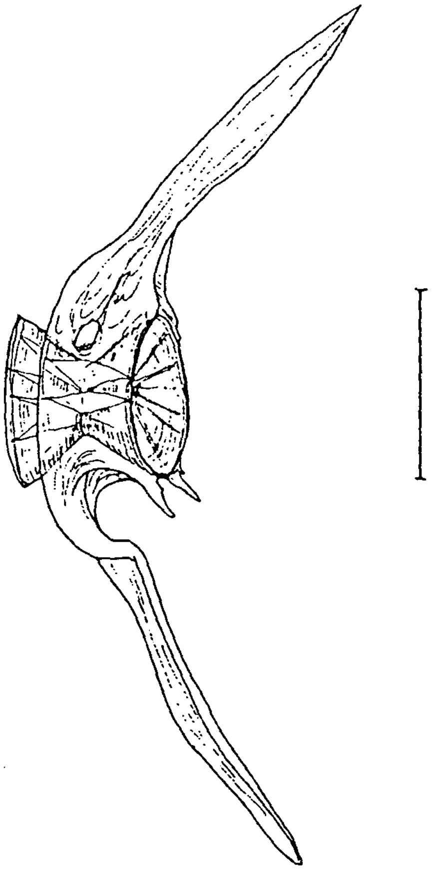


Plaice <u>Pleuronectes platessa</u>

Pleuronectidae

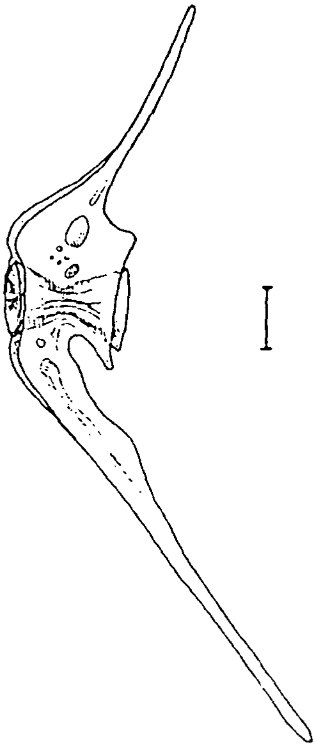
LUMPSUCKER Cyclopteridae

Cyclopterus lumpus

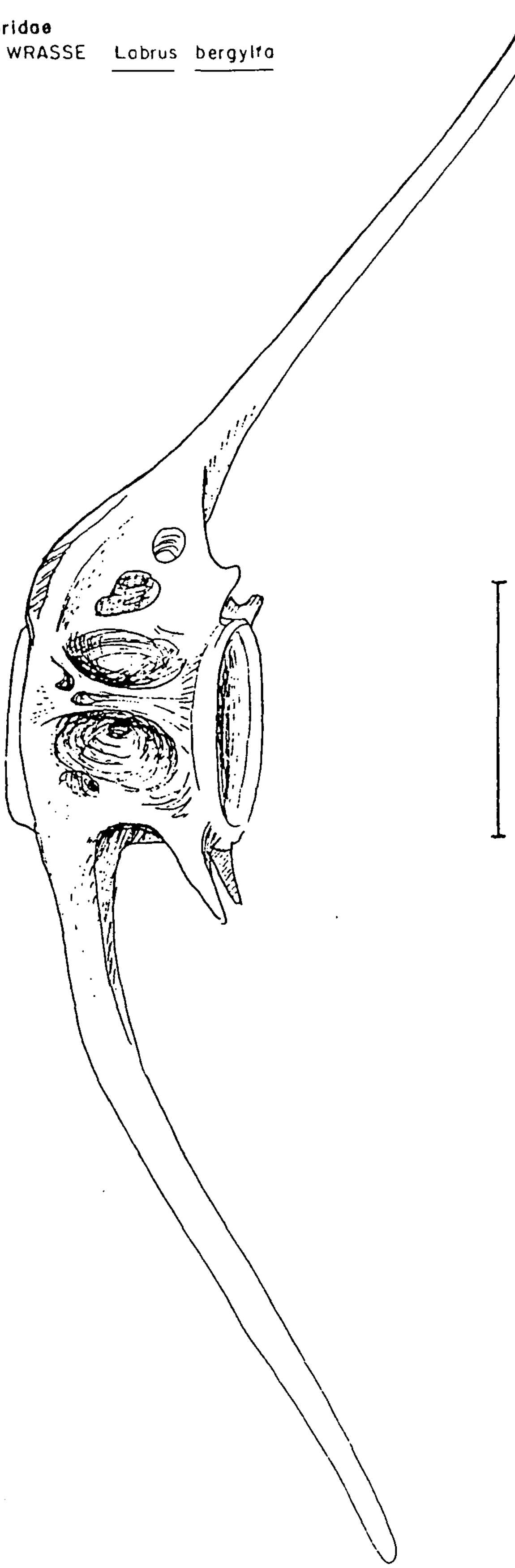


Cyclopteridae

SEA SNAIL *Liparis sp.*

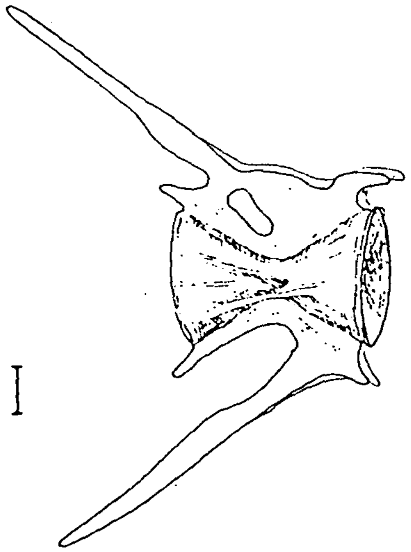


Labridae
BALLAN WRASSE *Labrus bergylta*



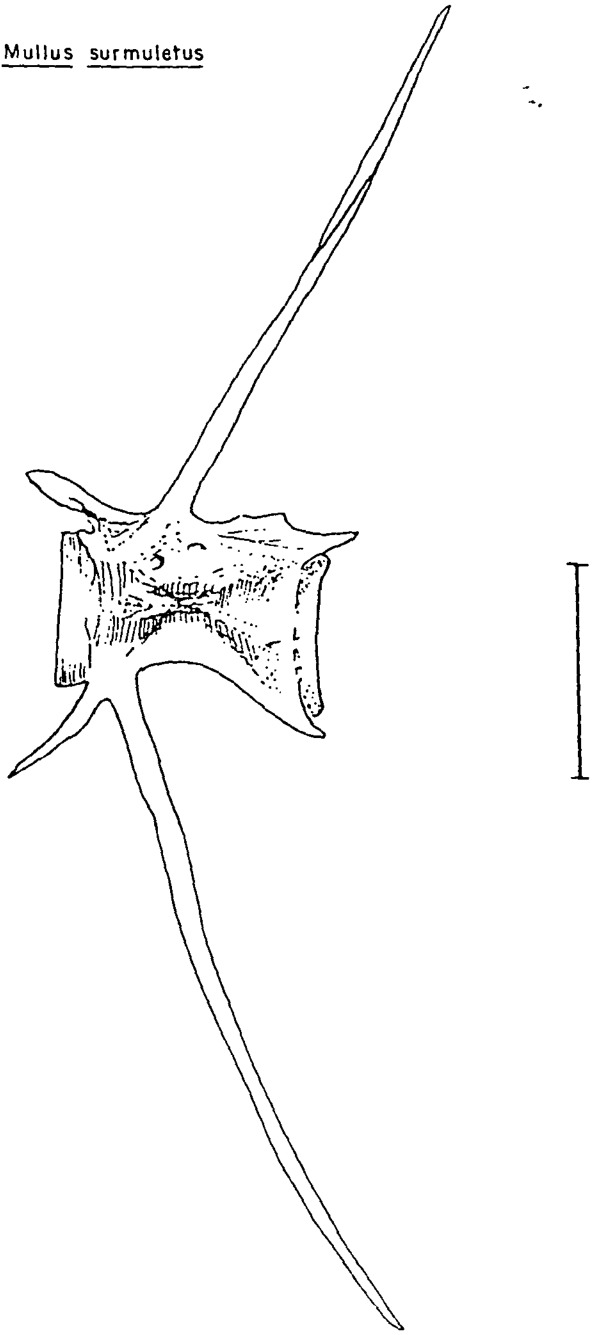
SAND EELS Ammodytidae

Ammodytes sp.



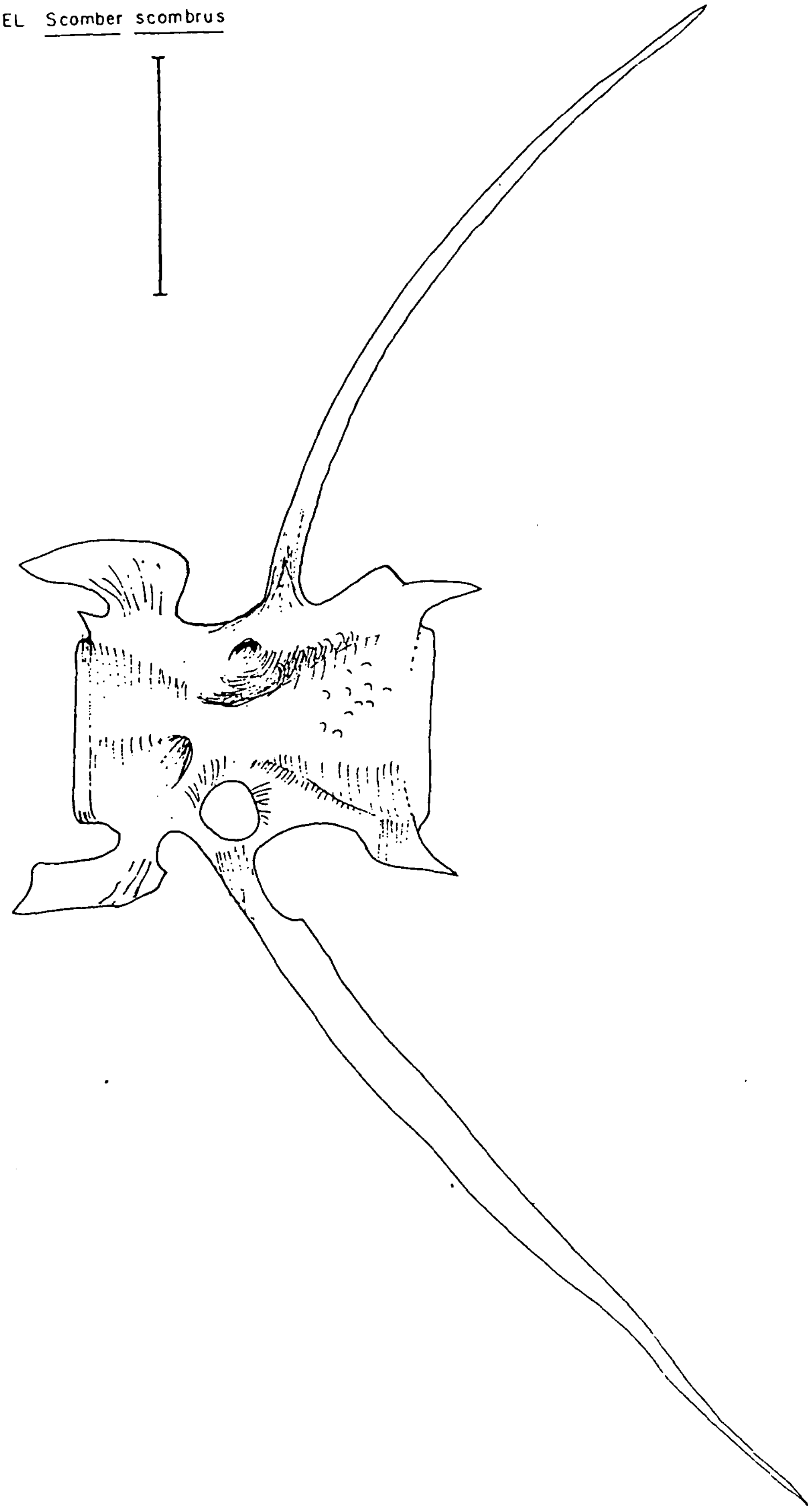
Mullidae

RED MULLET *Mullus surmuletus*



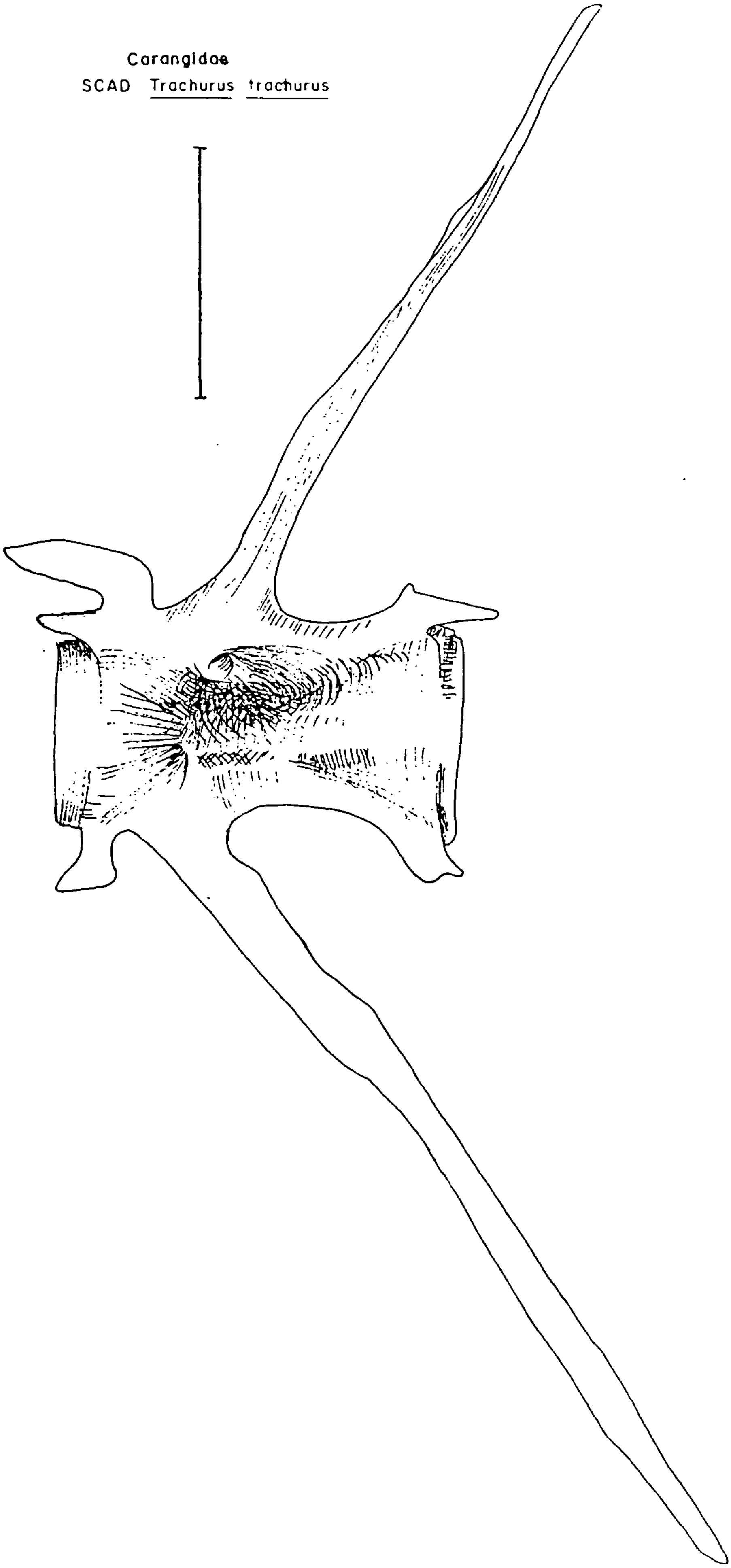
Scombridae

MACKEREL _Scomber_ _scombrus_



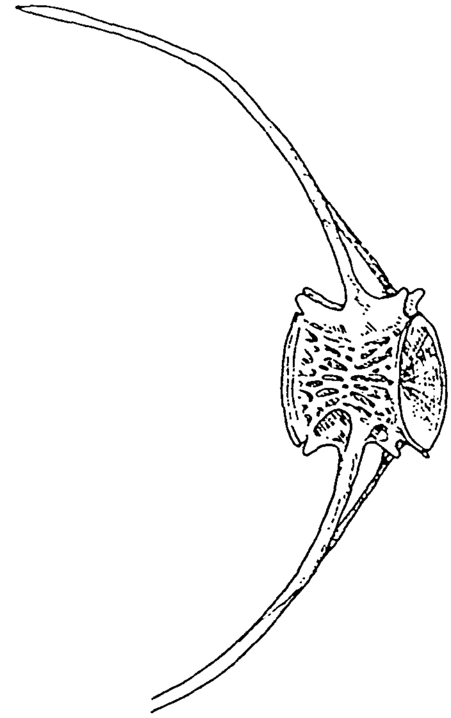
Carangidae

SCAD Trachurus trachurus



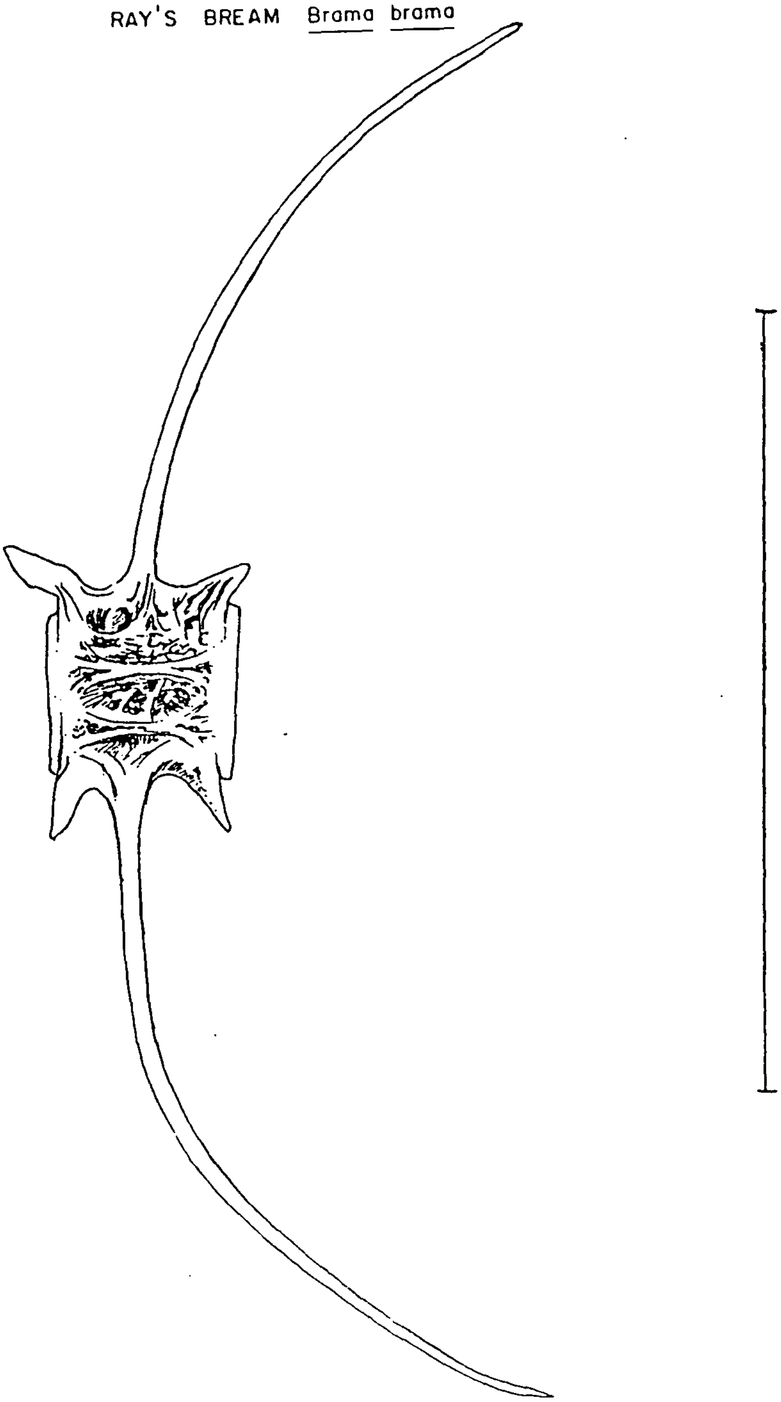
TROUT Salmonidae

Salmo trutta



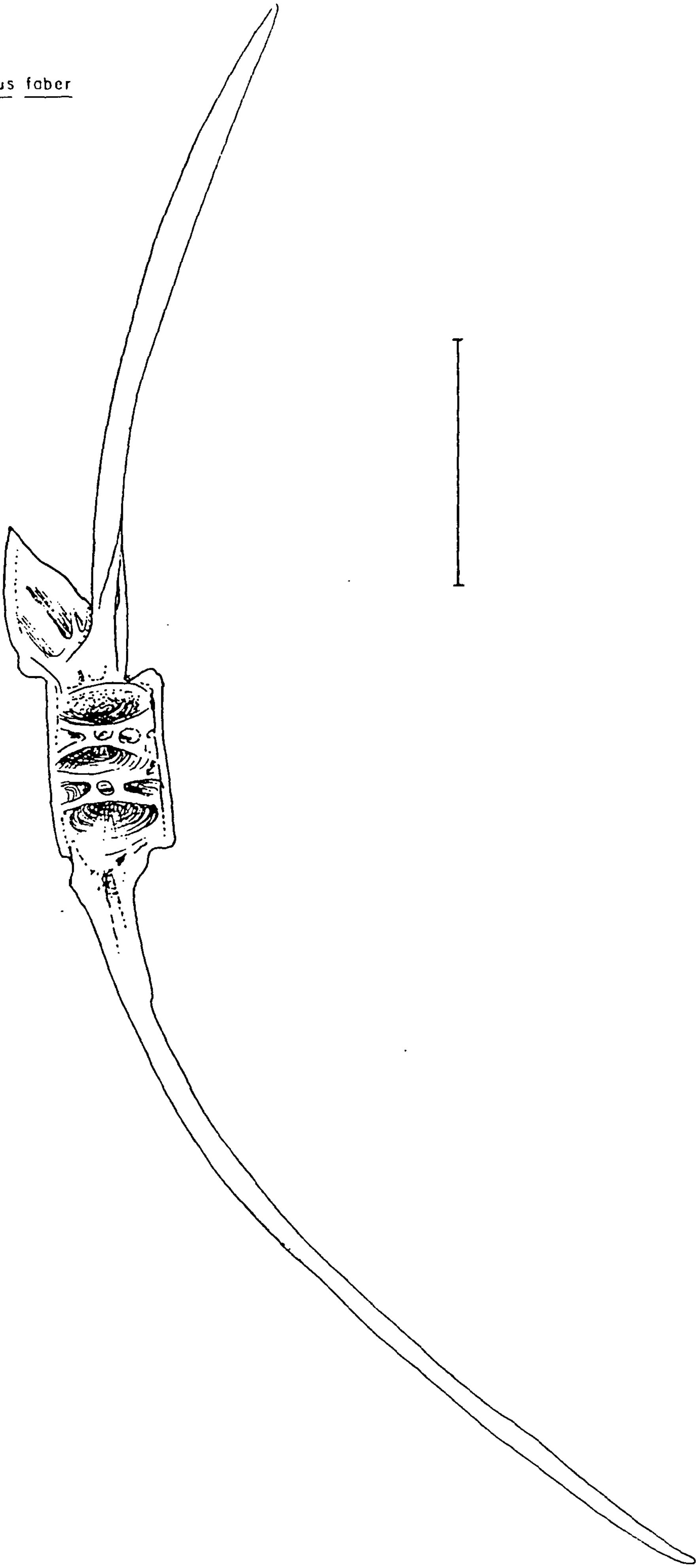
Bramidae

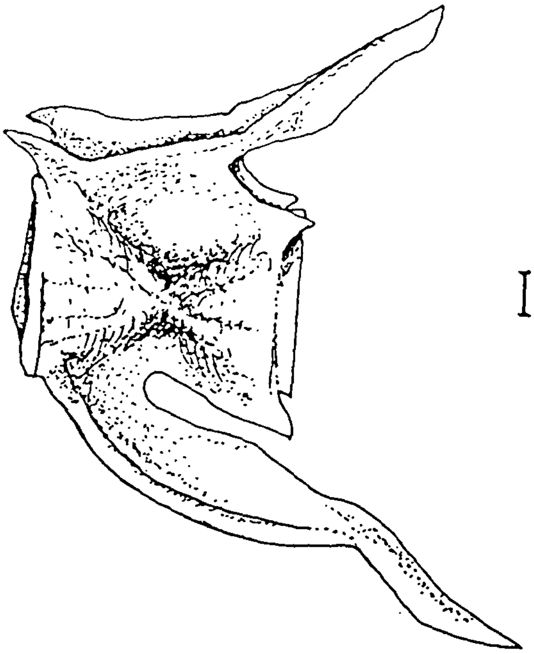
RAY'S BREAM Brama brama



Zeidae

JOHN DORY *Zeus faber*



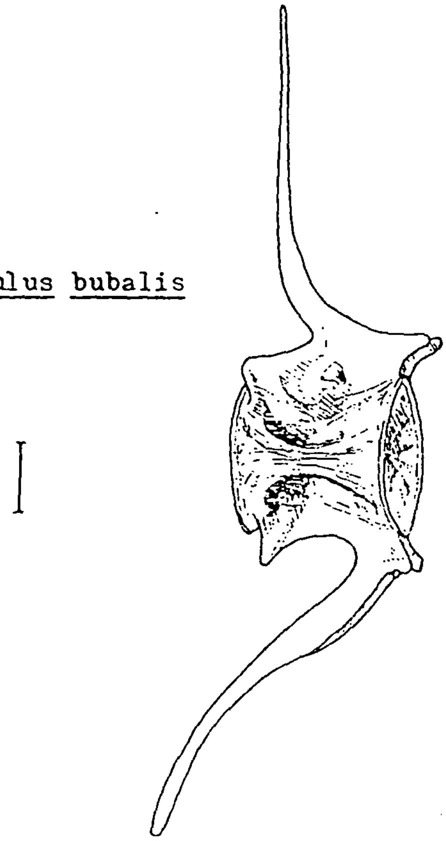


Agonidae

HOOKNOSE *Agonus cataphractus*

Cottidae

Long-Spined Sea Scorpion *Taurulus bubalis*

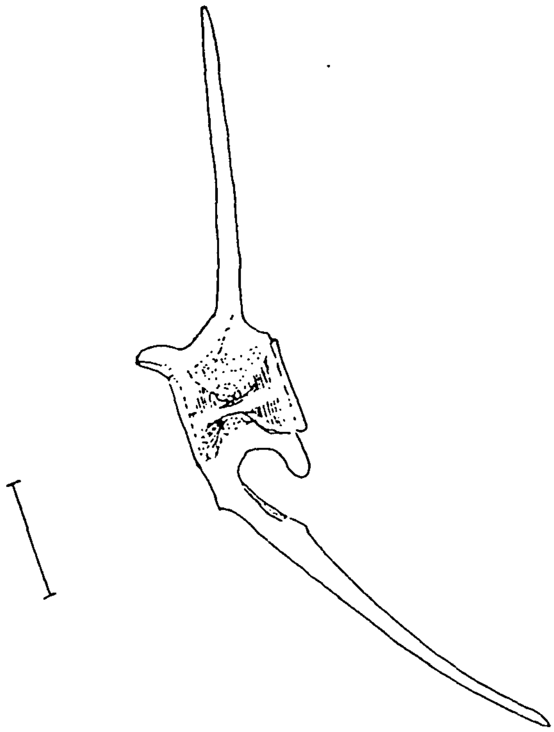


Cottidae

FATHER – LASHER *Myoxocephalus scorpius*

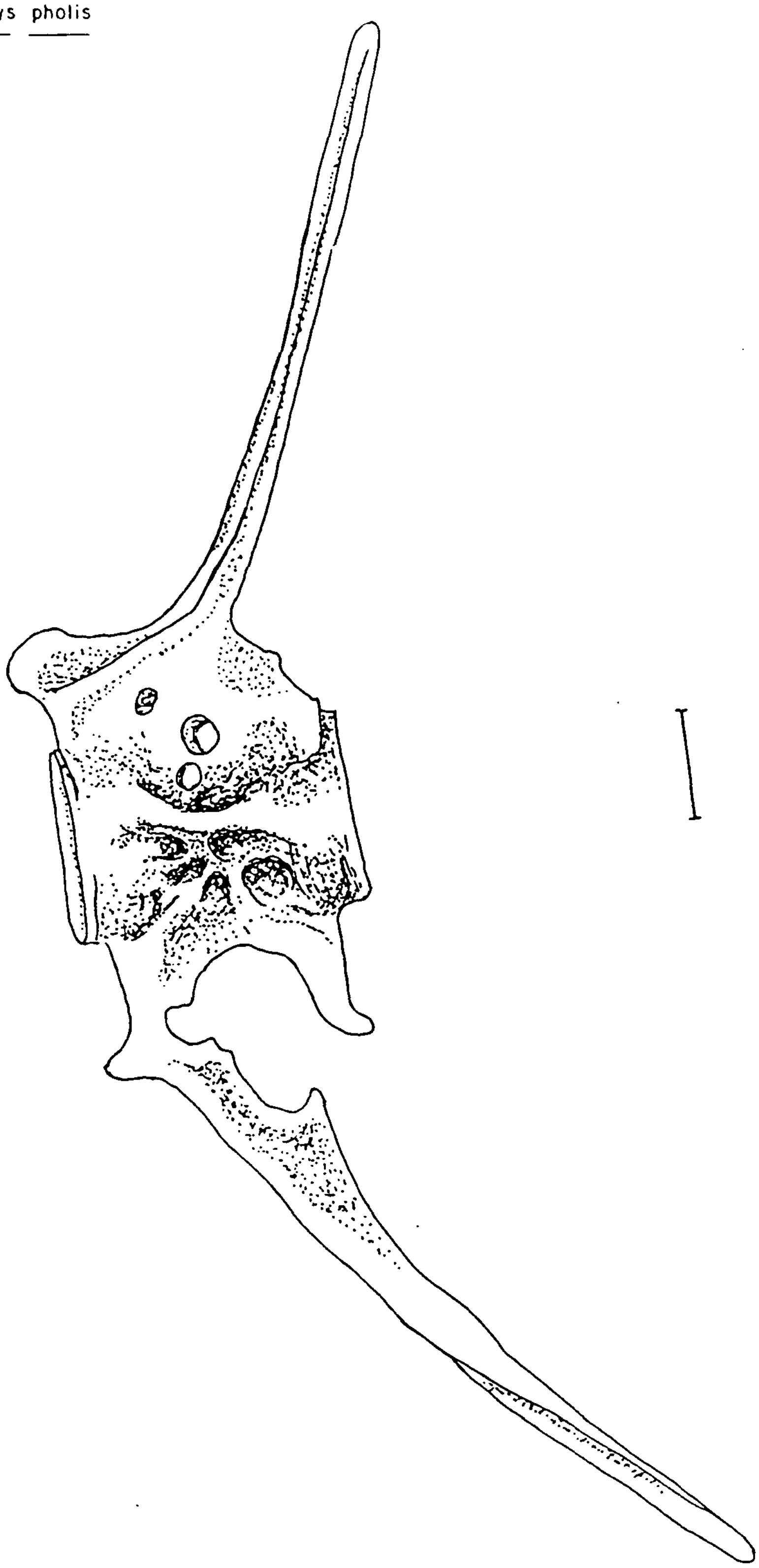
Trachinidae

LESSER WEEVER *Epiichthys vipera*

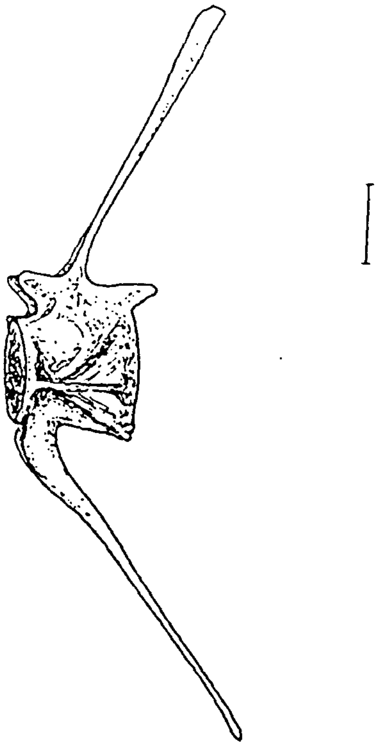


Blenniidae

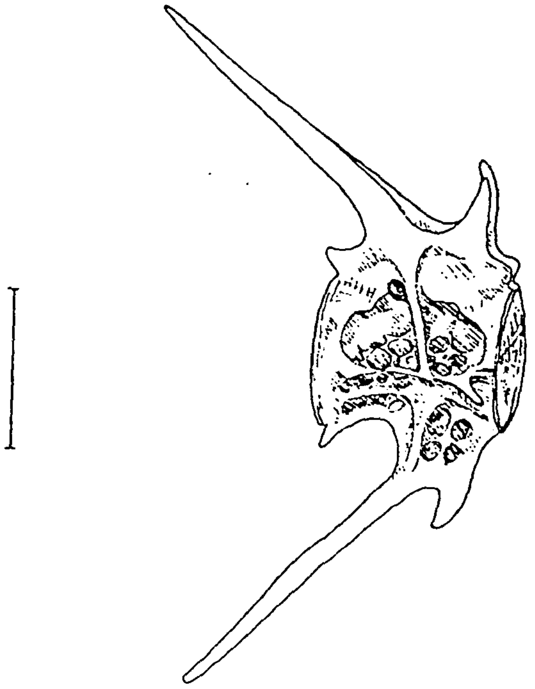
SHANNY *Lipophrys* *pholis*



BUTTERFISH Pholidae
Pholis gunnellus

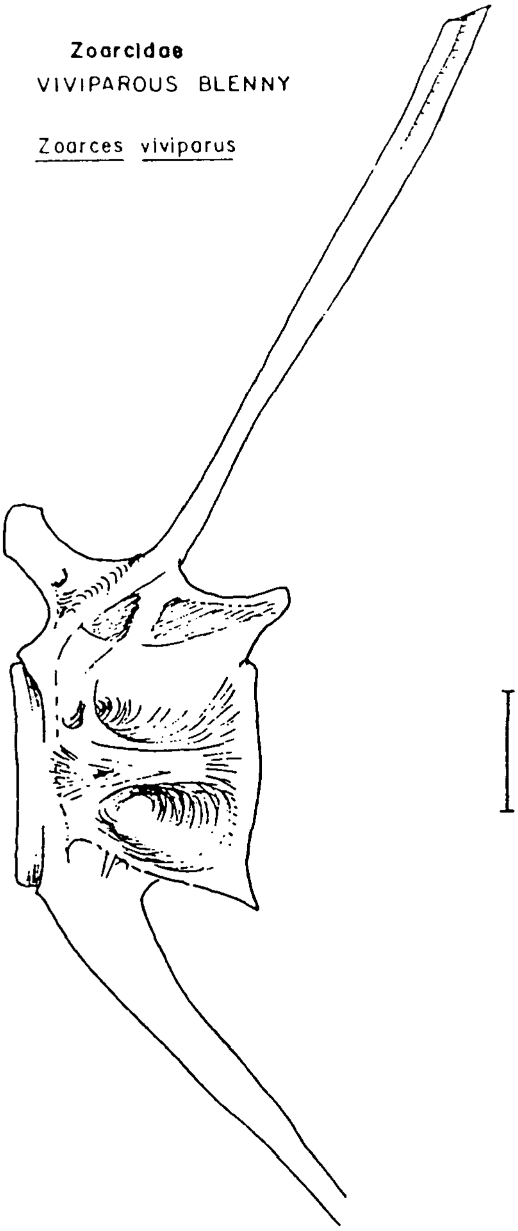


CONGER EEL Congridae
Conger conger

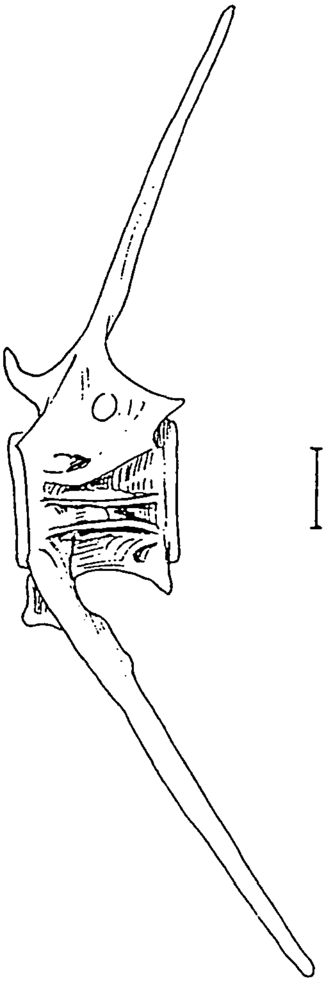


Zoarcidae
VIVIPAROUS BLENNY

Zoarces viviparus

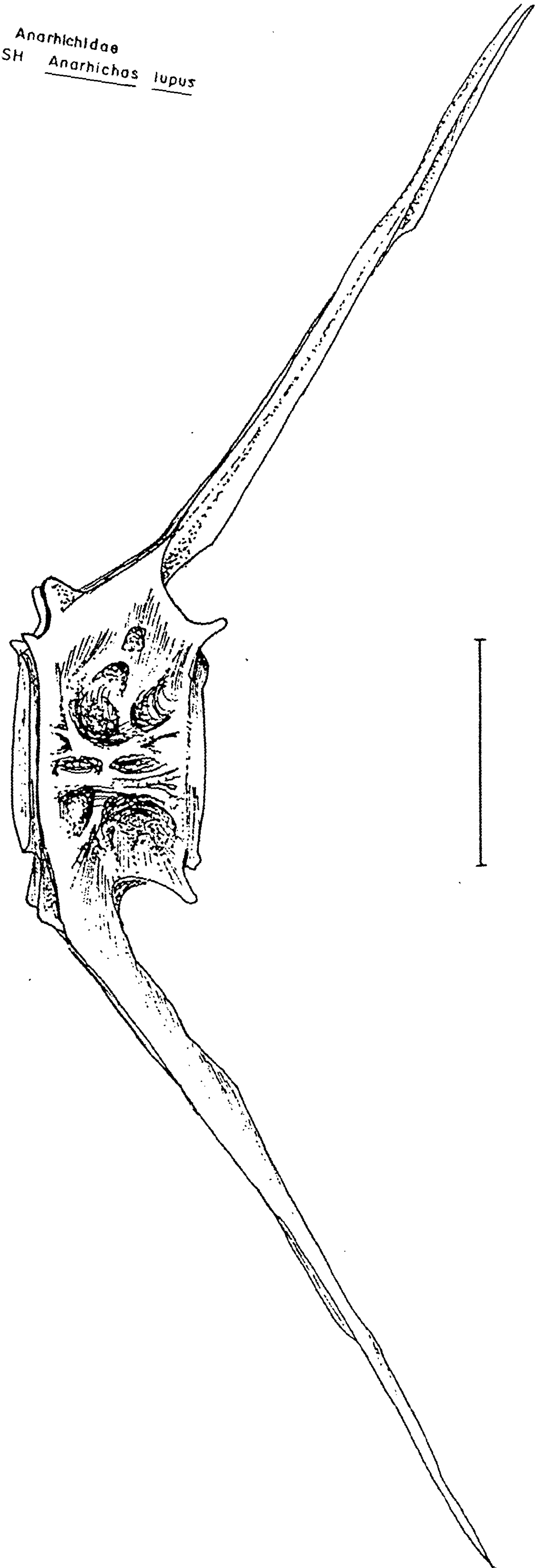


YARRELL'S BLENNY *Chirolophis ascanii*
Stichaeidae



Anarhichidae

CATFISH *Anarhichas lupus*



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