Condition Indices, Energy **Density and Water and Lipid Content of Atlantic Herring** (Clupea harengus harengus) of southeastern Newfoundland

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Fisheries and Aquatic Sciences 958

August 1980

CONDITION INDICES, ENERGY DENSITY AND WATER

AND LIPID CONTENT OF ATLANTIC HERRING (CLUPEA

HARENGUS HARENGUS) OF SOUTHEASTERN NEWFOUNDLAND

by

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ABSTRACT

McGurk, M. D., J. M. Green, W. D. McKone, and K. Spencer. 1980. Condition indices, energy density and water and lipid content of Atlantic herring (Clupea harengus harengus) of southeastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 958: iv + 41 p.

Condition indices, energy densities and water and lipid contents of the soma and the gonads of Atlantic herring were measured for the period March 1977-March 1978. Body condition index, somatic energy density and somatic lipid content reached a maximum in October and a minimum in early June, immediately after spawning, confirming earlier reports for this species. The testes growth rate was greatest over the summer and zero during the winter whereas the ovaries grew at a slower rate throughout the summer and winter. The ovaries had a consistently lower lipid content (1-2%) than the testes (2-4%) but the range of energy densities of the ovaries (7-8 kj·g-1) was higher than that of the testes (4-6 kj·g-1). The slope of the linear regression of energy density on percent water for the soma was higher than the slopes of the gonads and higher than the slope of a similar regression reported in the literature.

Key words: Atlantic herring, Clupea harengus, condition, energy, lipid, gonads, soma, seasonal

RÉSUMÉ

McGurk, M. D., J. M. Green, W. D. McKone, and K. Spencer. 1980. Condition indices, energy density and water and lipid content of Atlantic herring (Clupea harengus harengus) of southeastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 958: iv + 41 p.

De mars 1977 à mars 1978, on a mesuré la condition physique, la densité énergétique et la teneur en eau et en lipides des parties somatiques et germinales du hareng de l'Atlantique. L'indice de condition physique ainsi que la densité énergétique et la teneur en lipides du soma ont atteint un maximum en octobre et un minimum au début de juin, immédiatement après la fraie, ce qui a confirmé ce qu'on savait déjà de cette espèce. La croissance des testicules a été maximale l'été et nulle l'hiver tandis que celle des ovaires était lente l'été et l'hiver. La teneur en lipides des ovaires (1 à 2%) était inférieure à celle des testicules (2 à 4%), mais la densité énergétique y était supérieure (7 à 8 contre 4 à 6 kj·g⁻¹). Pour le soma, la pente de la droite de régression du rapport de la densité énergétique sur la teneur en eau était supérieure aux pentes calculées pour les gonades et supérieure à la pente d'une régression similaire trouvée dans une publication.

INTRODUCTION

The seasonal cycles of the condition indices, the energy densities and the water and lipid content of the body tissues of the Atlantic herring are important for two reasons. First, they are important to those engaged in the herring fishery, for the body condition index and the lipid content influences the commercial value of the fish. Second, the phenomenon of the transfer of material from the musculature to the gonads is important to those studying the reproductive biology of the herring. It is quite possible that environmental factors regulate the allocation of energy between the soma and the gonads and this has important implications for those attempting to understand the reasons behind the success or failure of year-classes.

There have been several studies of the chemical composition of herring from the Canadian Atlantic, however none of these have examined the soma and the gonads as separate compartments. Most of these studies were concerned with whole-body analysis (Leim 1957, 1958; Stoddard 1967, 1968; Hodder et al. 1973; Varga et al. 1977) and one with the analysis of the fillets (Ackman and Eaton 1976).

Direct calorimetric measurements of the seasonal cycle of the energy content of herring from the Canadian Atlantic have not been reported. An indirect estimate of the whole-body energy content of overwintering herring of southwest Newfoundland was made by Winters (1977) who used lipid and water data from Hodder et al. (1973) and standard factors for the energy density of lipid and solids.

This report presents the results of a study of the seasonal cycle of the condition indices of the body and the gonads and the seasonal cycle of the lipid and water content and the energy density of the body and gonads. The samples were taken from the southeast Newfoundland herring stock complex.

MATERIALS AND METHODS

SAMPLING

Ten samples of herring were obtained from commercial catches between March, 1977 and February 6, 1978. Samples were taken every six to eight weeks except during the pre-spawning and spawning period when they were taken every two to three weeks.

The seasonal nature of the inshore herring fishery made it impossible to obtain all samples from one popu-Eight of the samples were taken from the lation. Placentia Bay-St. Mary's Bay management unit, one was taken from the adjacent Conception Bay-Southern Shore management unit and one from the Bonavista Bay management unit (Fig. 1). It is assumed that the energy cycles of these three units are synchronous. This is reasonable since the mean date of spawning for the spring-spawners in each unit are within a week of each other (G. Winters, personal communication). Also recent tagging studies (G. Winters, personal communication) have shown that migration occurs between the first two units but because the extent of intermixing is unknown they are separated for management purposes.

A sample consisted of 50-60 specimens taken from the catch of a commercial vessel. The catch was sampled either on board the ship or in the fish processing plant several hours after off-loading. The fish were packed in ice and transported to the laboratory. There 10-15 fish of each sex were chosen and length, defined as the distance from the tip of the snout to the end of the longest caudal ray, was measured to 0.1 cm. Wet body

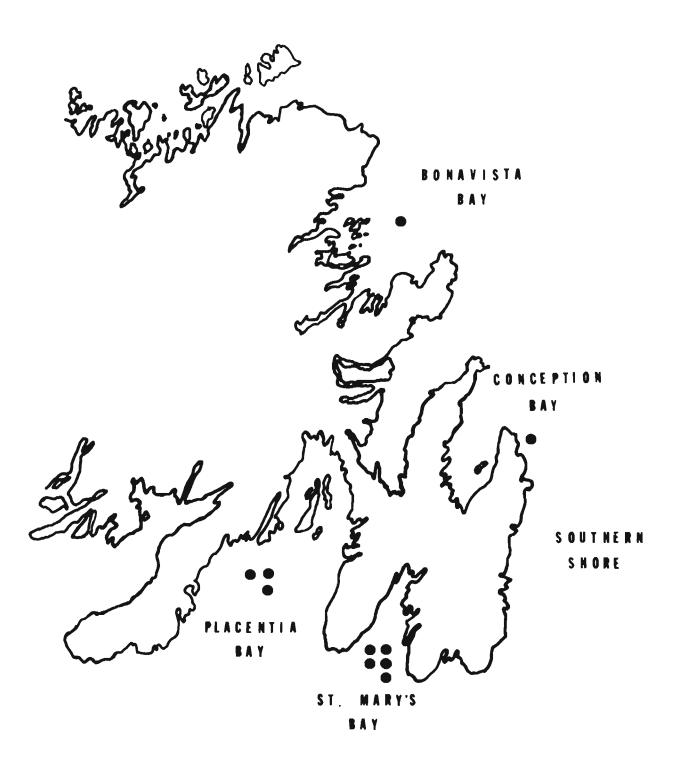


Fig. 1. Map showing the east coast of Newfoundland and the locations of the samples. Each dot represents one sample.

weight was measured to 0.1 g. The otoliths were removed for age determination. The weight of the stomach contents, if any, was taken to 0.1 g and was later used to correct the wet body weight. The gonads were weighed to 0.1 g, sexed and assigned a maturation stage (Anonymous 1964).

The body was separated into three compartments: the head, the gonads and the soma. The head was treated as a separate entity because it is assumed to play a negligible role in the internal energy flows of the body due to its lack of energy storage organs. A subsample of gonad tissue was placed in a plastic bag which was immediately sealed and frozen at -20°C for later lipid and water analysis. The remainder of the gonad was reserved for calorimetry. The head and the vertebral column, including the caudal fin, were removed and weighed to 0.1 g. The fillets and the viscera, hereafter referred to as the soma, were combined and minced in a meat grinder and then homogenized in a heavy duty Waring blender. A subsample of the homogenate was placed in a plastic bag which was immediately sealed and frozen at -20°C for later lipid and water analysis. Another subsample was reserved for calorimetry.

Twice during the year a number of heads were ground, homogenized and subsampled for lipid and water analysis and for calorimetry.

WATER

The frozen subsamples were thawed, then transferred to tared aluminum pans, weighed and dried in an oven at 100°C for two days. The pans were cooled in a desiccator and then weighed again. Mean percent water was computed from duplicate samples and never differed by more than 1%.

LIPID

Percent lipid was determined by the Soxhlet method (Association of Official Analytical Chemists 1975) using ether as a solvent. Mean percent lipid was computed from duplicate samples of dried tissue. A third replicate was performed if the difference between the duplicates was greater than 1% and the mean percent lipid was then computed using the two values which differed by less than 1%.

CALORIMETRY

The fresh subsamples of gonad and soma were dried in an oven at 100°C for two days and then ground to a fine powder using either a mortar and pestle or a ball mill grinder. All subsamples were stored in a desiccator until bombed. Ten subsamples of soma and ten subsamples of gonad of each sex were bombed in duplicate with a Parr adiabatic calorimeter. All energy values were corrected for the heat of fuse wire combustion and for the heat of acid formation. An additional test was performed if the first two tests differed by more than 126 joules g⁻¹. All tests were done within 30 days of procuring a sample in order to avoid possible inaccuracies due to tissue oxidation.

RESULTS

CONDITION INDICES

The sample number, date, location and the number of specimens processed of each sample are listed in Table 1. The measurements of length and weight of each specimen are listed in Appendix l.

The mean body condition index, C, is defined as (1) $C = W \times 10^6/L^3$, where W is body weight in grams and L is the length in millimeters. The mean C of each sex of each sample is shown in Table 2. T-tests revealed that, except for the sample taken on October 25, there are no significant differences between the mean C's of the two sexes. The means of the sexes were combined and are shown in Fig. 2A. There is a decrease in mean C over the winter and spring followed by an increase over the summer months to a peak in December. The sudden drop in mean C at the time of spawning was calculated by subtracting the mean gonad weight at spawning from the mean body weight at spawning. The post-spawning mean C was calculated as 6.60 for a wide range of body weights. The dotted line was drawn by eye.

The monthly gonad condition index I, defined as (2) $I = W_{gonad}/W,$

is shown in Fig. 2B and 2C. The ovaries appear to increase in condition throughout the winter and spring whereas the testes appear to remain constant or even to decrease in condition over the same period. The testes grow rapidly over the summer and reach their maximum condition in October. The ovaries grow at a slower rate, reaching their maximum condition immediately before spawning.

Table 1. List of dates and locations of the herring samples analyzed.

Sample number	Date	Area	Number of fish measured	Number for lipid and water	Number for calorimetry
1	Mar. l	Placentia Bay	36	22	0
2	Mar. 31		26	24	12
3	Apr. 29	St. Mary's Bay	36	0	14
4	May 18	St. Mary's Bay	28	23	19
5	June 3	St. Mary's Bay	26	23	22
6	Aug. 12		23	17	17
7	Oct. 25		45	20	20
8	Dec. 20	St. Mary's Bay	24	21	18
9	Jan. 17		24	0	0
10	Feb. 6	St. Mary's Bay	24	20	0
		Total	292	170	122

Table 2. The mean body condition index (\pm 1 s.d.) of each sex of each sample. The bracketed number is the sample size. NS means there is no significant difference between the means and S means there is a significant difference.

Sample	M-3-	D. 1	
Date	Male	Female	
Mar. 1, 1977	8.88 ± 0.94 (14)	8.69 ± 0.55 (22)	NS
Mar. 31, 1977	8.27 ± 0.62 (12)	8.57 ± 0.46 (13)	NS
Apr. 29, 1977	7.80 ± 0.31 (17)		NS
May 18, 1977	7.67 ± 0.68 (12)	7.92 ± 0.66 (16)	NS
June 3, 1977	7.96 ± 0.39 (12)	7.78 ± 0.74 (13)	NS
Aug. 12, 1977	7.66 ± 0.49 (14)	7.46 ± 0.41 (9)	NS
Oct. 25, 1977	8.23 ± 0.39 (21)	7.69 ± 0.41 (24)	(P < 0.01)
Dec. 20, 1977	8.56 ± 0.68 (12)	8.20 ± 0.37 (12)	NS
Jan. 17, 1978	8.47 ± 0.53 (12)		NS
Feb. 6, 1978	7.80 ± 0.54 (12)		NS

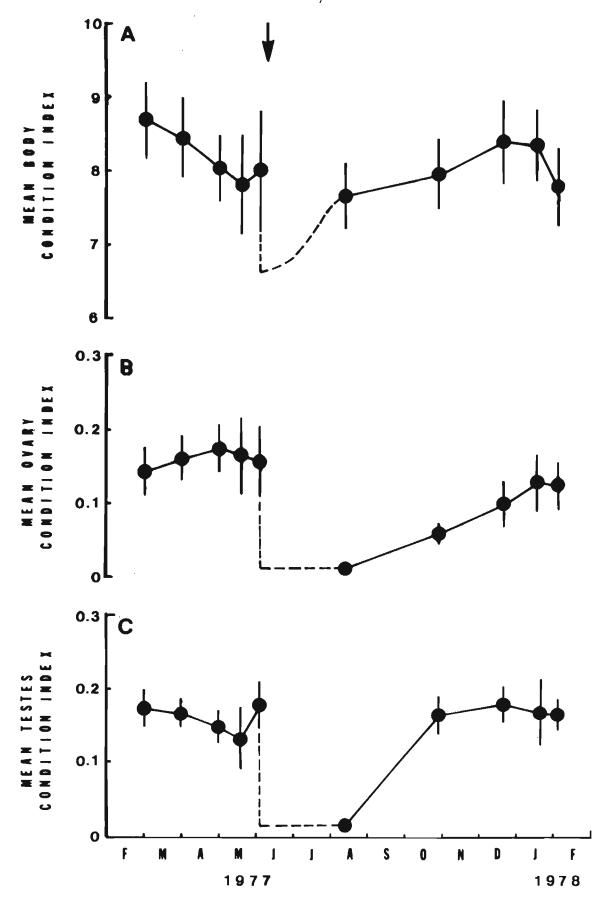


Fig. 2. Annual cycle of: A. mean (\pm 1 s.d.) body condition of the combined data of both sexes; B. mean (\pm 1 s.d.) ovary condition index and C. mean (\pm 1 s.d.) testes condition index. The arrow indicates mean time of spawning.

In order to determine if there is any variation of condition index with age the mean condition indices of each sample were separated into age classes as is shown in Tables 3, 4 and 5. Immatures were not included in these tables. Examination of the tables shows that there is a possible positive correlation between the condition indices and age. In order to test this an index, D, of the deviation of the monthly means at age from the monthly mean for the entire sample, \overline{C} , was first calculated. It is defined as

 $D_{i} = (j(C_{ij} - C_{j})n_{ij})/jn_{ij}$

where n is the sample size of the monthly mean at age, i is age and j is the sample number. The D of the body condition index is significantly correlated with age $(r=0.83;\ 0.01 < P < 0.05)$ as is that of the ovaries $(r=0.97;\ P > 0.01)$. The D of the testes is not correlated with age $(r=0.011;\ P < 0.05)$. The scatter of the points is shown in Fig. 3A, 3B and 3C. A regression of D on age was calculated for the body and the ovary respectively.

body: (4a) D = 0.0660 (Age) -0.5105; $R^2 = 0.70$ ovary: (4b) D = 0.0094 (Age) -0.0835; $R^2 = 0.95$

LIPID AND WATER

The percent lipid and percent water of each compartment, based on the net weight of the compartment, of each specimen analyzed are listed in Appendix 2. T-tests revealed that there were no significant differences (P > 0.05) between the percentages of lipid and water of the soma of the males and that of the females at any time of the year. The two sets of data were therefore pooled. The annual cycles of mean (t 1 s.d.) percent water and mean (± 1 s.d.) percent lipid of the soma, the ovaries and the testes are shown in Fig. and 5. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The percent water of all these compartments increased over the winter and spring to a maximum immediately before spawning. The percent water of the soma was at a minimum in mid-summer and gradually increased over the fall and early winter, whereas the percent water of both the ovary and the testes steadily decreased from a peak in October. The percent lipid of the soma, ovary and testes followed a pattern that is essentially the opposite of that of the percent water.

Table 3. Mean monthly body condition index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in the calculation of the mean. See text for explanation of D.

Month	3	4	5	6	7	8	9	10	11+	Mean ± 1 s.c.
Feb.	-	-	8.65 (7)	-	8.85 (1)	8.45 (4)	8.48 (10)	-	8.92 (13)	8.68 ± 0.53 (35)
March	-	_	8.13 (7)	8.86 (1)	_	8.27	8.71	8.25 (3)	8.64	8.43 ± 0.54 (26)
April	-	-	-	-	-	7.96 (11)	8.02 (18)	- -	8.22	8.03 ± 0.44 (35)
May	-	-	7.51 (3)	6.73 (1)	7.45 (3)	7.99 (5)	7.83	8.18 (1)	8.08 (6)	7.81 ± 0.67 (28)
June	-	8.30 (1)			8.09 (1)	7.90 (11)	7.66 (9)	-	8.14	7.98 ± 0.83 (25)
July	~	-	-	-	_	_	_	_	-	-
Aug.	-	-	-	-	-	7.59 (4)	7.72 (11)	7.42 (1)	7.38 (7)	7.64 ± 0.45 (23)
Sept.	_	-	_	_	-	_	_	_	_	_
oct.	-	-	-	-	-	8.57 (3)	7.92 (29)	7.78 (2)	7.86 (11)	7.94 ± 0.48 (45)
lov.	_	-	-	-	_	_	_	_	_	_
Dec.	-	-	8.32 (2)	-	-	-	8.35 (6)	-	8.40 (16)	8.38 ± 0.57 (24)
Jan.	~	8.06 (8)	7.85 (1)	8.45 (6)	-	-	-	-	8.54	8.33 ± 0.49 (24)
Peb.	-	7.56 (3)	7.32 (4)	7.65	8.27	-	-	7.87 (10)	8.05	7.77 ± 0.53 (24)
	_	-0.206	-0.234	-0.017	-0.050	-0.015	-0.025	0.017	0.405	

Table 4. Mean monthly ovary index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in calculating the mean. See text for explanation of D.

Month	3	4	5	6	7	8	9	10	11+	Mean ± 1s.d.
Feb.	-	-	0.1003 (5)	-	0.1546 (1)	0.0976 (1)	0.1524 (6)	-	0.1640	0.1429 ± 0.0331 (22)
March	-	-	0.1252	0.1664 (1)	-	0.1728	0.1697 (6)	0.1592 (1)	0.2040	0.1612 ± 0.0303 (13)
April	-	-	-	-	-	0.1491 (5)	0.1790	-	0.2007	0.1743 ± 0.0315 (18)
May	-	-	0.1108 (2)	0.0464 (1)	0.1434 (2)	0.1988	0.2066	0.2088 (1)	0.1722 (5)	0.1656 ± 0.0504 (16)
June	-	0.0745	_	-	_	0.1722	0.1513	-	0.1755	0.1559 ± 0.0484 (12)
July	_	_	_	_	_	-	-	_	-	-
Aug.a	-	-	-	-	-	0.0136 (3)	0.0123	0.0145 (1)	0.0150 (1)	0.0133 ± 0.0021 (9)
Sept.	_	_	_	_	_	_	_	_	_	_
Oct.	-	-	-	-	-	-	0.0607 (15)	0.0592 (2)	0.0605 (7)	0.0605 ± 0.0128 (24)
Nov.	_	_	_	-	_	_	-	_	_	_
Dec.	-	-	-	-	-	-	0.1046 (2)	_	0.0979 (10)	0.0990 ± 0.0296 (12)
Jan.	-	0.0901 (2)	0.0886 (1)	0.1291 (4)	-	-		_	0.1498	0.1279 ± 0.0391 (12)
Feb.	-	0.0623	0.1113	-	0.1072	_	-	0.1378 (4)	0.1453	0.1238 ± 0.0310 (12)
D		-0.0546	-0.0362	-0.0208	-0.0136	-0.0073	0.0059	0.0106	0.0119	

a. Probably sexed incorrectly and so represents mean value for both sexes

Table 5. Mean monthly testes index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in the calculation of the mean. See text for explanation of D.

				_	_					
Month	3	4	5	6	77	8	9	10	11+	Mean ± 1s.d.
Feb.	-	-	0.1381 (3)	-	~	0.1711 (2)	0.1778	-	0.1929	0.1723 ± 0.0252 (13)
March	-	-	0.1615	-	_	0.1571	0.1736 (2)	0.1809 (2)	0.1683	0.1664 ± 0.0181 (13)
April	-	_		_	-	0.1542	0.1394	-	0.1553	0.1474 ± 0.0225 (17)
May	-	-	0.1187 (1)	-	0.0541 (1)	0.1421 (4)	0.1453 (5)	~	0.1092 (1)	0.1314 ± 0.0422 (12)
June	-	-		-	0.1486 (1)	0.1806 (6)	0.1927 (4)	_	0.1181 (1)	0.1768 ± 0.0313 (12)
July	_	_	_		_		, <u> </u>	_	`	` <u> </u>
Aug.a	-	_	_	-	_	0.0405 (1)	0.0148 (7)	-	0.0143 (6)	0.0164 ± 0.0079 (14)
Sept.	-	_	_	-	-	-	_	_	· - ·	_
Oct.	-	-	-	-	-	0.1830 (3)	0.1602 (14)	-	0.1694 (4)	0.1640 ± 0.0270 (21)
Nov.		_	-	-	-	-	_	_	_	-
Dec.		-	0.1501 (2)	-	-	-	0.1796 (4)	-	0.1881 (6)	0.1789 ± 0.0245 (12)
Jan.	-	0.1333 (6)	_	0.2067 (2)	-	~	-	-	0.1987	0.1673 ± 0.0459 (12)
Feb.	-	0.1521 (2)	0.1609	0.1663 (2)	-	-	-	0.1674 (6)	0.1785	0.1651 ± 0.0206 (12)
D	-	-0.0288	-0.0179	0.0203	-0.0528	0.0063	0.0031	0.0054	0.0109	

a. Probably sexed incorrectly and so represents a mean value for both sexes.

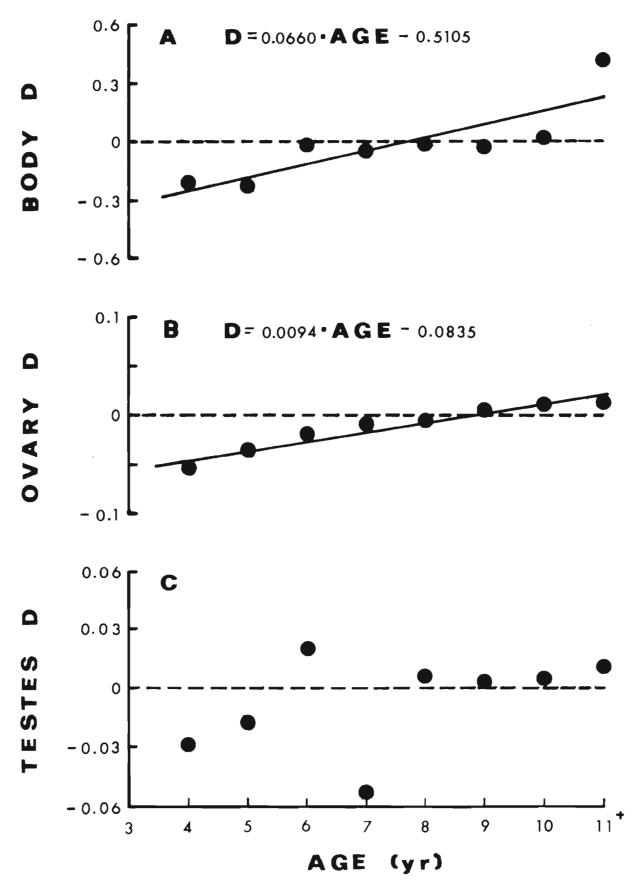


Fig. 3. The relationship between D and age for: Λ , the body; B, the ovary and C, the testes.

In order to determine if the percent lipid of the soma varies with body length the data on percent lipid of each sample was grouped into length classes and a mean value for each length class calculated as is shown in Table 6. Examination of Table 6 shows that there is no apparent trend of percent lipid of the soma with length.

Examination of the percent lipid and percent water of the compartments of individual specimens suggest that lipid and water make up a constant percent of the wet weight of a compartment. The mean (\pm 1 s.d.) combined percent is 80.21 \pm 0.99% for the soma, 75.89 \pm 2.84% for the testes and 68.10 ± 3.29% for the ovaries. Correlation analysis revealed that the percent lipid of the soma is highly negatively correlated with the percent water (r = -0.98; P < 0.01), as are the percent lipid and percent water of the testes (r = -0.70; P < 0.01). The percent lipid of the ovaries, however, is not significantly correlated with the percent water (r = 0.24; P > 0.05). This means that it is possible to use percent water as a prediction of percent lipid for the soma and the testes. The ovaries have a mean (t 1 s.d.) percent lipid of 1.23 ± 0.33% at all times of the year. Percent lipid was linearly regressed on percent water for the soma and the testes and the following equations were obtained

(Fig. 6) soma:

(5a) % lipid = 86.71 - 1.095 (% water), Testes:

(5b) % lipid = 13.81 - 0.150 (% water).

ENERGY DENSITY

The energy densities (kj · g⁻¹ wet weight) of each compartment of each specimen are listed in Appendix 3. T-tests revealed that there is no difference between the mean energy densities of the soma of males and those of the soma of females for any sample and so the two sets of data were pooled. The annual cycle of mean energy densities of the three compartments are shown in Fig. 7.

In order to determine the energy conversion factors for lipid and solid the percentages were converted to weights and the energy densities to total energies by multiplying the percentages by the wet weight of the tissue. Solid is defined as the tissue residue left after extraction of lipid and water. Then total energy was regressed on the weight of lipid and the weight of solid to obtain the following equations for the soma, the testes and the ovaries respectively:

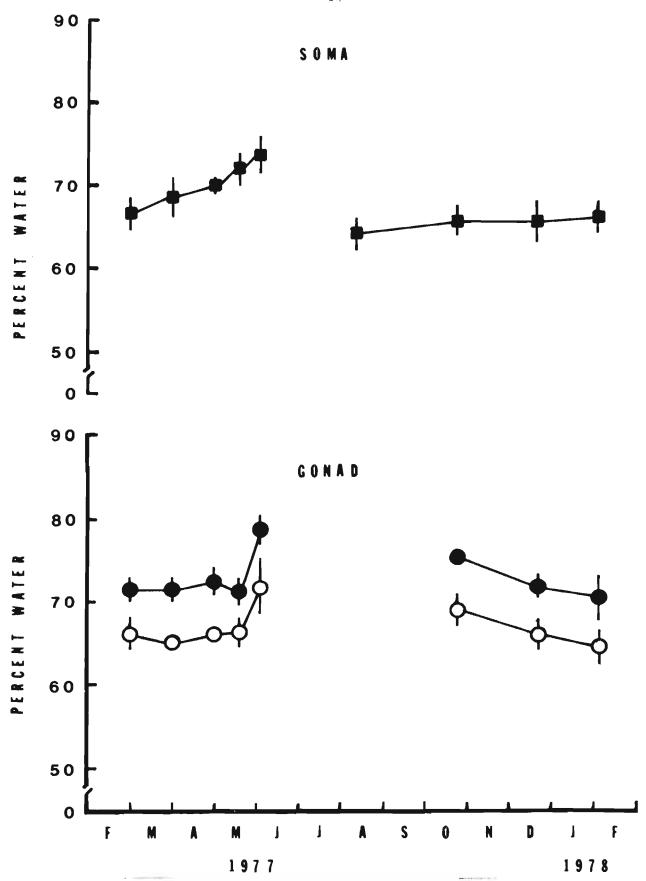


Fig. 4. The mean (\pm 1 s.d.) percent water of the soma of the combined sexes and of the gonads. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The open circles are females, the closed circles are males and the squares are pooled males and females.

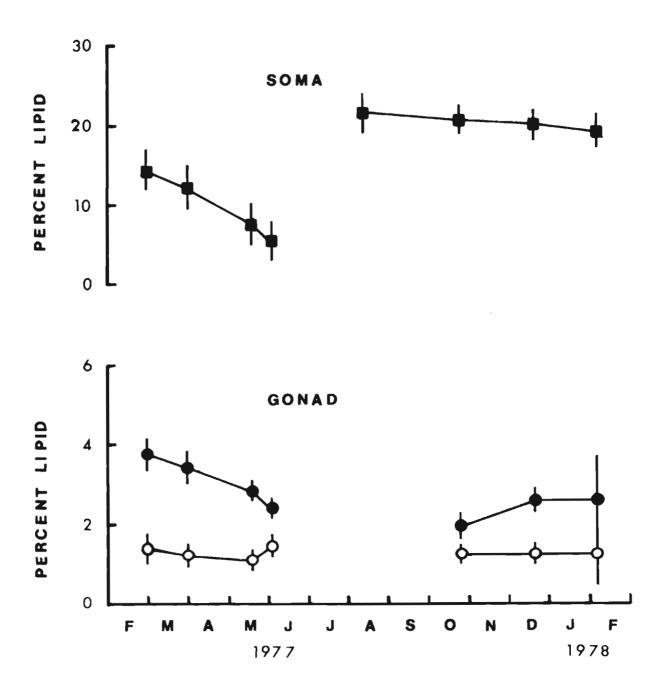


Fig. 5. The mean (\pm 1 s.d.) percent lipid of the soma of the combined sexes and of the gonads. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The open circles are females, the closed circles are males and the squares are pooled males and females.

Table 6. The mean percent lipid of the soma of the combined sexes separated into length classes for each sample. The number of specimens is in parentheses.

Sample Number	29.1- 30.0	30.1- 31.0	31.1- 32.0	32.1- 33.0	33.1- 34.0	34.1- 35.0	35.1- 36.0	36.1- 37.0	47.1- 38.0
1	_			_	_				
2	-	-	-	16.94 (2)	13.88 (6)	15.14 (8)	12.50 (5)	16.41 (1)	-
3	-	-	-	13.00	12.36 (9)	10.96	13.57	14.18	-
4	_	_	_		_		_		_
5	-	-	8.26 (3)	5.66 (5)	5.61 (4)	8.05 (6)	9.41 (3)	7.43 (2)	_
6	7.48 (1)	-	3.70 (1)	6.22 (5)	5.20 (8)	5.39 (5)	6.17 (3)	_	_
7	-	-	_	-	16.66 (8)	16.03	16.67 (5)	16.58 (1)	_
8	-	-		15.27 (2)	14.88	16.02	16.13	17.00	_
9	-	-	_	15.88	15.94	14.32	14.65	15.36 (4)	-
10	_	-	_	-	_	-	_	-	_
11	-	16.34	13.45	14.65 (2)	15.00 (5)	13.98 (4)	12.89	10.76	17.22 (1)

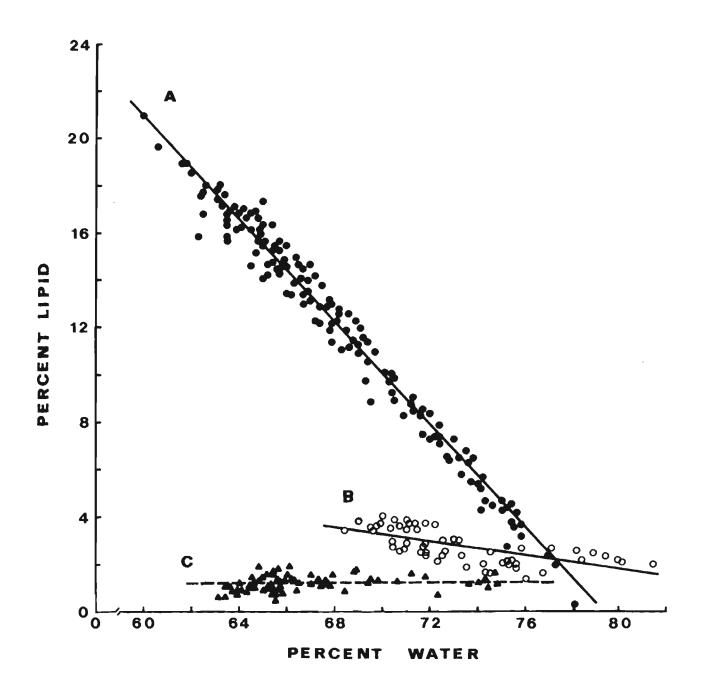


Fig. 6. The relationship between the percent lipid and the percent water of: A, the soma of the combined sexes; B, the testes and C, the ovaries. The regression equation for A is: % lipid = 86.710 - 1.095 (% water); r = -0.98; $R^2 = 0.97$; n = 140. The regression equation for B is: % lipid = 13.81 - 0.150 (% water); r = -0.70; $R^2 = 0.49$; n = 59. The dashed line, C, is the mean percent lipid of the ovaries. The sample size of C is 69.

soma: Energy = 50.48 + 38.80 (lipid) + 20.30 (solid) (6a) testes: Energy = -1.45 + 20.59 (lipid) + 22.07 (solid) (6b) ovaries: Energy = -5.80 + 18.13 (lipid) + 25.19 (solid) (6c) The equations are significantly different from each other (t-test, P < 0.001). The equation for somatic energy, (6a), was found to be not significantly different (t-test, P > 0.1) from the equation, (7) Energy = 39.75 (lipid) + 20.92 (solid). The coefficients in equation (7) are those commonly used in the ecological literature (1 g lipid = 9500 cal = 39.75 kj; 1 g solid = 5000 cal = 20.92 kj) (Beamish et al. 1975). However, both equations (6b) and (6c) are significantly different from equation (7) (P < 0.001). The use of equations (6b) and (6c) introduces a 4.42% and an 11.79% error, respectively, in the estimation of total energy.

The energy density of a tissue can be estimated by determining the percent water content and then by substituting that value into equations (5) and (6). The calculations can be simplified by deriving one expression for the dependence of energy density on percent water. Energy density was regressed on percent water to obtain the following equations for the soma, the testes and the ovaries respectively:

soma:

- (8a) Energy density = 36.17 0.400 (% water) testes:
- (8b) Energy density = 24.08 0.248 (% water) ovary:
- (8c) Energy density = 25.52 0.260 (% water)
 The slopes and the elevations of all three lines are significantly different from each other (t-test, P < 0.001). The lines are shown in Fig. 8. Kitchell et al. (1977) derived a linear regression between energy density and percent water using data from the literature and their line is presented for comparison.

DISCUSSION

There is a continuous decrease in the body condition index and the somatic energy density of the Atlantic herring throughout the winter and spring. If one assumes, as did Winters (1977), that overwintering herring of the Newfoundland area feed negligibly or not at

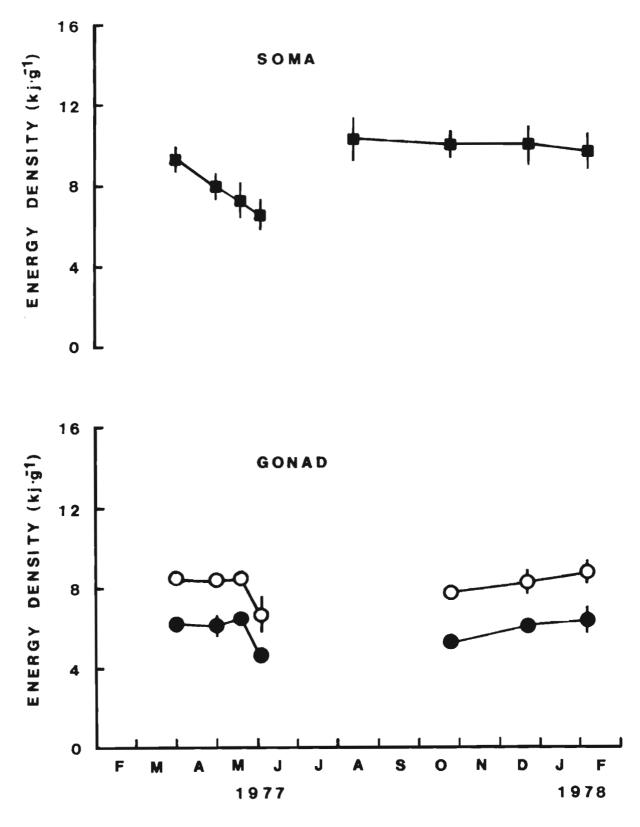


Fig. 7. The annual cycle of the mean (\pm 1 s.d.) energy density of the soma, the testes and the ovaries. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The open circles are females, the closed circles are males and the squares are pooled males and females.

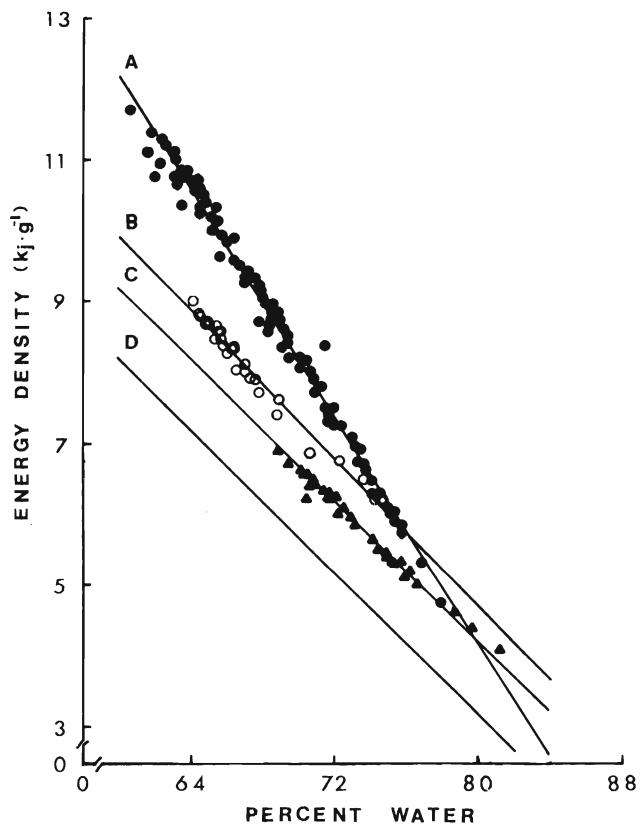


Fig. 8. The relationship between the energy density and the percent water of: A, the soma of the combined sexes; B, the ovaries and C, the testes. The line from Kitchell et al. (1977), D, is presented for comparison. The regression equation of A, B and C are, respectively: Energy Density = 36.172 - 0.400 (% water); r = -0.99; $R^2 = 0.99$, n = 121. Energy Density = 25.522 - 0.260 (% water); r = -0.99; $R^2 = 0.99$, n = 43. Energy Density = 24.082 - 0.248 (% water); r = -0.99; $R^2 = 0.98$; n = 48.

all then this loss of body weight and somatic energy density represents energy expended in metabolism. Making this assumption Winters (1977) calculated a mean overwintering metabolic rate of Atlantic herring.

The significantly higher mean body condition index of the males compared to that of the females of the October 25 sample is most probably the result of the fact that the testes grow faster than the ovaries (Table 2 and Fig. 2B and 2C). This sexual difference in the scheduling of gonad growth is a phenomenon that has also been observed in North Sea herring (Iles 1964). be speculated that the testes begin growth sooner than the ovary because the male has a higher total body energy content than the female after spawning. The testes, being approximately half as energy rich as the ovaries would represent less of an energy drain to the prespawning male than the ovaries do to a pre-spawning fe-This implies that a threshold of body energy exists above which gonad growth is possible but below which gonad growth is suppressed. One piece of supporting evidence for this hypothesis is the observation by Wilkins (1967) that juvenile Atlantic herring that had been starved for four months in captivity did not undergo sexual maturation, whereas their wild counterparts had begun to mature sexually during that period.

There is a large body of data on the seasonal cycle of the percent lipid and the percent water of the flesh and the gonads of many species of fish. Herring have been particularly well studied in this respect (reviewed by McBride et al. 1959; Leim 1957; Stoddard 1967, 1968; Hodder et al. 1973; Ackman and Eaton 1976; Varga et al. 1977). There is general agreement among the aforementioned that the percent lipid of the herring tissue varies seasonally depending upon the amount of food available and upon the state of maturation of the gonads. There is also agreement that the percent lipid and the percent water of the flesh vary inversely with each other and that the percent solid varies little with season.

Hodder et al. (1973) found no correlation between the percent lipid and the length of the fish, which is in agreement with this study (Table 6). They did, however, find that, on the average, females have a 5% higher absolute lipid content than males over the entire range of the lipid content values. It was not tested to determine if there is a statistically significant difference. No significant differences in percent lipid and percent water between sexes were found in this study. Perhaps the 5% difference is related to the sampling method, Hodder et al. (1973) performed whole body analysis while this study considers the body as three separate compartments.

The reported seasonal cycle of percent lipid of Hodder et al. (1973) is virtually identical to that reported here (Fig. 5); a maximum of approximately 15% in January and a minimum of approximately 6% in June, immediately after spawning. They also reported that the lipid/water relationship did not appear to be strictly linear and so fitted the data with a second degree polynomial regression. Since equation (5a) has a very high correlation coefficient (r = -0.98) (Fig. 6) and it explains 98% of the variance of the data it is not considered necessary to attempt to improve the fit by using

polynomial regression.

The energy density of a tissue can be determined directly by bomb calorimetry or indirectly by conversion of the weights of lipid and solid to energy units with standard energy density factors. The energy density of lipid is commonly reported as $38.91 - 39.75 \text{ kj} \cdot \text{g}^{-1}$ (Beamish et al. 1975). However, Niimi (1972, referenced in Beamish et al. 1975) reports a value of $35.56 \text{ kj} \cdot \text{g}^{-1}$ which suggests that the value should be revised or at least reexamined. Also, since solids can consist of differing proportions of protein (23.64 kj \cdot g⁻¹), carbohydrate (16.74 kj \cdot g⁻¹) and ash the energy density coefficient of solid of 20.92 kj \cdot q^{-1} can serve only as a mean value. These standard factors are appropriate for determining the energy content of herring soma but introduce error if used to determine that of the gonads. This is likely due to the difference in the proportions of protein and other solids in the soma and the gonads.

The significant differences between equations (8a), (8b) and (8c) can be explained as due to the differing proportions of lipid, water and solid found in the soma and the gonads. The close fit of these equations (R^2 = 0.99) indicates that they can be used to calculate the energy density of a body compartment with high accuracy. Their use would greatly simplify the task of monitoring the energy content of a herring population should such a program be initiated. The greatest source of inaccuracy in the estimates of energy content would lie in the estimation of the compartment weights.

Kitchell et al. (1977) proposed the following relationship between the energy density and the percent water of fish flesh:

Energy density = 23.17 - 0.25 (% water). The slope of the regression is almost indistinguishable from that of equations (8b) and (8c) but is quite different from equation (8a), (Fig. 8). Both (8b) and (8c) have a higher elevation than Kitchell's regression and this is almost certainly due to the fact that many of Kitchell's samples were whole-body samples which include bone. This would tend to lower the energy density of a

sample and therefore lower the elevation of Kitchell's regression. The reason for the higher slope of equation (8a), 0.400 as compared to 0.25, lies in the life-history of the herring. It must store large amounts of energy in the form of lipid in its musculature in order to survive long periods of nonfeeding. Therefore the seasonal change in the energy density of the herring soma is greater than most fish, especially if one considers tropical fish such as tuna as did Kitchell et al. (1977).

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APPENDIX 1: Lengths and Weights of Samples

Sample number	Length (cm)	Weight (g)	Sex ¹	Age	Mat. stage	Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
1-002 1-003 1-004 1-006 1-007 1-010 1-010 1-011 1-012 1-013 1-015 1-016 1-017 1-018 1-019 1-021 1-023 1-023 1-023 1-023 1-033 1-033 1-033 1-033 1-033 1-033 1-033 1-033 1-033 1-033 1-044 1-044 1-045 1-045 1-045	31333333333333333333333333333333333333	32738.80.59.50.00.50.00.00.00.00.00.00.00.00.00.00.	1 2 1 2 2 1 1 1 2 2 2 2 1 1 1 2 2 1 1 2 2 1 1 2 2 1 1 2 2 1 1 2 2 1 1 2 2 1 1 2 2 1 1 1 2 2 1 1 2 2 1 1 1 2 2 1 1 2 2 1 1 1 2 2 1 1 1 2 2 1 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 1 2 1 1 1 2 1 1 1 2 1	11119	444411444444444444444444444444444444444	836607800641815240192011774695553542556 730 63295007800641815240192011777469555334584 8499 63725742547543484265855011777469555334584 8499			
2-005 2-006 2-007 2-008 2-009	32.2 33.8 35.4 34.2	307.2 330.0 393.4 353.8	1 2 2 2	8 9 11 7	4 4 4 4	57.9 62.0 54.7	- - - -	- - - -	- - - -

 $¹_1 = male; 2 = female$

Sample number		Weight (g)	Sex	Age	Mat. stage	Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
2-010 2-011 2-012 2-013 2-014 2-015 2-016 2-017 2-018 2-019 2-020 2-021 2-022 2-023 2-024 2-026 2-027 2-028 2-029 2-030 2-031 2-032 2-033 2-034 2-035 2-037 2-038 2-039	334.59 34.59 354.6.59 354.6.59 354.6.59 354.6.6.79 354.6.6.79 356.6.888 356.6.79 356.6.79 356.6.79 356.6.79 356.6.888 357.6.6.79 357.6.888 357.6.6.79 357.6.888 357.6.6.79 357.6.888 357.6.6.79 357.6.888 357.6.6.79 357.6.888 357.6.688 357.6.688 357.6.688 357.6.688 357.6.688 357.6888 357.6	305.5 305.2 305.2 305.2 305.2 392.7 305.2	1 2 1 1 1 1 2 2 1 2 2 1 2 2 1 2 2 1 2 2 1 2 1 2 1 2 2 1 2 2 1 2 1 2 2 1 2 2 1 2 2 1 2 2 1 2 2 1 2 2 2 1 2 2 2 2 1 2 2 2 2 2 1 2	95911891159991119511185 11185 11185	***************************************	51.30 51.30 51.30 51.32 51.30 51.32 51			
3-001 3-002 3-003 3-004 3-005 3-006 3-007 3-010 3-012 3-020 3-021 3-026 3-027 3-028 3-029 3-030	34.2 32.7 36.1 34.0 33.2 33.3 35.3 32.8 33.3 32.8 33.0 35.0 35.0 34.4 33.6	332.3 298.7 408.8 375.0 298.7 360.8 3071.6 359.1 278.9 304.2 299.3 304.1 385.7 312.9 329.0 297.1	1 1 2 2 1 1 1 2 2 2 1 2 1 2 1 2 1 1 2 1	9 5 11 9 8 11 5 8 9 5 8 5 10 10 9 11 10 8	444444444444444444444444444444444444444	64.3 47.4 83.4 726.1 67.2 64.7 65.1 534.6 60.5 61.0 62.1 40.0			

Sample number	Length (cm)	Weight (g)	Sex	Age		Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
3-031 3-032 3-033 3-034 3-036 3-038 3-039 3-040	34.8 34.0 33.4 34.0 34.6 34.8 34.3 32.7	350.0 330.2 285.5 334.2 357.8 373.2 311.9 285.4	1 2 1 2 2 2 2 1	9 9 5 9 6 5 5	4 4 4 4 4 4 4 4	53.8 39.8 49.6 55.7 61.2 62.1 33.3 44.0	- - - - -	- - - - - -	-
4-034 4-035 4-036 4-037 4-038 4-040	33333333333333333333333333333333333333	310.0 340.3 328.2 280.4 310.0 328.2 280.4 310.0 375.2 310.0 375.2 3721.8 3755.2 3721.8 3755.2 37321.9 3755.2 37321.9 3755.3	1 2 2 2 1 1 2 2 2 2 1 1 2 1 2 1 1 1 1 1	8 9 1 1 9 9 8 9 9 8 8 1 1 9 8 9 8 8 9 9 9 1 1 1 1		0.6.2.1.0.7.7.0.4.2.7.0.7.7.8.2.5.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.5.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.9.3.4.2.2.8.1.8.2.4.4.9.3.3.3.5.0.6.2.2.8.1.8.2.4.4.9.3.3.3.4.2.2.8.1.8.2.4.4.9.3.3.3.4.2.2.8.1.8.2.4.4.9.3.3.3.4.2.2.8.1.8.2.4.4.9.3.3.3.4.2.2.8.1.8.2.4.4.9.3.3.3.4.2.2.8.1.8.2.4.4.9.3.3.3.4.2.2.8.1.2.2.8.1.2.2.2.2.2.2.2.2.2.2.2.2		- 0289809529320469180085374519102 - 264.89809529320469180085374519102	- 1 14.1 17.6 13.8 16.3 13.6 10.8 11.9 10.8 11.4 13.6 11.7 12.8 11.7 12.8 12.9 10.6 11.1 11.1 11.1
5-001	34.9	306.4	1	9	4	40.3	3.32	25.2	19.8

Sample number		Weight (g)	Sex	Age		Gonad wt.(g)			Back wt.(g)
5-002 5-004 5-006 5-007 5-007 5-001 5-012 5-013 5-018 5-018 5-022 5-022 5-023 5-033 5-	354.92.76.94.00.91.084.99.54.95.34.85.00 354.92.76.94.00.91.084.99.54.95.34.85.00	369.4 361.0 382.4 283.4 301.6 30	2 2 2 1 1 2 2 2 2 1 1 2 2 2 2 2 1 1 1 2	11 8 11 9 8 9 11 7 5 9 7 11 8 9 5 10 8 7 6 9 9 9 11 5 8 11 5 8 7 6 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9	444444444444444444444444444444444444444	65.1 71.8 74.4 30.1 36.7 62.1 53.1 21.5 72.2 55.1 53.5 72.5 83.6 93.6 93.6 93.6 93.6 93.6 93.6 93.6 9	6.4653 6.	26.4 27.4 29.4 29.4 23.8 27.9 21.0 21.8 25.7 21.9 21.0 21.8 22.2 21.0 21.0 21.0 21.0 21.0 21.0 21.0	22.9 18.9 18.2 14.0 15.0 16.5 17.1 13.5 12.5 10.1 13.6 13.6 13.6 13.6 13.6 13.6 14.6 12.7 14.0 17.9
6-001 6-002 6-003 6-004 6-005 6-007 6-008 6-009 6-010 6-011 6-013 6-014 6-015 6-017 6-018 6-019	33.0 33.6 33.6 33.3	265.0 316.0 331.0 268.0 325.0 275.0 277 276 322 279 268 401 316 330 363 302 260 311 309	2 1 1 2 1 2 1 1 2 1 2 1 2 1 2 1 2 1 2 2 1 2 2 1 2	8 8 9 9 9 8 8 9 9 9 3 1 1 1 1 1 9 7 8 9 9 7 8 9	555655555566566556	470.858.2064.7954.07468.85 759.82064.7954.0746.85 748.3553.9946.95.468.85 933745.82.3643.5	3.91 2.26 3.06 4.62 3.08 4.51 2.91 3.92 2.15 53.81 53.67 3.63	22.0 26.0 25.0 24.0 27.0 24 27 23 16 31 28 24 28 26 19 24	12.0 12.0 14.5 12.5 13.0 10.0 9 13 11 9 7 12 10 9 12 13 8 10 12

Sample number		Weight (g)	Sex	Age	Mat. stage	Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
6-020 6-022 6-023 6-024 6-025 6-026	32.9 32.1 32.7 33.8 32.0 30.9	249 263 325 311 264 245	2 1 2 1 1 2	8 8 8 8 4	6 5 5 5 5 5	33.5 42.8 67.5 55.2 48.1 18.3	2.87 2.86 3.10 2.58 3.38 5.72	23 22 25 24 23 18	11 8 9 10 11
7-002 7-003 7-005 7-006 7-007 7-010 7-011 7-012 7-013 7-014 7-016 7-017 7-018 7-019 7-020 7-021 7-023 7-024 7-025 7-028	36.4 36.4 37.8 37.8 37.8 37.1 37.8 37.1 37.8 37.1 37.8 37.1	335.2 326.5 262.6 320.0 329.4 313.3 292.6 311.3 300.0 321.0 271.4 340.4 318.3 279.6 315.1 335.6 309.7 309.7 309.7 309.8 296.2 334.1 301.3	1 1 2 1 1 2 1 2 1 2 1 2 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 2 1 1 1 1 2 1 1 1 1 2 1 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 1 2 2 1 2 1 2 1 2 1 2 1 1 2 1 2 1 2 1 2 1 2 1 2 1 2 1 2 1 2 1 2 2 1 2 2 1 2 2 1 2 2 1 2 1 2 2 1 2 1 2 2 1 2 2 1 2 2 1 2 2 1 2 2 2 1 2	11 11 8 8 11 9 9 8 9 9 11 10 9 9 11 11 9	2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	4.5.2.5.0.8.0.5.6.1.5.6.2.1.6.5.6.1.7.2.0.2.8.5.1.4.3.6.4.6.3.4.3.5.4.4.3.3.5.2.4.4.4.4.4.4.4.4.4.4.4.4.4.4.4.4.4.4	564.48590222441262244490129 564.7556653553544665554	30.5 23.5 23.6 23.6 24.9 23.6 25.7 26.9 27.5 27.7 27.9 27.9 27.9 27.9 27.9 27.9 27.9	14.7 13.5 11.7 11.2 14.6 11.5 10.0 9.7 9.3 11.1 9.6 11.4 11.8 11.2 10.3 10.7
8-002 8-003 8-004 8-005 8-006 8-007 8-008 8-010 8-011 8-012 8-013 8-014 8-016 8-017 8-018 8-019 8-020	34.9 35.8 33.3 33.4 35.4 35.4 35.6 33.7 33.7 33.7 33.7 33.7 33.7 33.7 33	376.6 349.4 310.0 317.3 336.2 338.9 270.3 391.1 330.2 293.3 364.3 299.2 299.7 293.2 344.4 263.6 296.3	1 2 1 1 2 1 2 2 2 1 1 2 2 2 1 1 1 2 1	11 11 9 11 11 11 11 9 9 9 9 9 9	44444443443444444	68.8 28.9 40.7 65.7 24.9 47.1 17.2 21.3 13.1 61.8 23.5 12.2 19.3 39.1 48.3 38.2 17.8 53.9	2.97 6.38 3.69 1.80 7.46 7.38 7.50 5.70 5.72 2.83 3.48 1.93	29.3 28.8 24.8 24.8 25.9 28.5 27.5 27.5 27.5 27.6 31.7 27.5 24.7 25.0	12.5 11.9 10.1 9.1 12.1 12.1 11.7 11.7 11.7 11.4 13.6 10.8 11.3 11.9 11.2 9.9

Sample number		Weight (g)	Sex	Age	Mat. stage	Gonad wt.(g)	hiver wt.(g)	Head wt.(g)	Back wt.(g)
8-021 8-022 8-023 8-024 8-025 8-026 8-027 8-028 8-030 8-031 8-033 8-033 8-033 8-033 8-033 8-041 8-044 8-044 8-044	33.4.9.3.9.6.0.4.3.5.5.9.2.7.0.2.9.8.0.7.4.7.7.5.9.8.9.5.3.3.3.3.3.3.3.3.3.3.3.3.3.3.3.3.3.3	317.1 326.1 309.6 313.5 284.8 305.0 317.9 2725.1 32725.1 32725.1 3284.6 2911.6 292.1 282.1 282.1 282.2 312.2	1 1 2 1 2 1 1 2 2 2 1 1 1 2 2 2 1 1 2	9 9 9 9 9 9 9 9 9 9 9 9 9 11 9 9 9 9 9	44343444333444433443443333	57.9 57.9	1.89 3.01 1.91 1.92 1.92 1.42 1.42 1.42 1.42 1.42 1.43 1.43 1.43 1.43 1.43 1.43 1.43 1.43	24.4 226.4 226.6 236.5 236	9.4 10.4 10.1 9.8 11.9 11.4 10.7 11.0 9.9 10.6
9-001 9-002 9-003 9-004 9-005 9-006 9-007 9-010 9-011 9-012 9-013 9-014 9-015 9-017 9-018 9-019 9-020 9-021	33.9 35.7 35.0 36.2 36.3 36.4 35.1 35.0 35.6 35.7 35.7 37.3 37.3 37.3	315.5 383.7 308.5 392.2 3950.3 416.3 416.9 416.5 350.4 350.5	2 1 1 2 1 1 2 1 1 2 1 2 1 1 2 1 2 1 2 1	9 9 11 11 11 11 11 9 11 11 11 11 11 11	444444444444444444444444444444444444444	29.3 44.6 50.6 82.7 57.5 66.1 29.3 44.2 67.6 63.4 769.4 769.4 769.4 38.5 93.0 87.9	7.26 13.50 2.98 3.48 7.57 3.19 3.27 3.03 2.34 7.32 3.69 2.76 7.08 3.31 2.55 8.12 10.53 3.74 10.29	25.3 31.4 28.5 31.8 30.5 29.2 29.5 30.4 28.2 23.4 26.7 31.6 22.3 25.6 29.4 30.0 37.0 30.0	15.9 21.1 16.3 19.5 16.3 15.0 16.4 15.0 12.1 12.2 12.2 12.4 155.1 17.0 16.0 13.0 15.0

	Length (cm)		Sex	Age				Head wt.(g)	Back wt.(g)
9-022 9-023 9-024	34.8 35.4 35.5	355.5 372.6 372.0	2 2 2	11 11 11	4 4 1 ₁	35.5 57.5 46.5	8.39 6.48 8.49	27.0 29.7 26.8	11.8 13.9 14.7
10-001 10-002 10-003 10-004 10-005 10-006 10-009 10-010 10-011 10-012 10-013 10-014 10-015 10-016 10-017 10-018 10-019 10-020 10-021 10-023 10-024	33.6 35.6 35.6 37.6 37.6 31.1 31.7 31.6	390.1 314.6 378.2 313.9 481.1 258.9 2400.6 2463.2 3241.1 398.3 378.6 2463.2 3241.1 398.3 378.6 3	2 1 2 2 1 1 2 1 1 2 1 1 2 2 1 1 2 2 1 1 1 2 1	11 6 5 11 6 4 4 6 4 11 4 11 11 11 11 11 11 11 11 11 11 11	444444444444444444444444444444444444444	62.7 77.4 88.2 77.2 83.3 77.5 74.4 62.6 7.7 7.5 7.4 10.0 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 10.6 7.7 7.7 7.7 7.7 7.7 7.7 7.7 7.7 7.7 7	7.68 4.72 2.77 6.33 4.12 9.49 1.23 9.49 1.25 1.21	31.4 22.9 25.4 21.9 26.1 27.5 31.2 29.3 31.7 29.3 29.3 27.3 29.3 27.3 29.3 27.3 29.3 27.3 27.3 27.3 27.3 27.3 27.3 27.3 27	11.6 9.9 12.2 11.0 12.8 10.4 7.9 8.0 10.9 7.6 10.9 7.6 10.9 7.8 11.6 7.8 9.8 11.6 7.7 7.7
11-012 11-013 11-014 11-015 11-016 11-017 11-018 11-019	36.1 35.1 35.1 35.1 37.5 37.6 37.6 37.6 37.6 37.6 37.6 37.6 37.6	277.2 393.8 322.5 259.4 340.0 394.0 322.7 290.0 328.6 423.8 309.2 2267.5 307.2 228.2 348.5 358.9 264.1 216.9 320.9	2 2 1 1 1 2 2 1 2 1 2 1 2 1 2 1 2 1 2 1	5 11 10 10 10 10 5 10 11 6 5 10 11 6 7 10	444444444444444444444444444444444444444	21.1 59.8 29.4 29.5 60.5 31.7 52.9 31.6 41.6 42.5 53.2 44.1 42.5 53.2 44.1 42.5 63.3 44.1 42.5 63.3 44.1 43.3 63.3 63.3 63.3 63.3 63.3 63.3 63.3	5.69 8.12 3.47 8.37 6.50 8.97 1.98 7.70 8.97 1.98 7.88 7.88 7.98 8.44	28.1 25.6 19.8 29.0	10.0 14.1 12.0 10.0 13.0 12.2 12.0 12.0 9.9 14.3 10.6 9.7 11.0 7.2 11.3 11.6 10.3 9.1 10.0 14.2

						Gonad wt.(g)			
11-021 11-022 11-023 11-024	36.1 33.6	313.6 382.7 271.7 279.5	1 1	11 10	4	44.0 68.3 39.3 45.0	3.11 2.50	24.4	10.2 14.0 10.8 9.9

APPENDIX 2: Percent Lipid and Percent Water

Complo	%	Lipid		%	Water	
Sample number	soma	testes	ovary	soma	testes	ovary
2-001 2-004 2-005 2-006 2-008 2-009 2-010 2-011 2-012 2-013 2-014 2-015 2-016 2-017 2-018 2-019 2-020 2-021 2-022 2-023	12.57 11.53 13.55 17.13 15.34 14.07 13.27 16.85 15.72 17.42 14.71 9.08 12.82 14.96 16.94 14.96 16.91 16.75 12.29	3.57 -3.57 -3.75 3.89 3.68 3.74 -	1.03 0.89 - 0.86 1.24 - 1.01 1.20 - - 1.16 1.44 - 1.62 0.99 1.75 1.61	68.22 68.79 66.94 63.30 65.70 66.60 67.47 65.04 67.01 71.33 68.79 66.34 63.73 65.40 66.91 64.54 68.07	70.02 75.22 71.32 71.07 71.01 72.19 71.23 71.68	65.16 66.37 - 65.02 64.73 - 65.36 66.56 - - 67.73 63.96 - 65.15 64.74 65.37 65.37
3-001 3-002 3-003 3-004 3-005 3-006 3-007 3-008 3-010 3-012 3-020 3-021 3-026 3-027 3-028 3-029 3-031 3-032 3-033 3-034 3-038 3-039	11.02 16.29 14.18 12.91 11.42 10.11 14.71 12.59 15.28 15.45 8.80 14.54 13.80 8.47 5.70 6.46 12.77 15.03 11.30 13.88 11.99 12.94 13.15	3.51 2.55 - 3.52 3.65 3.06 - 3.91 - 3.55 - 3.60 3.48 3.63 3.03 - - -	1.12 0.86 - 0.95 1.19 1.10 - 1.95 0.99 - - - 1.60 - 1.21 1.12 1.95 1.29	69.68 64.90 67.18 67.98 67.39 68.61 65.16 65.16 65.17 67.52 71.29 74.18 73.15 66.42 67.43 69.42 67.49 66.43 67.49 66.43	70.37 74.54 - 71.00 70.72 72.52 - 70.52 - 70.35 - 69.47 71.38 69.75 73.20 - 71.79	64.44 64.32 - 64.99 64.58 64.60 65.57 - 67.00 64.73 64.48 64.81 65.70

	% Lipid			% Water	
soma	testes	ovary	soma	testes	ovary
11.61	2.92	_	69.18	71.78	-
-	-	-	71.71 68.54 71.69 69.19 68.41 71.45 70.67 70.14 68.90 71.01 71.12 69.07 69.53 70.85	71.47 - 71.66 72.23 - 72.60 - 71.92 76.28 71.65	65.47 66.25 66.37 - 65.47 65.56 - 66.36 65.64
8.95 8.37 9.75 11.26 5.21 3.84 6.36 9.70 9.86 4.60 10.60 5.51 7.36 9.99 	2.55 - 2.70 3.02 2.97 - 2.82 - - - - - - - - - - - -	1.42 1.11 0.97 - 0.81 - 1.07 1.52 1.08 0.77 - 0.52 0.73 - 1.01 - 1.53 1.41	70.48 72.34 68.96 73.48 75.86 75.86 75.49 76.16 71.42 73.46 71.42 73.46 73.46 71.76 71	71.79 70.86 70.50 71.01 - 71.67 70.87 71.64 75.85 69.91 70.55 70.17 68.92	65.59 65.67 64.11 - 65.78 65.62 64.94 67.42 65.35 - 65.51 65.52 65.26 - 65.01 71.76 69.48
6.28 3.24	2.22	1.59	73·55 75·83	79.83	65.99 -
	11.61	soma testes 11.61 2.92	Soma testes Ovary	soma testes ovary soma 11.61 2.92 - 69.18 - - 71.71 - - 68.54 - - - 71.69 - - 68.54 - - - 69.19 - - 68.41 - - - 69.19 - - 68.41 - - - 71.45 - - 70.67 - - 70.67 - - 70.14 - - - 70.14 - - - 71.01 - - 71.01 - - - 71.01 - - - 71.01 - - - 71.01 - - - 71.01 - - - 71.01 - - - 71.01 - - - 71.01 - - - - - - - - - -	Soma testes Ovary Soma testes

Sample	Ý	Lipid		% Water			
number	soma	testes	ovary	soma	testes	ovary	
6-003 6-004 6-005 6-006 6-007 6-008 6-009 6-010 6-011 6-012 6-013 6-014 6-015 6-016 6-017 6-018 6-019 6-020 6-021 6-022 6-023 6-025 6-026	6.58 8.32 6.57 8.35 6.37 6.33	2.10 -2.28 -2.51 2.36 -2.02 	1.35 1.36 2.05 - 1.17 1.43 1.69 1.14 - 1.07 1.28	73.17 70.91 74.56 75.00 73.34 76.85 75.03 78.00 71.65 74.10 72.05 75.41 75.78 73.02 73.77 72.43 69.00 77.18 71.30 77.00 71.30	79.98 79.38. 78.82 79.26 81.29 	76.02 67.57 - 72.28 - 73.56 74.67 74.92 - 74.37 74.02 - 68.92 - 66.60	
7-002 7-003 7-005 7-006 7-007 7-010 7-011 7-012 7-013 7-014 7-016 7-017 7-018 7-019 7-020 7-021	16.58 18.08 19.66 18.95 18.97 16.15 17.84 16.36 17.80 11.07 18.59 11.89 17.46 12.19 14.49 17.92		-	63.47 62.56 60.62 61.80 61.56 64.47 62.50 63.11 68.25 62.02 67.84 63.13 67.88 65.59 63.11			
8-003 8-006 8-007 8-008 8-009	18.04 18.14 13.20 16.68 17.16	1.66	1.18 1.09 1.72 1.43	63.14 63.15 67.84 64.76 63.82	- 76.72 - -	66.45 67.84 - 68.78 67.25	

	7	i Lipid		9	water (
Sample number	soma	testes	ovary	soma	testes	ovary
8-010 8-011 8-012 8-013 8-014 8-016 8-017 8-019 8-020 8-021 8-022 8-022 8-022 8-025 8-027 8-027 8-029 8-030 8-031 8-036 8-044 8-047	13.04 	2.18 - 1.42 2.12 1.86 - 2.15 1.91 2.21 - 2.07 2.02	- - - - - - - - 1.58 1.65 1.35 1.22 0.90 0.74	67.89 65.92 63.64 66.02 67.60 65.87 64.04 65.93 68.89 65.10 64.73 64.51 64.23 68.52 65.48	75.42 - 76.01 75.03 75.59 - 75.36 75.74 75.19 - 75.63 75.30	67.89 71.22 69.77 69.38 68.38 72.26
9-001 9-002 9-003 9-004 9-005 9-006 9-007 9-010 9-011 9-012 9-013 9-014 9-015 9-016 9-017 9-018 9-019 9-021	15.90 15.10 14.25 14.697 16.488 15.35 12.888 12.37 14.637 14.37 15.37 15.37 16	2.42 2.41 	1.30 1.35 - 1.41 - 0.93 - 1.17 - 1.28 1.36 - 1.50 1.13	63.47 64.65 65.20 65.20 65.49 65.39 67.69 67.15 62.38 64.78 65.38 64.68 64.69 64.17 67.17	71.80 73.25 -72.59 70.41 70.46 -74.20 -73.01 72.49 -72.27 70.74	65.68 65.87 - 66.27 - 65.65 64.17 - 65.28 - 70.55 64.80 - 64.48 66.98
11-001 11-002	13.43	-	1.85 1.09	66.66 -	-	65.61 63.43

Sample	%	Lipid		g	Water	
number	soma	testes	ovary	soma	testes	ovary
11-003 11-004 11-005 11-006 11-007 11-008 11-009 11-010 11-011 11-012 11-013 11-014 11-015	14.77 15.86 11.14 12.76 11,40 13.36 14.63 17.22 12.26 15.66 14.31 16.34 16.85	1.71 1.88 3.76 3.45 - - 3.00 - 3.45 1.63	0.65 - - 0.63 0.94 1.11 - 0.88	65.35 - 68.74 68.21 67.94 65.69 65.73 63.34 67.23 63.49 65.73 64.06 62.48	74.33 73.53 69.88 69.62 70.36 68.36 74.51	63.42 - - 63.13 63.91 63.64 - 63.85
11-016 11-017 11-018 11-019 11-020 11-022	8.87 14.74 13.45 17.71 11.18 12.22	3.84	1.39	69.53 65.16 65.47 63.37 68.61 67.42	- - - - 68.96	66.15

Sample	llea	.d
number	% lipid	% water
7-027	9.07	69.23
7-028	9.07	69.23
11-008	11.37	67.99
11-009	11.31	68.98
11-010	11.53	68.80

APPENDIX 3: Energy Density

Energy Density (kilojoules/g wet wt.)

Sample	(kilo	ojoules/g v	wet wt.)	
number	soma	testes	ovary	head
3-002 3-003 3-004 3-005 3-010 3-012 3-028 3-031 3-032 3-034 3-039 3-040	10.474 9.444 9.063 8.491 8.968 10.016 - 8.966 9.787 9.584 9.270 8.608	5.499 - 6.415 - 6.217 6.718 5.835	8.802 - 8.667 - - 8.091 8.685 8.414	
4-001 4-002 4-004 4-005 4-006 4-008 4-009 4-010 4-011 4-012 4-013 4-018 4-024 4-025	7.258 8.754 7.423 8.459 8.653 7.984 8.653 7.684 7.688 8.1924 7.924	6.329 - - 6.253 - 6.084 - 6.232 5.207 6.306	8.553 8.317 8.321 	-
5-001 5-002 5-004 5-006 5-007 5-008 5-010 5-012 5-013 5-014 5-015 5-016 5-018 5-020 5-021 5-024	7.973 7.497 8.125 8.725 6.574 5.934 7.0318 6.477 8.483 7.253 8.164 6.034 8.415 6.920 6.720	6.312 - 6.498 6.578 6.445 - 6.243 - - 6.484	8.511 8.502 8.981 - 8.350 - 8.702 7.903 8.638 - 8.506 8.481	

Energy Density (kilojoules/g wet wt.)

Sample	(kilo	ojoules/g v	wet wt.)	
number	soma	testes	ovary	head
5-037	7.884	6.592	-	_
5-038 5-039	7.735 7.500	6.625 6.891	-	-
6-001	-	-	8.240	_
6-002	5.751	4.383	-	-
6-003 6-004	6.956 7.712	4.358	- 5.777	_
6-005	6.310	4.472	-	-
6-006	6.097	-	7.868	-
6-007 6-008	6.743 5.328	4.622 4.457	-	-
6-009	6.065	-	6 . 753	_
6-010	4.745	4.078	-	-
6-011	7.323	-	- (1,01,	-
6-012 6-013	6.357 6.290	-	6.484 6.193	_
6-014	7.269	4.745	-	-
6-015	7.262	-	6.201	-
6-016 6-017	6.040 5.842	- 5.326	6.092	-
6-018	7.079	4.742	_	_
6-019	6.631	-	6.201	-
6-020	7.198	_	6.289	-
6-021 6-023	7.066 7.761	_	7.591	~
6-026	7.783	-	-	-
7-002	10.707	-	-	-
7-003 7-005	11.214 11.685	-	-	_
7-006	11.376	_	-	_
7-007	11.112	-	_	-
7-009 7-010	10.253 10.942	<u>.</u>	-	~
7-010	10.373	_	-	_
7-012	10.772	_	-	-
7-013	8.564	~	-	-
7-014 7-016	10.772 8.709	_	-	_
7-017	10.662	_	-	-
7-018	10.710	-	-	-
7-019 7-020	8,680 9,635	-	-	-
7-020	10.757	_	-	-
7-024		-	-	6.735
7-025	-	-	-	6.802
7-026	-	-	-	6.735

Energy Density (kilojoules/g wet wt.)

Sample	(kil	(kilojoules/ g wet wt.)					
number	soma	testes	ovary	head			
8-003	11.013	_	8.016	_			
8-006	11.119	-	7.687	-			
8-007	9.234	5.012	-				
8-008	10.399	-	7.398	-			
8-009	10.839	-	7.889	_			
3-010	9.155	-	+	_			
3-011	-	5.314	-	-			
3-012	9.892	-	_	_			
3-013	10.763	-	-	-			
3-014	9:843	_	_	-			
3-016	9.325	5.109	-	_			
3-017	9.930	5.377 5.276	-	-			
3-018	10.705	5,276	~	_			
3-019	9.949	-	-	-			
3-020	8.840		_	-			
3-021	10.197	5.340	-	-			
3-022	10.521	5.285		-			
3-024	10.593	5.371	-	-			
3-025	10.565	-	_	_			
3-026	8.835	5.281	-	_			
3-027	10.130	5.329	-	_			
9-001	-	_	8.443	_			
0-002	10.430	_	-	_			
9-004	10.122	-	_	-			
9-005	10.325	-	8.286	-			
-006	10.328	6.090	-	_			
0-007	10.663	6.557	_	-			
7-008	10.854	_	-	_			
7-009	9.224	-	8.466	-			
-010	10.961	5.642	_	-			
0-011	8.355	8.901	-	_			
-012	8.196	5.966	-	~			
0-013	9.953	6.039	_	_			
-014	11,288	-	8.439	-			
0-015	10.179	6.016	-	-			
-016	9.935	6.410	-	_			
-017	10.478	_	6.874	-			
-018	9.508	-	8.673	-			
0-021	10.717	-	8.765	-			
9-022	9.307	-	7.984	_			

