

COMPOSITION AND ENERGY CONTENTS OF MATURE INSHORE SPAWNING CAPELIN (*MALLOTUS VILLOSUS*): IMPLICATIONS FOR SEABIRD PREDATORS

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Abstract—1. Lipid levels of capelin are highest in late fall and lowest during the summer spawning season; protein levels are constant at 13–14% body wt throughout the year.

2. Ovid females contained significantly more lipid and protein and less water and had higher energy densities than males and spent females.

3. Surgically-removed egg masses made up $34.2 \pm 10.3\%$ female body wt and were very similar in composition and energy density to gravid females, differing from spent females and males in similar respects. Owing to the ovarian development of females, sexes differ in energy density only during the spawning season.

4. Sexes were similar in amino acid composition. Analysis of capelin and three other seabird forage species revealed that isoleucine levels were lower than minimum avian maintenance and growth requirements.

5. Implications for the foraging behaviour and food preferences of diving seabird predators (murre, puffins) are discussed.

INTRODUCTION

Capelin (*Mallotus villosus*) are the most abundant and important forage fish in the northwest Atlantic (Carscadden, 1983). Besides being the predominant summer prey of many fish and marine mammal species in the Newfoundland region (Winters and Carscadden, 1978), they are an extremely important food for many marine birds (e.g. Montevecchi *et al.* (1984); see also Norderhaug *et al.*, 1981), especially for alcids of the genera *Uria* and *Fratercula* (e.g. Mahoney, 1979; Brown and Nettleship, 1983). A drastic decrease in Newfoundland capelin stocks after 1976 (Carscadden, 1983) has generated concern about possible detrimental effects on avian predators, especially Atlantic puffins, *Fratercula arctica* (Brown and Nettleship, 1983).

Models of energy flow through seabird communities in the North Atlantic, North Pacific and off South Africa have yielded estimates that marine birds consume 22–29% of the available commercial fisheries stocks in ocean areas around colonies (Wiens and Scott, 1975; Furness, 1978, 1982; Furness and Cooper, 1982). Energy modelling is dependent upon data from studies of chick growth and feeding ecology. The interpretation of such studies requires accurate determinations of the nutritive compositions and energy contents of seabird prey.

Research on the organic composition of capelin has been conducted in the Barents Sea (e.g. Jangaard, 1974), although few data are available on capelin composition from the inshore waters of eastern Newfoundland (e.g. Montevecchi and Porter, 1980). The present study reports on the organic composition and energy contents of mature male and female capelin (and eggs) collected in eastern Newfoundland. Data from other sources are reviewed and drawn together.

Implications for the food preferences and foraging behaviour of alcids that feed heavily on capelin are discussed.

METHODS

Spawning capelin were collected in June 1982 at Torbay (47° 39'N, 53° 16'W) and Cape Broyle (47° 06'N, 53° 03'W), Newfoundland, Canada. Fish were frozen, then measured (total length, ± 0.05 mm, Helios dial calipers), weighed (± 0.01 g, Mettler balance) and eggs were surgically removed from 10 gravid females about 16 weeks after collection.

Fifteen mature males, 10 ovid females, 10 spent females, 10 females with egg masses surgically removed and 10 corresponding egg masses taken from gravid females were oven dried to constant weight (102°C for 18–24 hr) to determine moisture contents (fresh – dry weight). Lipids were extracted in baths of diethyl ether, and protein contents were determined by the Kjeldahl method. Ash contents were obtained by combusting extracted samples in a muffle furnace at 550°C for 8 hr (see Ricklefs and Montevecchi, 1979). Two dry, powdered homogenates of males, ovid and spent females and of eggs were subjected to HCl hydrolysis, and amino acids were determined on a Beckman amino acid analyser. Carbohydrates make up a minute fraction of fish tissue (Wheeler, personal communication) and were not analysed. Conversion factors of 20 kJ/g protein and 38 kJ/g lipid were used to calculate energy contents (Ricklefs, 1974).

RESULTS

Organic composition

The protein content of capelin remains at 13–14% of body wt throughout the year (Table 1). Lipid and water contents, however, fluctuate markedly, with lowest fat and highest water levels occurring during the spawning season (June, July; see Table 1). Water contents are lowest and lipid contents highest in late fall/early winter.

Table 1. Approximate monthly composition and energy content of capelin*

Month	Source†	% Composition			Energy‡
		Lipid	Protein	Water	(kJ/g) (wet)
Jan	1	13	13	72	7.5
Feb	1, 3	13	13	72	7.5
Mar	1, 3, 5	13	13	72	7.5
Apr	1, 3, 5	9	14	75	6.2
May	1, 3, 5	6	13	79	4.9
Jun	1, 2, 4, 6, 7	3	14	81	3.9
Jul	1, 2, 5	3	14	81	3.9
Aug	1, 2	8	14	76	5.8
Sep	1, 2	11	14	73	7.0
Oct	1, 2, 5	15	13	70	8.3
Nov	1, 2, 5	16	13	69	8.7
Dec	1	18	13	67	9.4

*Compiled from "sources". Some data on the seasonal composition of capelin from the Barents Sea are included and have been adjusted for differences in spawning times between the Barents Sea and Newfoundland. Percentages combined equal 98%, with the assumption that ash content is consistent at 2%.

†Sources: (1) Jacobsen and Henn, in Jangaard, 1974; (2) Eaton *et al.*, 1975; (3) Winters, 1970; (4) this study; (5) Anon in Jangaard, 1974; (6) prokorov, in Jangaard, 1974; and (7) McCallum in Jangaard, 1974.

‡Energy content of lipid and protein equals 38.0 and 20.0 kJ/g, respectively (Ricklefs, 1974).

Table 2. Average (\pm SD) size, percentage organic composition and energy contents of adult spawning capelin from the southeastern shore of Newfoundland, June 1982. All sample sizes = 10, except for males for which $N = 15$

Measurement	Female				
	Male*	Ovid	Spent	Egg mass removed†	Egg mass
Length (mm)	183 \pm 6.2	158 \pm 18.6	158 \pm 12.7	168 \pm 9.4	
Weight (g)	42.1 \pm 4.2	26.2 \pm 8.4	20.7 \pm 5.5	29.4 \pm 6.1	10.2 \pm 3.0
% water	80.2 \pm 1.4	76.5 \pm 1.0	80.0 \pm 2.6	80.5 \pm 1.6	74.8 \pm 1.0
% protein	14.2 \pm 0.4	15.5 \pm 0.5	14.3 \pm 0.9	15.2 \pm 0.7	15.7 \pm 0.8
% lipid	2.4 \pm 1.3	4.1 \pm 0.8	2.7 \pm 2.0	1.6 \pm 1.1	3.8 \pm 0.5
% ash	2.0 \pm 0.4	1.9 \pm 0.3	2.1 \pm 0.2	2.1 \pm 0.2	1.4 \pm 0.1
Energy values‡					
Total \bar{X} (kJ)	158 \pm 26.7	121 \pm 38.8	78.4 \pm 18.2	105 \pm 21.3	46.8 \pm 13.2
kJ/g (wet)	3.8 \pm 0.5	4.6 \pm 0.3	3.9 \pm 0.8	3.6 \pm 0.5	4.6 \pm 0.3

*In varying stages of maturity though all spawning.

†Egg mass removed from ovid females to simulate spent condition.

‡Energy content of lipid and protein equals 38.0 and 20.0 kJ/g, respectively (Ricklefs, 1974).

Table 3. Analyses of variance:* comparisons of adult capelin composition in Table 2

		Female		
		Ovid	Spent	Egg mass removed
Male	% water	***	NS	NS
	% protein	***	NS	***
	% lipid	**	NS	NS
	% ash	NS	NS	NS
	kJ/g	**	NS	NS
Ovid female	% water	—	***	***
	% protein	—	**	NS
	% lipid	—	NS	***
	% ash	—	NS	NS
	kJ/g	—	**	**
Spent female	% water	—	—	NS
	% protein	—	—	*
	% lipid	—	—	NS
	% ash	—	—	NS
	kJ/g	—	—	NS

*Significance levels: *** $P < 0.001$; ** $P < 0.01$, * $P < 0.025$, NS—no significant differences.

Table 4. Comparisons of male and female capelin composition and energy densities before, during, and after spawning (late June-early July)

	Male \bar{X} (%)						Female \bar{X} (%)					
	N	Length (mm) \bar{X} or range	Fat	Water	Protein*	(kJ/g) (wet)	N	Length (mm). \bar{X} or range	Fat	Water	Protein*	(kJ/g) (wet)
29 Mar-	5	190-210	11.9	71.2	14.9	7.5	5	180-200	11.9	71.6	14.5	7.4
3 Apr 1968†	5	170-190	8.4	74.7	14.9	6.2	5	160-180	8.4	74.1	15.5	6.3
	5	150-170	5.5	77.1	15.4	5.2	5	140-160	6.0	76.2	15.8	5.4
24-28	15	183.3	2.4	80.2	14.2	3.8	10§	158.0	4.1	76.5	15.5	4.6
June 1982‡							10	158.0	2.7	80.0	14.3	3.9
June 1972¶	60	—	2.7	81.6	13.7	3.8	80**	—	3.2	80.3	14.5	4.2
July 1972¶	200	159	0.8	82.7	14.5	3.2	200**	141	1.9	81.3	14.8	3.7
Oct 1972¶	60	—	18.4	67.2	12.4	9.5	60	—	18.4	67.1	12.5	9.5

*%Protein extrapolated assuming constant ash composition of 2.0%.

†From Winters (1970).

‡This study.

§Ovid females.

||Spent females.

¶From Eaton *et al.* (1975).

**Condition unknown.

The proportionate organic composition of eggs and fishes in our sample are presented in Table 2. Males, which are significantly longer and heavier than females, contained significantly more water, less lipid and protein than ovid females but did not differ significantly from spent females in any respect (Table 3). Ovid females had significantly more fat and protein and less water than spent females and differed from females with egg masses surgically removed in the same respects except that protein levels were similar (Tables 2 and 3). Females with egg masses surgically removed also contained proportionately more protein than males and spent females (Tables 2 and 3).

Egg masses averaged 10.2 ± 3.0 g, comprising $34.2 \pm 10.3\%$ ($N = 18$) of female body weight. The water, lipid and protein levels of egg masses were very similar to those obtained from ovid females and differ from the other fish sample groups in similar respects (see Tables 2 and 3).

Energy contents

Table 2 also shows the energy values of the eggs and different fish samples. A comparison of energy density (kJ/g) values shows that owing to higher lipid and lower water levels, ovid females are per unit weight the energetically richest prey type (Table 3).

Comparisons of the organic compositions and energy densities of different size-classes of male and female capelin before, during and after the spawning season are presented in Table 4. Overall these findings show that while composition and energy density vary considerably across size-classes and throughout the year, there are no compositional differences between the sexes except during the spawning season (June, July).

Amino acid composition

Table 5 shows that male and female capelin have very similar amino acid compositions. Females with

Table 5. Amino acid composition expressed as nm/mg protein and as ratio to threonine of inshore spawning capelin and eggs

Amino acid	Male		Female egg mass removed		Egg mass	
	nm/mg protein	Threonine ratio*	nm/mg protein	Threonine ratio	nm/mg protein	Threonine ratio
Taurine	76	0.24	61	0.18	71	0.18
Hydroxyproline	43	0.14	21	0.06	0	0.0
Aspartic acid	671	2.1	671	2.0	591	1.5
Threonine†	321	1.0	333	1.0	393	1.0
Serine	379	1.2	370	1.1	598	1.5
Proline	301	0.94	297	0.89	422	1.1
Glutamic acid	816	2.5	825	2.5	708	1.8
Glycine†	648	2.0	657	2.0	406	1.0
Alanine	593	1.8	602	1.8	708	1.8
Valine†	328	1.0	375	1.1	432	1.1
Methionine†	191	0.60	177	0.53	156	0.40
Isoleucine†	234	0.73	282	0.85	322	0.82
Leucine†	533	1.7	527	1.6	537	1.4
Tyrosine	167	0.52	145	0.44	170	0.43
Phenylalanine†	200	0.62	201	0.60	216	0.55
Lysine†	492	1.5	476	1.4	411	1.0
Histidine†	106	0.33	105	0.31	138	0.35
Tryptophan†	n.d.	—	n.d.	—	n.d.	—
Arginine†	311	0.97	305	0.92	305	0.78

*Expressed as ratio to threonine for comparative purposes (Fisher, 1972).

†Essential amino acids for poultry (Fisher, 1972).

eggs surgically removed had slightly lower concentrations of the nonessential amino acids taurine, hydroxyproline, proline and tyrosine and slightly higher levels of the essential amino acids valine and isoleucine.

Eggs were analysed separately and showed many substantial differences in composition from both sexes of capelin. Eggs contained no hydroxyproline, lower levels of aspartate, glutamate, glycine, methionine, lysine and higher concentrations of serine and proline. In view of our finding that egg mass may account for > 30% of female body wt at spawning, the different amino acid compositions of eggs and fishes (and therefore between ovid females and males or spent females) may be biologically significant for predators.

The relative amino acid compositions of four commercially exploited forage species in Newfoundland are compared in Table 6. With the exception of isoleucine, the relative levels of the amino acids identified as being essential for avian (poultry) maintenance and growth met or exceeded minimum requirements (Fisher, 1972). The proportionate levels of some amino acid concentrations (taurine, hydroxyproline, proline, glycine and alanine) are highly variable across species, whereas others (aspartate, threonine, serine, methionine and isoleucine) show very little interspecific variation.

Lipids, the major determinant of energy-density in capelin, are very similar to those found in other North Atlantic pelagic fish. These lipids consist largely of triglyceride oils of long-chain mono-unsaturated fatty acids, short-chain saturated acids and a relatively low amount of long chain poly-unsaturated acids (Jangaard, 1974; Eaton *et al.*, 1975). Other minor components include free phospholipids and unsaponifiable constituents (hydrocarbons, fatty alcohols and sterols).

Fat levels in capelin show marked seasonal variation. Levels are lowest during the spawning season,

when predation on capelin is greatest (Winters and Carscadden, 1978), and when local murre and puffin population energy demands are maximal (e.g. Wiens and Scott, 1975). Water content varies inversely with lipid content throughout the year, while the proportion of protein is constant at 13–14%.

Ovid females and capelin eggs contained the highest proportionate amounts of lipid and protein and the lowest water levels of the samples analysed. Consequently, their energy densities were also the highest. Because males and spent females do not differ in composition or energy density, and because males and females are virtually identical in these regards outside the spawning season, sex differences in composition and energy density clearly derive from the breeding condition of females. Egg masses contained significantly higher proportions of fat and protein and lower proportions of water than those found in either male or female body tissues. Some invertebrate prey of seabirds also show significant sex differences in caloric value during the spawning season (e.g. Clarke and Prince, 1980).

Females with egg masses artificially removed had significantly higher percentages of protein than either spent females or males. The act of spawning may in some way deplete protein from body tissues. Although such effects are beyond the scope of the present study, other potential reasons for such a difference are not obvious.

Winters (1970) found that from March to May the fat levels of immature capelin (0.8–1.4%) were much lower than that of adults (5.6–11.9%) and found no seasonal trend in fat contents among immatures, as was the case among adults (see above). Based on Winters' (1970) data, and assuming an ash content of 2%, we calculated an energy density of 3.5 kJ/g (wet) for immature fish. Thus, during spawning season, immatures are nearly equivalent in energy to adult males and spent females. The small size (~10% adult wt) of immatures certainly lowers their value as a

Table 6. Relative amino acid composition* of four commercially exploited Newfoundland fishery species that are important prey for different marine birds

Amino acid	Minimum required†	Capelin‡	Squid	Herring	Mackerel
Taurine	—	0.28	0.87	0.19	0.34
Hydroxyproline	—	0.12	0.12	0.06	0.28
Aspartic acid	—	1.9	1.8	1.9	1.9
Threonine	1.0	1.0	1.0	1.0	1.0
Serine	—	0.97	1.0	0.92	1.0
Proline	—	0.80	1.1	0.68	0.98
Glutamic acid	—	2.4	2.4	2.2	2.0
Glycine	0	2.1	2.0	1.8	3.3
Alanine	—	1.8	1.8	1.8	2.7
Valine	1.0	1.1	0.91	1.1	1.6
Methionine	0.3	0.56	0.54	0.54	0.46
Isoleucine	0.9	0.76	0.75	0.77	0.82
Leucine	1.0	1.5	1.4	1.5	1.4
Tyrosine	—	0.48	0.46	0.49	0.34
Phenylalanine	0.1	0.59	0.61	0.61	0.61
Lysine	0	1.4	1.2	1.5	1.3
Histidine	0	0.32	0.32	0.38	0.48
Tryptophan	0.1	n.d.	n.d.	n.d.	n.d.
Arginine	1.0	0.89	1.0	0.85	1.0

*Amino acid concentrations expressed as ratios to threonine for comparative purposes (Fisher, 1972).

†Minimum requirement of essential amino acids for poultry—defined as the lowest amino acid concentrations required to maintain nitrogen equilibrium (Fisher, 1972).

‡Based on two males collected inshore during spawning season.

prey item, although their greater abundance may increase their availability to predators.

In a small mixed sample of male and female capelin taken in late March/early April 1968 (before the spawning season), Winters (1970) found that, owing to increasing lipid level and decreasing moisture contents, energy density increased directly with body length. If this relationship holds outside the alcids' nesting season, then the birds might select the largest sized capelin that they are capable of capturing and handling effectively, a situation unlike that during the breeding cycle (see below). In our spawning season sample, there were no significant correlations between any of the organic components or energy density and fish length.

In addition to energetic considerations, nutritive aspects of food must be considered in comprehensive studies of seabird feeding ecology, growth and development. Ricklefs (1979) and others have suggested, for instance, that certain nutrients, such as sulphur-bearing amino acids, may produce "bottle necking" effects on growth processes when present in limiting concentrations. Protein quality is essential for growth and maintenance and has direct effects on fat metabolism, sexual maturation and reproduction in birds (e.g. Fisher, 1972; Hazelwood, 1972). The amino acid requirements of most animals are unknown, and only a few avian species have been studied (Fisher, 1972). The levels of all essential amino acids except isoleucine in capelin and other seabird forage species met or exceeded minimum avian (poultry) requirements. Isoleucine levels were higher in capelin eggs and spent females than males. Of the forage species analysed isoleucine levels were highest in mackerel. Studies of the effects of limiting isoleucine (or other essential amino acids) concentration on growth and maintenance would allow for a more complete assessment of protein quality on post-hatch development.

Protein levels in mackerel (*Scomber scombrus*, 16.2%), sand lance (*Ammodytes ammodytes*, 19.4%) and squid (*Ilex illecebrosus*, 15.9%) are slightly higher than those in capelin during summer (Montevocchi and Porter, 1980; Montevocchi, unpublished data). All fish protein levels are considerably higher than those required for basal maintenance in many avian species (4–12%, Fisher, 1972).

During the breeding season in Newfoundland both common murres (*Uria aalge*) and Atlantic puffins feed on adult capelin and both species feed their chicks immature as well as adult capelin (Mahoney, 1979; Brown and Nettleship, 1983; Piatt, unpublished data; A. Burger, personal communication). Preliminary analysis of summer diets suggests that breeding murres feed on males, females and immatures, whereas puffins eat females almost exclusively (Piatt, unpublished data). Being considerably larger than puffins, murres can take larger prey (e.g. male capelin), in addition to smaller female and immature capelin, and can consume more fish in a single foraging effort (Piatt, unpublished data). Murres carry single prey items back to offspring, whereas puffins are multiple prey loaders. These species differences could make it beneficial for puffins to select high energy-density food items (i.e. ovid females) and for murres to select large prey (i.e. male capelin) with a higher total energy content. Central

place foraging theory predicts that in similar circumstances single prey loaders should be more selective than multiple prey loaders (Orians and Pearson, 1978). This problem deserves more research attention, as it appears that the single prey loaders, the murres, have a wider prey spectrum than the multiple prey loaders, the puffins.

Further study is also needed to determine whether the swimming characteristics of male and female capelin and puffins and murres have preadapted different predators to specific prey. Male capelin remain in inshore waters longer than females, and females and immatures tend to range more pelagically and stay higher in the water column than males (Templeman, 1948; Bakke and Bjorke, 1973; Gjo-saeter *et al.*, 1975), patterns that would impose different foraging pressures on avian predators. Murres dive to greater depths than puffins (Piatt *et al.*, 1983; Piatt and Nettleship, in preparation), and may allow them to exploit male capelin that remain low in the water column. The ways in which utilization of different sex classes of capelin may affect interspecific competition and foraging behaviour remains to be investigated.

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