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Food and Feeding Chronology of American Plaice (*Hippoglossoides platessoides*) in the North Atlantic

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**Abstract**

Food and feeding of 5 592 individuals of American plaice (*Hippoglossoides platessoides*, Fabricius) was examined from Grand Bank (NAFO Divisions 3NO), Flemish Cap (NAFO Div. 3M) and Svalbard Area (ICES Div. IIb). Differences in diet composition were observed by areas. Feeding intensity was higher on Flemish Cap (77.6%) and lower in the Svalbard (4.7%). There was significant seasonal feeding variation in the Svalbard, with higher feeding intensity in summer. The main groups of prey were Pisces (46%), Echinodermata (20%), Crustacea (16%) and Mollusca (10%). The prey spectrum was larger in the south of the Grand Bank, the main prey being Pisces (64%), while both on Flemish Cap and in Svalbard the main prey was Ophiuroidea (39%). Feeding pattern indicated that American plaice is a daytime feeder, and no marked differences were noted over a 24 hour period. Low cannibalism intensity was observed on Grand Bank. A greater similitude was present between the diets on Flemish Cap and in Svalbard. Composition and overlapping diet, by length classes, were also analyzed.

| **Key words:** American plaice, food, daily feeding, Grand Bank, Flemish Cap, Svalbard

**Introduction**

American plaice (*Hippoglossoides platessoides*, Fabricius) is an economically and ecologically important flatfish. American plaice or long rough dab (common name in Europe) is an arctic-boreal pleuronectid flatfish that inhabits both sides of the North Atlantic. In the eastern Atlantic, it is found from Iceland and Spitzbergen south to the North Sea, the western Baltic, and as far south as the English Channel. In the western Atlantic, it is common from the outer coast of Labrador, south from Hamilton Inlet, Newfoundland, on the Grand Banks, in the Gulf of St. Lawrence, west and south to Cape Cod. It occurs as far south as Montauk Point, NY (Johnson *et al.*, 1999).

The main interest of this study is the analysis of the feeding habits of American plaice in terms of the geographical and ontogenic differences, besides the study of daily feeding behaviour following on from a previous study (Bruno *et al.*, 2000).

Spatial and temporal variation in food habitats of three populations of American plaice are examined to gain a more in-depth knowledge of changes in diet and habitat during ontogeny, partition food resources between length classes, behaviour and period of activity. Specifically, we set out to gain knowledge of and compare American plaice feeding patterns in three areas of the North Atlantic. A study is also presented of the daily feeding pattern of this species with data from the Grand Bank.

The data presented in this study were collected in the course of several research bottom trawl survey and commercial fishing survey, with scientific observers developing the Observers on Board Plan for Commercial Vessels, by the Instituto Español de Oceanografía.

Survey	Vessel	Dates	Area
Research bottom trawl survey: Platuxa 98	Playa de Mendiña	06 – 26 May 1998	Grand Bank
Research bottom trawl survey: Platuxa 02	Vizconde de Eza	29 April – 19 May 2002	Grand Bank
Research bottom trawl survey: Flemish Cap 98	Cornide de Saavedra	17 July- 02 Aug. 1998	Flemish Cap
Research bottom trawl survey: Flemish Cap 01	Cornide de Saavedra	03 - 20 July 2001	Flemish Cap
Research bottom trawl survey: Flemish Cap 02	Cornide de Saavedra	30 June - 17 July 2002	Flemish Cap
Research bottom trawl survey: Fletán Ártico 01	Garoya Segundo	03 – 26 October 2001	Svalbard
Research bottom trawl survey: Fletán Ártico 02	Garoya Segundo	05 – 27 October 2002	Svalbard
Commercial fleet: Pair trawl, targeting cod	León Marco V	01 May – 24 July 2002	Svalbard
Commercial fleet: Targeting shrimp	Garoya Segundo	31 Oct. – 24 Nov. 2001	Svalbard
Commercial fleet: Targeting shrimp	Garoya Segundo	03 Nov. – 06 Dec. 2002	Svalbard

### Materials and Methods

In the south area of the Grand Bank (NAFO Div. 3NO), 3165 individuals were sampled in April and May in samplings taken in 1998 and 2002; in the Flemish Cap area (NAFO Div. 3M), 630 individuals were sampled in July and August in samplings taken in 1998, 2001 and 2002; and in the Svalbard area (ICES IIb), 1797 individuals were sampled in June, October, November and December in samplings taken in 2001 and 2002 (Fig.1). Data were compiled and analyzed different years in each area. Table 1 presents the characteristics for the individuals sampled in each geographic area, year and size range, including month, mean depth (m), mean size (cm), mean weight (g), number of individuals and weight of stomach contents (g).

Data were compiled for this study on the feeding habits of American plaice as a stratified sampling by size range of the fishes. To do so, size groups of 10 cm each were established (0-9, 10-19, 20-29, 30-39, 40-49 and  $\geq 50$  cm). In some geographic areas, it was not possible to collect individuals from all the size ranges, or alternatively, a number less than that required was collected. Food contents was analyzed on board, except in the Platuxa 98 Research Survey (Grand Bank) and on the commercial fishing survey targeting cod, *Gadus morhua* (Svalbard) in 2002. On these two occasions, stomachs were subsequently collected, frozen and analyzed at the laboratory of the Instituto Español de Oceanografía in Vigo.

The data collection for the daily feeding behaviour study was carried out on Grand Bank (Platuxa 98 Research Survey). Five time periods were considered (dawn, midday, afternoon, dusk and night). Samples were taken from 19 to 27 May in 1998, until gathering 50 individuals picked up at random in each size range and time period. The  $\geq 50$  cm range has less individual number in some time periods. However, we prefer to maintain this size groups, due to the interest on the knowledge of their behaviour. In this study, we considered one less time period –morning, than in the same study carried out the previous year, due to the necessity of adapting to the survey schedule and their main objectives. The morning interval was included in midday. We sampled 928 individuals (Fig. 2). The main characteristics of the haul and individual sampled are showed in the Tables 2 and 3, respectively. The data of the individuals sampled for the daily feeding behaviour study were also included in the feeding habit study.

Regurgitated individuals were not taken into consideration. Data from each individual collected on board the vessel were on size (TL to the nearest lower cm), sex, maturity and degree of stomach repletion. Weight of the fish in some of samplings was calculated according to the length-weight relationship with the data on samplings obtained in the respective survey.

Subsequently at the laboratory, when the stomachs were collected and frozen, they were then thawed out, having removed any liquid, proceeding to separating, identifying and weighing the different preys at the lowest taxonomic level possible. With these wet weights, the total stomach content weight for each stomach and the percentage in weight for each type of prey were calculated.

### Data analysis

In the quantitative diet analysis, gravimetric methods were used on prey items (Hannson, MS 1980; Hyslop, 1980; Amezcaga, 1988; Cortés, 1997). This measurement was expressed as a weight percentage of each prey item of the

total weight of stomach contents by each size range ( $\%W_{pi}$ ) or by each time period ( $\%W_{pt}$ ). In this manner, we analyzed predator preferences in terms of size or the different periods of the day. These measurements reflect dietary nutritional value (Macdonald *et al.*, 1983).

$$\%W_{pi} = w_{pi} / W_{ti} \times 100$$

$\%W_{pi}$  was the percentage in weight (gr) of the prey item  $p$  in the size range  $i$ .

$w_{pi}$  was the weight (gr) of the prey item  $p$  in the size range  $i$ .

$W_{ti}$  was the weight (gr) of total preys in the size range  $i$ .

$$\%W_{pt} = w_{pt} / W_p \times 100$$

$\%W_{pt}$  was the percentage in weight (gr) of the prey item  $p$  in the time period  $t$ .

$w_{pt}$  was the weight (gr) of the prey item  $p$  in the time period  $t$ .

$W_p$  was the total weight (gr) of prey item  $p$  in the overall time periods.

The Feeding Intensity Index (FI) and Mean Weight Fullness Index (MWFI) were calculated to analyze the feeding intensity for each size range and for each period of the day in the daily feeding behaviour study.

- Feeding Intensity Index (FI): percentage of individuals with stomach content.

$$FI_{ti} = (n_{ti} / N_{ti}) \times 100$$

$n_{ti}$  was the number of individuals with stomach content in size range  $i$  (and time period  $t$ ).

$N_{ti}$  was the total number of individuals sampled in size range  $i$  (and time period  $t$ ).

- Mean Weight Fullness Index (MWFI): weight percentage of stomach content weight in terms of predator weight. This index reduces the effect of predator size on stomach content weight.

$$MWFI_{ti} = \Sigma [(Pc_{pti} / Pt_{pi}) \times 100]$$

$Pc_{pt}$  was the stomach content wet weight of the individual  $p$ , in the size range  $i$  (and time period  $t$ ).

$Pt_{pi}$  was the wet weight of individual  $p$ , in the size range  $i$  (and period  $t$ ).

Differences in feeding intensity by fish size, month, area were tested by  $\chi^2$ . Differences in mean weight fullness index were tested by the Kruskal-Wallis test. All statistical inferences were based on the 0.05 significance level.

The degree of diet overlap was measured by using the Simplified Morisita's Index ( $C_{jk}$ ) (Horn, 1966; Krebs, 1989; Hall *et al.*, 1990) – based on %W. This index is used when resources are expressed as proportions (Caillet *et al.*, 1979; Cortés, 1997). Also in this index, the quantitative measures not influenced by the number of food categories considered.  $C_{jk}$  vary between 0 (no categories in common) and 1 (identical categories). Overlap is generally considered to be a biological significant when the value exceeds 0.60 (Zaret *et al.*, 1971; Wallace, 1981). We used  $C_{jk}$  to measure the diet overlap between size classes by inter and intra-area and overall diet by area, without considering length classes.

$$C_{jk} = \frac{2 * \sum_{i=1}^s w_{ij} \times w_{ik}}{\sum_{i=1}^s w_{ij}^2 + \sum_{i=1}^s w_{ik}^2}$$

$C_{jk}$  was the Simplified Morisita's Index for predators  $j$  and  $k$ .

$j, k$  was the groups (size classes or area).

$w_{ij}$  was the proportion of food category  $i$  in the diet of predator  $j$ .

$w_{ik}$  was the proportion of food category  $i$  in the diet of predator  $k$ .

$s$  was the number of food category.

In order to analyze the differences in feeding times over a 24-hour period and to interpret if there is a daily feeding cycle (Jenkins *et al.*, 1977) in this species, differences in feeding intensity and mean weight fullness index by size range and time period were tested by  $\chi^2$  and Kruskal-Wallis test respectively. All statistical inferences were based on the 0.05 significance level.

## Results

### Feeding intensity

The percentage of individuals with stomach content (Feeding Intensity Index, FI) was far higher on Flemish Cap (77.6%), followed by Grand Bank (42.1%), while in Svalbard this was far lower (4.7%) (Table 1 and Fig. 3).

**Feeding intensity in relation to size classes, month and area.** On Grand Bank, the feeding intensity falls as the size rises to the maximum (75%) in 0-9 cm, and the minimum (36%) in  $\geq 50$  cm (Table 4), with a significant variation with size ( $\chi^2 = 54.47$ , d.f. 5,  $p < 0.0001$ ). On Flemish Cap, all the ranges presented a high FI (ranging from 69% to 100%), and in Svalbard quite the opposite was observed (ranging from 3% to 16%). None of these two areas showed a clear tendency in the FI value in terms of size (Tables 5, 6 and Fig. 3), and only the FI in Svalbard showed significant differences in size ( $\chi^2 = 17.94$ , d.f. 4,  $p < 0.005$ ).

In Svalbard samplings were taken in June, October, November and December, the June FI being far higher (89%) than in the autumn and winter months (Table 6), with significant differences for the three higher ranges ( $\chi^2 = 265.47$ , 347.52 and 36.77, d.f. 2, 3 and 2,  $p < 0.0001$ ).

### Mean Weight Fullness Index

The highest MWFI values were recorded on Flemish Cap (0.44%), and the lowest were in Svalbard (0.04%) (Table 1, Fig. 4).

**Mean Weight Fullness Index in relation to size classes, month and area.** On Grand Bank, the maximum MWFI corresponded to the 0-9 cm group (2.00%), and the lowest in 20-29 cm (0.28%) (Table 4). These differences between size ranges were significant ( $\chi^2 = 76.141$ , d.f. 5,  $p < 0.0001$ ). On Flemish Cap, the maximum corresponded to 10-19 cm (0.77%) and the minimum to the 40-49 cm range (0.38%) (Table 5). In this area, no significant differences in MWFI appeared between size ranges. Finally, in Svalbard (Table 6), the maximum corresponded to  $\geq 40$  cm (0.47%) and the minimum to 20-29 cm (0.02%). In this area, the MWFI was significantly different between the size ranges ( $\chi^2 = 19.66$ , d.f. 4,  $p < 0.001$ ) and this was also the case for the sampling month ( $\chi^2 = 741.01$ , d.f. 3,  $p < 0.0001$ ) with the maximum in June (0.75%) and the minimum in October (0.11%).

### Food

Considering the three areas as a whole, the large groups of prey found in the stomach contents of American plaice were Pisces (46%, 73% of which was northern sand lance, *Ammodytes dubius*), Echinodermata (20%, 72% of which was Ophiura), Crustacea (16%) and Mollusca (10%, 96% of which was Bivalvia). By areas, the most important groups of prey on Grand Bank were Pisces (64%), Bivalvia (14%), Echinoidea (7%) and Decapod Crustacea (4%). The most important groups of prey on Flemish Cap were Ophiuroidea (39%), Amphipoda and Decapod Crustacea (16% and 12%, respectively), Ctenophora (15%) and Pisces (6%). The most important groups of prey in Svalbard were Ophiuroidea (39%), Pisces (10%), Decapod Crustacea (8%) and offal (fishing processed remnant, 25%).

### Diet composition in relation to size classes by area

**Grand Bank.** The most important preys in the 0-9 cm range were the small crustaceans (gammaridean amphipods and copepods, 38 and 27%, respectively) and polychaetes (14%); in the 10-19 cm range the small crustaceans were, once again, the most important preys (mysids and gammaridean amphipods, 45 and 25%); in the 20-29 cm range, the most important were the mysids (34%), and northern sand lance (22%). Fishes were the most important preys in the 30-39 and 40-49 cm ranges, accounting for 80% and 84%, respectively, especially northern sand lance (52 and 67%, respectively); in the  $\geq 50$  cm range, the most important were bivalves (*Lutraria*, 28%), northern sand lance (27%) and sand dollars, *Echinarachnius parma*, (12%). The phenomenon of cannibalism only occurred in the 20-29 cm group, accounting for only 1% of stomach contents (Table 4 and Fig. 5).

**Flemish Cap.** The most important preys in the 10-19 cm range were snake blenny, *Lumpenus lampretaeformis*, (86%), and mysids (14%); in the 20-29 cm range were the ophiuroids (23%) and northern shrimp, *Pandalus borealis*, (21%). In the 30-39 and 40-49 cm ranges, the most important preys were the ophiuroids (50% and 51%, respectively). Nevertheless, the following were the most important, in order, in the 30-39 cm range: snake blenny (10%) and northern shrimp (9%), whereas in the 40-49 cm range, the most important were the hyperids (23%); in the  $\geq 50$  cm range, the most important were Ctenophora (33%) and ophiuroids (24%) (Table 5 and Fig. 5).

**Svalbard.** In this area, we noted a far smaller spectrum of prey than in the other two areas. The most important preys in the 0-9 cm range were crustaceans (63%) (due to their state of digestion, they were not classified, but they may have been Natantia) and polychaetes (13%); crustaceans were also the most important preys in the 10-19 cm group (decapods and amphipods, 55 and 23%, respectively) and polychaetes (16%); in the 20-29 cm range the most important were the ophiuroids (50%) and decapod crustaceans (17%); in the 30-39 and 40-49 cm ranges, the most important preys were the ophiuroids (34 and 46%, respectively) and offal (20 and 43%, respectively). The Pisces were only present in two ranges, 20-29 and 30-39 cm (5% and 16% respectively) (Table 6 and Fig. 5).

The greatest abundance in prey weight from the individuals captured was in June. In that month, ophiuroids (61%) and polychaetes (6%) predominated; in October, there was less stomach content but more crustaceans (37%), fishes (37%) and bivalve molluscs (20%); with a higher percentage of ophiuroids (12%) in November. Remains of fishing processed also appeared in stomach contents in June (23%) and November (70%) in considerable quantities.

#### **Diet composition in relation to time period on Grand Bank**

The Pisces appeared in stomach contents in all periods, and their presence was basically limited to northern sand lance. This prey appeared at all times of the day, although the highest percentages appeared in the afternoon and at night (36% and 31%, respectively), with the minimum at dusk (4%). In almost all periods, however, we found digested fishes, and assumed that a substantial part could be northern sand lance. The other fishes present in the stomach contents did not appear at all times of the day. Capelin (*Mallotus villosus*) appeared at midday and dusk; sculpin (*Triglops sp*) appeared at all times except at dusk; and American plaice at dawn and midday (Table 7 and Fig. 6).

Bivalvia practically only appeared from dawn to the afternoon with the maximum (48%) at dawn, decreasing in other time periods. Sand dollars appeared in the same time periods in terms of the latter with the maximum (53%) in the afternoon. However, the ophiuroids only appeared at midday (68%) and dusk. Snow crab (*Chionoecetes opilio*) appeared mainly at dusk and night (47% and 48%, respectively).

Some small crustacean appeared at all day times, gammaridean amphipods and mysids, in a higher percentage at midday (85%) and in the afternoon (44%) respectively; cumaceans only appeared at dawn and midday (92%); Caprellidae appeared at midday and in the afternoon (86%); isopods appeared from dawn to dusk (maximum at dusk, 49%); and crustacean larvae appeared from the afternoon to night (maximum in the afternoon, 79%).

Finally, the polychaetes and cnidarians appeared at all times of the day, although with a more marked presence at midday (62%) and at dawn (74%) respectively (Table 7 and Fig. 6).

#### **Feed overlapping**

The Simplified Morisita's Index ( $C_{jk}$ ) used to compare the total preys for each area, without taking into consideration the size classes, showed overlapping between the diets on Grand Bank with Flemish Cap ( $C_{jk} = 0.63$ ), and between the diets on Flemish Cap with Svalbard ( $C_{jk} = 0.75$ ) (Table 8).

When comparing the same size ranges in the three study areas, the size ranges presenting overlap were: 20-29 cm ( $C_{pk} = 0.64$ ), 30-39 cm ( $C_{pk} = 0.84$ ), and 40-49 cm ( $C_{pk} = 0.65$ ) on the Flemish Cap with Svalbard (Table 8).

Comparison between all the size classes in each area showed a high overlap on Grand Bank between 30-39 / 40-49 cm ( $C_{pk} = 0.99$ ) and a lower overlap between 10-19 / 20-29 cm ( $C_{jk} = 0.74$ ), 20-29 / 30-39 cm ( $C_{jk} = 0.67$ ), and 20-29 / 40-49 cm ( $C_{jk} = 0.62$ ).

On Flemish Cap we also found a high overlap between 30-39 / 40-49 cm ( $C_{pk} = 0.90$ ), and a lower overlap between 20-29 / 30-39 ( $C_{jk} = 0.64$ ), 30-39 /  $\geq 50$  cm ( $C_{jk} = 0.61$ ), and 40-49 /  $\geq 50$  cm ( $C_{jk} = 0.65$ ).

In Svalbard, a fairly high overlap occurred between 20-29 / 30-39 cm ( $C_{pk} = 0.81$ ), and 30-39 / 40-49 cm ( $C_{pk} = 0.81$ ), and slightly less between 20-29 / 40-49 cm ( $C_{jk} = 0.68$ ) (Table 9).

### Daily feeding pattern

Feeding intensity values in general reached a maximum FI during the dawn-midday-afternoon periods, whereas the minimum was recorded at dusk. The 20-29 cm range reached its maximum (78%) in the afternoon and the minimum at night (42%); furthermore, this range showed less variation in feeding intensity over the 24 hour period than the other ranges. The 30-39 cm range reached its maximum FI at midday (76%); the 40-49 cm group reached its maximum at night (52%), although at midday it presented a high FI (50%); the  $\geq 50$  cm range reached its maximum FI (60%) at dawn. These latter three ranges presented the lowest FI at dusk, which fluctuated from 12 to 30% (Fig. 7).

The FI values for the size ranges and times periods showed significant differences in all the size ranges, with the exception of the 40-49 cm group ( $\chi^2 = 6.38$ , d.f. 4,  $p > 0.05$ ). The other three size classes showed significant differences in the FI values over the 24 hour period: the 20-29 cm group ( $\chi^2 = 15.21$ , d.f. 4,  $p < 0.05$ ), 30-39 cm ( $\chi^2 = 23.78$ , d.f. 4,  $p < 0.001$ ), and  $\geq 50$  cm ( $\chi^2 = 23.39$ , d.f. 4,  $p < 0.001$ ).

In terms of the MWFI, we noted that the maximum values correspond to the night period in all ranges (0.64% in the 30-39 cm group; 0.75% in 40-49 cm, and 0.93% in  $\geq 50$  cm), except in the 20-29 cm range whose maximum occurred at midday (0.43%), with minimum values at dusk for all the ranges with values from 0.10% to 0.25% (Fig. 8).

We noted significant differences in the MWFI values in all size ranges, with the exception of the 40-49 cm group ( $\chi^2 = 7.694$  df = 4,  $p > 0.05$ ). The other three showed significant differences in the MWFI values over the 24 hour period: 20-29 cm ( $\chi^2 = 13.25$ , d.f. 4,  $p < 0.05$ ), 30-39 cm ( $\chi^2 = 23.49$ , d.f. 4,  $p < 0.001$ ), and  $\geq 50$  cm ( $\chi^2 = 19.74$ , d.f. 4,  $p < 0.001$ ).

### Discussion

In this study, we compared three distribution areas of American plaice, finding differences in the food and feeding. These differences may be due to geographical reasons but also to seasonality. On Flemish Cap, a high feeding intensity was noted, as occurred in Svalbard in June. Both cases were sampled in summer. In a study on long rough dab (American plaice) in the North Sea, Ntiba *et al.* (1993) noted that lowest feeding intensity occurred in December-January (31%), with the maximum in May (90%) to July. These same characteristics were found on Flemish Cap; Rodríguez-Marín *et al.* (1994) observed 83% FI in summer, as opposed to 6% in winter; Konstantinov *et al.* (1985) found an 86-94% FI in summer. The same seasonal behaviour in feeding intensity was found in the south of Grand Bank (Zamarro, 1992) with a maximum in April-September and a minimum in October-February. In the study on Grand Bank, Pitt (1973) found a higher proportion of empty stomachs in February and March.

This same characteristic was observed in Sable Island Bank (Martell *et al.*, 1994), with samplings taken in February (FI=36%) and June (FI=86%). Pedersen *et al.* (1991) found 68% of individuals with stomach content in his study in West Greenland waters conducted from June to November.

Other studies note this generalized seasonal nature throughout the distribution of American plaice in the West Atlantic (Johnson *et al.*, 1999) with periods of lower feeding intensity in January and February, increasing until May-September; this fact would allow for a higher degree of feeding in summer for generating energy for metabolic use and gonad maturation.

In our study, the FI values are in agreement with the MWFI values obtained. These results may reflect this seasonal behaviour, with greater feeding intensity in the summer months (samplings on Flemish Cap, and those in June in Svalbard). A slightly lower feeding intensity occurs in spring (samplings on Grand Bank) and finally, a far lower feeding intensity in the winter months (samplings in Svalbard). In these results, we should also take into

consideration the fact that they were taken in different years, which may lead to significant inter-annual changes, as described by other authors (Pitt, 1973; Link *et al.*, 2002) that are not dealt in this study.

The analysis of feeding intensity and the mean weight fullness index showed a relationship with the size, decreasing with the increase of size, but with a slight increase in the larger sizes, particularly on Flemish Cap and Svalbard. In the area where feeding intensity was high (Flemish Cap), the differences in these indices between the size ranges were less and not significant.

Diet composition presented a greater prey diversity on Grand Bank and a small spectrum in Svalbard. American plaice diet in the three areas was different, although this species preys on the same large groups of prey, the importance of these in each area varied. Pisces was the dominant group on Grand Bank (64% in weight) with a large difference over other prey. Ophiuroidea was the main group, both on Flemish Cap and in Svalbard.

The most abundant species of Pisces varied according to the area. On Grand Bank, the main species was northern sand lance, followed by capelin but with considerably less importance. On Flemish Cap, snake blenny was the most important species; and in Svalbard, blue whiting (*Micromesistius poutassou*) and haddock (*Melanogrammus aeglefinus*) were the most important fish species. The Echinodermata group mostly comprised Echinoidea (sand dollars) on Grand Bank, as opposed to the Ophiuroidea (mainly brittle stars) in the other two study areas. The bivalve molluscs also presented differences according to the areas, with *Lutraria* predominating on Grand Bank, with the considerable presence of Pectinidae in Svalbard, or the scarce importance of this group on Flemish Cap. On Grand Bank, the main decapod crustacean was the snow crab, and on Flemish Cap and Svalbard it was northern shrimp. This variation reflects the geographic distribution and availability of the possible preys, and so, American plaice will consume the more abundant and accessible preys.

Variation in the specific distribution of prey not only appears when studying the distant geographic areas as in our study; this variation is also present in more immediate geographic areas (Pitt, 1973; Scott, 1973; Klemetsen, 1993; Ntiba *et al.*, 1993; Johnson *et al.*, 1999; Bowman *et al.*, 2000). Some of these studies, however, indicate the variation in specific prey without affecting the general pattern of predation in the larger taxonomic groups.

Geographic variation in diet may influence the differences in growth rates, the size of first maturation and the  $L_{\infty}$  observed in the different areas concerned. This fact would be influenced by the differences in the energy content of the different preys (Steimle *et al.*, 1985; Lawson *et al.*, 1998). American plaice presented a higher growth on Flemish Cap than on Grand Bank (Zamarro, 1992), and differences in growth were observed in the individuals from different areas on Grand Bank (Pitt, 1967b). Growth rates are higher and maturity is reached earlier in the southern areas of Northwest Atlantic (Scotian Shelf, Gulf of Maine) than in the north (Johnson *et al.*, 1999). Bowering *et al.* (1994), however, found similar sizes at 50% maturity on Flemish Cap to those for American plaice in other areas of the Northwest Atlantic, although the ages at 50% maturity were considerably lower.

In this study, we found cases of cannibalism, although only on Grand Bank and in the 20-29 cm range. This fact is in line with the study by Ntiba *et al.* (1993) where this feeding phenomenon appeared in individuals larger than 10 cm and progressively decreased with size.

In Svalbard, one of the prey items appearing in sizes  $\geq 30$  cm was the offal from the fishery activity. This fact shows the “opportunistic” nature as this food is more available and “easy” to obtain.

Diet presents changes in size. On Grand Bank, sizes <10 cm exclusively fed of polychaetes and small crustaceans; sizes from 10 to 30 cm mostly preyed on “soft” and “small” preys (cnidarians, polychaetes, mysids, copepods, gammaridean amphipods, hyperids); the intermediate sizes (from 30 to 49 cm) practically fed on fishes; sizes  $\geq 50$  cm mostly fed on “hard” and larger size preys (snow crab, echinoderms, bivalve molluscs). The spectrum of preys in the  $\geq 50$  cm size range was less than for the other ranges, and the importance in weight was still focussed on a lower number of prey. In Svalbard, the sizes <20 cm almost exclusively fed on polychaetes and small crustaceans (mainly *P. borealis*); the 20 to 39 cm size have a more varied diet including northern shrimp, ophiuroids and fishes as the most important preys; the  $\geq 40$  cm sizes feed on “hard” preys. This behaviour has been well recorded in numerous studies conducted in different locations (Pitt, 1973; Scott, 1973; Martell *et al.*, 1992; Zamarro, 1992; Rodríguez-Marín *et al.*, 1994; Johnson *et al.*, 1999; Methven, 1999; Link *et al.*, 2002). Morphology, form and size of the mouth, ontogenetic changes, the size of food in relation to fish and habitat characteristics during the larval,

juvenile and adult phases are determining factors in feeding, as witnessed in different species (De Groot, 1971; Labropoulou *et al.*, 1997; Labropoulou *et al.*, 1999; Bruno *et al.*, 2000).

In our study, this feeding pattern was not clearly noted on Flemish Cap, showing a greater homogeneity in presence and percentages of prey per size ranges than the other two areas studied. All size ranges fed on “soft” and “hard” preys in this area.

Seasonality is another factor that affects to the diet (Klemetsen, 1993; Martell *et al.*, 1994). In some studies, although, the seasonality causes more quantitative than qualitative variation (Pitt, 1973; Scott, 1973). These diet seasonal changes would reflect the habit changes, both in predators and in preys. In our study, only the samplings taken in Svalbard covered different seasons of the year, and thus showed seasonal variation.

Diet overlap indicated a considerable difference between the diets in individuals on Grand Bank as distinct from in Svalbard, and a greater proximity in the diets on Flemish Cap and Svalbard. In terms of overlapping between size ranges, in all areas, overlap occurs from the intermediate sizes and larger (from 10 to 49 cm on Grand Bank, from 20 to  $\geq 50$  cm on Flemish Cap and from 20 to 49 cm in Svalbard). The most considerable overlap was between 30-39 and 40-49 cm ranges in all areas. When comparing the diets in the same ranges, in different areas, we found that on Grand Bank and on Flemish Cap diet overlap does not appear among individuals of the same size range.

Traditionally, American plaice is considered a specialist species, fully depending on the benthos for eating, as shown in various studies on Flemish Cap (Rodríguez-Marín, 1995; Torres *et al.*, 2000), on the continental shelf off USA and parts of Canada (Link *et al.*, 2002). American plaice, however, is also able to feed on a wide variety of types of prey (Langton *et al.*, 1990; Methven, 1999) and for this reason, we must consider that this speciality varies with size, area and season.

#### *Feeding chronology*

On Grand Bank, predation on different types of prey was not the same for the different time periods of the day. Cnidarians were most preyed on at dawn; bivalve molluscs from dawn to midday; polychaetes at midday; ophiuroids from midday to the afternoon; the different crustaceans varied from dawn to night; and the different fishes present in the diet presented different times for catching. This fact may reflect the different behaviour patterns (habits, movements) both in American plaice and in the preys. In our study, the benthic fauna and fauna living in the sediment or the fauna with small movements were the most preyed on with light, and the pelagic or benthopelagic fauna were preyed on at different time periods.

Boujard *et al.* (1992) considers that there is evidence to indicate that fish activity follows a circadian rhythm. It is synchronized by the alternation of light/dark. Our results show that American plaice is a daytime feeder, although we must not overlook the fact that feeding intensity at night-dawn was not excessively low, only diminishing considerably at dusk. Similar results were obtained by analyzing the mean weight fullness index, although this index shows a high value in all size ranges at night time. The 40-49 cm range was the only one with no significant differences in the values of these two indices throughout the periods considered.

Beamish (1966) and Pitt (1967a) suggested that American plaice are daytime feeders, as indicated by differences in diel catch and feeding rates, although Casey *et al.* (1998) reached different conclusions. Zamarro (1992), when studying individuals measuring over 40 cm in the south of Grand Bank, observed that this species preferably feeds during the day and that its behaviour shows a flexible timetable to feed off its prey when they are more accessible. Ntiba *et al.* (1993) in his study of daily feeding pattern in the western central North Sea at North Shields, found that feeding intensity increased from morning to dusk, peaking in the afternoon. But this study only considered three size ranges (10-14, 15-19 and 20-24 cm). Bruno *et al.* (2000) obtained similar results in their study on Grand Bank, analyzing the FI values, but only found significant differences in the 30-39 and 40-49 cm ranges. In our study, the results varied slightly in terms of the latter, particularly at dusk. We found that the midday-afternoon period had a greater feeding intensity for all ranges, reaching the minimum at dusk.

Other biological aspects inter-related with those previously dealt with are present, such as sex and maturity. These would cause, or rather, would explain, changes in food and feeding intensity and, therefore, should be considered. Some studies on American plaice have already dealt with aspects such as density-dependent effects on temperature



preference; the sex-specific temperature distribution and its relation to age and abundance with females distributed in warmer waters (Swain *et al.*, 1996; Swain, 1997; Swain *et al.*, 2001); the seasonal distribution (Morgan *et al.*, 1991); the time and location of spawning (Morgan, 2001); the distribution at non-habitual depths (Iglesias *et al.*, 1996); the abundance and surficial sediments (McConnaughey *et al.*, 2000); rates of digestion of different preys (MacDonald *et al.*, 1982). This all assumes a combination of factors (geographic distribution, depth, temperatures and competence), which lead to changes in habits, both in the predator and in the preys in the course of their life history, factors which may change inter-annually. All this points suggest to continue studying feeding in the long term.

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TABLE 1. Area, month, mean depth (m), size range (cm), mean weight  $\pm$  Standard Deviation (g), number of individuals sampled, Feeding Intensity Index (FI), weight of stomach contents (g), and Mean Weight Fullness Index (MWFI) of American plaice sampled.

Area	Month (n° indiv.)	Mean Depth (m)	Size range (cm)	Mean size (cm)	Mean weight $\pm$ SD (g)	No indiv. sampled	FI (%)	Weight stom. cont. (g)	MWFI (%)
Gand Bank (3NO) 1998	May (928)	44	20 - 29	27 $\pm$ 2	163.2 $\pm$ 35.3	250	58.4	98.20	0.263
			30 - 39	35 $\pm$ 3	367.2 $\pm$ 104.4	250	50.8	349.90	0.322
			40 - 49	43 $\pm$ 3	740.9 $\pm$ 156.6	250	44.4	1041.89	0.575
			$\geq 50$	54 $\pm$ 4	1649.5 $\pm$ 472.7	178	44.9	993.90	0.351
			<i>Total</i>	39 $\pm$ 1	658 $\pm$ 576.2	928	50.0	2483.89	0.380
2002	April (128)	234	0 - 9	8 $\pm$ 1	4.7 $\pm$ 1.7	8	75.0	0.64	2.002
			10 - 19	15 $\pm$ 3	28.4 $\pm$ 15.5	428	56.3	52.89	0.509
	May (2109)	20 - 29	24 $\pm$ 3	115.6 $\pm$ 41.5	653	37.8	214.90	0.283	
		30 - 39	35 $\pm$ 3	373.4 $\pm$ 104.7	478	33.7	667.68	0.346	
		40 - 49	44 $\pm$ 3	812.1 $\pm$ 188.4	466	33.3	1498.40	0.391	
		$\geq 50$	54 $\pm$ 4	1571.3 $\pm$ 484.1	204	28.4	740.48	0.261	
<i>Total</i>	32 $\pm$ 1	431.4 $\pm$ 491.8	2237	38.8	3174.98	0.366			
<b>Total</b>						<b>3165</b>	<b>42.1</b>	<b>5658.88</b>	<b>0.370</b>
Flemish Cap (3M) 1998	July (104) August (37)	236	20 - 29	26 $\pm$ 3	162.1 $\pm$ 61.0	11	81.8	15.68	0.887
			30 - 39	36 $\pm$ 2	456.5 $\pm$ 73.7	49	89.8	241.65	1.076
			40 - 49	44 $\pm$ 3	838.5 $\pm$ 214.3	66	89.4	439.90	0.803
			$\geq 50$	52 $\pm$ 1	1493.3 $\pm$ 130.4	15	93.3	212.21	0.957
			<i>Total</i>	41 $\pm$ 7	722.64 $\pm$ 380.3	141	89.4	909.44	0.921
2001	July (320)	179	10 - 19	17 $\pm$ 3	50.6 $\pm$ 20.4	5	100	1.95	0.767
			20 - 29	26 $\pm$ 3	172.8 $\pm$ 53.2	16	50.0	12.42	0.420
			30 - 39	37 $\pm$ 2	474.8 $\pm$ 85.6	90	71.1	78.51	0.202
			40 - 49	44 $\pm$ 3	850.0 $\pm$ 216.6	118	76.3	150.48	0.147
			$\geq 50$	52 $\pm$ 2	1485.6 $\pm$ 178.9	91	68.1	556.42	0.418
<i>Total</i>	43 $\pm$ 8	878.9 $\pm$ 464.3	320	71.6	799.78	0.263			
2002	July (169)	199	20 - 29	28 $\pm$ 2	203.0 $\pm$ 46.9	5	100	3.74	0.402
			30 - 39	36 $\pm$ 3	459.1 $\pm$ 109.2	41	65.9	54.62	0.324
			40 - 49	45 $\pm$ 3	926.5 $\pm$ 260.0	77	84.4	317.54	0.385
			$\geq 50$	52 $\pm$ 2	1474.5 $\pm$ 214.1	46	80.4	284.13	0.411
			<i>Total</i>	44 $\pm$ 7	940.8 $\pm$ 443.5	169	79.3	660.03	0.378
<i>Total</i>						<i>630</i>	<i>77.6</i>	<i>2369.25</i>	<i>0.441</i>
Svalbard (IIb) 2001	Octob. (791) Novemb. (259)	562	0 - 9	8 $\pm$ 1	3.7 $\pm$ 1.2	44	6.8	0.03	0.019
			10 - 19	15 $\pm$ 3	26.7 $\pm$ 14.4	120	0.8	0.05	0.002
			20 - 29	26 $\pm$ 2	164.1 $\pm$ 45.4	472	2.1	6.15	0.009
			30 - 39	34 $\pm$ 3	408.4 $\pm$ 118.7	392	1.3	15.75	0.013
			$\geq 40$	41 $\pm$ 1	730.3 $\pm$ 100.5	22	4.5	7.50	0.045
<i>Total</i>	27 $\pm$ 8	244.8 $\pm$ 179.3	1050	1.9	29.48	0.011			
2002	June (44) Oct. (478) Nov. (222) Decemb. (3)	575	0 - 9	9 $\pm$ 1	4.9 $\pm$ 1.9	10	10.0	0.05	0.100
			10 - 19	14 $\pm$ 3	23.0 $\pm$ 26.9	64	9.4	1.05	0.062
			20 - 29	26 $\pm$ 2	159.0 $\pm$ 106.9	334	5.1	15.80	0.028
			30 - 39	34 $\pm$ 3	411.0 $\pm$ 112.6	317	10.7	114.95	0.091
			$\geq 40$	42 $\pm$ 2	734.9 $\pm$ 138.1	22	27.3	66.77	0.428
<i>Total</i>	28 $\pm$ 7	269.2 $\pm$ 193.9	747	8.6	198.62	0.071			
<i>Total</i>						<i>1797</i>	<i>4.7</i>	<i>228.10</i>	<i>0.036</i>

TABLE 2. Characteristics of hauls sampled for the daily feeding study of American plaice on Grand Bank (May-1998).

Haul	Reference	Mean time of haul (hr UTC)	Tow duration (min)	Location		Depth min-max (m)	Date
1	Dawn	07:13	31	43° 27'23N	50° 33'15W	60 - 62	20.05.98
2	Dawn	07:13	31	43° 27'20N	49° 59'95W	62	21.05.98
3	Dawn	07:15	32	43° 56'98N	50° 11'34W	53 - 59	26.05.98
4	Midday	12:17	31	43° 17'08N	50° 29'76W	71	20.05.98
5	Midday	11:29	31	43° 14'92N	49° 55'02W	59	21.05.98
6	Midday	11:26	35	43° 59'68N	49° 45'38W	49 - 53	24.05.98
7	Midday	12:31	33	43° 38'91N	49° 49'28W	60	25.05.98
8	Midday	12:00	31	43° 50'11N	50° 20'91W	60	26.05.98
9	Afternoon	15:57	31	43° 24'70N	50° 17'69W	58 - 60	20.05.98
10	Afternoon	18:10	31	43° 42'73N	50° 37'31W	64 - 69	22.05.98
11	Afternoon	17:57	33	43° 46'64N	49° 38'16W	49 - 51	25.05.98
12	Afternoon	16:51	34	43° 32'56N	49° 55'14W	60 - 62	26.05.98
13	Dusk	21:03	33	43° 40'92N	50° 50'75W	69 - 71	19.05.98
14	Dusk	21:53	34	43° 00'54N	50° 14'78W	77 - 80	21.05.98
15	Dusk	21:54	31	43° 30'54N	50° 39'16W	64 - 66	26.05.98
16	Night	02:35	110	43° 22'71N	50° 21'27W	55 - 58	27.05.98

TABLE 3. Time interval (hr UTC), size range (cm), mean weight  $\pm$  Standard Deviation (g), number of individuals sampled, Feeding Intensity Index (FI), weight of stomach contents (g), and Mean Weight Fullness Index (MWFI) of American plaice sampled for the daily feeding study on Grand Bank (May-1998).

Haul (time interval, hr UTC)	Size range (cm)	Mean weight $\pm$ SD (g)	No indiv. sampled	FI (%)	Weight stomach contents (g)	MWFI (%)
Dawn (06:58 – 07:31 h)	20 - 29	170.2 $\pm$ 30.2	50	60.0	11.72	0.144
	30 - 39	390.2 $\pm$ 111.4	50	54.0	80.85	0.352
	40 - 49	717.9 $\pm$ 150.1	50	42.0	212.17	0.599
	$\geq$ 50	1628.4 $\pm$ 488.2	50	60.0	295.50	0.329
Midday (11:09 – 12:48 h)	20 - 29	162.8 $\pm$ 38.4	50	62.0	28.33	0.431
	30 - 39	352.2 $\pm$ 109.0	50	76.0	65.17	0.311
	40 - 49	749.8 $\pm$ 158.9	50	50.0	198.80	0.547
	$\geq$ 50	1518.0 $\pm$ 397.4	50	56.0	289.59	0.378
Afternoon (15:42 – 18:26 h)	20 - 29	167.3 $\pm$ 31.6	50	78.0	32.22	0.395
	30 - 39	346.0 $\pm$ 100.2	50	46.0	45.54	0.207
	40 - 49	739.4 $\pm$ 172.8	50	48.0	286.63	0.730
	$\geq$ 50	1767.3 $\pm$ 458.7	39	43.6	269.43	0.437
Dusk (20:47 – 22:10 h)	20 - 29	152.2 $\pm$ 43.3	50	50.0	8.57	0.135
	30 - 39	363.8 $\pm$ 96.1	50	28.0	22.64	0.101
	40 - 49	785.7 $\pm$ 172.4	50	30.0	87.58	0.249
	$\geq$ 50	1746.4 $\pm$ 548.1	33	12.1	66.59	0.135
Night (01:40 – 3:30 h)	20 - 29	163.3 $\pm$ 29.7	50	42.0	17.36	0.210
	30 - 39	384.0 $\pm$ 101.4	50	50.0	135.70	0.638
	40 - 49	711.6 $\pm$ 117.2	50	52.0	256.71	0.752
	$\geq$ 50	1622.0 $\pm$ 396.5	6	16.7	72.79	0.927

TABLE 4. Prey items (% weight by size range or month, + indicates presence but <0.5%), stomach content weight, individual number, Feeding Intensity Index (FI) and Mean Weight Fullness Index (MWFI) found in American plaice stomach contents by length classes or month on Grand Bank (1998, 2002).

Prey taxa	%W of prey on Grand Bank						Month		Total prey weight (gr)
	Size range (cm)						April	May	
	0-9	10-19	20-29	30-39	40-49	≥50			
CNIDARIA		0.9	0.8	+	+	+	2.4	+	12.67
CTENOPHORA			+	+	+	+	0.8	+	9.64
CHAETOGNATA		+						+	0.02
ANNELIDA	14.1	6.1	5.4	1.5	+	+	+	0.9	48.02
SIPUNCULIDA						+		+	3.68
<b>CRUSTACEA</b>	<b>78.9</b>	<b>77.4</b>	<b>54.0</b>	<b>11.0</b>	<b>3.9</b>	<b>9.3</b>	<b>22.1</b>	<b>10.0</b>	<b>583.43</b>
Isopoda		+	+	+	+		+	+	2.21
Mysidacea		44.6	34.0	5.5	1.3	+	+	4.0	219.48
Euphausiacea		1.8	3.6	1.2	+	+	+	0.7	36.86
Copepoda	26.7	+						+	0.19
Cumacea		0.7	+		+		+	+	0.63
<b>AMPHIPODA</b>	<b>38.1</b>	<b>28.5</b>	<b>7.8</b>	<b>3.3</b>	<b>0.8</b>	<b>+</b>	<b>5.1</b>	<b>1.6</b>	<b>95.63</b>
Gammaridea	38.1	25.0	7.1	2.7	0.8	+	5.0	1.4	84.87
Caprellidae				+				+	0.40
Hyperiidea		3.3	+	+	+			+	3.56
Other amphipods		+	0.5	0.5	+		+	+	6.80
<b>DECAPOD CRUSTACEAN</b>		<b>0.5</b>	<b>7.4</b>	<b>0.8</b>	<b>1.3</b>	<b>9.2</b>	<b>16.7</b>	<b>3.6</b>	<b>223.67</b>
Northern shrimp ( <i>P. borealis</i> )		+	+					+	0.57
Crustacean larvae			7.2	+				+	23.80
Other Natantia crustaceans				+				+	0.61
Hermit crab (Paguridea)					+			+	0.81
Snow crab ( <i>Ch. opilio</i> )					0.9	7.6		2.8	154.69
Hyas sp			+			1.4	16.7	+	24.77
Other Brachyura		+		0.6	+	+		+	18.42
Unidentified and digested crustac.	14.1	1.0	1.0	+			+	+	4.76
<b>ECHINODERMATA</b>		<b>8.5</b>	<b>3.2</b>	<b>4.0</b>	<b>9.4</b>	<b>15.8</b>	<b>7.9</b>	<b>10.1</b>	<b>567.13</b>
Ophiuroidea		4.8	2.5	1.1	3.2	4.0	2.0	3.1	171.03
Sand dollars ( <i>E. parma</i> )		+	0.7	2.9	6.0	11.8	4.6	7.0	389.79
(Echinoidea)									
Holothurioida		3.6			+		1.3	+	6.31
<b>MOLLUSCA</b>		<b>+</b>	<b>1.2</b>	<b>1.4</b>	<b>1.9</b>	<b>41.3</b>	<b>+</b>	<b>14.2</b>	<b>782.43</b>
Bivalvia		+	1.2	1.4	1.8	41.1		14.2	778.54
Lutraria						27.8		8.8	482.86
Other bivalves		+	1.2	1.4	1.8	13.3		5.4	295.68
Gasteropoda					+	+		+	3.23
Placophora			+		+		+	+	0.66
<b>PISCES</b>		<b>6.0</b>	<b>34.5</b>	<b>80.4</b>	<b>83.6</b>	<b>33.1</b>	<b>66.5</b>	<b>64.1</b>	<b>3628.17</b>
Northern sand lance ( <i>A. dubius</i> )			22.2	52.4	66.6	27.1	56.4	48.7	2765.47
American plaice ( <i>H. platessoides</i> )			1.1					+	3.43
Capelin ( <i>M. villosus</i> )			6.5	18.7	12.3	6.0		11.4	627.94
Sculpin ( <i>Triglops</i> spp)		0.8	1.1	2.5	0.9		+	0.9	51.90
Snakeblenny ( <i>L. lamprætaeformis</i> )		1.3	+		1.9		+	0.9	51.03
Grenadier ( <i>Nezumia bairdi</i> )					+			+	2.04
Lampfish			0.5				1.1		1.67
Seasnail fish ( <i>Liparis</i> sp)		1.1	+	1.8	+		8.5	+	25.52
Digested fishes		2.8	2.4	4.9	1.6		0.5	1.7	99.17
Unidentified and digested preys	7.0	0.9	0.9	1.5	+	+	+	+	23.71
Stomach content weight (gr)	0.6	52.9	313.1	1017.6	2540.3	1734.4	147.6	5511.3	5658.9
No. indiv. sampled	8	428	903	728	716	382	128	3037	3165
FI (%)	75.0	56.3	43.5	39.6	37.2	36.1	64.1	41.2	42.1
MWFI (%)	2.000	0.508	0.278	0.338	0.456	0.303	0.676	0.357	0.370

TABLE 5. Prey items (% weight by size range or month, + indicates presence but <0.5%), stomach content weight, individual number, Feeding Intensity Index (FI) and Mean Weight Fullness Index (MWFI) found in American plaice stomach contents by length classes or month on Flemish Cap (1998, 2001, 2002).

Prey taxa	%W of prey on Flemish Cap						Month		Total prey weight (gr)
	Size range (cm)								
	10-19	20-29	30-39	40-49	≥50	July	August		
CNIDARIA			+	0.8	+	0.5		11.79	
CTENOPHORA				2.1	32.7	16.8		362.86	
BRYOZOA				+		+		0.19	
CHAETOGNATA		4.8	0.7	2.2	1.2	1.7		35.80	
ANNELIDA		1.6	2.7	3.9	2.5	3.1	2.3	72.22	
CRUSTACEA	13.8	65.7	24.1	31.2	30.5	33.1		716.06	
Isopoda		0.6				+		0.19	
<i>Mysidacea</i>	13.8	+	+	+		+		1.27	
Euphausiacea		9.0	3.1	2.4	1.4	2.3		50.69	
Copepoda			+	+	+	+		1.29	
<i>AMPHIPODA</i>		0.9	4.6	23.4	14.1	17.5		379.12	
Gammaridea			+	+	+	+		2.96	
Hyperiidia		0.9	4.4	23.3	14.1	17.4		375.97	
Other amphipods				+		+		0.19	
DECAPOD CRUSTACEAN		53.3	15.9	5.2	14.9	13.0		280.91	
Northern shrimp ( <i>P. borealis</i> )		20.9	9.3	4.1	14.2	10.5		227.90	
Hermit crab (Paguridea)				+	+	+		0.97	
Other Natantia crustaceans		32.4	6.6	1.0	0.7	2.4		52.04	
Unidentified and digested crustac.		1.7	0.4	+	+	+		2.58	
<i>ECHINODERMATA</i>		24.3	51.8	52.9	28.3	36.0	97.6	979.82	
Ophiuroidea		23.1	50.4	51.1	24.2	33.0	97.5	914.95	
Sand dollars ( <i>E. parma</i> ) (Echinoidea)		1.2	1.4	1.8	3.7	2.8	+	60.73	
Holothurioidea					0.4	+		4.14	
<i>MOLLUSCA</i>			3.5	2.2	+	1.7	+	36.30	
Bivalvia			+		+	+	+	2.61	
Gasteropoda			0.6	2.1	+	1.0	+	22.65	
Cephalopoda			2.9	+		0.5		11.04	
<i>PISCES</i>	86.2	3.8	17.0	4.4	4.3	7.0		151.16	
Eelpout ( <i>Lycodes</i> spp)					+	+		4.56	
Red fish ( <i>Sebastes</i> sp)				0.5		+		4.38	
Wolf-fish ( <i>A. lupus</i> )			2.7		1.9	1.4		29.61	
Snakeblenny ( <i>L. lamprotaeformis</i> )	86.2	0.9	10.2	2.0	+	2.8		60.87	
Grenadier ( <i>Nezumia bairdi</i> )		2.9	2.3			+		9.68	
Sculpin ( <i>Triglops</i> spp)			1.8	1.0	0.7	1.1		23.41	
Ribbon barracudina ( <i>N. rissoi</i> )					0.7	+		6.85	
Digested fishes				0.9	+	0.5		11.80	
Unidentified and digested preys				+		+		3.10	
Stomach content weight (gr)	1.95	31.8	374.8	907.9	1052.8	2164.4	204.9	2369.3	
No. indiv. sampled	5	32	180	261	152	593	37	630	
FI (%)	100	68.8	75.0	82.0	74.3	76.3	78.9	77.6	
MWFI (%)	0.767	0.578	0.468	0.383	0.469	0.437	0.512	0.441	

TABLE 6. Prey items (% weight by size range or month, + indicates presence but <0.5%), stomach content weight, individual number, Feeding Intensity Index (FI) and Mean Weight Fullness (MWFI) found in American plaice stomach contents by length classes or month on Svalbard (2001, 2002).

Prey taxa	%W of prey on Svalbard									Total prey weight (gr)
	Size range (cm)					Month				
	0-9	10-19	20-29	30-39	≥40	June	Oct.	Nov.	Dec.	
CNIDARIA				6.2			4.4		100	8.04
BRYOZOA			+				+			0.09
ANNELIDA	12.5	16.4	6.3	5.2	+	5.6	0.8	1.0		8.55
<b>CRUSTACEA</b>	<b>62.5</b>	<b>83.6</b>	<b>23.7</b>	<b>11.2</b>		<b>1.1</b>	<b>36.6</b>	<b>6.0</b>		<b>20.75</b>
Cumacea				+		+				0.15
<i>Mysidacea</i>			5.1	0.7			4.4			2.06
<i>AMPHIPODA</i>		22.7	1.4	+		0.4	+	0.7		0.88
Gammaridea		22.7	1.4	+		0.4	+	0.7		0.88
<b>DECAPOD CRUSTACEAN</b>		<b>54.5</b>	<b>17.1</b>	<b>10.1</b>		<b>0.5</b>	<b>32.1</b>	<b>5.0</b>		<b>17.55</b>
Northern shrimp ( <i>P. borealis</i> )			5.7	8.1			22.8	3.4		11.86
Shrimp ( <i>P. tarda</i> )			11.4				5.4			2.50
Hermit crab (Paguridea)				2.0		0.5	4.0			2.58
Other Natantia crustaceans		54.5	+					1.6		0.61
Unidentified and digested crustac.	62.5	6.4						+		0.12
<b>ECHINODERMATA</b>			<b>49.9</b>	<b>34.3</b>	<b>45.8</b>	<b>61.1</b>	<b>1.6</b>	<b>12.1</b>		<b>89.77</b>
Ophiuroidea			49.9	33.6	45.8	60.5	1.6	12.1		88.90
Sand dollars ( <i>E. parma</i> ) (Echinoidea)				0.7		0.6				0.88
<b>MOLLUSCA</b>			<b>10.5</b>	<b>3.5</b>	<b>10.1</b>	<b>0.9</b>	<b>19.6</b>	<b>10.8</b>		<b>14.42</b>
Bivalvia			10.5	3.5	10.1	0.9	19.6	10.8		14.42
Pectinidae			7.1	3.3		0.9	1.4	10.8		5.92
Other bivalves			3.4	0.2	10.1		18.2			8.50
<b>PISCES</b>			<b>4.6</b>	<b>15.7</b>		<b>3.3</b>	<b>36.8</b>			<b>21.68</b>
Eelpout ( <i>Lycodes</i> spp)			4.6				2.1			1.00
Blue whiting ( <i>M. poutassou</i> )				5.7			16.1			7.50
Haddock ( <i>M. aeglefinus</i> )				5.6			15.8			7.36
Digested fishes				4.4		3.3	2.8			5.82
Unidentified and digested preys	25.0		4.6	3.9	1.3	5.1		+		7.14
Offal (fishing procesed remant)				19.9	42.6	22.9		70.0		57.66
Stomach content weight (gr)	0.08	1.1	22.0	130.7	74.3	138.4	46.6	37.1	6.0	228.1
No. indiv. sampled	54	184	806	709	44	44	1269	481	3	1797
FI (%)	7.4	3.8	3.3	5.5	15.9	88.6	1.8	4.6	0.0	4.7
MWFI (%)	0.034	0.023	0.017	0.048	0.236	0.752	0.011	0.032	0.440	0.036



TABLE 7. Prey items (% weight by time period, + indicates presence but <0.5%), stomach content weight, individual number, Feeding Intensity Index (FI) and Mean Weight Fullness Index (MWFI) found in American plaice stomach contents by period on Grand Bank in May 1998.

Prey taxa	%W by time period on Grand Bank					Total prey weight (g)
	Dawn	Midday	Aftern.	Dusk	Night	
CNIDARIA	74.4	4.6	1.6	8.5	10.9	1.29
ANNELIDA	16.3	61.8	3.2	11.6	7.1	13.39
CRUSTACEA	2.5	17.1	15.6	29.0	35.8	277.93
Cumacea	8.3	91.7				0.12
Isopoda	16.8	29.2	5.1	48.9		1.37
Mysidacea	2.3	10.7	40.2	7.1	39.7	30.53
AMPHIPODA	6.8	74.3	1.4	0.7	16.8	46.51
Gammaridea	7.0	84.8	0.8	0.9	6.5	38.31
Caprellidae		12.5	87.5			0.40
Hyperiidea	11.5	34.5			54.0	1.13
Other Amphipoda	4.8	24.3			70.9	6.67
DECAPOD CRUSTACEAN	1.4	4.3	15.1	39.0	40.3	196.40
Crustacean larvae			79.1	17.2	3.7	23.80
Other Natantia crustacean		100				0.61
Hermit crab (Paguridea)			100			0.81
Snow crab ( <i>Ch. opilio</i> )		5.0		47.4	47.6	152.85
Other Brachyura	14.5	1.0	55.0		29.5	18.33
Other crustacean	7.0	31.3	19.7	25.7	16.3	3.00
ECHINODERMATA	24.7	24.8	45.4	5.1		231.66
Ophiuroidea		67.5		32.5		34.48
Sand dollar ( <i>E. parma</i> ) (Echinoidea)	29.0	17.4	53.4	+		197.18
MOLLUSCA BIVALVIA	47.8	38.3	12.9		1.0	624.10
Lutraria	51.5	34.2	14.3			482.86
Other Bivalvia	35.3	52.2	8.3		4.2	141.24
PISCES	17.5	17.1	30.4	6.8	28.2	1326.80
Northern sand lance ( <i>A. dubius</i> )	13.7	15.3	35.6	4.3	31.1	1119.78
Capelin ( <i>M. villosus</i> )		61.1		38.9		55.12
Sculpin ( <i>Triglops</i> spp)	33.5	31.6	14.5		20.4	27.88
Snakeblenny ( <i>L. lampraeformis</i> )	100					41.1
American plaice ( <i>H. platessoides</i> )	31.0	69.0				2.55
Digested Pisces	35.5	13.6		25.4	25.5	80.33
Unidentified and digested preys	21.8	33.7	9.9	12.2	22.4	8.72
Stomach content weight (g)	600.2	581.9	633.8	185.4	482.6	2483.9
No. indiv. sampled	200	200	189	183	156	928
FI (%)	54.0	61.0	54.5	31.7	46.8	50.0
MWFI (%)	0.356	0.416	0.442	0.157	0.548	0.380

TABLE 8. Simplified Morisita's Index between size classes (cm) and area in American plaice.

Grand Bank (GB) – Flemish Cap (FC) – Svalbard (SV)							
Total	GB-FC	0.630	GB-SV	0.261	FC-SV	0.752	
	0-9	10-19	20-29	30-39	40-49	≥50	
0-9	GB-ART	0.337					
10-19		GB-FC	0.215				
		GB-SV	0.233				
		FC-SV	0.000				
20-29			GB-FC	0.212			
			GB-SV	0.234			
			FC-SV	0.643			
30-39				GB-FC	0.304		
				GB-SV	0.316		
				FC-SV	0.843		
40-49					GB-FC	0.111	
					GB-SV	0.030	
					FC-SV	0.651	
≥50						GB-FC	0.018

TABLE 9. Simplified Morisita's Index between size classes (cm) of American plaice in each area.

	Grand Bank					Flemish Cap				Svalbard			
	10-19	20-29	30-39	40-49	≥50	20-29	30-39	40-49	≥50	10-19	20-29	30-39	40-49
0-9	0.431	0.154	0.035	0.008	0.001					0.142	0.051	0.049	0.008
10-19		0.737	0.178	0.121	0.079	0.059	0.273	0.070	0.075		0.315	0.222	0.001
20-29			0.667	0.620	0.461		0.638	0.454	0.502			0.810	0.683
30-39				0.996	0.579			0.899	0.614				0.811
40-49					0.583				0.654				

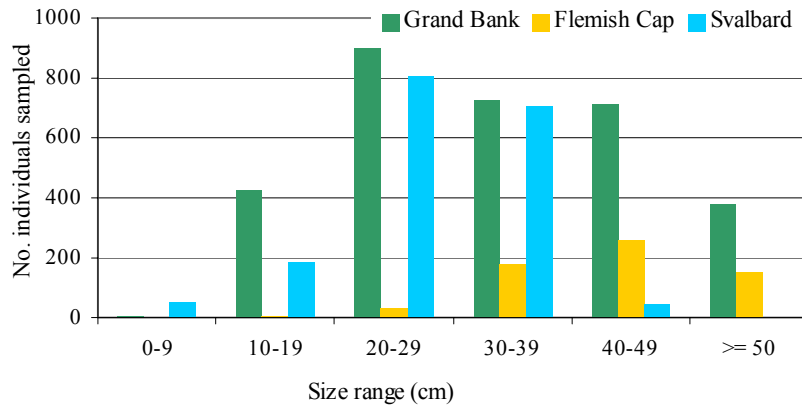


Fig. 1. No. of individuals sampled by size range and area (Grand Bank 1998, 2002; Flemish Cap 1998, 2001, 2002; and Svalbard 2001, 2002) in feeding habit study of American plaice.

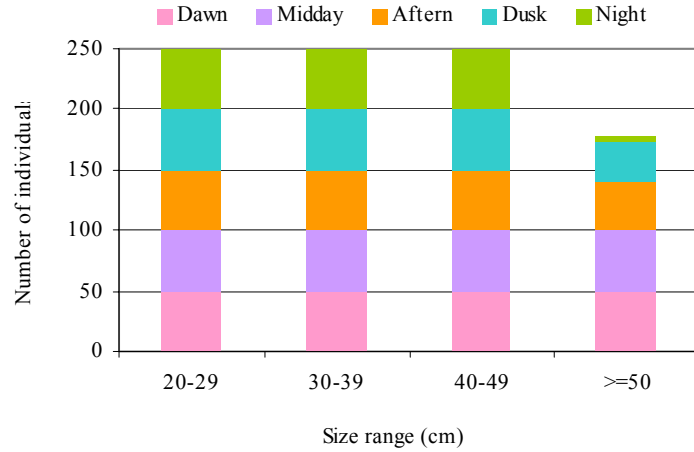


Fig. 2. No. of individuals sampled by size range and time period in daily feeding behaviour study of American plaice from Grand Bank in May-1998.

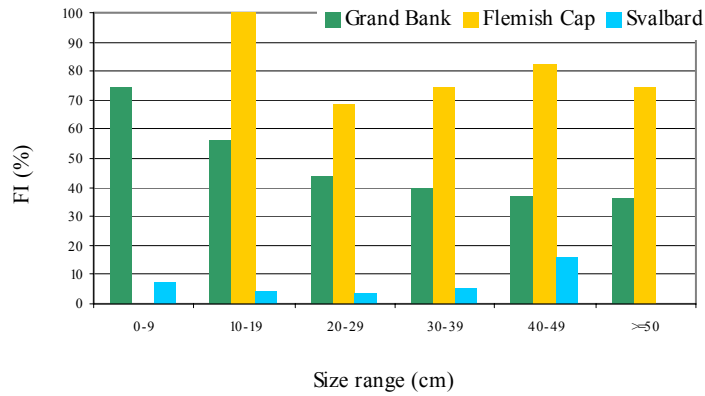


Fig. 3. Feeding intensity (%) by size range and area (Grand Bank 1998, 2002; Flemish Cap 1998, 2001, 2002; and Svalbard 2001, 2002) of American plaice.

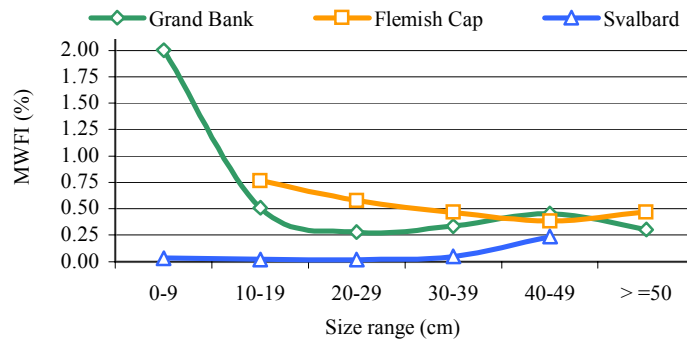
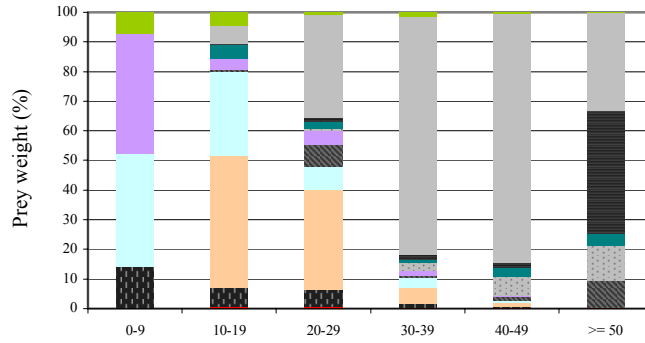
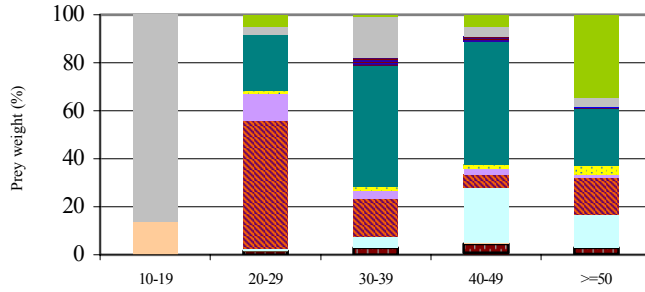


Fig. 4. MWFI (%) by size range by area (Grand Bank 1998, 2002; Flemish Cap 1998, 2001, 2002; and Svalbard 2001, 2002) of American plaice.

Grand Bank (April-May)



Flemish Cap (July-August)



Svalbard (June-Oct.-Nov.-Dec.)

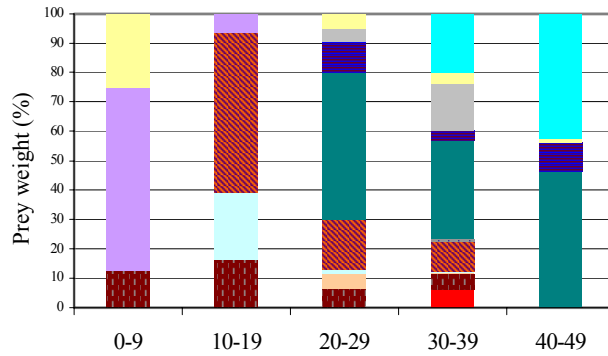


Fig. 5. Main prey weight (%) by size range (cm) and area (Grand Bank 1998, 2002; Flemish Cap 1998, 2001, 2002; and Svalbard 2001, 2002) of American plaice.

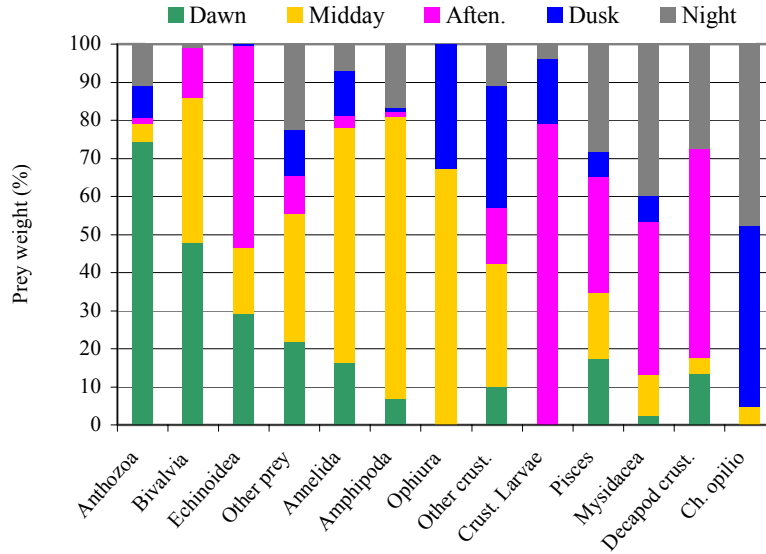


Fig. 6. Main prey weight (%) by time period of American plaice sampled on Grand Bank in May-1998.

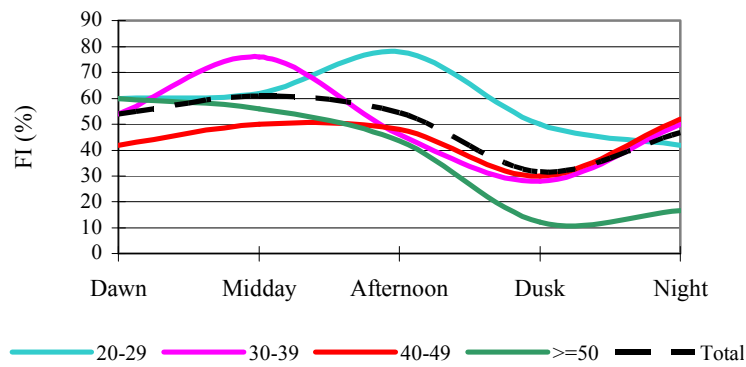


Fig. 7. Feeding intensity by time period and size range over 24-h of American plaice on Grand Bank (May-1998).

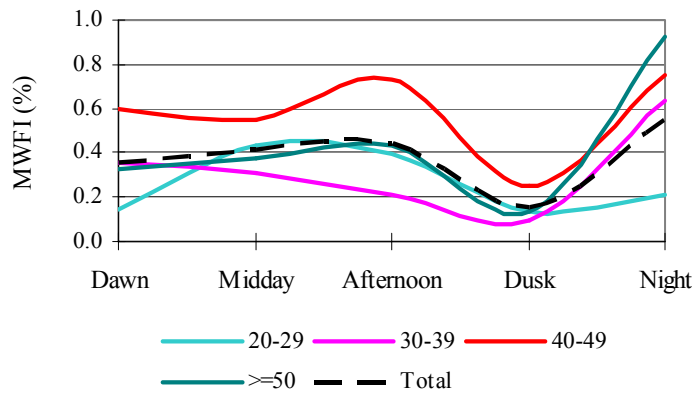


Fig 8. Mean Weight Fullness Index by time period and size range over 24-h of American plaice on Grand Bank (May-1998).