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Feeding Habits of Wolffishes (*Anarhichas denticulatus*, *A. lupus*, *A. minor*) in the North Atlantic

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Abstract

Feeding habits of 7 995 individuals of three wolffish species distributed in the north Atlantic were analyzed: 1 016 of northern wolffish (*Anarhichas denticulatus*), 4 783 of Atlantic wolffish (*A. lupus*) and 2 196 of spotted wolffish (*A. minor*). The individuals sampled were taken in the NAFO Area Divisions 3NO in spring in the period 2002-2005, Div. 3L in summer in the period 2003-2004, Div. 3M in summer in the period 1993-2005, and in the ICES Area Div. IIb in autumn in the period 2004-2005. Feeding intensity was higher in the NAFO Area than in the northeast Atlantic (spring-summer *vs.* autumn), mainly in spotted wolffish in Div. 3M. The importance of each prey taxa was evaluated using the weight percentage. Wolffish species diet showed geographical differences. Ontogenic diet changes and prey variation throughout the studied period were observed, mainly in Atlantic and spotted wolffishes. This two species preyed primarily on bottom (echinoderms, gastropods and bivalves) and benthopelagic (northern shrimp and redfish) organisms on Flemish Cap and Grand Bank. However fish and northern shrimp predation were more important on the Flemish Cap, mainly in spotted wolffish, showing periods with higher predation on these prey when the biomass of these prey species increased. This fact might have been the cause of diet overlap between Atlantic and spotted wolffishes in some periods in Div. 3M. Less ontogenic, annual and geographical diet variations were found in northern wolffish in NAFO Area, feeding mainly on ctenophores; however in Svalbard area, this species showed to be highly piscivore. Three species showed cannibalism but only in the Div. 3M.

Introduction

Three species of wolffishes (Family Anarhichadidae, genus *Anarhichas*) commonly inhabiting northern Atlantic waters, *A. lupus* (Atlantic or striped wolffish), *A. minor* (spotted wolffish), *A. denticulatus* (northern or broadhead wolffish). In the northwest Atlantic, all three species are distributed from Labrador and northeast Newfoundland Shelves to the southern Grand Banks and Flemish Cap. In the late 1990s, two species (spotted and northern wolffishes) were designated by COSEWIC as threatened due to the declines in both abundance and biomass (Kulka, 2002; Simpson and Kulka, 2003).

Although they are not a target species of Spanish fleet, they constitute by-catch species taken in these northwester Atlantic fisheries (González *et al*., 2005). All three species declined in abundance during the 1980s and they have been stable since the mid-1990s. Reductions in extent of distribution and abundance were minimal on the Grand Banks, however they were much greater north of 48º (Simpson and Kulka, 2002). The Atlantic wolffish is concentrated on the southern Grand Bank and at shallower depths than the other two species.

Ecosystem model approach is needed for the study and management of the marine resources. Ecological studies focused on fish communities, assemblages, and other aspects of fish ecology such as feeding habits and habitat requirements are necessary to provide advice in relation to ecosystem, biodiversity and nature conservation issues. In this sense, food and feeding allow to know the niche dimensions (Krebs, 1989). Fish display a wide adaptive range of feeding habits, and it is unusual for fish to specialize in one particular prey category throughout their entire life cycle. Fish usually show ontogenetic changes in feeding habits and prey selection (Jobling, 1995).

Studies on feeding habits of wolffish species have been reported (Albikovskaya, 1983; Nelson and Ross, 1992; Rodríguez-Marín *et al*., 1994; Torres *et al*., 2000; Román *et al*., 2004a). We report the study and comparison of the diet and feeding habits of Atlantic, spotted and northern wolffishes in summer on Flemish Cap (NAFO Area, Div. 3M) in the period 1993 to 2005. Feeding habits of these species in spring-summer in Div. 3NO (Grand Bank) and 3L, and in Div. IIb (Svalbard Area, ICES) in autumn are also presented. Changes in food habits with predator size and interspecific overlap were examined in each area. Diet changes through the years and the interspecific overlap in relation to the depth range and a three-year periods in Div. 3M were also analyzed. Data on yield in EU Flemish Cap survey in the same period were indicated.

Material and Methods

Stomach contents of 7 995 individuals of three wolffish species distributed in the north Atlantic were analyzed: 1 016 of northern wolffish (*A. denticulatus*), 4 783 of Atlantic wolffish (*A. lupus*) and 2 196 of spotted wolffish (*A. minor*) (Table 1). The individuals sampled were taken in the NAFO Area Div. 3NO by the Spanish Bottom Trawl Research Survey *Platuxa* 2002-2005 in spring (González Troncoso *et al*., 2006a), the EU Survey *Flemish Cap* 1993-2005 in Division 3M in summer (González Troncoso *et al.*, 2006b), the Spanish Bottom Trawl Research Survey *Fletán Negro-3L* 2003-2004 in summer (*unpublished data*) and in ICES Area Div. IIb by the Spanish Bottom Trawl Research Survey *Fletán Ártico* 2004-2005 in autumn (Paz *et al.,* 2006). These research surveys were carried out by the Instituto Español de Oceanografía (I.E.O., Spain) (Fig. 1). The depth range (m), median, percentiles, extreme values and outliers of the samples carried out for each species and area are shown in Fig. 2.

Sampling was performed randomly and it was stratified by predator size range. Size groups of 10 cm were established (0-9, 10-19, 20-29, 30-39, 40-49, 50-59, 60-69, 70-79, 80-89, 90-99, 100-109 and ≥110 cm). The stomach contents were analyzed on board. Fish whose stomach was everted or contained prey ingested in the fishing gear were discarded. Specimens that presented total or partial regurgitation were taken into account to estimate the emptiness index.

The data collected for each predator were: total length (TL) to the nearest lower cm; volume of stomach content quantified in c.c. using a trophometer (Olaso, 1990); percentage of each prey in the total volume, and digestion stage and number of each prey. Prey were identified to the lowest possible taxonomic level.

Data Analysis

Feeding intensity was evaluated using the Feeding Intensity Index (*FI*): percentage of individuals with stomach content, where *n* was the individual number with stomach content and *N* was the total individual number sampled.

$$FI = (n / N) * 100$$

The importance of each prey taxa was evaluated using the weight percentage (W_{pi}) of each prey item (or prey group) of total weight of the stomach content by each size range (or year), where w_{pi} was the weight (g) of the prey item *p* in the size range or year *i* and W_{ti} was the total prey weight (g) of the size range or year *i*. This measure reflects dietary nutritional value (Hansson, MS 1980; Hyslop, 1980; Macdonald and Green, 1983; Amezaga, 1988; Cortés, 1997).

$$W_{pi} = w_{pi} / W_{ti} * 100$$

Diet overlap was measured using the Simplified Morisita´s Index (C_H) (Krebs, 1989) –based on *%W*. C_H varies between 0 (no categories in common) and 1 (identical categories). Overlap is generally considered to be biological significant when the value exceeds 0.60 (Wallace, 1981). We used C_H to measure the interspecific diet overlap at different depth ranges and periods in each area. Food categories in the diet were considered at the higher taxonomic levels: Pisces, Crustacea, Mollusca (Gastropoda, Bivalvia and Cephalopoda), Echinodermata (Asteroidea, Echinoidea, Ophiuroidea); "*Other Groups*" (Annelida, Anthozoa, Cnidaria, Ctenophora, Scyphozoa); Other Prey (offal, eggs, unidentified/digested prey) (Bowman *et al.,* 2000).

$$C_H = \frac{2 \sum p_{ij} * p_{ik}}{\sum p^2_{ij} + \sum p^2_{ik}}$$

C_H was the Simplified Morisita´s Index.
j, k was the predator groups (division, depth, year period).
p_{ij} was the proportion of food category *i* in the diet of predator *j*.
p_{ik} was the proportion of food category *i* in the diet of predator *k*.
i (i = 1,2,3,…n) was the number of food category.

Differences in feeding intensity by area and sex were tested by χ^2. The GLM Univariate procedure (General Linear Model) has been used to test the differences in the mean weight of prey groups among years in each predator. Pearson correlation coefficient (*r*) was used to measure the inter-annual relation among mean weight of different prey groups in each predator.

Results

Feeding Intensity

This index showed the highest value in NAFO Divisions (39 to 63%). Feeding intensity (*FI*) was slightly higher in spotted and Atlantic wolffishes (63% and 54%, respectively). Only the northern wolffish showed a feeding intensity significantly different among three divisions ($\chi^2_{(2)}$ = 44.59 $p \leq 0.000$) with values of 22% in Div. IIb and 53% in Division 3M; and this species was also the only one with significantly different *FI* between sexes in Div. 3M ($\chi^2_{(1)}$ = 9.74 $p \leq 0.002$), with a higher value in males than in females (47 and 35%, respectively) (Table 2).

In Div. 3LNO, feeding intensity of northern and Atlantic wolffishes showed an increasing trend with length. And this index had less variation among size ranges in Div. 3M (Fig. 3).

Food Habits, Diet Changes and Overlap in Division 3M in the Period 1993-2005

Northern wolffish. Ctenophores (71% in weight), they were included in "*Other groups*" in Tables and Figures, were the main prey of northern wolffish. Fishes (*Macrourus berglax* 9% and *Sebastes* sp. 7%) were the following important prey group. This species showed little cannibalism (<1%) (Table 3). The individuals <40 cm preyed on hyperids; ctenophores were preyed by individuals of 40-99 cm. Fish predation began to be important in the diet of individuals ≥70 cm, and practically they were the only prey in individuals ≥100 cm (Fig. 4).

Predation on ctenophores of northern wolffish was important through the period 1993-2005. This predation decreased for some years and this fact coincided with an increase of fish predation on *M. berglax* (the first years, 1996-97) and redfish (since 1999), and there was also an increase of crustacean (*Pandalus borealis*) predation (since 2002) (Fig. 5). The weight of the prey groups showed no significant differences among years ($F_{(39,7437)}$ = 1.16, p >0.05). A significant positive correlation was found only between the mean weight of crustaceans and echinoderms consumed through the studied period (r = 0.85, $p \leq 0.01$).

Atlantic wolffish. This species presented a higher prey spectrum. Several prey groups had importance in their diet: echinoderms (29%) in particular brittle stars (Ophiura) (13%), fish (28%) mainly redfish (13%), crustaceans (26%) primarily northern shrimp (*P. borealis*) (18%) and molluscs (9%) with bivalves (7%). The Atlantic wolffish showed cannibalism (2%) and offal was also present in the stomach contents (2%) (Table 3). When the size range of the predator increased, the importance of brittle stars, bivalves and northern shrimp decreased and fish increased. Individuals <20 cm preyed polychaetes and hyperiids (Fig. 4).

Atlantic wolffish showed a period (1993-1999) in which fish predation (redfish and Atlantic cod, *Gadus morhua*) gradually decreased and predation on echinoderms and molluscs increased. Since 2000, fish predation (on redfish) showed an opposite trend, gradually increasing until year 2005. This same trend was appreciated in the crustacean consumption (mainly northern shrimp) since 1998; however the consumption of echinoderms was minimal in the last years (Fig. 5). The weight of the prey groups showed significant differences among the years ($F_{(57,1079)}$ = 12.92,

$p \leq 0.000$). No correlation in the increase or decrease of the mean weight of the different prey groups was found throughout the series.

Spotted wolffish. This species preyed mainly on Pisces (50%) in this division with a high number of different fish prey species, but mainly on redfish (26%). Northern shrimp (11%), brittle stars (6%) and starfish (Asteroidea) (5%) were the following remarkable prey. Cannibalism (6%) was found, and offal (<1%) was consumed by bigger individuals (Table 3). Predation of northern shrimp was observed in individuals of 10-59 cm, and fish predation was found in individuals ≥40 cm (Fig. 4).

Fish predation showed variations in the spotted wolffish diet, increased in the period of 1993-1995, based on Atlantic cod and redfish predation. In the period 1998-2005, there was an increase on redfish as prey. The importance of crustaceans (northern shrimp) also had some oscillations. During the years when the previous prey diminished in the stomach contents, they were replaced by ctenophores (period of 1998-2001), and echinoderms were important in other periods (Figure 5). The weight of the prey group showed significant differences among years ($F_{(56,4079)} = 2.16$, $p \leq 0.000$). Only the mean weight of molluscs and echinoderms preyed presented a significant positive correlation ($r = 0.71$, $p \leq 0.01$).

Only Atlantic and spotted wolffish diets in Div. 3M showed overlapping ($C_H = 0.67$) considering all the years (Table 4); it was just observed in depths of 400-599 m ($C_H = 0.76$). Spotted wolffish showed a slight diet overlap with the other two wolffish species in shallower areas (200-399 m) (Table 5). Food habits showed changes on main prey groups preyed in the studied period, mainly in Atlantic and spotted wolffishes. We have considered interspecific diet overlap in a three-year periods, and Atlantic and spotted wolffishes showed diet overlap in the periods 1993-95 ($C_H = 0.89$) and 2002-2005 ($C_H = 0.75$). Northern and spotted wolffish diet overlapped in the period 1996-2001 ($C_H = 0.72$ and 0.60) (Table 6 and Fig. 5).

Food Habits in the Period 2002-2005 in Divisions 3LNO

The main food components in the diet of northern wolffish were ctenophores (56%) and Pisces (31%) with redfish (17%) and roughhead grenadier (*M. berglax*) (12%). Offal was also found but with a minimal percentage (1%) (Table 3). Ctenophores were the main food in the diet of all individuals except for some size ranges. It was possibly due to having a small sample and not to a behaviour rule. Fish prey began important in the diet of individuals ≥80 cm (Fig. 6). In the period of 2002-2005, the percentage of fish (mainly redfish) in the northern wolffish diet decreased considerably, and "*Other Groups*" increased due to the predation on ctenophores (Fig. 7).

Atlantic wolffish presented higher prey spectrum than the other two wolffish species in this area. All the prey groups considered had an importance in their diet, except for Pisces. Gastropoda (43%) were the most important prey; and ctenophores (15%), Paguridae (8%) and sand dollar (*Echinarachnius parma*) (6%) were the following prey in importance (Table 3). The consumption of these components increased when the size of the predator also increased. The individuals <30 cm ate polychaetes, toad crab (*Hyas* sp), and brittle stars (Fig. 6). In the Atlantic wolffish diet, molluscs (gastropods) showed a great variation in the annual series, diminishing remarkably their importance. When these prey decreased, there was an increase of crustacean consumption (snow crabs, pagurids or northern shrimp) and echinoderms (sand dollars and brittle stars) (Fig. 7).

Spotted wolffish preyed mainly on echinoderms (59%), especially sand dollars and starfish (37 and 13%). Other important prey were redfish (15%) and snow crab (*Chionocetes opilio*) (10%) (Table 3). Predation on brittle stars diminished, and sand dollars and snow crab predation increased when the predator size increased (Fig. 6).

Echinoderms were the main component in the spotted wolffish diet in year 2002, but they were replaced by fish in the diet in year 2003; and both groups have had the same importance in the last two years (Fig. 7).

Food Habits in the Period 2004-2005 in Division IIb

Prey spectrum in the stomach contents of wolffishes in Div. IIb was low. Northern wolffish showed a piscivorous diet (81%) based on Greenland halibut (*Reinhardtius hipoglossoides*, 54%) and redfish (16%), but the importance of these prey was due to the individuals ≥90 cm. Brittle stars and gastropods were the following remarkable prey (7 and 5%, respectively), and these prey appeared in the diet of individuals <90 cm. Northern wolffish showed a minimal offal predation (<1%). The diet showed the same trend in the two years studied (Table 3 and Fig. 8). Spotted wolffish in this division preyed on northern shrimp (67%) and on echinoderms (23%) (Table 3).

Discussion

Flemish Cap Survey wolffish catches have declined until the low levels found in year 2000 and a slight recovery within low levels has been observed in the last years (González Troncoso *et al*., 2006b). This general trend has been reported in other areas of the northwest Atlantic (Simpson and Kulka, 2002).

In the EU Flemish Cap Survey in NAFO Div. 3M, the most abundant species was the Atlantic wolffish (*A. lupus*) and the spotted wolffish (*A. minor*) had the lowest catches. However, the Atlantic wolffish yield decreased in the last period (Fig. 9). The distribution of the three species showed a clear different depth pattern: shallower for the Atlantic wolffish, intermediate for the spotted wolffish and a deeper distribution for the northern wolffish (Fig. 10).

Wolffish species showed medium feeding intensity values. It was slightly higher in spotted wolffish and in Div. 3M (Albikovskaya, 1983; Rodríguez-Marín *et al*., 1994; Torres *et al*., 2000; Román *et al*. 2004a).). The feeding intensity in Div. IIb was low. This fact was observed in other fish species in this area (González Iglesias *et al*., 2003; Román *et al*., 2004b; González Iglesias *et al*., 2005). It is also important to take into account that the samplings were carried out in different seasons.

Prey spectrum of the three wolffish species was higher in NAFO Divisions than in the northeast Atlantic, mainly in Atlantic and spotted wolffishes in Div. 3M. These two species showed a size-dependent predation and ontogenetic changes. They ate bottom and benthic organisms (echinoderms, gastropods, bivalves, crabs) and benthopelagic prey (redfish) increased with the predator size. There were found geographical differences in prey. Predation on fish was more important in Div. 3M, mainly in spotted wolffish. In Div. 3LNO, hard-shelled organisms prevailed in the diets of both species (Templeman, 1985; Rodríguez-Marín *et al*., 1994; Rodríguez-Marín, 1995; Torres *et al*., 2000; Román *et al*., 2004a). This fact is remarkable because fish predation of most fish species (American plaice *Hippoglossoides platessoides*, Greenland halibut *Reinhardtius hippoglossoides*, smooth skate *Malacoraja senta*, thorny skate *Amblyraja radiata*, spinytail skate *Bathyraja spinicauda*) was more important on the Grand Bank than on the Flemish Cap (González Iglesias *et al*., 2005, González Iglesias *et al*., 2006). The Atlantic wolffish diet in the Gulf of Maine-Georges Bank Region also showed hard-shelled prey, but mainly bivalve molluscs (Nelson and Ross, 1992).

Geographical differences in feeding habits have been reported in wolffish species (Albikovskaya, 1983). The northern wolffish had a benthypelagic diet with a higher predation on ctenophores in all size ranges in NAFO Divisions. This species showed a specialist feeder (González Iglesias *et al*., 2006) and a smaller connection with the bottom behaviour. However, their diet was very different in Div. IIb, showing a more diversified diet and a higher predation on fish (redfish and Greenland halibut) in particular in bigger individuals.

Predation on fish and crustaceans in Div. 3M has oscillated throughout the studied period. The decrease of these prey in the stomach contents of Atlantic and spotted wolffishes in the period of 1995-2000 coincides with the decreased catches of juvenil *Sebastes*, however there is not a clear relationship with the trend of the total redfish catch (González Troncoso, 2006b). Nevertheless, the increase of the crustacean consumption since 1999 coincides with the good catches of northern shrimp obtained in the late 1990s in this division (Casas *et al.,* 2005; González Troncoso, 2006b). The diet changes of Atlantic wolffish showed a relationship with the evolution of biomass of Atlantic cod, redfish and northern shrimp.

Diet overlap was only found between Atlantic and spotted wolffishes in Div. 3M in the range of depth 400-600 m. A different behaviour in the diet between both species on Grand Bank in the same depth range was observed (González Iglesias *et al*., 2006). However, the changes in diet habits were noted in the three species through the period studied on Flemish Cap. Spotted wolffish showed a similar and overlapped diet with northern wolffish in a period (1996-2001). It was more similar to the diet of Atlantic wolffish in previous and subsequent years to this period. The diet overlapping between spotted and Atlantic wolffishes took place in periods in which the Atlantic cod and the redfish (in more recent years) increased.

This overlapping coincided with the bathymetric distribution of the species. Spotted wolffish showed an intermediate behaviour of bathymetric distribution and feeding habits. Therefore, in Div. 3M, it has been observed as a part of the same assemblage as the northern wolffish in the period of 1989-1994 (Paz and Casas, 1996), and as a part of the same assemblage as the Atlantic wolffish in the period of 1995-2002 (Fig. 10) (*unpublished data, personal comment D. González-Troncoso*). This fact is reflected in the bottom range of the samples carry out for this study (Fig. 2).

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Table 1. No. individuals sampled of *Anarhichas denticulatus*, *A. lupus* and *A. minor* by Division and year (NAFO Div. 3M in 1993-2005, 3LNO in 2002-2005, and ICES Div. IIb in 2004-2005).

Specie	Year	3M No. indvs.	3LNO No. indvs.	IIb No. indvs.	*Total*
Anarhichas denticulatus	1993				
	1994	15			*15*
	1995	26			*26*
	1996	59			*59*
	1997	40			*40*
	1998	53			*53*
	1999	25			*25*
	2000	48			*48*
	2001	37			*37*
	2002	91	14		*105*
	2003	65	56		*121*
	2004	112	63	48	*223*
	2005	106	88	70	*264*
	Total	*677*	*221*	*118*	*1 016*
Anarhichas lupus	1993	236			*236*
	1994	90			*90*
	1995	234			*234*
	1996	266			*266*
	1997	251			*251*
	1998	312			*312*
	1999	235			*235*
	2000	229			*229*
	2001	267			*267*
	2002	307	189		*496*
	2003	639	282		*921*
	2004	347	184		*531*
	2005	430	285		*715*
	Total	*3 843*	*940*		*4 783*
Anarhichas minor	1993	121			*121*
	1994	99			*99*
	1995	187			*187*
	1996	189			*189*
	1997	229			*229*
	1998	204			*204*
	1999	144			*144*
	2000	88			*88*
	2001	80			*80*
	2002	118	4		*122*
	2003	149	13		*162*
	2004	278	77	2	*357*
	2005	172	36	6	*214*
	Total	*2 058*	*130*	*8*	*2 196*
Total		***6 578***	***1 291***	***126***	***7 995***

Table 2. No. individuals sampled and Feeding Intensity (*FI* %) of *Anarhichas denticulatus, A. lupus* and *A. minor* by Division and sex (NAFO Div. 3M in 1993-2005, 3LNO in 2002-2005 and ICES Div. IIb in 2004-2005).

Specie	Div	Males		Females		Indeterm.		*Total*	
		No. indv.	*FI* (%)	No. indv.	*FI* (%)	No. indv.	*FI* (%)	*No. indv.*	*FI (%)*
Anarhichas denticulatus	3M	373	46.9	297	35.0	7	100	*677*	*52.9*
	3LNO	119	38.7	102	39.2			*221*	*38.9*
	IIb	57	17.5	61	26.2			*118*	*22.0*
	Total	*549*	*49.5*	*460*	*41.7*	*7*	*55*	*1016*	*46.3*
Anarhichas lupus	3M	1991	52.8	1772	58.2	80	0.0	*3843*	*53.2*
	3LNO	485	54.2	440	55.2	15	73.3	*940*	*55.0*
	IIb								
	Total	*2476*	*53.8*	*2212*	*53.0*	*95*	*57.9*	*4783*	*53.5*
Anarhichas minor	3M	999	55.3	1041	59.1	18		*2058*	*62.9*
	3LNO	64	57.8	63	60.3	3	66.7	*130*	*59.2*
	IIb	*3*	33.3	*5*	20.0			*8*	*25.0*
	Total	*1066*	*55.4*	*1109*	*54.6*	*21*	*66.7*	*2196*	*62.6*

Table 3. Prey (% weight) in the stomach contents of the *A. denticulatus*, *A. lupus* and *A.minor* in NAFO Div. 3M (summer 1993-2005), 3LNO (spring-summer 2002-05) and ICES Div. IIb (autumn 2004-05). (* in values <1%).

Prey group	Prey	*A. denticulatus*			*A. lupus*		*A.minor*		
		3M	**3LNO**	**IIb**	**3M**	**3LNO**	**3M**	**3LNO**	**IIb**
Other Groups	***Total***	***71.6***	***58.8***	***2.1***	***4.5***	***17.9***	***20.1***	***0.1***	
	Anthozoa			1.9	*	*	*	*	
	Ascidiae				*	*			
	Bryozoa	*			*		*		
	Chaetognatha	*	*		*	*	*		
	Cnidaria	*		*	*	*	*		
	Ctenophora	70.8	55.9		1.2	14.5	18.8		
	Placophora					*			
	Annelida	*	*	*	1.8	*	*	*	
	Aphroditidae					3.0	*		
	Porifera	*		*	*		*		
	Priapulida				*				
	Scyphozoa	*	2.9		*	*	*		
	Sipunculida				*				
Echinodermata	***Total***	***1.1***	***2.5***	***9.3***	***29.4***	***15.7***	***11.8***	***58.6***	***23.4***
	Asteroidea	*	*	1.6	5.6	*	4.6	12.5	
	Crinoidea	*					*		
	Echinoidea	*			1.4	*	*		
	Echinarachnius parma					6.1		36.7	
	Holothurioidea				*	*			
	Ophiuroidea	*	2	7.1	12.7	4.4	5.6	6.2	
	Unid. and Dig. Echinodermata	*	*	*	9.7	4.5	1.3	3.3	23.4
Mollusca	***Total***	***1.1***	***0.3***	***5.2***	***8.9***	***45.6***	***1.2***	***0.6***	
	Scaphopoda				*		*		
	Gastropoda (total)	*0.7*		*5.2*	*1.4*	*42.6*	*0.3*	*0.6*	
	Buccinum sp					18.7			
	Nudibranchia				*				
	Opisthobranchia	*			*	*			
	Unid. and dig. Gastrop.	*		5.2	1.4	23.8	*	*	
	Bivalvia (total)	*0.0*			*7.1*	*3.1*	*0.2*	*0.0*	
	Unid. Bivalvia	*			7.0	2.6	*		
	Pectinidae				*	*	*	*	
	Cephalopoda (total)	*0.4*	*0.3*		*0.3*		*0.7*		
	Illex coindetii				*		*		
	Illex illecebrosus				*				
	Unid. Oegopsida	*					*		
	Octopoda		*						
	Histioteuthis sp	*					*		
	Bathypolipus arcticus				*		*		
	Unid. Cephalop. Decap.				*		*		
	Unid. and dig. Cephalop.	*			*		*		
	Unid. and dig. Mollusca				*		*		
Crustacea	***Total***	***5.3***	***5.8***	***2.2***	***25.9***	***15.8***	***14.8***	***13.6***	***66.5***
	Copepoda				*	*			
	Euphausiacea	*	*		*	*	*	*	
	Mysidacea				*	*			
	Isopoda				*	*	*		
	Amphipoda (total)	*2.3*	*4.3*	*0.1*	*3.5*	*0.4*	*0.7*	*0.0*	
	Gammaridea	*		*	*	*	*		
	Caprellidae		*			*			
	Hyperiidea	2.3	4.2		3.4	*	*	*	
	Unid. and dig. Amphip.				*	*	*		
	Decapoda Natantia (total)	*2.8*	*1.1*	*0.8*	*19.0*	*1.5*	*11.2*	*1.0*	*66.5*
	Crangonidae				*		*		
	Caridea						*		
	Metacrangon jacqueti					*			
	Acanthephyra purpurea		*						
	Lebbeus polaris	*			*	*			
	Pandalus borealis	2.7		*	18.2	1.4	11.0	1.0	66.5
	Pandalus montagui					*			
	Pontophilus norvegicus				*				
	Sabinea sarsi				*				
	Sergestes arcticus	*	*	*	*	*	*		
	Sergia robusta		*						
	Spirontocaris lilljeborgi				*		*		
	Unid. and dig. Natantia	*	*		*		*		
	Decapoda Brach. (total)	*	0.1	*0.2*	*2.1*	*5.9*	*2.8*	*12.4*	
	Chionocetes opilio	*	*		2.0	4.1	2.3	10.3	
	Lithodes maja				*		*		
	Hyas sp		*			1.7		2.1	
	Unid. and dig. Brachyura			*	*	*	*		
	Dec. Anomura (Total)	*0.0*		*0.8*	*0.7*	*8.0*	*0.1*		
	Paguridae	*		*	*	8.0	*		
	Galatheidae				*		*		
	Unid. and dig. Dec. Crust.			*	*	*			
	Unid. and dig. Crustacea	*	*		*	*	*	*	
Pantopoda	Pycnogonida				*		*		

Table 3 (cont.). Prey (% weight) in the stomach contents of the *A. denticulatus*, *A. lupus* and *A.minor* in NAFO Div. 3M (summer 1993-2005), 3LNO (spring-summer 2002-05) and ICES Div. IIb (autumn 2004-05). (* in values <1%).

Prey group	Prey	*A. denticulatus*			*A. lupus*		*A.minor*		
		3M	**3LNO**	**IIb**	**3M**	**3LNO**	**3M**	**3LNO**	**IIb**
Pisces	***Total***	***20.2***	***30.9***	***81.0***	***28.1***	***4.0***	***50.2***	***26.9***	
	Amblyraja radiata				*				
	Ammodytes dubius				*	*	*	*	
	Anarhichas denticulatus	*					2.1		
	Anarhichas lupus	*			1.6		1.3		
	Anarhichas minor						1.3		
	Anarhichas sp	*			*		1.1		
	Batilagus euriops						*		
	Benthosema glaciale	*	*				*		
	Ceratoidea						*		
	Chauliodus sloani	*			*		2.8		
	Chiasmodon niger						*		
	Cottunculus microps							*	
	Gadidae				*				
	Gadus morhua				4.6		3.9		
	Gaidropsarus ensis				*			4.4	
	Hippoglossoides platessoides					*	*		
	Lampadena speculigera	*			*		*		
	Larva of fish				*	*			
	Leptagonus decagonus				*				
	Liparidae	*	*				*		
	Liparis sp					*	*		
	Lumpenus lumpretaeformis	*			*		*		
	Lycodes reticulatus				*	*			
	Lycodes sp						*	2.2	
	Lycodes valhii				*				
	Macrourus berglax	8.9	11.6		*		1.8		
	Magnisudis atlantica						*		
	Mallotus villosus				*	1.2			
	Myctophidae		*		*		*		
	Nemichthys scolopaceus	*					*		
	Nezumia bairdi		1.1		1.0		*		
	Notolepis risso						*		
	Paralepididae						*		
	Phycis chesteri				*		*		
	Protomictophum arcticum						*		
	Pseudoscopelus scriptus						*		
	Reinhardtius hippoglossoides	*	*	54.3					
	Rajidae	*			*		*		
	Scomberesox saurius						*		
	Sebastes sp	7.3	16.7	15.7	13.3	0.2	26.2	15.2	
	Serrivomer beani	*			*		2.9		
	Stomias boa	*			*	*			
	Triglops murrayi				*		*		
	Unidentif. Macruridae	*			*		1.1		
	Urophycis sp				*				
	Urophycis tenuis							4.4	
	Unid. and dig. fish	*	*	11.0	2.5	*	3.2	*	
Other prey	***Total***	***0.8***	***1.7***	***0.2***	***3.1***	***1.0***	***1.9***	***0.1***	***10.0***
	Chlorophyceae				*				10.0
	Rhodophyceae				*				
	Offal		1.0		2.0		*		
	Eggs	*	*		*	*	*	*	
	Unidentified	*	*	*	*	*	1.0		
Number of prey		47	29	18	83	50	80	22	3
Number of individuals sampled		677	221	118	3843	940	2058	130	8

Table 4. Interspecific niche overlap among the wolffish species in each Division (Div. 3M 1993-2005; 3LNO 2002-05; and Div. IIb 2004-05).

	Division				
	3M		3LNO		IIb
	A. lupus	***A. minor***	***A. lupus***	***A. minor***	***A. minor***
A. denticulatus	0.08	0.49	0.34	0.10	0.01
A. lupus		0.67		0.21	

Table 5. Interspecific niche overlap among the wolffish species by depth range in Div. 3M (1993-2005).

	Division 3M							
	0-199 m		200-399 m		400-599 m		600-799 m	
	A. lupus	***A. minor***	***A. lupus***	***A. minor***	***A. lupus***	***A. minor***	***A. lupus***	***A. minor***
A. denticulatus	0.12	0.42	0.09	0.59	0.08	0.25	0.00	0.01
A. lupus		0.44		0.58		0.76		0.00

Table 6. Interspecific niche overlap among the wolffish species by three year period in Div. 3M (1993-2005).

	Division 3M							
	1993-1995		1996-1998		1999-2001		2002-2005	
	A. lupus	***A. minor***	***A. lupus***	***A. minor***	***A. lupus***	***A. minor***	***A. lupus***	***A. minor***
A. denticulatus	0.00	0.12	0.01	0.72	0.03	0.60	0.34	0.40
A. lupus		0.89		0.22		0.34		0.75

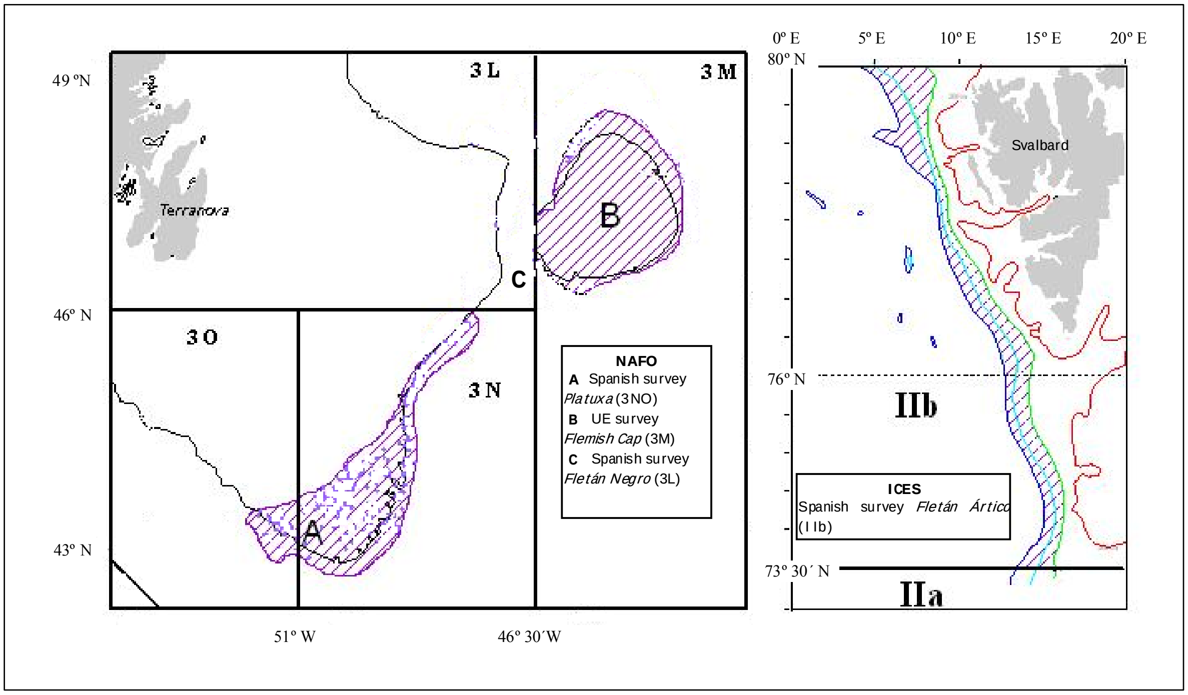

Fig. 1. NAFO and ICES Areas where the bottom trawl research surveys were carried out.

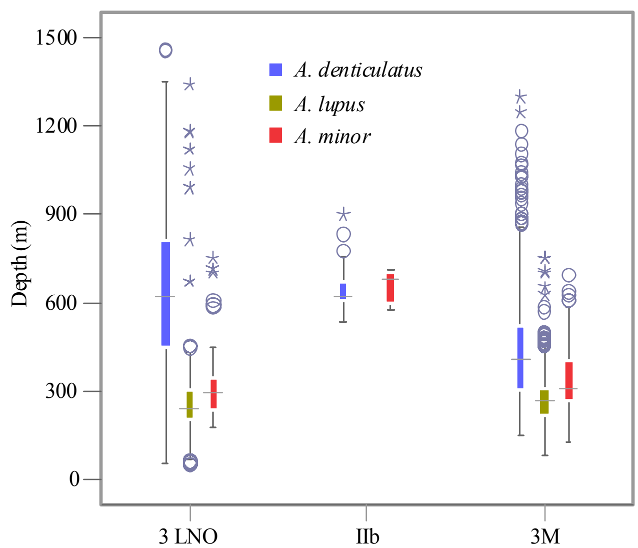

Fig. 2. Depth (m) of wolffish species samplings according by Division showing the median, percentiles, extreme values and outliers (NAFO Div. 3M in 1993-2005; 3LNO in 2002-2005; and ICES Div. IIb in 2004-2005, with depth range of survey 500-1 450 m).

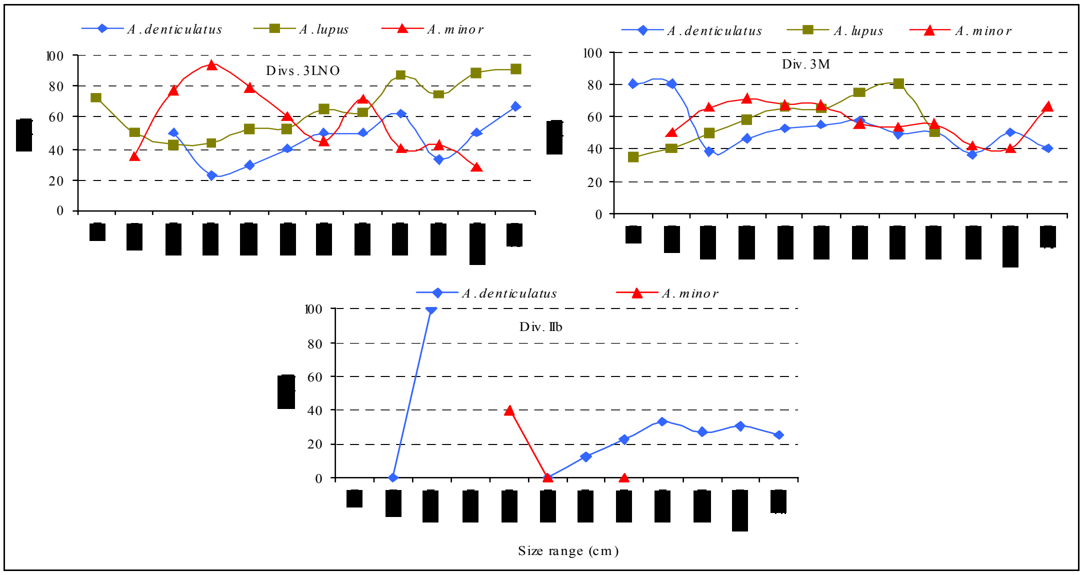

Fig. 3. Feeding Intensity (FI%) of *A. denticulatus*, *A. lupus* and *A. minor* by size range in each Division (NAFO Div. 3M in 1993-2005, 3LNO in 2002-2005, and ICES Div. IIb in 2004-2005).

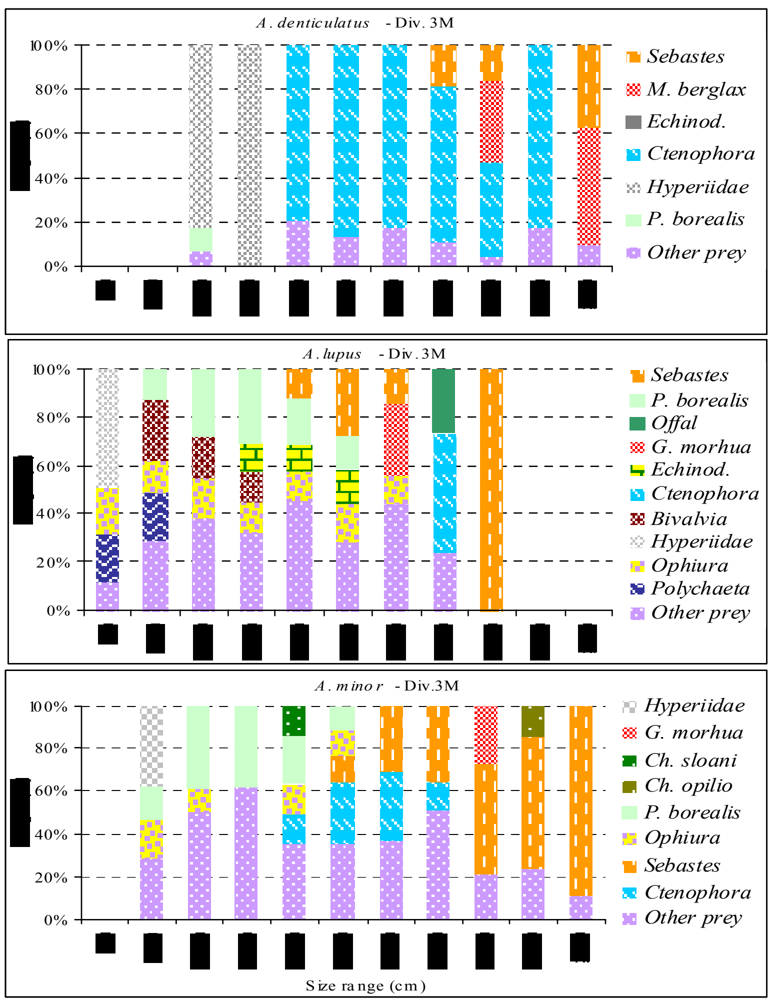

Fig. 4. Weight (%) of main prey of wolffish species by size range (cm) in NAFO, Div. 3M (1993-2005).

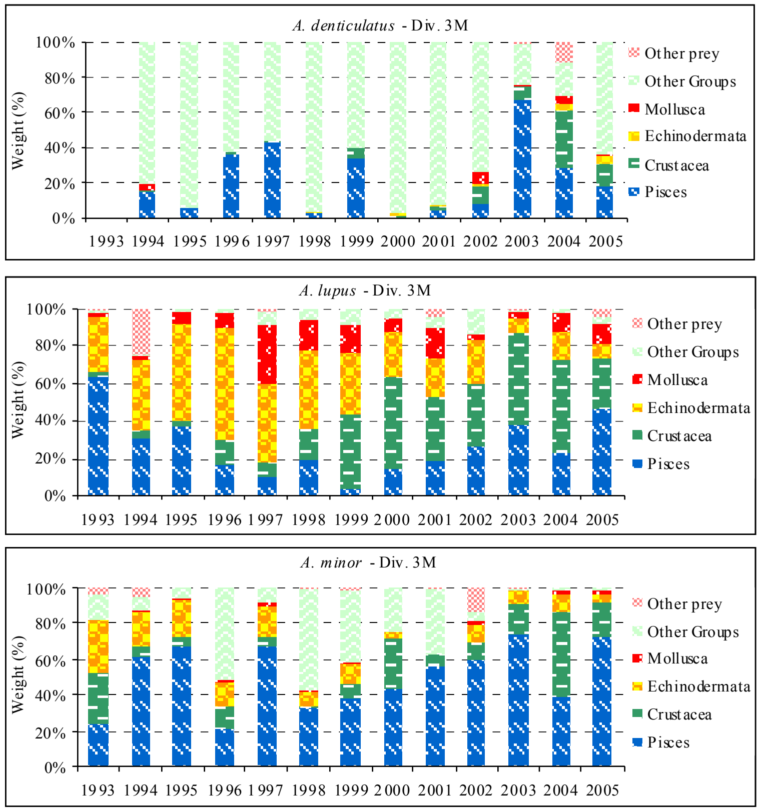

Fig. 5. Weight (%) of the prey groups of wolffish species by year in NAFO, Div. 3M (1993-2005).

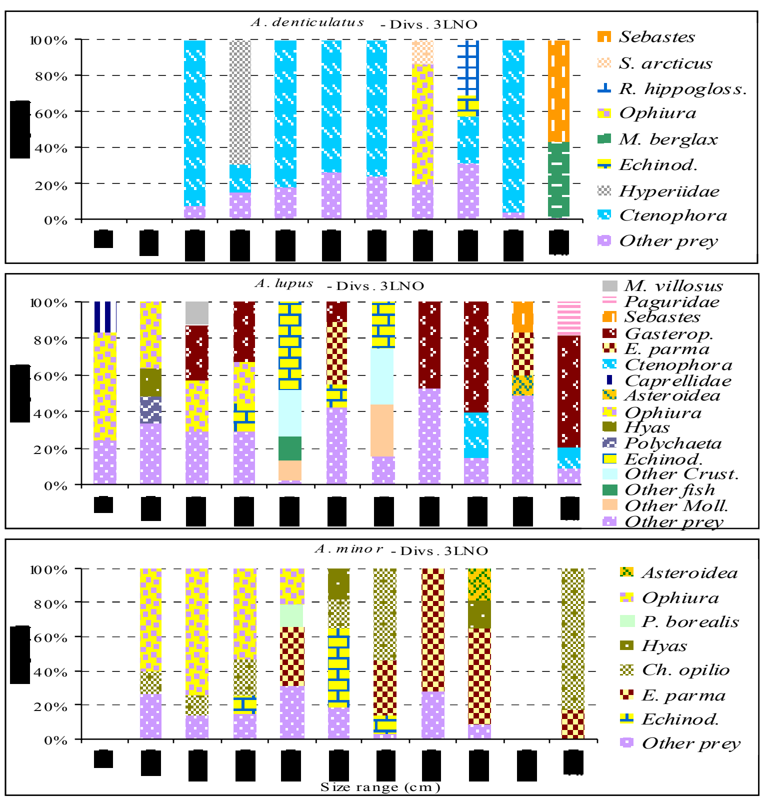

Fig. 6. Weight (%) of main prey of wolffish species in NAFO, Div. 3LNO (2002-2005).

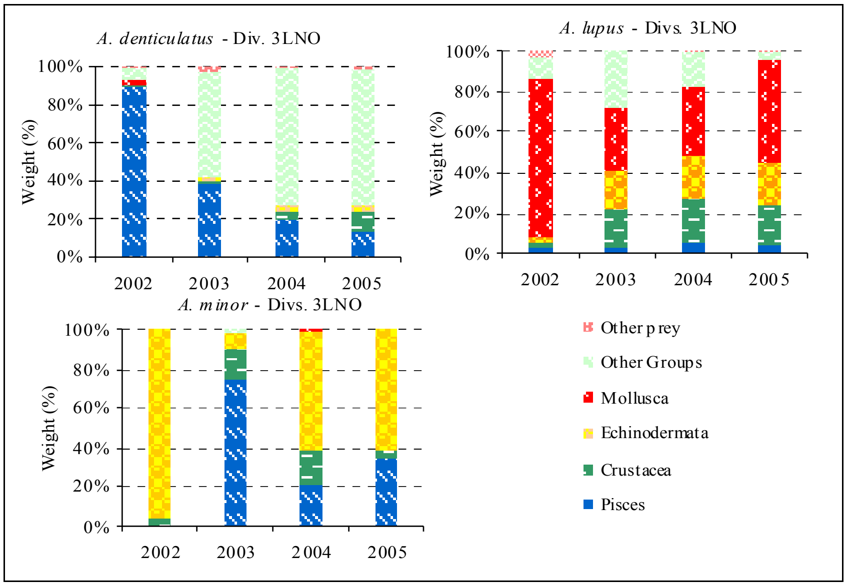

Fig. 7. Weight (%) of the prey groups of wolffish species by year in NAFO, Div. 3LNO (2002-2005).

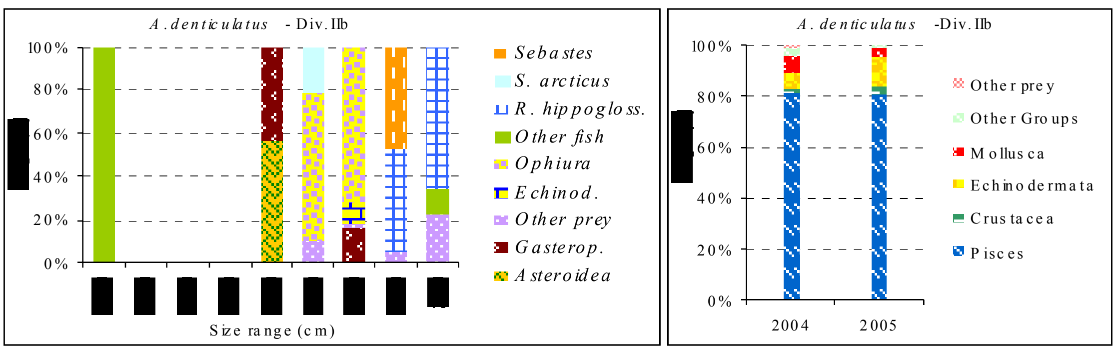

Fig. 8. Weight (%) of main prey by size range (cm) and weight (%) of prey group by year of *A. denticulatus* in ICES, Div. IIb (2004-2005).

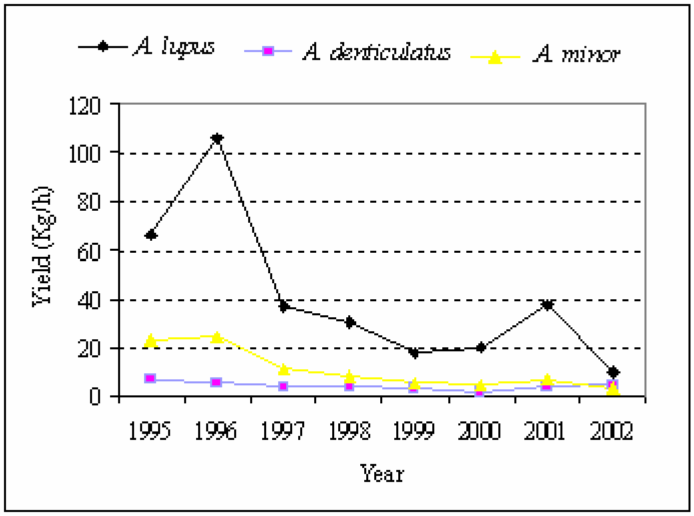

Fig. 9. Wolffish yield trends from EU Flemish Cap Survey, 1995-2002.

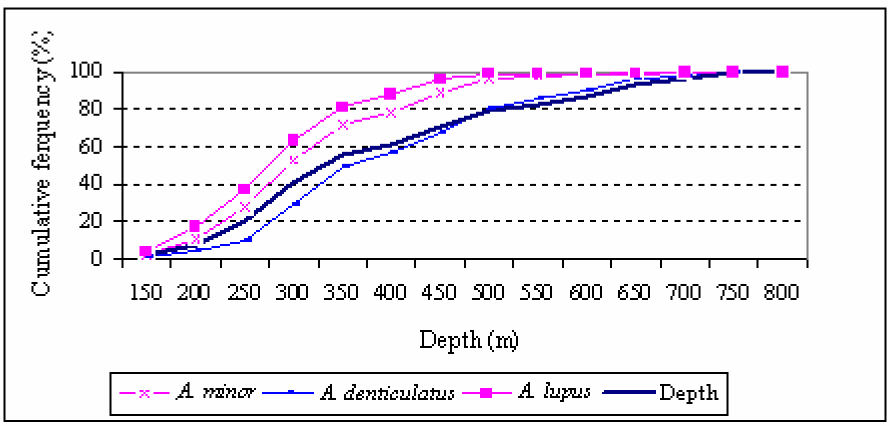

Fig. 10. Wolffish presence by depth from EU Flemish Cap Survey, 1995-2002.