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Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds

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(With 2 figures in the text)

Wet and dry calorific values (energy densities) and total energy content of lesser sandeel *Ammodytes marinus*, sprat *Sprattus sprattus*, Atlantic herring *Clupea harengus*, whiting *Merlangius merlangus*, saithe *Pollachius virens* and cod *Gadus morhua*, were measured. Calorific values varied both within and between species. Larger fish tended to have higher calorific values than small ones, particularly when considered in terms of wet weight, but there was considerable temporal variation. The calorific values and body weights of sandeels larger than 10 cm showed marked seasonal trends and in consequence the total energy content of a sandeel of given length in summer is approximately double the spring value. The calorific values of herring and sprat also varied from month to month but seasonal cycles were less obvious. Whiting varied least. Both calorific values and total energy content of individual sprat were very variable in summer (the spawning season of this species). Because there is so much intraspecific variation, care must be taken when assessing the relative merits (in terms of energy) of different species as prey. The practical difficulties of obtaining reliable data on wet calorific values are discussed and the use of dry calorific values and dry weight/length relationships is recommended.

Contents

Introduction

There is increasing interest in the use of models to study interactions between seabirds (and other top predators) and fish. Often these models are based on energy transfer between predator

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and prey, e.g. case studies which consider possible competition between seabirds and man in the exploitation of fish stocks (Furness, 1978; Bailey, 1986), or the cost-effectiveness of feeding on different prey or using different feeding strategies (Harris & Hislop, 1978; Costa, 1988). Although many models require information on calorific values and/or energy content of fish of the species and size on which seabirds feed, few data of this kind have been published (but see Montevecchi & Piatt, 1984 for information on capelin (*Mallotus villosus*)). In addition, many of the data available in the literature (e.g. Murray & Burt, 1969; Cummins & Wuycheck, 1971) or figures calculated from equations relating calorific value and fish length (e.g. Harris & Hislop, 1978), can be misleading, because they fail to take into account that many species of fish show pronounced seasonal changes in body composition. These cycles are most prominent in 'oily' fish such as the Clupeidae (herrings and anchovies) and Scombridae (mackerels and tunas), whose body fat can range from <1% to >25% of their wet body weight (e.g. Wood, 1958; Hardy & Keay, 1972; Wallace & Hulme, 1977; Wallace, 1986; Almatar, 1989), but also occur in 'non-fatty' species such as plaice (*Pleuronectes platessa*) (Dawson & Grimm, 1980).

In this paper we present information on seasonal and size-related changes in the proximate composition, calorific value (energy density) and total energy content of the lesser sandeel *Ammodytes marinus*, common prey of seabirds, fish and marine mammals in north Scottish waters, and less detailed information on calorific value and energy content of Atlantic herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and gadoids (mainly whiting, *Merlangius merlangus*). We concentrate our attention on fish of the size ranges usually eaten by most British seabirds (<15 cm long, see Pearson, 1968). The results are pertinent to current studies investigating the relationships between seabirds, sandeels and other fish in the North Sea (e.g. Bailey, 1986; Monaghan *et al.*, 1989). The practical difficulties of determining the energy content of fish are discussed.

Methods and materials

In this paper, the term calorific value refers to kJ/g^{-1} (wet or dry weight) and is a measure of energy density. Energy content refers to the energy (kJ) in an entire fish and chemical composition is the proximate (gross) composition of an entire fish. The use of terms such as high and low quality food in the **Discussion** refers solely to the calorific value or energy content of the fish and takes no account of possible differences in proteins, vitamins or trace elements.

The sandeels in all fishery samples and the majority of the samples from seabirds were definitely *A. marinus*. However, we cannot exclude the possibility that a few sandeels collected from birds may have been other species.

Samples of fish from fishing boats and research vessels (fishery samples)

In 1986, commercial landings of sandeels caught in northern Scottish waters (the North Minch, North Rona, Fair Isle, Foula and several inshore locations round the Shetland Islands) were sampled. Several kg from each landing were placed in polythene bags and frozen (−20 °C) as soon after capture as possible. Later, the fish were allowed to thaw overnight in a refrigerator, sorted into 2 cm length classes (snout to tip of tail) and homogenized. Any water which had accumulated in the containers into which the fish were sorted was poured into the homogenizer. In a few cases, where the number of fish was small, the length range of the sample was increased to give sufficient weight for a full analysis. To determine water content, samples of approximately 10 g of homogenate were weighed in silica crucibles and dried for 24 h at 105 °C. Fat content was determined by the method of Bligh & Dyer (1959) as modified by Hanson & Olley (1963). Nitrogen analysis was carried out using a Kjeltac Auto 1030 Analyser after digestion with sulphuric acid, and crude protein content estimated by multiplying g nitrogen/100 g by 6·25 (Crisp, 1971). The resulting data were originally grouped by length class, month and area of capture; no systematic between-area differences could be detected and data from all sites were pooled.

In 1987 sandeel, sprat, herring and whiting were obtained from research vessel catches in the northern North Sea. Shortly after capture the fish were sorted into 0·5 or 1 cm length classes and known numbers of fish of known length were sealed in polythene bags of known weight and frozen at −20 °C. The mean wet weight of a fish in each length class was determined. When the fish were thawed and homogenized prior to analysis, any ice or water remaining in the bag was included in the homogenate. Water content was determined by drying weighed samples in an oven at 105 °C for 24 h. The calorific values of the dried samples were determined in triplicate using a Gallenkamp Autobomb Calorimeter and a Cam Metric galvanometer. Wet calorific value was calculated as: dry calorific value ×(1 − proportion of water).

Samples of fish collected from seabirds

To feed their young, guillemots *Uria aalge* and puffins *Fratercula arctica* bring back intact fish to the breeding colony. In 1976 and 1986–88 undamaged and apparently freshly caught sandeel, sprat, herring, whiting, saithe (*Pollachius virens*) and cod (*Gadus morhua*) were collected from these birds on the Isle of May (Firth of Forth), Canna (Inner Hebrides) and St Kilda (Outer Hebrides). Each fish was either placed in a polythene bag or wrapped in cling-film and frozen (−20 °C) in the field. After thawing, the fish were measured, weighed (together with any moisture inside the wrappings) and then freeze-dried to constant weight. Calorific determinations of a subsample of each fish were made with a Gallenkamp Autobomb Calorimeter, using the method described in Allen (1989).

Some of the data presented here were included in the results of Harris & Hislop (1978).

Estimates of energy content

For the 1987 fishery samples, and the fish collected from birds, the energy value of a fish was obtained by multiplying the fish weight (wet weight in the former case, dry in the latter) by the determined calorific value of the same fish.

Indirect methods were applied to the 1986 fishery samples of sandeels. The mean wet weight of a sandeel in each length class in each month was calculated using the monthly weight/length relationships given by Coull *et al.* (1989). Mean weight was then multiplied by wet calorific value obtained by: (a) the relationship found between water content and calorific value (**Appendix VI**); and (b) from the body composition using energy equivalents of 39·6 kJ/g^{-1} for fat and 23·7 kJ/g^{-1} for protein (Crisp, 1971).

Results

The results of the analyses are given in **Appendices I–V** and regression equations in Fig. 1 and **Appendices VI–VII.**

Calorific values

Calorific values (both wet and dry) of the 1987 fishery samples are given in **Appendices I–IV** and dry calorific values of fish taken from seabirds in Table I. Within each species, calorific values varied from month to month and in some cases these differences were as large as, or larger than, differences between species. The smaller fish of each species tended to have lower wet calorific values than larger individuals. This was largely due to the fact that small fish have a relatively high

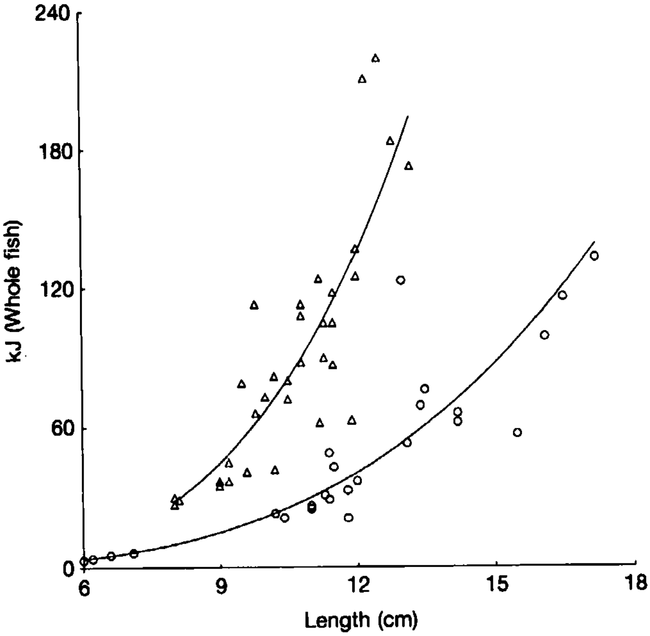

FIG. 1. Relationship between energy content and length of whole sprats (△) and sandeels (○) collected from seabirds. Equations for the fitted lines are:

$$\text{Sandeel } E = 0{\cdot}0081\ L^{3{\cdot}427}\ (r = 0{\cdot}965,\ N = 25,\ P < 0{\cdot}001)$$

$$\text{Sprat } E = 0{\cdot}0096\ L^{3{\cdot}845}\ (r = 0{\cdot}891,\ N = 34,\ P > 0{\cdot}001)$$

TABLE I

Mean (±S.D.) calorific values (kJ/g⁻¹ dry weight) of herring, sprat, sandeel and gadoids (whiting, saithe, cod) collected from seabirds in June and July, 1976–1988

Mean length (cm)	Herring N	Herring	Sprat N	Sprat	Sandeels N	Sandeels	Gadoids N	Gadoids
4·5							2	19·20 (1·70)
5·5					3	20·13 (2·23)	2	20·90 (1·27)
6·5	2	18·55 (1·20)			19	21·87 (1·51)		
7·5	4	19·50 (1·00)			9	22·12 (1·01)	1	17·70
8·5	1	20·00	7	21·57 (3·10)	1	23·40		
9·5			9	25·33 (1·50)	1	15·30		
10·5			11	26·00 (2·41)	4	20·93 (2·32)		
11·5			13	26·23 (2·55)	10	21·47 (2·10)		
12·5			7	26·43 (2·30)	6	22·18 (2·79)		
13·5			2	27·00 (1·41)	7	23·07 (1·81)		
14·5					4	24·00 (1·57)		
15·5					2	24·00 (2·83)		
16·5					2	23·75 (1·06)		
17·5					1	24·30		
20·5					1	20·00		

water content (see next section) and the difference is less obvious when calorific value is expressed on a dry weight basis. The calorific values of whiting and other gadoid (cod-like) species were generally lower, and varied less between months and length classes, than those of sandeel, sprat and herring.

Chemical composition of A. ***marinus***

The gross body composition of sandeels differed between months and length classes. Fat content increased rapidly (and water content declined) between April and June and remained relatively stable throughout June, July and August (**Appendix** V). Protein content varied comparatively little from one month to the next. Within each month, except April, large sandeels had a higher fat content than small ones.

There was a strong negative correlation between the percentages of fat (F) and water (W).

$$F = -0{\cdot}777 \times W + 64{\cdot}094 \ (r = -0{\cdot}949, N = 143, P < 0{\cdot}001) \quad (1)$$

Relationships between fat and water have been previously calculated for Atlantic herring: $F = -1{\cdot}139\ W + 90{\cdot}45$ (Iles & Wood (1965)) and for sprat, pilchard (*Sardina pilchardus*) and Atlantic mackerel (*Scomber scombrus*): $F = -1{\cdot}049\ W + 85{\cdot}58$ (Wallace & Hulme (1977)). Mackerel, herring, sprat and pilchard can attain much higher fat values than sandeel, but over the range of fat and water levels we observed in sandeel the relationships for the other species lie mostly within the 95% confidence limits of our regression.

Relationship between calorific value and water content

As might be expected, there were highly significant negative correlations between both wet and dry calorific value and water content in sandeel, herring and sprat (**Appendix VI**). The whiting data showed a similar trend but were more scattered. It appears, therefore, that determining water content may prove to be a useful 'short-cut' method of predicting calorific value.

The energy content of whole fish

Although information on calorific value (energy density) is useful in itself, in the study of energy flow it is often desirable to know the total energy content of a prey item of a given size or weight. This varies both with the month and with the length of the fish.

Monthly relationships between measured and calculated energy content (kJ) and fish length (cm) for fishery samples of sandeels collected in 1986 and 1987 are given in **Appendix VII**. Within each month there was good agreement between the three estimates (Table II).

The energy content of sandeel increases rapidly with length, the value of the exponent being significantly greater than three in every case, which confirms previous findings (e.g. Harris & Hislop, 1978). The energy content of sandeels of the same length increased markedly between April and June, then remained more or less constant during June, July and August.

Although there were some marked month to month differences in the energy content of sprat in the 1987 fishery samples, there were no obvious seasonal trends (**Appendix II**).

Sampling of herring was patchy and we have few data for small herring (< 15 cm). Seasonal changes were not apparent, although energy content was relatively low at the beginning of the year (**Appendix III**).

TABLE II

Total energy content (kJ) of sandeels in the fishery samples as predicted by equations in Appendix VII. (a) Calorific value determined by calorimetry; (b) calorific value estimated from water content; and (c) calorific value calculated from proximate composition. Predictions based on sandeels collected from seabirds (Fig. 2) are given in the final column. Extrapolated values are shown in parentheses

	April			May			June			July			August			June/July
Length (cm)	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	Fish from seabirds
5	(1·1)	(0·9)	(1·0)	(1·1)	(0·9)	(1·1)	(1·1)	1·1	1·3		1·2	1·3		(1·3)	(1·5)	(2·0)
7	(3·4)	2·9	(3·0)	(3·7)	(3·2)	(3·7)	4·0	4·1	4·5		4·3	4·6		4·7	5·1	6·4
9	7·7	6·8	7·1	(9·3)	8·2	9·1	10·3	10·9	11·6		11·6	12·0		12·3	12·8	15·1
11	14·8	13·6	14·1	(19·3)	17·4	18·7	23·1	23·8	24·6		25·4	25·4		26·4	26·7	30·0
13	25·5	24·2	24·8	35·4	32·4	34·0	41·7	45·5	46·0		48·9	47·6		50·0	49·4	53·2
15	40·5	39·6	40·4	59·5	55·1	56·8	71·9	79·2	78·7		85·6	81·5		86·4	83·5	86·9
17	60·9	60·8	61·9	93·7	87·9	88·9	115·7	128·6	125·7		139·8	130·4		139·2	132·3	133·4
19	(87·4)	89·1	90·4	140·3	133·0	132·4	(176·7)	197·8	190·7		216·2	198·1		212·9	(199·0)	(195·3)

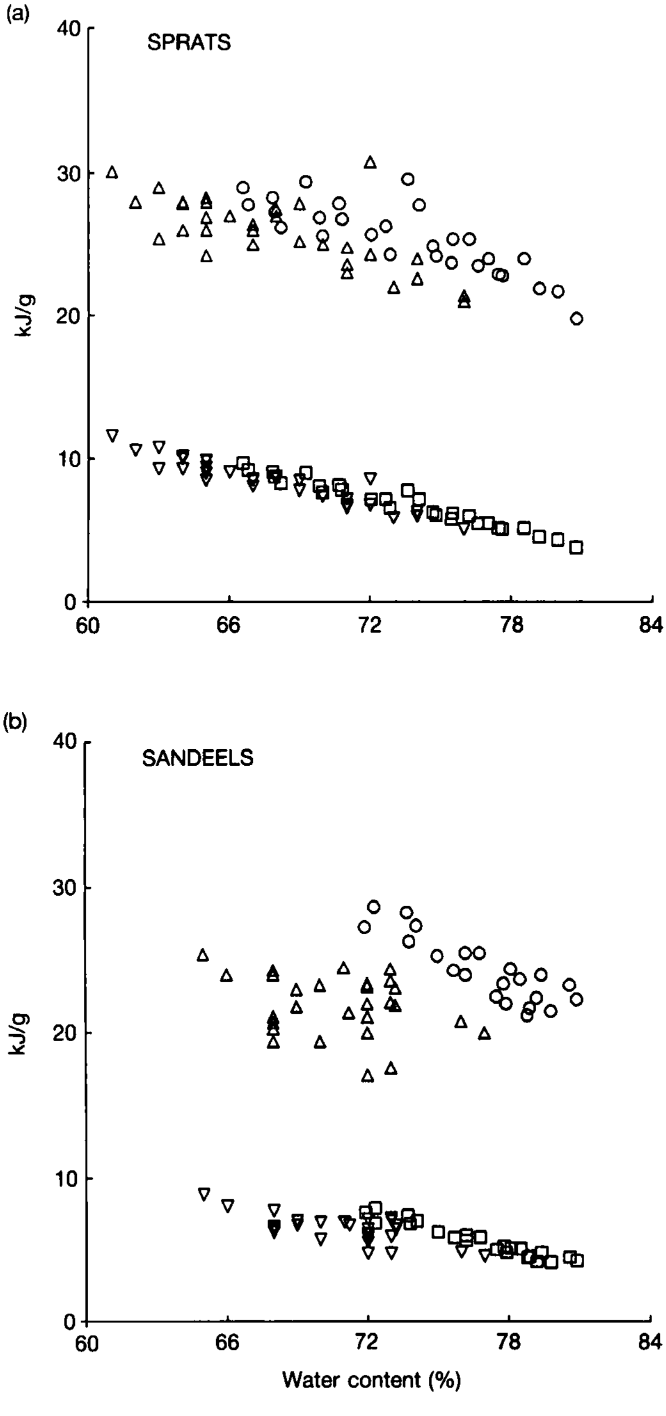

FIG. 2. Comparison of relationships between dry (upper) and wet (lower) calorific values and water content of (a) sprats and (b) sandeels from fishery samples (○, □) and from seabirds (△, ▽).

There was markedly less monthly variation in the energy content of whiting than in the other three species (**Appendix IV**).

Direct measurements (dry weight × dry calorific value) of the energy content of sandeel and sprat collected from birds in June and July are plotted against fish length in Fig. 1.

The predicted energy content of larger sandeels (> 11 cm), based on fish collected from seabirds, agrees closely with the fishery estimates for June, July and August, but agreement was not so good for the smaller length classes (Table II).

The sprat data were more scattered about the fitted line than those from sandeel. This is to be expected because, in contrast with the lesser sandeel, which spawns in winter (Gauld & Hutcheon, 1990), sprat in the northern North Sea spawn in late spring and summer (Bailey & Braes, 1976), and our samples were probably a mixture of reproductive stages ranging from pre-spawning fish with high body weights and calorific values, through fish in the process of spawning, to spent (sexually exhausted) individuals with depleted energy reserves and low calorific values (Montevecchi & Piatt, 1984; Almatar, 1989). We did not assess the reproductive state of the fishery samples but examination of some of the sprats from seabirds indicated that the sample was a mixture of spawning and spent fish.

The calorific values of sandeels and sprats from birds and from fishery samples are plotted against water content in Fig. 2. Most of the points relating to fish collected from birds lie well to the left of those from the fishery samples, suggesting that the former fish had lost some water.

Discussion

The deceptively simple questions asked of fishery biologists by avian ecologists such as 'what is the calorific value of species X?', and 'what is the energy content of a fish of size Y?' cannot be answered unless very specifically phrased. There are three main problems, which will be dealt with in turn.

Changes in calorific value within a species

Wet calorific value often increases with fish length and in consequence total energy content increases more rapidly with length than would be predicted by a simple weight/length relationship. This implies that when several predators exploit the same fish prey, those capable of taking bigger individuals will get a better return, in terms of energy per gram of prey captured, than predators who are only able to exploit small prey, although the energy costs of searching for and handling large prey may be greater.

The energy content of a fish depends not only on its size but also on the time of year (see also Steimle & Terranova, 1985). We have demonstrated that the energy content of sandeels of a given length can virtually double over the period April–June, although the increase is less for small (< 10 cm) individuals (Table II). Seasonal cycles in fat content and, consequently, in calorific value are generally associated with the annual reproductive and feeding cycles of the fish, and tend to be greater amongst the larger, mature members of the population. Different species of fish spawn at different times of year and, within a species, spawning may take place at different times in different areas (Daan *et al.*, 1990). In consequence, the condition cycles of the various prey species are out of phase to a greater or lesser extent. Thus, in the summer months in the northern North Sea *A. marinus*, which spawn in winter, are relatively fat whereas sprat, which spawn in summer, may have a lower energy content than in winter. The condition cycles of Atlantic herring are particularly complex, because this species consists of several 'races', which spawn at different times (Daan *et al.*, 1990).

Calorific value and energy content of different species

Because fish demonstrate intraspecific length-related and seasonal changes in calorific value and energy content, it can be unwise to generalize about the relative food values of different prey species to predators. The calorific value of whiting, a typical gadoid fish, is relatively low (usually <5 kJ/g^{-1} wet weight) and varies little from month to month. By comparison, clupeids and scombrids exhibit marked seasonal differences in condition and mean fat levels may be as high as 20-25% of the wet body weight (Iles & Wood, 1965; Wallace & Hulme, 1977; Wallace, 1986). This is reflected in some of the high calorific values (>10 kJ/g^{-1} wet weight, >30 kJ/g^{-1} dry weight) in our June and August samples of herring (**Appendix III**). However, it is important to realize that these high levels are only attained by the larger (>20 cm) maturing or mature herring; the calorific values and energy content of herring small enough to be exploited by the majority of seabirds are not much higher than those of whiting. Barrett *et al.* (1987) also recorded that small herring (3–7 cm) had low calorific values (4·6–6 kJ/g^{-1}). Thus, although herring may represent a concentrated source of energy for predators capable of capturing large fish, this is not true of the small herring on which young seabirds are fed. The calorific values of mature sprat can equal those of mature herring (**Appendices II** and **III**). Because sprat rarely grow larger than 15 cm they reach sexual maturity, and hence have high levels of energy density, at a much smaller length (10–12 cm). They would thus appear to be a high quality food suitable for exploitation by a large size range of predators, although in summer there is considerable individual variation in the energy content of sprats of a given length (Fig. 1).

Sandeel have maximum calorific values intermediate between those of gadoids and clupeoids. Although they are locally extremely abundant and reach peak body condition during the summer months, when birds are feeding young, sandeels contain less energy, length for length, than most other possible prey species because their bodies are needle-shaped. The difference between the energy content of sandeel and similarly sized sprat in summer is clearly demonstrated in Fig. 1. Juvenile sandeels (<10 cm), which have low body weights and a high water content, would seem, on purely energetic grounds, to be low quality food, even though they are usually, or can often be, the commonest prey brought to young puffins, razorbills (*Alca torda*), kittiwakes (*Rissa tridactyla*), arctic terns (*Sterna paradisaea*), common terns (*S. hirundo*), sandwich terns (*S. sandvicensis*) and fulmars (*Fulmarus glacialis*), species which feed at or within a few tens of metres of the surface (Pearson, 1968; Harris & Hislop, 1978; Furness, 1984; Harris & Wanless, 1986; Fowler & Dye, 1987; Monaghan *et al.*, 1989). Puffins can carry more than 60 small fish in their beak so that when forced to feed on small sandeels they can still bring back several grams of fish from each feeding trip. There is, however, a significant negative relationship between the weight of the load and the size of the fish comprising the load (Harris, 1984) and puffins feeding their young on small fish, and on 'low quality' gadoids, tend to have low breeding success (Harris & Hislop, 1978). Seabirds which can dive deeper, e.g. guillemot and shag (*Phalacrocorax aristotelis*), usually feed their young on larger sandeels, of higher energy value, though these also on occasions bring back numbers of small individuals (Pearson, 1968; Martin, 1989, pers. obs.).

The practical difficulties of determining calorific value and energy content

Fish prey collected at seabird breeding colonies have often undergone partial dehydration during transit from the birds' feeding area to their breeding site. The extent of this water loss will depend on many factors, including ambient temperature, flying speed and flight duration, the surface area of the fish and the degree to which the fish is enclosed by the bill of the bird. Montevecchi & Piatt (1987) simulated carriage of capelin by auks by tying fish to a drying rack mounted on a pick-up truck which was driven at 60 kph (representing the cruising speed of an auk). After one hour, weight loss averaged 9% for male capelin and 11·5% for females.

After a fish has been collected by a researcher, it will continue to lose water until transferred to a suitable container, such as the pre-weighed impermeable bags used to hold the 1987 fishery samples. Although samples are often stored frozen before their moisture content is determined and/or chemical analyses are performed, freezing itself causes additional dehydration; water loss may be substantial if fish are stored unwrapped or loosely wrapped. Figure 2 indicates that some of the fish collected from auks must have been partially dehydrated by the time they were analysed, even though the fish were wrapped as soon after collection as possible. The difference is greater for sandeel than sprat, presumably because the needle-shaped sandeels, with a high surface: volume ratio, are more susceptible to dehydration than sprats, which have compact bodies.

In the estimation of total energy content, problems arising from dehydration are avoided if energy content is determined by multiplying dry body weight by dry calorific value. This is rarely done. More commonly, calorific value is multiplied by the body weight of the fish as predicted by a weight/length relationship. However, whereas calorific values are initially determined on a dry weight basis, weight/length relationships are almost always expressed in terms of wet weight. It is therefore necessary to convert the 'dry' calorific value to its 'wet' equivalent, using information on the water content of the sample, but if dehydration has occurred the observed water content will be lower, and the calculated 'wet' calorific value higher, than the real values. The effect of partial dehydration on estimates of wet calorific value can be large. For example, if a fish whose initial water content is 70% suffers a 10% loss in body weight through dehydration, its water content falls to 66·7%. If the dry calorific value is 25 kJ/g, the observed wet calorific value will be $(1-0{\cdot}667)\times 25=8{\cdot}3$ kJ, compared with the original value of $(1-0{\cdot}7)\times 25=7{\cdot}5$ kJ. For any given percentage loss in body weight, the discrepancy between the initial and final water levels will be greatest for fish with a relatively low initial water content. Water content can be used to predict the calorific value of fish (**Appendix VI**) but this method will give spurious results if a regression based on 'fresh' material is applied to dehydrated samples, or vice versa.

Montevecchi & Piatt (1987) urged seabird biologists to compare dry weight energy densities across studies. Although, regrettably, their appeal has had a very limited response, we strongly support it and recommended that for very critical studies it may be best to obtain both dry calorific value and a dry weight/length relationship, after which field samples could be measured, rather than weighed. However, Montevecchi & Piatt (1987) acknowledged that wet weights are biologically important (e.g. for assessing the energy costs of transporting prey). For this reason, we have included wet calorific values both in the present paper and earlier (Harris & Hislop, 1978). These wet weight data must be used with care, and it must be recognized that it is probably not possible to get true wet weights of fish collected at seabird colonies, although water loss may be minimized by suitable handling methods, such as used for our 1987 fishery samples.

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Appendix I

*Mean length, calorific values (kJ/g^{-1}), wet weight (W, g) and total energy content (E, kJ) of lesser sandeel **Ammodytes marinus** in 1987 fishery samples*

Mean length (cm)	March				April				May				June			
	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E
6·5													21·2	4·5	0·6	2·7
7·5					21·5	4·2	1·0	4·2					22·0	4·9	1·1	5·4
8·5	22·3	4·3	1·3	5·6												
9·5	23·3	4·5	1·7	7·7												
10·5					24·0	4·8	2·8	13·4					24·3	5·9	3·1	18·3
12·5					22·4	4·2	5·1	21·4	25·5	5·9	6·5	38·4	27·4	7·1	5·6	39·8
14·5					21·7	4·6	7·6	35·0	24·0	5·7	8·9	50·7	28·3	7·5	9·2	69·0
16·5					24·4	5·2	11·1	57·7	23·4	5·3	12·5	66·3	25·8	6·9	13·5	93·2
17·0									22·5	5·1	14·5	74·0				
18·0									25·5	6·1	16·6	101				
18·5					23·7	5·1	15·5	79·1					28·7	8·0	18·8	150
19·0									25·3	6·3	20·7	130				
20·0									26·3	6·9	27·7	191				
20·5									27·3	7·7	31·6	243				

Appendix II

Mean length, calorific values (kJ/g^{-1}), wet weight (W, g) and total energy content (E, kJ) of sprat in 1987 fishery samples

Mean length (cm)	December/January				February				March				June				November			
	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E
4·0													19·8	3·8	0·3	1·1				
5·5	21·7	4·4	1·4	6·2																
7·5	23·5	5·8	3·3	19·1																
9·0													25·6	7·7	5·7	43·9				
9·5	24·2	6·1	6·8	41·5	24·9	6·3	4·9	30·9	24·0	5·9	4·6	27·1								
10·0													28·3	9·1	8·1	73·7				
10·5																	26·2	8·3	8·2	68·1
11·0													29·6	7·8	10·9	85·0				
11·5	25·9	6·6	10·6	70	27·9	8·2	9·1	74·6	22·9	5·2	9·3	48·4					27·3	8·8	10·9	95·9
12·0					27·8	7·2	12·4	89·3					24·0	5·5	12·8	70·4				
12·5	25·7	7·2	14·1	102													27·8	9·2	14·0	129
13·0													23·7	5·8	16·5	95·7				
13·5	26·8	7·8	17·3	134					25·4	6·2	15·2	94·2					29·0	9·7	18·4	179
14·5	24·3	6·6	24·5	162													29·4	9·0	20·6	185
15·5	26·9	8·1	25·9	210					35·5	12·4	30·5	378								

Appendix III

Mean length, calorific values (kJ/g^{-1}), wet weight (W, g) and total energy content (E, kJ) of herring in 1987 fishery samples

Mean length (cm)	December/January				February				March				June				August				November			
	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E
8·5	23·8	4·6	3·3	15·2																				
9·5	21·7	4·2	4·7	19·7																				
10·5					20·0	4·0	6·2	24·8																
11·5	23·2	4·6	8·4	38·6																				
12·0					22·3	4·8	11·8	56·6																
13·5	24·6	5·2	14·0	72·8					23·1	4·7	12·0	56·4												
14·5					20·2	4·4	16·7	73·5																
15·5	24·6	6·7	19·5	131					22·5	4·6	18·6	85·6					28·9	7·5	41·6	312				
17·5					22·9	5·5	37·0	204																
20·0	28·3	8·2	59·7	490					25·4	7·0	50·4	353	33·0	10·5	65·5	688	33·8	11·0	62·9	692	30·5	8·4	61·2	514
22·5					25·5	6·7	75·2	504																
25·0	26·3	7·9	119	940					23·9	5·8	123	713	27·3	6·7	113	757	34·4	10·6	116	1230	27·4	7·5	111	833
27·5					28·4	8·5	117	995																
30·0	24·3	6·1	194	1183									30·5	8·5	197	1675					27·4	6·9	186	1283

Appendix IV

Mean length, calorific values (kJ/g^{-1}), wet weight (W, g) and total energy content (E, kJ) of whiting in 1987 fishery samples

Mean length (cm)	February				March				June				August			
	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E	Dry CV	Wet CV	W	E
5·0									19·8	3·9	1·0	3·9				
7·5													19·6	3·7	3·4	12·6
9·5													20·5	3·0	6·1	23·8
11·5					18·5	3·5	9·9	34·7								
13·5	20·6	4·2	16·4	68·9	18·3	3·5	15·9	55·7					20·9	3·9	17·7	69·0
14·5	20·4	4·2	19·4	81·5												
15·5					19·3	4·0	25·8	103					21·4	4·0	26·6	109
17·5	20·3	4·3	34·0	146												
20·0					20·8	4·6	63·6	293	22·5	4·8	71·3	342	21·9	4·0	63·2	278
22·5	20·1	4·3	82·2	354												
25·0									23·9	4·7	106	498	20·1	4·0	118	496
27·5	19·5	4·4	154	678												
30·0									24·4	5·2	212	1102	26·1	5·2	208	1227

Appendix V

Mean monthly percentages (±S.D.) of water, protein and fat in lesser sandeel ***Ammodytes marinus*** *in 1986 fishery samples. N is the number of samples analysed: each sample was a homogenate of several fish*

Length class (cm)	April						May						June					
	N	Water	N	Protein	N	Fat	N	Water	N	Protein	N	Fat	N	Water	N	Protein	N	Fat
4·1–6·0													2	81·6 (1·13)	2	14·5 (0·99)	2	2·3 (0·64)
6·1–8·0													4	78·8 (2·57)	3	15·5 (0·85)	4	4·1 (2·02)
8·1–10·0	4	79·5 (0·28)	2	16·5 (0·21)	4	2·1 (0·41)	1	79·0 (—)	1	16·0 (—)	1	3·8 (—)	3	77·1 (1·39)	2	16·0 (0·64)	4	5·1 (1·27)
10·1–12·0	4	79·4 (0·45)	2	16·6 (0·71)	5	2·3 (0·43)	6	76·5 (1·43)	5	17·4 (0·64)	5	4·2 (0·90)	3	74·2 (1·33)	2	17·3 (0·28)	6	7·0 (2·06)
12·1–14·0	6	79·1 (0·32)	4	16·7 (0·25)	6	2·2 (0·32)	8	76·0 (1·36)	7	17·6 (0·43)	7	4·9 (1·62)	5	72·3 (1·88)	4	17·8 (0·58)	6	7·9 (2·33)
14·1–16·0	8	78·5 (0·66)	7	17·1 (0·49)	8	2·5 (0·32)	8	75·0 (2·02)	7	17·8 (0·76)	8	5·5 (2·35)	6	71·7 (1·71)	5	18·1 (0·64)	6	8·9 (1·57)
16·1–18·0	4	78·0 (0·70)	3	17·2 (0·25)	5	2·5 (0·69)	7	74·9 (2·25)	6	17·7 (0·35)	8	5·5 (2·39)	4	72·3 (1·06)	3	18·2 (0·68)	6	8·5 (1·32)
18·1–20·0	2	78·8 (0·35)	1	17·1 (—)	2	2·6 (0·92)	4	74·7 (1·90)	3	17·5 (0·10)	4	5·8 (2·26)	3	73·6 (1·21)	2	18·7 (1·48)	3	6·4 (1·38)

Appendix V *(cont.)*

Length class (cm)	July						August						September and October					
	N	Water	N	Protein	N	Fat	N	Water	N	Protein	N	Fat	N	Water	N	Protein	N	Fat
4·1–6·0	5	80·0 (0·54)	5	15·2 (0·55)	5	2·0 (0·28)												
6·1–8·0	6	79·5 (0·92)	6	15·9 (0·47)	6	2·9 (0·98)	4	78·8 (0·94)	3	16·7 (0·53)	4	3·0 (0·37)						
8·1–10·0	4	76·2 (2·38)	3	17·1 (1·23)	4	5·3 (1·25)	5	75·3 (1·22)	3	17·1 (0·76)	5	5·9 (1·00)	2	76·5 (1·70)	2	17·6 (1·48)	2	5·0 (0·42)
10·1–12·0	4	74·7 (1·64)	1	18·5 (—)	6	6·0 (1·69)	5	73·9 (1·04)	3	17·4 (0·62)	5	7·2 (1·13)	2	75·1 (0·64)	2	17·1 (0·92)	2	5·3 (1·20)
12·1–14·0	6	72·8 (1·52)	5	18·1 (0·90)	7	7·1 (1·88)	4	72·1 (0·87)	3	18·0 (0·35)	4	8·3 (0·75)	1	73·5 (—)	1	18·3 (—)	1	7·1 (—)
14·1–16·0	4	71·9 (1·22)	4	18·4 (0·43)	7	7·6 (2·20)	2	72·3 (1·20)	2	18·5 (0·14)	3	8·2 (1·14)	1	73·5 (—)	1	18·1 (—)	1	4·9 (—)
16·1–18·0	1	70·3 (—)	2	18·7 (0·92)	4	7·0 (2·76)	2	71·9 (1·41)	2	18·9 (0·21)	2	7·9 (1·13)						
18·1–20·0	1	70·3 (—)	1	18·8 (—)	1	8·8 (—)												

Appendix VI

Relationships between wet and dry calorific values and percentage water content

Sandeel
CV (kJ/g^{-1} wet) = -0.418 W + 37.785 ($r = -0.966$, N = 23, $P < 0.001$)
CV (kJ/g^{-1} dry) = -0.769 W + 83.566 ($r = -0.889$, N = 23, $P < 0.001$)

Sprat
CV (kJ/g^{-1} wet) = -0.382 W + 34.871 ($r = -0.978$, N = 28, $P < 0.001$)
CV (kJ/g^{-1} dry) = -0.494 W + 61.763 ($r = -0.884$, N = 28, $P < 0.001$)

Herring
CV (kJ/g^{-1} wet) = -0.469 W + 41.788 ($r = -0.958$, N = 28, $P < 0.001$)
CV (kJ/g^{-1} dry) = -0.797 W + 83.653 ($r = -0.856$, N = 28, $P < 0.001$)

Whiting
CV (kJ/g^{-1} wet) = -0.339 W + 31.271 ($r = -0.694$, N = 22, $P < 0.001$)
CV (kJ/g^{-1} dry) = -0.612 W + 69.813 ($r = -0.342$, N = 22, ns)

Appendix VII

Relationships between energy content (E, kJ) of whole sandeels and their length (L, cm), as determined by three methods

(a) Calorific value determined by calorimetry
April E $= 0.0061\ L^{3.250}$ ($r = 0.999$, N = 6, $P < 0.001$)
May $= 0.0032\ L^{3.630}$ ($r = 0.951$, N = 8, $P < 0.001$)
June $= 0.0024\ L^{3.806}$ ($r = 0.998$, N = 7, $P < 0.001$)

(b) Calorific value estimated from water content
April E $= 0.0036\ L^{3.436}$ ($r = 0.999$, N = 7, $P < 0.001$)
May $= 0.0023\ L^{3.724}$ ($r = 0.999$, N = 6, $P < 0.001$)
June $= 0.0022\ L^{3.874}$ ($r = 0.999$, N = 8, $P < 0.001$)
July $= 0.0021\ L^{3.920}$ ($r = 0.999$, N = 8, $P < 0.001$)
August $= 0.0028\ L^{3.817}$ ($r = 0.999$, N = 7, $P < 0.001$)

(c) Calorific value calculated from proximate composition
April E $= 0.0040\ L^{3.405}$ ($r = 0.999$, N = 7, $P < 0.001$)
May $= 0.0035\ L^{3.580}$ ($r = 0.999$, N = 6, $P < 0.001$)
June $= 0.0031\ L^{3.745}$ ($r = 0.999$, N = 8, $P < 0.001$)
July $= 0.0031\ L^{3.758}$ ($r = 0.999$, N = 8, $P < 0.001$)
August $= 0.0040\ L^{3.673}$ ($r = 0.999$, N = 7, $P < 0.001$)