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**Daily ration and energy content obtained from the diet of American plaice (*Hippoglossoides platessoides*) in the Grand Bank and the Flemish Cap**

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**Abstract**

The energy content obtained from the diets of American plaice (*Hippoglossoides platessoides*) in the Grand Bank and the Flemish Cap was estimated from the feeding composition of 6570 and 1290 individuals, respectively, sampled in spring-summer in the 2002-2006 period. This was related to the reported growth and longevity of this fish species in each area. To estimate energy values of food components, the daily ration for American plaice in the Grand Bank was calculated using Elliot and Persson, Eggers, and Swenson and Smith models. Results showed differences among models, the values obtained with the first two models were the closest; the third model gave higher values. Daily ration was higher in females and it increased with length. The values ranged between 1.61 to 2.24 %BW/d in females and 0.54 to 4.18 %BW/d in males with the Elliot & Persson model.

Results showed that the Flemish Cap diet had higher energy, and that the female diet was richer in energy in both areas. Differences in the energy component of the diet between areas decreased with increasing length for both sexes; it was linked to a diet change of the individuals in the Grand Bank from a length of 34 cm in males and 51 cm in females. This result agrees with the differences in growth and longevity observed in each area for both sexes. The influence of feeding on populational differences could be reflected. The observed trend of diminishing energy differences between areas where the individuals are >30 cm is even more marked in the biggest individuals. This would agree with the superior growth rate in the Flemish Cap, at the same time as a smaller  $L_{max}$  and longevity. The sizes where the growth pattern changes are close to those where the feeding pattern also changes.

**Introduction**

The amount of energy obtained from the food process which is then allocated to the physiological functions of the vital phases throughout the life history of the fish, will depend on many factors, some of which are specific (genetic and physiological) and others environmental, such as temperature, oxygen and feeding. The rate of food consumption will depend mainly on the ontogenetic characteristics, seasonal and geographical distribution, where physiological and reproductive stages both for predator and prey, prey availability and temperature interact, and population conditions (competition and overlap relationships) are also present. The lifetime phases will lead to different bioenergetic balances and metabolic allocation in movement, growth and reproduction; there will be marked differences between when individuals are sexually immature or adult (Lester *et al.* 2004). If the energy overcomes the metabolism costs, the surplus energy is allocated to growth (Persson and De Roos, 2006). Therefore, given the relationship between population and individual growth, the differences of well being and growth are reflected both within and between fish populations.

Fish species may feed continuously (consuming food particles and digesting them simultaneously), or discontinuously (large meal and then digest it later). Ration refers to the quantity of food eaten and diet to the quality or composition of the food. Feeding patterns vary with the type and abundance of food, and models to estimate ration should take this variance into account (Pitcher, 1992; Wootton, 1999). The most important factors influencing gastric evacuation are predator size, volume and surface of meal, food composition and nutrient content, frequency of feeding and temperature. Reviews on daily ration and gastric evacuation estimation in the field have been carried out and different models have been proposed and compared (Bromley, 1994; Hansson *et al.*, 1996; Diana, 2004). They are based on assumptions and are sensitive to different measuring of the variables that affect the gastric evacuation process, resulting in a model being better adjusted for certain species or situations (MacPherson, 1985; Héroux and Magnan, 1996; Maynou and Cartes, 1997). The application of the physiological model gives indications as to the mathematical expressions best suited for the calculation of gastric emptying rates of microphagus/planktivorous fish, which feed more or less continuously, and predators, which tend to consume large meals. However, there are fish species that do not fit into either of these distinct ecological categories, many fish feed opportunistically and, at any given time, the stomach may contain food items in various stages of digestion, therefore gastric emptying patterns are complex (Jobling, 1986). Temperature is probably the most studied variable influencing digestion and gastric evacuation rate. Evacuation rate usually increases with temperature, affecting enzyme reactions, which are essentially exponential processes (Bromley, 1994).

American plaice (*Hippoglossoides platessoides*) are distributed on both sides of North Atlantic. In the northwest, juveniles and adults show seasonal changes in density and abundance (Swain and Morin, 1996). Differences in spatial and depth distributions according to length and sex were observed, which were related to the temperature and salinity preferences (Swain and Morgan, 2001). This species exhibits geographical differences in sexual dimorphic growth and maturation rates (Bowering and Brodie, 1994; Lloret, 1997; Morgan and Colbourne, 1999; Barot *et al.* 2005), and ontogenetic shifts in diet with a gradual shift in size-selective preference of prey (Link *et al.* 2002; González *et al.* 2003). It is an opportunistic feeder; therefore, differences in prey spectrum reflect abundance or accessibility of prey (Johnson, 2004).

In the northwest Atlantic, the regulation area of Northwest Atlantic Fisheries Organization (NAFO) manages two stocks, in Divisions 3LNO and in Division 3M. Both stocks are at the moment in moratorium. The biomass and the SSB of American plaice in Division 3M are at very low levels, and there is no sign of recovery. Similarly, the 3LNO stock remains low compared to historical levels (NAFO, 2006, 2007). Feeding is fundamental for the success of a species and responds to geographical differences in the biological features of the species. We analyze the energy benefit that the Grand Bank and Flemish Cap American plaice populations obtain, starting from the corresponding observed diets and their possible relationship with the growth shown in each area.

The estimate of the daily ration provides us with the energy input obtained and enables us to quantify the predation. Few studies have approached the study of daily ration and bioenergetic equivalence in American plaice in the Grand Bank and Flemish Cap (Northwest Atlantic). Zamarro (1992) reported on daily ration in Grand Bank, but a narrow length range was treated, and it was not completely representative of the population. Pitt (1973) analyzed the energy differences that this species could obtain in some areas of the Grand Bank, estimating them directly from the diet composition.

The present study seeks to find out if the differences in feeding can explain the differences of growth and longevity noted between the two studied populations. The daily ration and energy equivalent content were calculated for this purpose, paying attention to diet differences related to sex and length.

## Material and methods

**Daily ration.** A study was carried out in May of 1998 with the purpose of finding out the daily feeding behavior of American plaice in the Grand Bank (González *et al.*, 2003). The design of the sample collection in the daily pattern study also allows us to use the same data to estimate the daily ration. Samples were taken at intervals of the daily cycle (dawn, midday, afternoon, dusk and night) throughout the period of 19 to 27 May 1998 (Table 1). The quantity and type of food in each stomach was recorded. Weight of stomach contents and prey items was expressed as a ratio of the fish weight (%BW = gr of prey per 100 gr of predator weight). Feeding intensity (%FI) is the percentage of individuals with food in their stomachs. Food components were grouped: soft or small foods (Hypsiidae, Anthozoa,

Amphipoda, Gammaridea, Caprellidae, Mysidacea, Isopoda, Cumacea, Annelida and Crustacea larvae), big or hard foods (Natantia, Crustacea and Brachyura unidentified, Paguridae, Bivalvia, Ophiura, Echinoidea, *Chionoecetes opilio*) and fish prey (*Ammodytes dubius* and other fish). Daily ration calculations were applied independently to each one of these groups, paying attention to the size and the sex of the predator. Total number of sampled individuals (fullness and emptiness of stomachs) was used. We consider 0.98 °C, as the temperature for the spring of 1998 in the Grand Bank area at depths of less than 100 m (Colbourne *et al.*, 2007).

Many studies have shown that the results are quite variable, and without a clear conclusion as to which model would be the most valid (Hansson *et al.*, 1996; Héroux and Magnan, 1996; Maynou and Cartes, 1997). We tested the daily ration estimation using three models:

- The Elliott and Persson (1978) model because it has probably been the most widely used and it fits well when feeding is more or less continuous.
- The model of Eggers (1979) (modification of Eggers of his 1977 model) has also been widely used. This model is less complex and is likely to give more robust estimates of food consumption than the Elliott & Persson model when there is large within-sample variability in the food weight. It can also be applied to species foraging for a wide range of prey types throughout the day, exhibiting occasional feeding peaks, and having no rigid feeding periods (Héroux and Magnan, 1996), as could be the case of American plaice (Zamarro, 1992; Bruno *et al.*, 2000; González *et al.*, 2003).
- Swenson and Smith model (1973) model. This is a model for non continuous feeders, which calculates daily ration over several time periods in a day, somewhat similar to the continuous feeding model.

The main characteristics, assumptions and problems of these three models are shown in Table 2.

The gastric evacuation rate ( $R$ ,  $h^{-1}$ ) is affected by temperature, food type and size, meal size and feeding regime, but the most important factors are temperature and food type. This calculation was made using the expression (Elliott, 1972):

$$R = a * \exp^{(bT)}$$

where  $T$  is the temperature (0.98 °C), and  $a$  and  $b$  are parameters dependent on prey type. The values used are indicated in the Table 3.

Energy value of the food components. The daily ration value obtained (from the data of the Grand Bank using Elliott and Persson model) was applied to the sampling data of stomach contents (qualitative and quantitative specific composition) taken in the Grand Bank in later spring and Flemish Cap in early summer for the period 2002 to 2006 (Table 4), with the purpose of estimating the energy input obtained by American plaice in each area. The prey spectrum in the stomach contents sampled in each area is shown in the Table 5; results are expressed as Mean Partial Fullness Index (%MPFI), which is the percentage of prey weight (gr) in terms of predator weight (gr) regarding the total number of individuals sampled.

$$\%MPFI_{ij} = (w_{ij} / W_j) * 100, \text{ where}$$

$w_{ij}$  is the wet weight of prey  $i$  in the stomach contents of the individual  $j$ .

$W_j$  is the wet weight of individual  $j$ .

In the sampling carried out to estimate the daily ration, males  $\geq 50$  cm were not caught, neither were individuals  $<20$  cm. Therefore the estimate of daily ration for female  $\geq 50$  cm was used for the males, and the value obtained for individuals 20-29 cm was applied for the individuals  $<20$  cm.

The applied caloric values for live weights of the prey species were obtained from bibliographic references (Percy and Fife, 1981; Steimle and Terranova, 1985; Wacasey and Atkinson, 1987; Steimle and Terranova, 1988). A value for similar species or average values were assumed when some species were present in food spectrum but not recorded in bibliographic data. This procedure has already been used by Pitt (1973).

Size of sample, length of individuals sampled and diet data regarding length groups and sex were previously visualized. The samplings carried out in the two areas in the 2002-2006 period were different in both the sample size and in the length of the individuals (Figure 1). The U of Mann-Whitney was used to compare the mean length of the

length groupings carried out for the sampling between areas. The test showed significant differences for all the length ranges: this should be kept in mind when the results are analyzed. However, the sampling intensity was reflective of the catch differences in both areas, allowing a wider sampling in the Grand Bank. Furthermore, the length range sampled in the feeding study and length distribution samplings (Table 6) were similar (Saborido-Rey and Vázquez, 2003; Casas, 2004; Casas and González-Troncoso, 2005; González-Troncoso *et al.*, 2006a; Casas and González-Troncoso, 2007; González-Troncoso *et al.*, 2007).

The Kruskal-Wallis test was carried out to compare the differences between areas on *MWFI* from main prey (17 items), which represented more than 95% of the total weight (Table 7) and showed significant differences among all of them, except for Anthozoa. Hierarchical analyses were performed using PRIMER 5 to assess the degree of similarity in the male and female diets in relation to length from Bray-Curtis similarity using a cluster mode of group average and Log (x + 1) transformation.

## Results

Spacial and ontogenetic variations in the diet. In the Grand Bank, both sexes showed a feeding behavior marked by a similarity of diet including clear size intervals. The length at which diet shift occurred was different in each sex. Males presented two main groups: individuals <34 and  $\geq 34$  cm. Females showed three groups: bigger individuals ( $\geq 51$  cm); smaller individuals (<25 cm) and intermediate lengths (Figure 2). However, feeding was more homogeneous throughout the length range in Flemish Cap, with groupings between non-contiguous sizes (Figure 3).

Daily ration. The values obtained from the three applied models showed differences among them (Table 8). Daily ration increased with the length and was higher in females, except in the individuals of 40-49 cm; the calculation, in this case, might have been overestimated due to the small number of individuals sampled. This problem might also affect the sample of females from 20-29 cm in length.

Elliott & Persson and Eggers models gave similar values in males and in the individuals  $\geq 50$  cm. Swenson & Smith model estimated higher values, however values were closer in the individuals  $\geq 50$  cm, and it minimizes the differences between sexes.

Energy equivalents of food components. Regarding the daily consumption, American plaice obtain more energy (Kcal per 100 gr of wet predator weight) with the diet of the Flemish Cap (Figure 4), where feeding intensity was also higher (Table 4). Both females and males obtain more energy over the lengths sampled (except males between 40-49 cm) in the Flemish Cap.

Inside each area, females obtain more energy from their diet than males, except the males of 40-49 cm in Grand Bank (Figure 5). In this area, the caloric value obtained by the smallest individuals (<10 cm) is high, but we must keep in mind that a value of daily portion for this group was not available, and the calculated value for the individuals of 20-29 cm was applied.

## Discussion

Daily ration. In general, comparisons between different models of the daily ration showed differences; this has been observed in Atlantic cod, *Gadus morhua* (Hansson *et al.*, 1996), yellowtail flounder, *Limanda ferruginea* (Collie, 1987), common sole, *Solea vulgaris*, (Lagardère, 1987) and deep-sea shrimp, *Aristeus antennatus* (Maynou and Cartes, 1997). Temperature, daily feeding pattern and gastric evacuation rate are the cause of considerable variations in daily ration estimates (MacPherson, 1985). The analysis should be considered in light of the assumptions made.

American plaice eats mostly during the daytime, but it shows feeding activity during 24 hours (there are food contents at different digestion stages all the time). This species is a continuous feeder with the maximum peak between midday-afternoon and the minimum at dusk (Bruno *et al.*, 2000; González *et al.*, 2003). This study reflects what was commented previously; the three models offered different results. Elliott & Persson and Eggers models came closer in values, which has already been reported (Bromley, 1994). Bigger differences (females 20-29 cm and males 40-49 cm) were found in the worst ranges sampled (low number of individuals). The models seem to approach each other for the males and when increasing the length. This also happens when both the weight of stomach contents regarding the predator weight (% BW) and the feeding intensity tend to diminish, which indicates a less continuous feeding pattern.

Geographical differences. The shallow water of the Flemish Cap combined with the proximity of large-scale oceanic circulation (Labrador and North Atlantic Currents) around the bank generate an anticyclonic gyre, elevate water temperatures and inorganic dissolved nutrients to enhance the possibility of high primary and secondary production (Maillet *et al.*, 2005). These conditions would provide conditions for more favorable food (in depth range and seasonal duration) in the bank of Flemish Cap than in the Grand Banks, along with high energy prey availability (as *Pandalus borealis* and Hyperiid) and smaller populational biomass thus diminishing the competition. All of these factors would facilitate a higher energy yield in American plaice in the Flemish Cap allowing higher growth rates than in other areas (Bowering and Brodie, 1994).

However, assemblages defining structural zonation and biogeography showed the Grand Bank to be a more complex system than the Flemish Cap (Gomes and Haedrich, 1992; González-Troncoso *et al.*, 2006b), with the corresponding repercussion in the feeding ecology. The individuals show ontogenetic changes defining feeding phases. The shift is not so clear in Flemish Cap, possibly the smaller specific diversity and different depth distribution pattern have an influence in this area. Similar results were reflected in feeding overlapping among different length classes (González *et al.*, 2003). Feeding shifts in the Grand Bank would be based on prey variation, while the predation on the same prey but at a different intensity would be a more habitual strategy in the Flemish Cap.

Amount and type of food have been considered as being responsible for the geographical differences of growth as well as for maturation (Stratoudakis, 1997; Morgan, 2004; Mateo, 2007; Kennedy *et al.*, 2008). In this way, comparisons of the caloric value of stomach contents of American plaice in Divisions 3L and 3N (NAFO Area, northwest Atlantic) showed lower values for Div. 3L, attributed to the inferior amount of fish consumed and the possible larger amount of expended energy in foraging (Pitt, 1973). This author suggested that the greater consumption of high energy food in Division 3N would cause the faster growth and earlier maturation observed; and the slightly higher temperature could increase the digestion rate with the consequent increase in energy production. A similar scenario could be happening between the Flemish Cap and the Grand Bank where, in general, American plaice presented better bioenergetic input with the food from Flemish Cap. But in this case, the fish consumption would not be responsible, since this diet and the piscivorous behavior increasing with the length are characteristic of Grand Bank (Román *et al.* 2004; González *et al.*, 2006a). Some prey, such as the ophiuroids, are an important food item in both areas despite their low caloric value. This can be compensated by greater abundance or accessibility compared with *Pandalus borealis*, *Ammodytes dubius* or *Mallotus villosus* (Pitt, 1973; Zamarro, 1992; Link *et al.*, 2002; González *et al.*, 2003) which have high caloric value but are highly mobile in terms of catchability.

Sex and length differences. Females showed bigger daily ration estimates than males and these increased with length. This corresponded to the annual period of greater feeding intensity (spring-summer). Our results show differences with other previous studies on American plaice. Berestovskiy (1995) found a daily ration (%BW) from 3-4 in juveniles to 1-2 in adults at 1.8-5.8 °C. However this author shows considerable differences in daily ration among different areas included in his study and also with the one obtained under experimental conditions. Furthermore, the daily ration did not always diminish with length. On the other hand, the number of individuals sampled, the temperature (T higher under experimental conditions to the one considered by us) and the length considered for juvenile/adult might be the causes of the differences with our study. Daily ration reported by Zamarro (1992) for individuals between 40-55 cm was 0.64% in April and 0.04% in January. This value is quite smaller than the one obtained in our study for similar length range individuals. Despite both studies being carried out in the same area (southern Grand Bank), season and the fact that he even considered a higher temperature (2.5 °C for spring-summer in the 1972-1986 period). However, the individuals were caught at a greater depth range than the one used in the present study, and in general, both feeding intensity and ingested meal amount tend to diminish with depth (González *et al.*, 2006a). The author, himself, highlights the low daily ration value and energy content achieved which are lower than the requirements estimated by other authors. This value would not allow for summer storage to be used in metabolism and gonad maturation (MacKinnon, 1972). In the Grand Bank, the abundance and biomass of American plaice has suffered a drastic fall in the last decades; changes in the food readiness have given rise to smaller competition in recent periods that would allow the daily ration to increase (Ware, 1980; Dwyer *et al.*, 2007).

Optimum temperature (smaller T causes lower metabolic consumption) and oxygen (when increasing the weight predator, it needs bigger oxygen consumption) are specific requirements; from it when the species have possibility to select the habitat, they are distributed according to the best use in their energy entrances (Morgan and Brodie, 1991; Morgan, 1993). Each species shows an optimum temperature and ration level that results in maximum growth. American plaice sex differences in distribution and aggregation depending on the temperature were recorded in Grand Banks and other areas (Swain and Morgan, 2001). The increment of the occupied area is more marked in

older females possibly due to intense foraging activity and high competition among them (Swain and Morin, 1996). The bioenergetic differences caused by the sexual dimorphism in food intake due to differences in the digestive tract size, hepatosomatic index, respiration and temperature requirements allow a higher surplus production for females (Lozán, 1992). The higher growth in females comes from a bigger energy benefit, increasing the feeding intensity or diminishing the intensity but consuming larger size prey; a more habitual strategy in American plaice when it increases its size.

In both areas, females in general presented higher energy equivalence from the diet. The considerations pointed out previously agree with the higher growth rates in females observed in this species in the north Atlantic (Bowering and Brodie, 1994; Lloret, 1997; Dwyer *et al.*, 2007). However a similar growth rate between the sexes up to age 3 reported for the Flemish Cap (Bowering and Brodie, 1994) is contradictory to these results. The environmental conditions in the Flemish Cap could be more favorable, but the expenditure would be also higher (larger metabolic expenditure due to superior temperature and greater expenditure in reproduction due to the low SSB). In this sense a gradual condition loss has been observed since the mid 90s (González *et al.*, 2006b). The longevity and maximum size diminish from south to north inside the area of the Grand Bank, as well as throughout the north-Atlantic distribution area of the species. However in the Flemish Cap, higher growth and fecundity were observed than in other areas of the northwest Atlantic and also smaller  $L_{max}$ ,  $A_{max}$ ,  $L_{50}$  y  $A_{50}$  (Walsh, 1994; Walsh, 1996), likewise the energy differences from diet between the areas compared diminished with the increase in length, and they tend to invert from >40 cm.

This shift is reflected in the American plaice geographical and sexual growth pattern for the two study areas. Results of the modeled growth showed a greater growth rate in Flemish Cap individuals than in Grand Bank individuals. However, a shift in the growth pattern was noted from a certain length, with a higher length at age and a bigger  $L_{max}$  being reached in Grand Bank. In males, this was noticed from a mean size of 38.1 cm considering the annual classes of 1993-1995 and 1998-1999, and in females from 50.9 cm corresponding to the annual classes of 1985-1995 and 1999. Feeding shift according to length in the mature phase is observed in Grand Bank, around the 34 and 50 cm for males and females respectively (personal communication of D. González-Troncoso).

From these results, it is clear that growth modeling is necessary to relate the growth rate and the food ecology. There are many factors that modify energy requirements and several estimates of daily ration would be necessary. A more complete annual study of food and feeding is necessary to improve the energetic equivalent estimate. Predator-prey interactions will also be needed to improve on consumption estimates for an energy flow model.

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Table 1. Characteristics of individuals and stomach contents of American plaice analyzed in daily ratio study (Grand Bank, spring 1998). Data from González *et al.*, 2003 modified.

Time interval	Length class (cm)	No. of individuals			Feeding intensity (%FI)			Mean weight of fish (g) ± SD		Mean stomach content (g) ± SD	
		Male	Female	Total	Male	Female	Total	Male	Female	Male	Female
Dawn	20-29	47	3	50	59.6	66.7	60.0	169 ± 30.7	182 ± 21.4	0.229 ± 0.64	0.313 ± 0.46
(07:13 to 07:15 h)	30-39	23	27	50	47.8	59.3	54.0	314 ± 84.4	455 ± 88.7	0.329 ± 0.77	2.714 ± 5.23
(53 to 62 m)	40-49	5	45	50	40.0	42.2	42.0	588 ± 42.0	732 ± 151.0	2.464 ± 3.38	4.441 ± 10.90
	≥ 50		50	50		60.0	60.0		1628 ± 488.2		5.910 ± 9.14
Midday	20-29	46	4	50	63.0	50.0	62.0	165 ± 37.5	132 ± 41.2	0.522 ± 1.14	1.080 ± 1.29
(11:26 to 12:31 h)	30-39	39	11	50	74.4	81.8	76.0	319 ± 91.1	471 ± 82.4	0.905 ± 2.15	2.715 ± 2.73
(53 to 71 m)	40-49	2	48	50	50.0	50.0	50.0	654 ± 0.0	754 ± 161.0	0.265 ± 0.00	4.131 ± 6.59
	≥ 50		50	50		56.0	56.0		1518 ± 397.4		5.792 ± 7.36
Afternoon	20-29	47	3	50	76.6	66.7	76.0	167 ± 31.1	177 ± 45.4	0.669 ± 1.01	0.267 ± 0.32
(15:57 to 18:10 h)	30-39	34	16	50	35.3	68.8	46.0	301 ± 70.5	443 ± 84.9	0.205 ± 0.93	2.411 ± 2.79
(49 to 69 m)	40-49	2	48	50	0.0	50.0	48.0	583 ± 32.4	746 ± 173.3	0	5.971 ± 12.54
	≥ 50		39	39		43.6	43.6		1767 ± 458.7		6.910 ± 11.49
Dusk	20-29	42	8	50	50.0	50.0	50.0	155 ± 43.1	135 ± 43.3	0.169 ± 0.28	0.186 ± 0.25
(21:03 to 21:54 h)	30-39	28	22	50	17.9	36.4	26.0	330 ± 83.7	406 ± 95.8	0.170 ± 0.71	0.812 ± 2.24
(64 to 80 m)	40-49	7	43	50	28.6	30.2	30.0	686 ± 174.6	802 ± 168.5	1.497 ± 2.59	1.793 ± 3.93
	≥ 50		33	33		12.1	12.1		1746 ± 548.1		2.018 ± 10.05
Night	20-29	45	5	50	40.0	60.0	42.0	163 ± 30.9	165 ± 16.5	0.301 ± 0.61	0.758 ± 0.99
(02:35 h)	30-39	20	30	50	30.0	63.3	50.0	308 ± 80.3	435 ± 80.7	1.931 ± 4.91	3.236 ± 5.31
(55 to 58 m)	40-49	1	49	50	100	51.0	52.0	758	711 ± 118.2	22.980	4.770 ± 7.50
	≥ 50		6	6		16.7	16.7		1622 ± 396.5		12.130 ± 29.72

Table 2. The main characteristics of the three daily ration and gastric evacuation models used.

Gastric evacuation model		Assumptions	Observations
Elliott and Persson (1978) $C_t = (S_t - S_0 * e^{-Rt}) / 1 - e^{-Rt}$	C is the food consumption (daily ration). The sum of values of $C_t$ provides an estimate of the daily food consumption. R is gastric evacuation rate. $S_0$ and $S_t$ are the mean stomach contents at the beginning and end of the interval (0 – t hours).	Continuous feeders. Food consumption is constant. Gastric evacuation is exponential and constant. A sampling interval of more than 3 h could produce very inaccurate estimates of the daily food consumption..	It was inadequate for larger fish and for fish that are feeding at a rate which increases or decreases markedly with time within the sampling interval. Not apply for several large particles in a meal. If feeding stops for only part of the period between sampling, when samples are taken at times with feeding has ceased, $C_t$ will be underestimated.
Eggers Modified (1979) $C_{24(E)C} = C_{24(E)} + (W_{t=24} - W_{t=0})$ $C_{24(E)} = S * R * 24$	$C_{24(E)C}$ is daily ration following the corrected Eggers model. $C_{24(E)}$ is the daily ration (Eggers, 1977). $W_0$ and $W_{24}$ is the mean weight of food content over 24 h (at the beginning and at the end of the sampling period). S is the mean stomach contents over a 24 h period. R is the instantaneous evacuation rate.	Gastric evacuation is exponential  When the weight of food in the stomach at the beginning and at the end of the 24 h cycle are significantly different. The modified model corrects when this assumption cannot be met.	It was not recommended for piscivorous fish that consume large prey periodically and have slow rates of evacuation.
Swenson & Smith (1973) $C = M * n / B * N$	C is the daily ration. M is the average size of an ingested meal. n is the number of fish with food in the stomach. B' is the number of days required for gastric evacuation. N is the total number of fish in the sample.	Non-continuous feeders but valid for the continuous feeders.	Model for non-continuous feeders but daily ration is calculated over several time periods in a day when fish feed synchronously at same time of day or feed a long time interval. It is not recommended for fish that do not eat synchronously.

Table 3. Parameters used to calculate the gastric evacuation rate.

Food type	<i>a</i>	<i>b</i>	<i>R</i>
Hard or large prey	0.198 <sup>(1)</sup>	0.115 <sup>(3)</sup>	0.222
Fish prey	0.0143 <sup>(2)</sup>	0.115 <sup>(3)</sup>	0.117
Soft or small prey <sup>(3)</sup>	0.041	0.111	0.046
<sup>(1)</sup> (MacDonald and Waiwood, 1982); <sup>(2)</sup> (Dwyier <i>et al.</i> , 1987); <sup>(3)</sup> (Durbin <i>et al.</i> , 1983).			

Table 4. Characteristics of individuals and stomach contents of American plaice analyzed in the food habit study (Grand Bank and Flemish Cap, 2002-2006 period).

Area	Length group (cm)	No. of individuals		Feeding intensity (%FI)		Mean weight of fish (g)± SD		Mean stomach content (g)± SD	
		Male	Female	Male	Female	Male	Female	Male	Female
Grand Bank (2002-2006) (May-June)	≤9	67	28	73.1	67.9	4 ± 1.6	4 ± 1.3	0.067 ± 0.0	0.068 ± 0.1
	10-19	575	590	70.6	72.0	34 ± 17.1	36 ± 18.2	0.238 ± 0.4	0.260 ± 0.4
	20-29	824	929	58.3	43.6	135 ± 49.1	134 ± 49.2	0.585 ± 1.2	0.533 ± 1.2
	30-39	720	751	44.2	44.3	350 ± 84.3	367 ± 112.2	1.470 ± 3.8	2.240 ± 4.9
	40-49	137	1121	43.1	42.6	646 ± 121.0	846 ± 175.4	3.076 ± 6.6	4.509 ± 9.9
	≥50		826		46.1		1775 ± 569.1		6.969 ± 12.9
Flemish Cap (2002-2006) (June-August)	20-29	42	46	76.2	73.9	163 ± 49.4	155 ± 48.1	0.668 ± 0.7	0.984 ± 1.0
	30-39	314	55	69.4	63.6	475 ± 103.9	425 ± 127.9	1.696 ± 3.2	1.198 ± 1.9
	40-49	270	219	73.3	75.8	711 ± 105.5	1050 ± 204.7	2.050 ± 3.8	4.902 ± 7.9
	≥50		335		77.9		1514 ± 220.4		7.715 ± 10.1

Table 5. Mean Partial Fullness Index by prey in American plaice individuals analyzed in the food habit study (Grand Bank and Flemish Cap, 2002-2006 period). \* is &lt;0.01

	Prey	Mean Partial Fullness Index (% MPFI)										Energetic value (Kcal/gr of prey)
		Grand Bank (NAFO, Divs. 3NO)					Flemish Cap (NAFO, Div. 3M)					
		2002	2003	2004	2005	2006	2002	2003	2004	2005	2006	
Echinodermata		0.02	0.02	0.03	0.08	0.11	0.06	0.04	0.04	0.03	0.07	
	Asteroidea								*	*	2.65	
	Crinoidea	*							*		1.22	
	<i>Echinarachnius parma</i>	*	*	*	*	0.02					0.86	
	Echinoidea							*			2.45	
	Echinoidea (irreg)						*	*	*	*	2.45	
	Echinoidea (reg)						0.02	*	*	*	0.04	
	Ophiuroidea	0.01	0.01	0.02	0.07	0.09	0.04	0.04	0.03	0.02	0.03	
	Holothurioida	*	*	*	*	*	*	*	*	*	2.80	
Mollusca		*	0.02	0.08	0.05	0.03	0.01	*	*	*		
	Bivalvia	*	0.01	0.04	0.01	0.02	*	*	*	*	4.00	
	Bivalvia Lutraria			0.05	0.03	*					4.34	
	Gasteropoda	*	*	*	*	*	*	*	*	*	4.47	
	Opisthobranchia			*							4.47	
	Unidentif. Mollusca		*								3.75	
	Cephalopoda		*		*						4.96	
	Oegopsida								*		5.26	
Crustacea		0.14	0.26	0.29	0.51	0.32	0.27	0.07	0.54	0.12	0.15	
	Amphipoda	*	*			*					3.67	
	Gammaridea	0.04	0.03	0.07	0.04	0.02	*	*	*	*	3.67	
	Caprellidae	*	*	*	*	*					3.97	
	Copepoda	*	*	*	*	*			*		5.01	
	Cumacea	*	*	*	*	*					1.99	
	Euphausiacea	*	*	*	0.02	*	0.02		0.02	*	*	
	Hyperiidia	*	*	0.05	0.01	*	0.17		0.42	*	5.17	
	Isopoda	*	*	*	*	*					3.83	
	Mysidacea	0.09	0.20	0.14	0.40	0.29	*	*	*	*	3.85	
	<i>Lebbeus polaris</i>						*	*	*	*	3.96	
	<i>Sergestes arcticus</i>						*	*	*	*	5.16	
	<i>Spirontocaris lilljeborgii</i>						0.03	*	0.04	*	0.01	
	<i>Argis dentata</i>			*	*					0.01	4.40	
	<i>Sabinea sarsi</i>								*		4.40	
	<i>Sclerocrangon ferox</i>								*		4.02	
	<i>Pandalus borealis</i>	*	*	*	0.01	*	0.04	0.06	0.05	0.07	0.12	
	<i>Pontophilus norvegicus</i>								*	*	5.09	
	<i>Chionoecetes opilio</i>	*	*	0.01	*	*				*	3.65	
	Crust. Decapoda		*						0.01		4.04	
	<i>Hyas coarctatus</i>					*					2.03	
	<i>Hyas</i> sp	*	*	*	*	*					2.03	
	Paguridae		*				*		*		3.55	
	Pycnogonidae								*	*	2.51	
	Unidentif. Natantia		*	*	*	*	*	*	*	*	4.26	
	Unidentif. Brachyura	*	*	*	*	*	*	*	*	*	3.65	
	Unidentif. Crustacea	*	*	*	*	*	*	*	*	*	4.02	
Pisces		0.17	0.19	0.22	0.29	0.20	0.02	0.02	0.02	0.03	0.03	
	<i>Anmodytes dubbius</i>	0.11	0.10	0.17	0.22	0.19					5.19	
	<i>Anarhichas</i> sp								*		5.00	
	<i>Hippoglossoides platessoides</i>	*			*						4.23	
	<i>Leptoclinus maculatus</i>								*		5.00	
	Liparidae				*						4.10	
	<i>Liparis</i> sp	*	0.01	*							4.10	
	<i>Lumpenus lumpretaeformis</i>	*	*	*	0.02	*	0.01	0.02	0.01	0.01	0.02	
	<i>Lycodes</i> sp				*						4.59	
	Macrouridae								*		4.36	
	<i>Mallotus villosus</i>	0.05	0.07	*	*	*		*	*	*	6.06	
	Myctophidae	*						*	*	*	5.95	
	<i>Nezumia bairdii</i>	*						*	*	*	4.36	
	<i>Pleuronectiformes</i>			*							4.34	
	<i>Reinhardtius hippoglossoides</i>		*								4.42	
	<i>Sebastes marinus</i>				*						4.42	
	<i>Sebastes</i> spp				*						4.42	
	<i>Tryglops murrayi</i>	*		0.01			*				4.33	
	<i>Tryglops</i> sp	*	*	*	*	*					4.33	
	Fish (eggs)	*									5.00	
	Fish (larvae)			*	0.01	*		*	*	0.01	0.02	
	Unidentif. fish	*	*	*	*	*	*	*	*	*	5.00	
Other Invertebrates		0.02	0.02	0.06	0.04	0.02	0.03	0.01	0.02	0.02	0.04	
	Anthozoa	*	*	*	*	*	*	*	*	*	3.72	
	Aphroditidae	*	*	*	*	*	*	*	*	*	3.20	
	Ascidacea	*	*	*	*	*	*	*	*	*	2.63	
	Chaetognata	*	*	*	*	*	0.01	*	*	*	5.04	
	Cnidaria							*	*	*	1.91	
	Ctenophora	*	*	*	0.02	*	*	*	*	*	1.64	
	Polychaeta	*	*	0.04	0.02	0.01	*	*	*	*	0.04	
	Polychaeta (err)	*	*	*	*	*	*	*	*	*	4.15	
	Polychaeta (sed)	*	*	*	*	*	*	*	*	*	4.15	
	Porifera			*							2.06	
	Scyphozoa		*	*	*	*	*	*	*	*	2.46	
	Siphonophora				*	*	*	*	*	*	2.46	
	Sipunculida	*	*	*	*	*	*	*	*	*	3.11	
Other groups		*	*	*	*	*	*	*	*	*	*	
No. Individuals sampled (males and females)		2237	2510	599	671	553	169	181	544	213	183	
Feeding intensity (%FI)		38.8	50.9	67.3	66.9	64.2	79.9	52.5	86.4	55.4	72.1	
Depth (m) of sampling (min.-max.)		38-1449	38-826	43-1378	51-324	50-242	130-352	130-534	136-372	132-401	134-367	

Table 6. Length range of the American plaice individuals in the length distribution and food samplings in the scientific survey (Spanish Spring and EU Flemish Cap surveys, 2002-2006 period).

		Length range (cm)							
		Grand Bank				Flemish Cap			
Year	Sex	Length sampling		Food sampling		Length sampling		Food sampling	
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
2002	Males	8	53	6	50	25	47	25	47
	Females	9	68	9	67	27	57	28	57
2003	Males	6	47	6	49	12	49	12	47
	Females	7	66	7	72	16	58	16	58
2004	Males	7	57	8	43	17	58	17	47
	Females	7	68	9	68	17	59	17	59
2005	Males	7	52	7	49	20	49	18	58
	Females	7	69	7	69	18	58	22	58
2006	Males	7	49	8	57	22	46	30	45
	Females	8	77	8	72	12	60	12	59

Table 7. Weight (%) of the main prey of American plaice in Grand Bank and Flemish Cap (2002-2006 period).

Prey	%Weight	
	Grand Bank	Flemish Cap
<i>Ammodytes dubbius</i>	<b>36.9</b>	
Ophiuroidea	<b>14.7</b>	<b>6.5</b>
Bivalvia	<b>13.0</b>	0.1
Mysidacea	<b>9.8</b>	0.0
<i>Mallotus villosus</i>	<b>9.5</b>	0.2
<i>Echinarachnius parma</i>	<b>4.9</b>	
Ctenophora	2.2	0.5
Gammaridea	1.2	0.2
Euphausiacea	0.6	2.8
Polychaeta	0.6	2.4
Hyperiidia	0.3	<b>57.1</b>
<i>Pandalus borealis</i>	0.2	<b>15.9</b>
Echinoidea	0.0	<b>3.4</b>
<i>Lumpenus lumpretaeformis</i>	0.4	2.8
<i>Spirontocaris liljeborgii</i>	0.0	1.5
Chaetognata	0.0	1.4
Anthozoa	0.7	0.7
<i>Lebbeus polaris</i>		0.4
Other prey	5.1	4.1

Table 8. Daily ration values estimated for American plaice in Grand Bank (Spanish Spring survey, 1998).

Length class (cm)		Daily Ration (%BW/d)		
		Model		
		Elliott & Persson (1978)	Eggers (1979)	Swenson & Smith (1973)
20-29	Female	1.61	1.44	1.79
	Male	0.54	0.50	1.14
30-39	Female	1.57	1.72	2.68
	Male	0.86	0.86	1.20
40-49	Female	1.90	1.88	2.90
	Male	4.18	3.93	3.88
≥ 50	Female	2.24	2.31	2.22

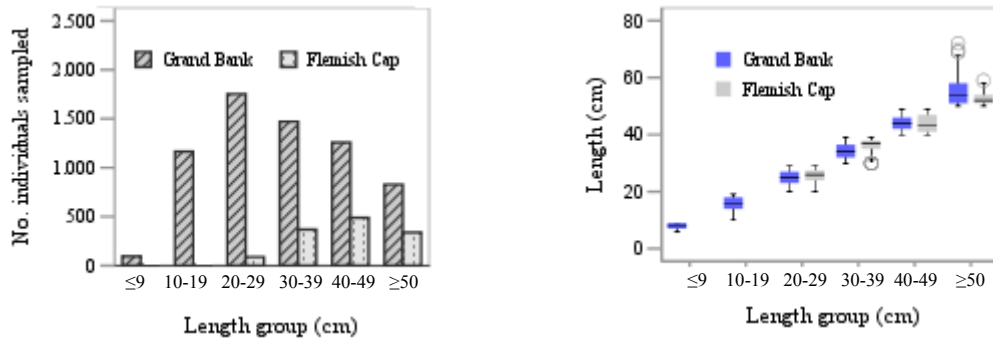


Figure 1. Food habit sampling in the Grand Bank and the Flemish Cap, period 2002-06: no. of individuals sampled (left), and mean length by length class (right).

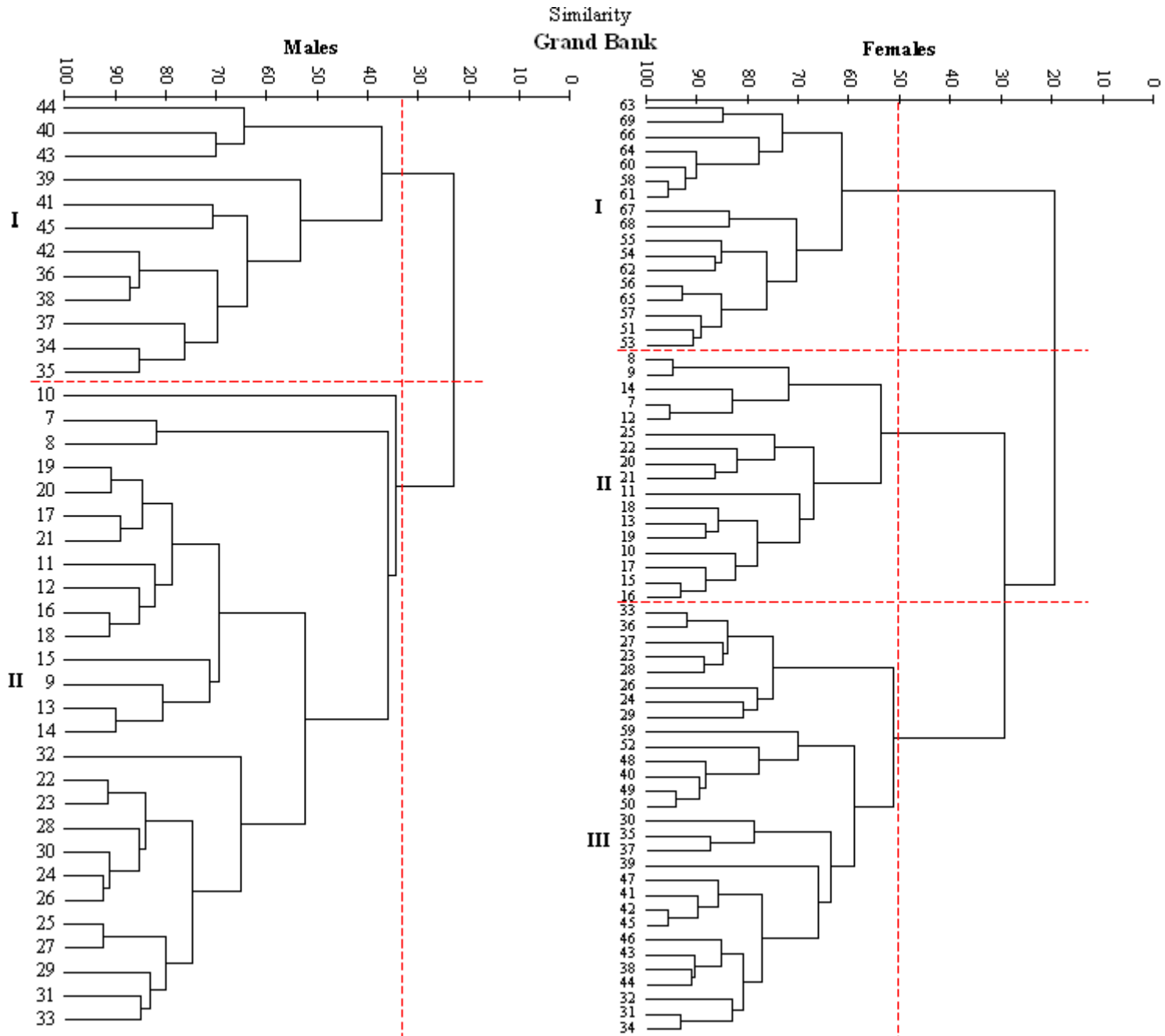


Figure 2. Dendrogram (Bray-Curtis similarity) based on %MPFI values of male and female diets in the Grand Bank.

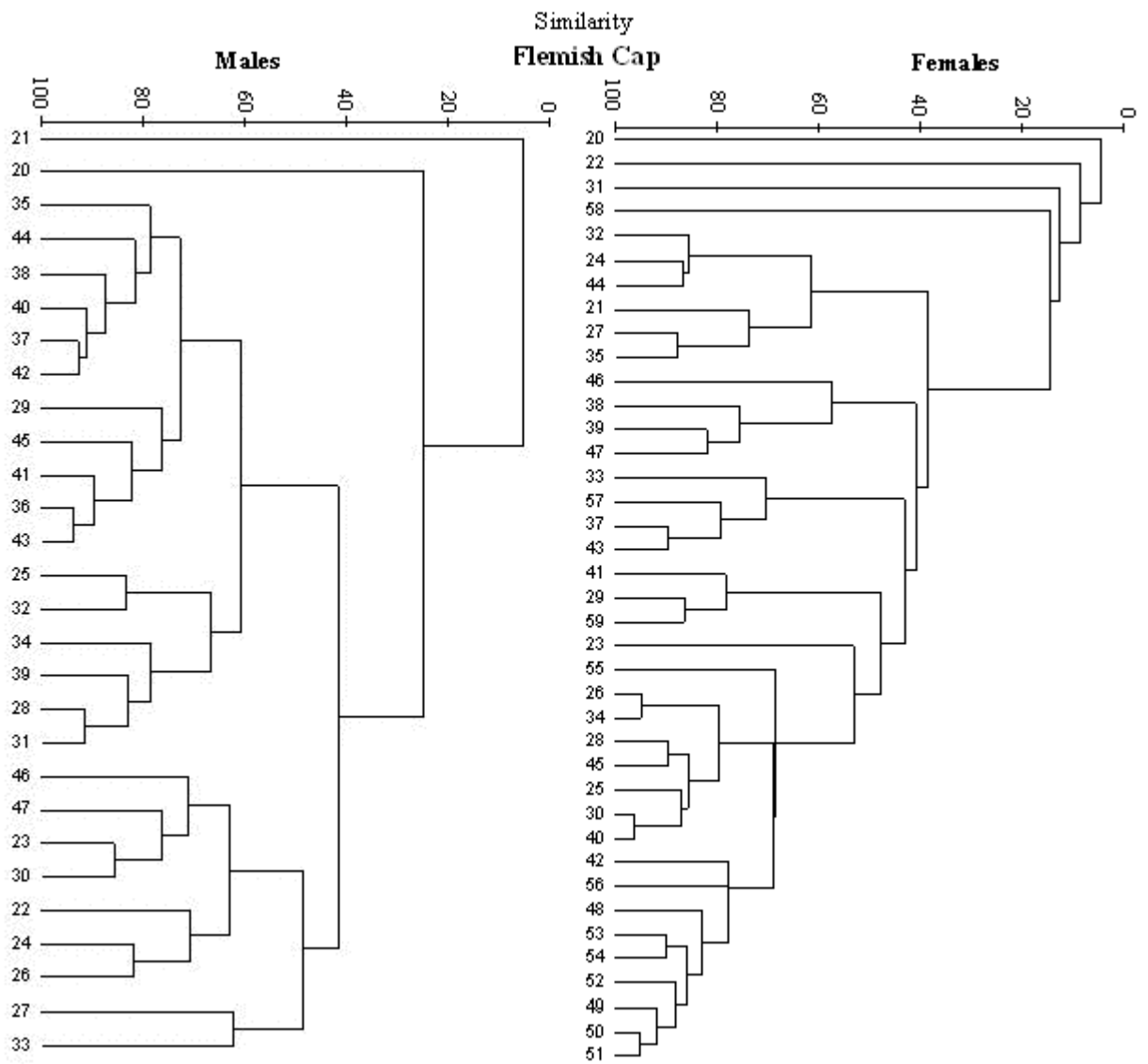


Figure 3 Dendrogram (Bray-Curtis similarity) based on %MPFI values of male and female diets in the Flemish Cap.



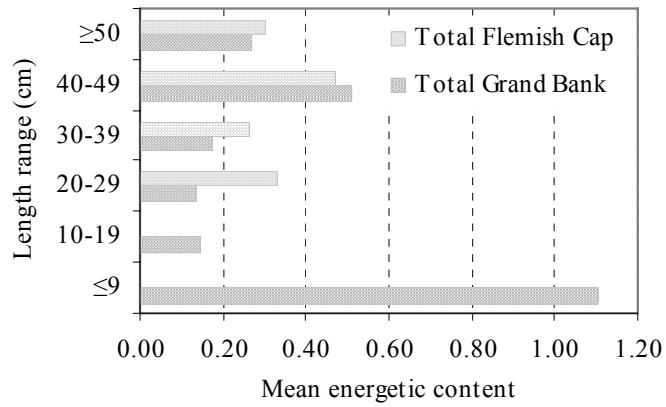


Figure 4. Energy content (energy values of the food consumption in kcal per 100 gr of wet weight of predator) estimated in each area.

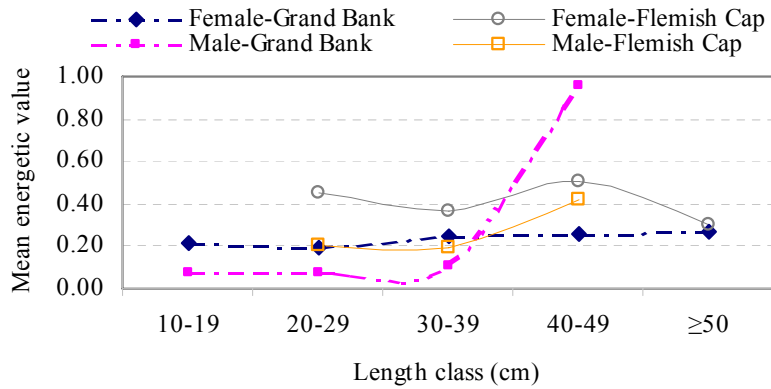


Figure 5. Energy content (energy values of the food consumption in kcal per 100 gr of wet weight of predator) for males and females in each area.