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A Study of Trophic Interrelations Between Cod (*Gadus morhua*) and Capelin (*Mallotus villosus*)
on the Newfoundland Shelf in Spring and Summer Seasons of 1985-1991

by

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ABSTRACT

Trophic interrelations between cod and capelin in the North of the Grand bank (Div. 3L) are studied with relation to differences in the geographical distribution and conditions in the habitat of young and mature capelin.

Optimal ratio of predator length (cod) and prey length (capelin) is within 17-24%. A relationship is established between the number of immature capelin in Div. 3L in spring and summer seasons and growth rate of cod at age 5-7.

Charts of distribution of principal capelin feeding areas are suggested and comparative characteristic of the intensity of consumption of capelin by cod in 1987-1991 is given. The strongest consumption was observed in May-June 1991.

INTRODUCTION

An analysis of trophic "predator-prey" relations between two species implies both the evaluation of the impact of predation on prey numbers and evaluation of a reverse relation - the impact of prey numbers variations on the status of predator population.

A question of "reverse relation" is more often in the centre of attention on occasions, when numbers of major prey of a certain commercial species have dropped drastically, which causes notable disturbances in the ecosystem trophic web as well as changes in predator numbers. However, the analysis of the "reverse relation" in situations, when prey numbers variations are not extreme, is of great interest and contributes to the comprehensive knowledge of how the ecosystem works.

Papers on trophic relations between cod and capelin over the Newfoundland and Labrador shelf suggest dif-

ferent methods and approaches to estimate daily and yearly consumption of capelin by cod (Popova, 1962; Campbell & Winters, 1973; Minet & Perodou, 1978; Turuk, 1978; Lilly, Wells & Carscadden, 1981; Lilly, 1987). In connection with a sharp drop of capelin biomass in the late 70s the year-to-year variability of capelin and other prey consumption by cod was studied (Lilly, 1989). In particular, it was studied whether cod are capable through feeding more intensively on other prey to compensate scarcity of capelin in the diet. It was found that other species can not be an adequate substitute for capelin, hence, variations of capelin numbers must in one way or another influence the biological condition of cod. However, the analysis of relation between capelin biomass and cod growth rate has not suggested clear conclusions. It was hypothesized, that the two species are not connected through any strong trophic relation (Akenhead et al., 1982; Millar et al., 1990).

In all above mentioned papers the population of capelin, its biomass and numbers are considered integrally, irrespective of their structure. However, it is known, that conditions in the habitat of young and mature capelin are different, especially in spring and summer seasons (Lilly, 1987). Therefore, the present paper suggests a differentiated approach to the study of trophic relations between capelin and cod.

MATERIAL AND METHODS

The paper uses materials on numbers and size-age compositions of cod and capelin, collected during complex research surveys in spring and summer seasons 1985-1991.

To analyse variations of the cod growth rate yearly weight increments in cod at age 3-9 were used. Weight increment was estimated as the difference between mean weights at age for two subsequent years.

Stomach contents of cod were studied in field and quantitative-weight analysis (Table 1). In the field analysis occurrence frequency of capelin in cod stomachs was determined as a ratio of stomachs with capelin to the total number of examined stomachs. In quantitative-weight analysis priority was given to the estimation of numbers and length of prey. Capelin length was measured from the tip of the snout to the end of the middle rays of the tail fin. The length of heavily digested capelin (SL) was restored from the length of the back bone (l) using the formula:

$$SL = 1.211 + 13.34$$

For comparative analysis and further calculations, all cod were distributed between 9 cm size groups. Total biomass of capelin in the diet of the whole cod stock in open waters of Div. 3L during the survey time was estimated from:

$$W = \sum_{i=1}^n w_i N_i K_i$$

where w_i - mean restored weight of capelin in stomachs of cod from group i ; N_i - numbers of fish in group i ; K_i - occurrence frequency of capelin in cod stomachs of group i ; n - number of 9 cm groups.

Similarly total numbers of capelin in the diet of the whole cod stock were estimated.

To evaluate the intensity of consumption of capelin by cod and to draw maps of the feeding areas, biomass of cod preyed on capelin was estimated for each catch (W_c):

$$W_c = W_{tot} K_c$$

where W_{tot} - catch of cod; K_c - occurrence frequency of capelin in cod stomachs in given catch. The calculated value was then multiplied by mean daily consumption of capelin by the whole cod stock, to estimate which it was assumed that it takes 4 days for digestion of food in cod stomachs (Bowering et al., 1984).

RESULTS

1. Size preference in cod in relation to capelin.

A ratio between prey length and predator length ($\frac{l}{L}$) was used as a main index of size preference exhibited by cod. Mean ratios for 1987-1991 are inversely proportional to cod length (Fig. 1):

$$\frac{l}{L} = e^{1.72L - 0.79} \quad (r = 0.98, P \geq 0.95)$$

55% in small cod and 11% in large cod (Table 2) can be considered as extreme values for the given ratio. Cod prey most intensively on capelin on occasions when the capelin length is 17-24% of the cod length - occurrence frequency of capelin in cod stomachs then is the highest (Table 3).

Data collected by many researchers indicate that cod of 40 to 70 cm are the main consumer of capelin over the Newfoundland shelf (Popova, 1962; Turuk, 1968; Lilly, 1987; 1989; Lilly & Rice, 1983). With account for the above given ratios it can be stated, that capelin of 7 to 18 cm in length experience the most heavy predation from cod, in other words, it affects both mature and young capelin. Since the numbers of capelin year classes vary notably between years, feeding condi-

tions for cod from different age groups within 40-70 cm can also vary considerably.

2. Relation between cod growth rate and capelin numbers.

Status of food supply may produce effects on the growth rate of fish, age of their maturation, fecundity and numbers. Of all mentioned indices the growth rate is most labile, responding fast to such prey biomass changes which are not extreme.

Div. 3L is not completely suitable for investigating the relationship between the growth rate of cod and capelin numbers, because of the complexity of the genetic structure of cod stock there (Postolaky, 1962; Lear, 1984, 1986). However, it is just in this area, that intensive feeding of cod on capelin is observed in spring and summer seasons concurrently with clear spatial separation of young and mature capelin.

The spawning stock of capelin is known to be composed of fish at age 4 and older, 2-yr-olds are mostly pre-recruits. The proportion of mature 3-yr-olds is on the average about 50%, however, this value can vary between years considerably.

Peak yearly increments in cod at age 3 to 5 coincided and fell at 1982-1986, 1988-1989 and 1990-1991 (Fig. 2). Assuming a relation between the growth rate of fish at the above age and capelin numbers (the young), it can be inferred, that 2-yr-olds were numerous in spring and summer of 1985, 1988 and 1990, i.e. the 1983, 1986 and 1988 year-classes of capelin were strong.

6-yr-olds of cod occupy an intermediate position with respect to the growth rate, while maximum increments in cod at age 7 to 9 again coincide and fall at 1985-1986, 1987-1988 and 1990-1991. Assuming a relation between the growth rate of cod from older age groups and numbers of mature capelin, it can be inferred that 4-yr-olds were numerous in 1985, 1987 and 1990 (1981, 1983 and 1986 year-classes). Following the same procedure the 1984, 1985 and 1987 year-classes of capelin can be evaluated as weak.

Data provided by capelin acoustic surveys in spring and summer are in general consistent with these assumptions (Bakaney & Mamylov, 1988; Bakaney & Zubov, 1991, Miller, 1991). 1987 is an exception - Canadian and Russian scientists have different opinions as about the strength of this year-class of capelin (Miller & Carscadden, 1989).

Therefore, on a qualitative level there is a certain

relation between the growth rate of cod and capelin numbers. Quantitatively this relation is somewhat difficult to express for many reasons, of which most important are: a) short data series, b) lack of data on capelin numbers and size-age composition of cod in inshore areas, c) rough estimates of capelin numbers as provided by acoustic surveys in spring and summer seasons. Performing a quantitative evaluation of the strength of relation, we use only the estimates of numbers of immature capelin from Russian surveys (Bakanev, Vaskov & Petrov, 1990; Bakanev & Zubov, 1991), presuming, that capelin pre-recruits, which stay in open waters of Div. 3L in spring time, can be estimated more precisely. As indicated by the results available, the most strong relation is found between the numbers of young capelin and growth rate of cod at age 5-7 (Table 4).

3. Spatial distribution of cod and its relation to capelin migrations in spring and summer 1987-1991

There are certain specific features in the distribution of cod over the northern part of the Grand bank in April-May, that are common for different years. For example, most dense concentrations develop, as a rule, in the west (along the eastern slope of the Newfoundland) and over the north-eastern slope of the bank (Fig. 3). Probably, these concentrations appear in connection with the preying of cod on capelin, although in April and May locations of intensive feeding on capelin were found, mainly, in the western part of the area (Fig. 4). An acoustic survey for capelin, which normally follows a bottom survey in Div. 3L, records, as a rule, concentrations of immature capelin in the north and north-east of the bank (Bakanev, Vaskov, Petrov, 1990; Mamylov & Bakanev, 1984; 1985).

The distribution pattern of cod in Div. 3L in 1991 was different from what was observed in previous years. The reason behind may be as follows. Since the bottom survey in 1991 was done later, it can be assumed, that the cod aggregating in the west of the area had by that time migrated towards coasts and were not available for surveying. However, it could well be, that in 1991 cod did not move inshore at all. Similar situation was observed in 1986, when the distribution of dense concentrations of immature capelin in offshore waters, where fish at age 3 (1985 year-class) prevailed, had an adverse effect on the inshore cod fishery. According to Canadian experts "food was so abundant offshore, most cod may have just stayed out there all summer rather

than follow the much smaller schools of spawning capelin to inshore waters" (The Science..., 1991). As indicated by our findings, in 1991 on the north-eastern slope of the bank cod preyed mainly on capelin at age 3 too (1988 year-class). It is worth noting, that in 1988 dense capelin concentrations offshore were dominated by smaller fish at age 2, conditions for cod fishing were good (The Science..., 1991).

4. Intensity of capelin consumption by cod.

Intensity of cod feeding on capelin can be characterized by absolute indices - total numbers and biomass of capelin in the food of the whole cod stock, and relative ones - occurrence frequency and daily intake of capelin by cod (Table 5). The biomass and numbers of capelin were the biggest in the food of cod in offshore waters of Div. 3L in April 1988. Fish at age 2 constituted a considerable part of the consumed capelin (Fig. 5). However, as for the relative indices of feeding intensity in that year, they were not peak ones. High absolute indices were to a great extent caused by high numbers of cod itself, in 1988 they were higher, than in other 4 years (Kuzmin, 1991).

Estimates of the total number of capelin in the food of cod in April-May 1987, 1989 and 1990 are fairly close, while those of the total biomass are more different, because of changes in the size frequency of capelin.

In May-June 1991 both absolute and relative indices of capelin consumption by cod were large. It can be assumed, that in previous years a survey for cod was conducted during capelin migration time, there was no complete overlapping of distributions of cod and capelin, it was varying all the time. In 1991, by the time of the cod survey capelin ceased to migrate, the overlapping of distribution areas of dense capelin concentrations and cod was steady and most vast, the intensity of cod preying on capelin reached its highest values.

On the other hand, a combination of such factors as: a) negative temperature anomalies over the Grand bank in 1990-1991 (Borovkov & Tevs, 1991); b) predominance of fish at age 3 in the capelin population, could be the reasons for unusual distribution and migration times of capelin in that year. It might be, that the proportion of mature individuals among 3-yr-olds was extremely low, therefore, capelin had not migrated inshore for spawning, but gathered over the north-eastern slope of the Grand bank. In case, the distribution of capelin in spring and summer 1991 was not

standard, its consumption by cod and other predators might be abnormally big.

DISCUSSION

The degree of geographical segregation of mature and immature capelin in the total stock during a year is not well studied. Data are especially scarce on times of autumn feeding and wintering, although there is evidence available, that in the beginning of December isolated concentrations of capelin at age 1+ dwelt in the north of Div. 3L, while the majority of the stock stayed in Div. 3K (Bakanev & Gorchinsky, 1985).

In spring and summer seasons mature capelin migrate for spawning in warm inshore waters or to the southern shallows over the Grand bank, whereas young cod gather in dense concentrations over the north-eastern slope of the bank, in the area influenced by the Labrador current (Dragesund & Monstad, 1973; Kovalev & Kudrin, 1973; Mamylov & Bakanev, 1984, 1985). In the day time young fish form small schools, dwelling in the mid-waters, pre-spawning capelin gather in dense concentrations near the bottom (Mamylov & Bakanev, 1984). Consequently, to prey on young cod the cod have to perform migrations into the pelagial, to cold intermediate layer, when feeding on pre-spawning capelin the cod can stay near the bottom, in warmer waters. Since pelagial feeding is more typical of younger cod, while bottom one - of older fish, the first hypothesis presented by this paper suggests a relation between the growth rate of cod from younger age groups in Div. 3L and numbers of immature capelin, and the growth rate of older cod and mature capelin numbers.

On the other hand, from geographical distribution of principal feeding areas it may be guessed, that besides size-age differences, the cod preying on young or mature capelin in Div. 3L can also have genetic ones. For example, concentrations of cod in the west and south-west of the area may contain migrants from the south, while in the north-east - fish from Div. 3K, the cod could migrate southwards along the eastern slope of the Grand bank as far as 45°30'N (Lear, 1986). It may also well be, that the intensity of cod migrations from the north to the south into Div. 3L in spring and summer is related to the density of capelin concentrations in the west and north-east of the Grand bank. Further, more detailed studies of trophic relations between cod and capelin can contribute to a better knowledge of this matter.

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Table 1. Total amount of materials used in cod feeding studies

Year	Number of stomachs	
	Field analysis	Quantitative & weight analysis
1987	744	42
1988	825	250
1989	1671	85
1990	1059	221
1991	1054	416

Table 2. Ratio between capelin length and length of predatory cod

Cod length, cm	Year	1987		1988		1989		1990		1991	
		l/L	min-max	l/L	min-max	l/L	min-max	l/L	min-max	l/L	min-max
18-26	-	-	-	-	-	-	-	-	-	0,47	0,43-0,52
27-35	0,39	0,35-0,45	0,34	0,23-0,53	0,41	0,38-0,45	0,33	0,25-0,50	0,42	0,30-0,54	
36-44	0,32	0,31-0,32	0,26	0,15-0,41	0,34	0,28-0,38	0,29	0,21-0,41	0,36	0,24-0,44	
45-53	0,26	0,15-0,34	0,25	0,16-0,36	0,24	0,18-0,36	0,30	0,24-0,38	0,29	0,18-0,37	
54-62	0,24	0,16-0,30	0,20	0,13-0,29	0,22	0,15-0,32	0,24	0,19-0,30	0,24	0,15-0,31	
63-71	0,22	0,12-0,26	0,19	0,12-0,26	-	-	0,20	0,14-0,25	0,20	0,14-0,26	
72-80	0,19	0,12-0,24	0,17	0,14-0,20	-	-	0,20	0,17-0,25	0,18	0,12-0,24	
81-89	-	-	-	-	-	-	0,17	0,12-0,20	0,17	0,12-0,21	
90-98	-	-	-	-	-	-	-	-	0,15	0,12-0,20	

Table 3. Occurrence frequency (%) and mean restored weight of capelin (g) in cod stomachs in Div. 3L in 1987-1991

Cod length, cm	Year	1987		1988		1989		1990		1991	
		I	2	I	2	I	2	I	2	I	2
18-26		-	-	-	-	-	-	-	-	8,9	9,6
27-35		10,0	10,0	12,8	15,7	29,4	11,5	12,7	14,7	28,3	15,0
36-44		19,8	3,7	31,7	27,7	29,8	17,2	19,2	16,5	39,2	43,2
45-53		29,6	57,4	34,4	35,7	36,9	30,5	24,5	64,2	47,8	117,8
54-62		37,6	61,2	43,9	79,8	33,3	24,1	28,9	90,6	51,4	111,2
63-71		39,7	63,0	58,0	104,0	28,5	2,5	28,4	46,6	63,0	144,2
72-80		28,6	98,0	72,2	111,0	26,1	no data	30,1	49,0	36,6	115,5
81-89		-	-	75,0	no data	25,9	no data	50,0	114,7	53,7	89,0
90-98		-	-	-	-	-	-	-	-	50,0	112,6

1 - occurrence frequency of capelin in cod stomachs, % of the total number of examined stomachs

2 - mean restored weight of capelin in cod stomachs of a given size group, g

Table 4. Correlation coefficients between numbers of young capelin and growth rate of cod at age

	Weight increment in cod											
	3-4	4-5	5-6	6-7	7-8	8-9	9-10	3-6	7-10	3-5	5-7	7-9
Numbers of 2-yr-olds of capelin	0,41	0,70	0,48	0,77	0,68	0,75	0,08	0,59	0,37	0,62	0,69	0,56
Numbers of immature capelin	0,37	0,68	0,56	0,80	0,70	0,75	-0,04	0,62	0,28	0,59	0,74	0,58

Table 5. Main indices of capelin consumption by cod in offshore waters of Div. 3L in spring and summer seasons of 1987-1991

Survey time	1987	1988	1989	1990	1991
	27.04-11.05	7.04-23.04	27.04-21.05	26.04-23.05	9.05-6.06
Occurrence frequency of capelin in cod stomachs, %	29,6	32,8	30,6	20,5	41,0
Total numbers of capelin in cod diet during survey time, fish $\times 10^{-6}$	112,0	615,3	98,5	112,5	331,7
Total biomass of capelin in cod diet during survey time	1623,3	6565,4	944,7	1601,6	6043,4
Mean daily consumption of capelin by cod, % of fish weight*	1,0	1,2	0,7	1,48	2,7

* Calculations have been done only for cod preying on capelin

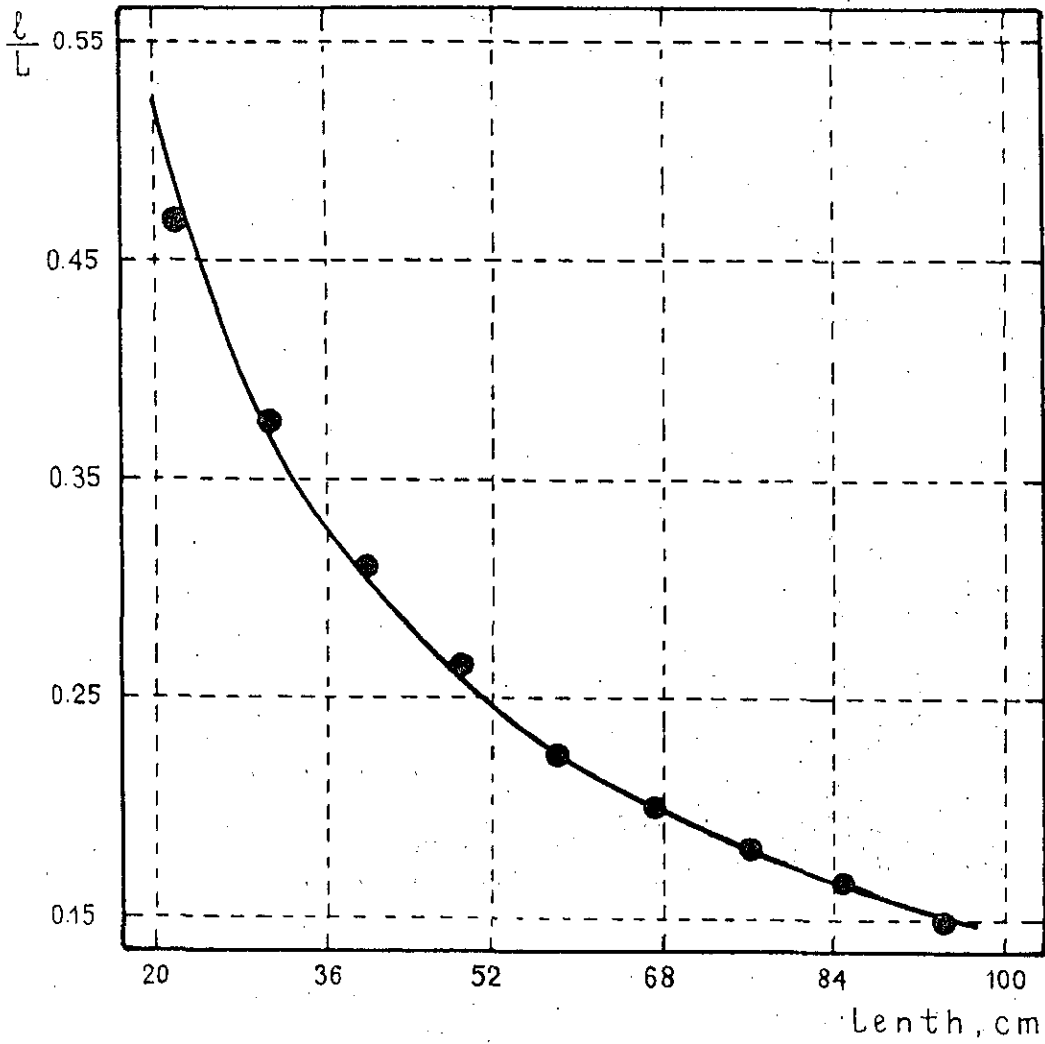


Fig. 1 Size preference in cod in relation to capelin. L - cod length; l - capelin length

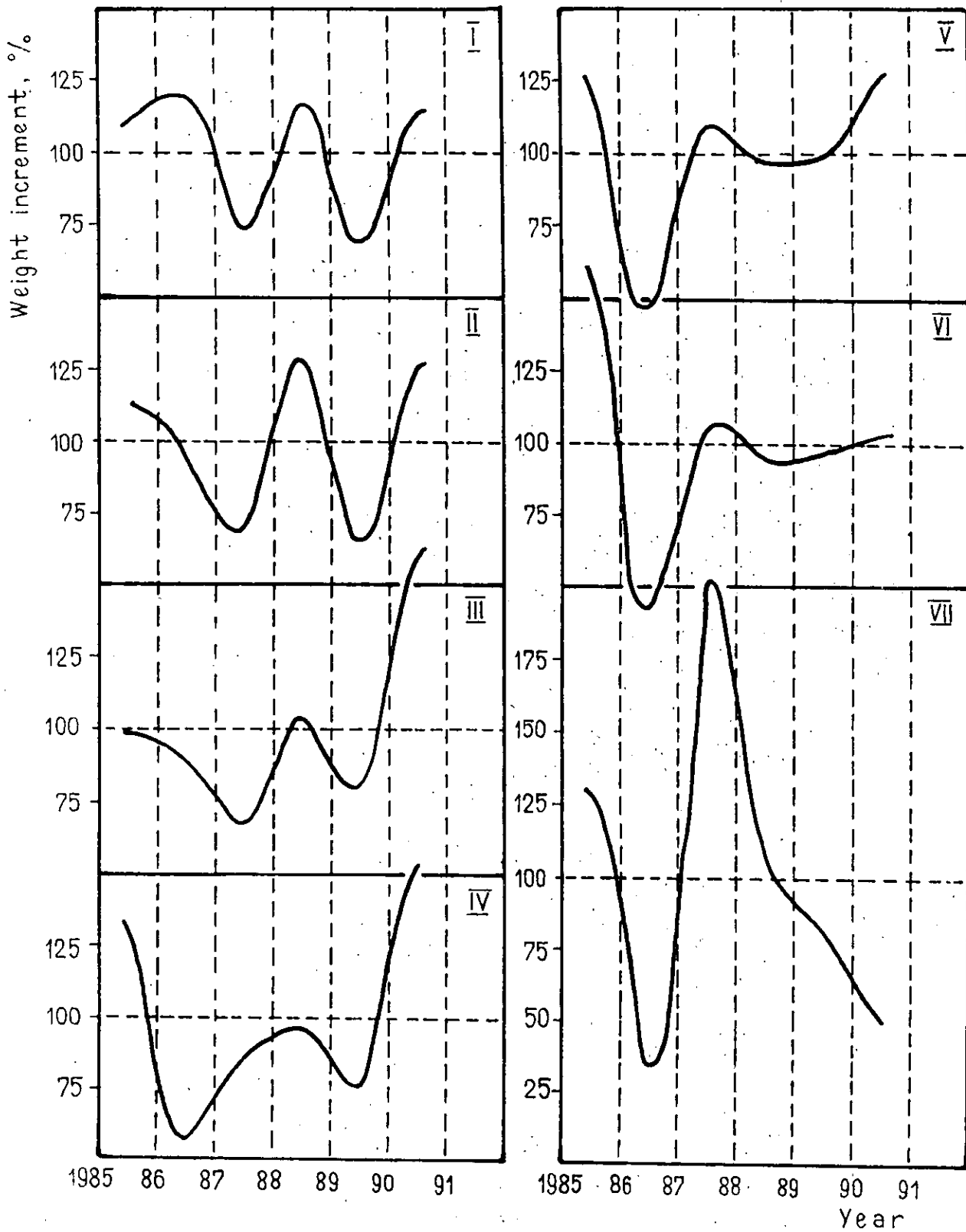


Fig. 2. Yearly increments in cod at age (% of mean yearly increment for 1985-1991)
I - cod at age 3-4; II - 4-5 years;
III - 5-6 years; IV - 6-7 years;
V - 7-8 years; VI - 8-9 years; VII - 9-10 years.

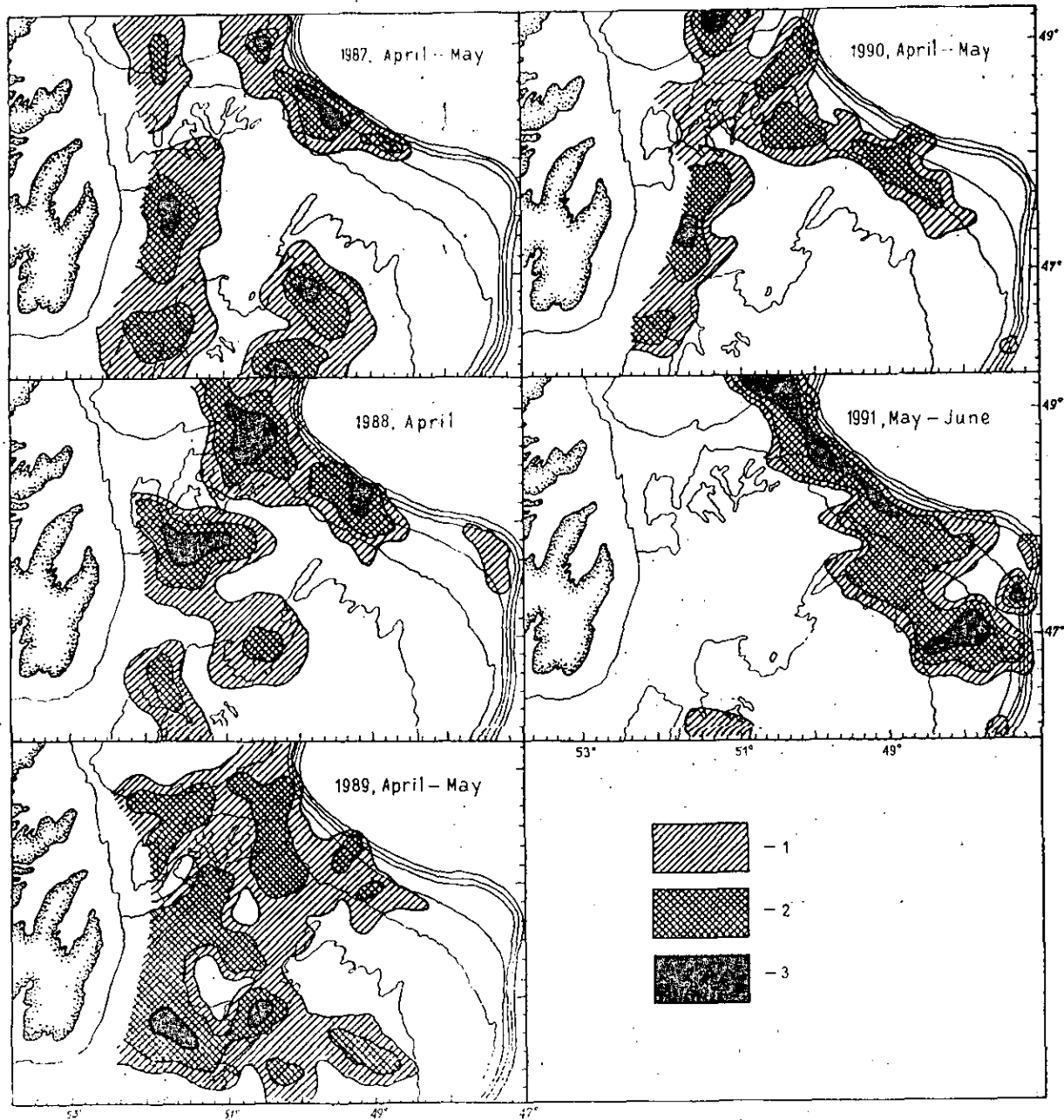


Fig. 3 Chart of distribution of main cod concentrations.

- 1 - 50-100 kg/hour tow
- 2 - 101-500
- 3 - over 500

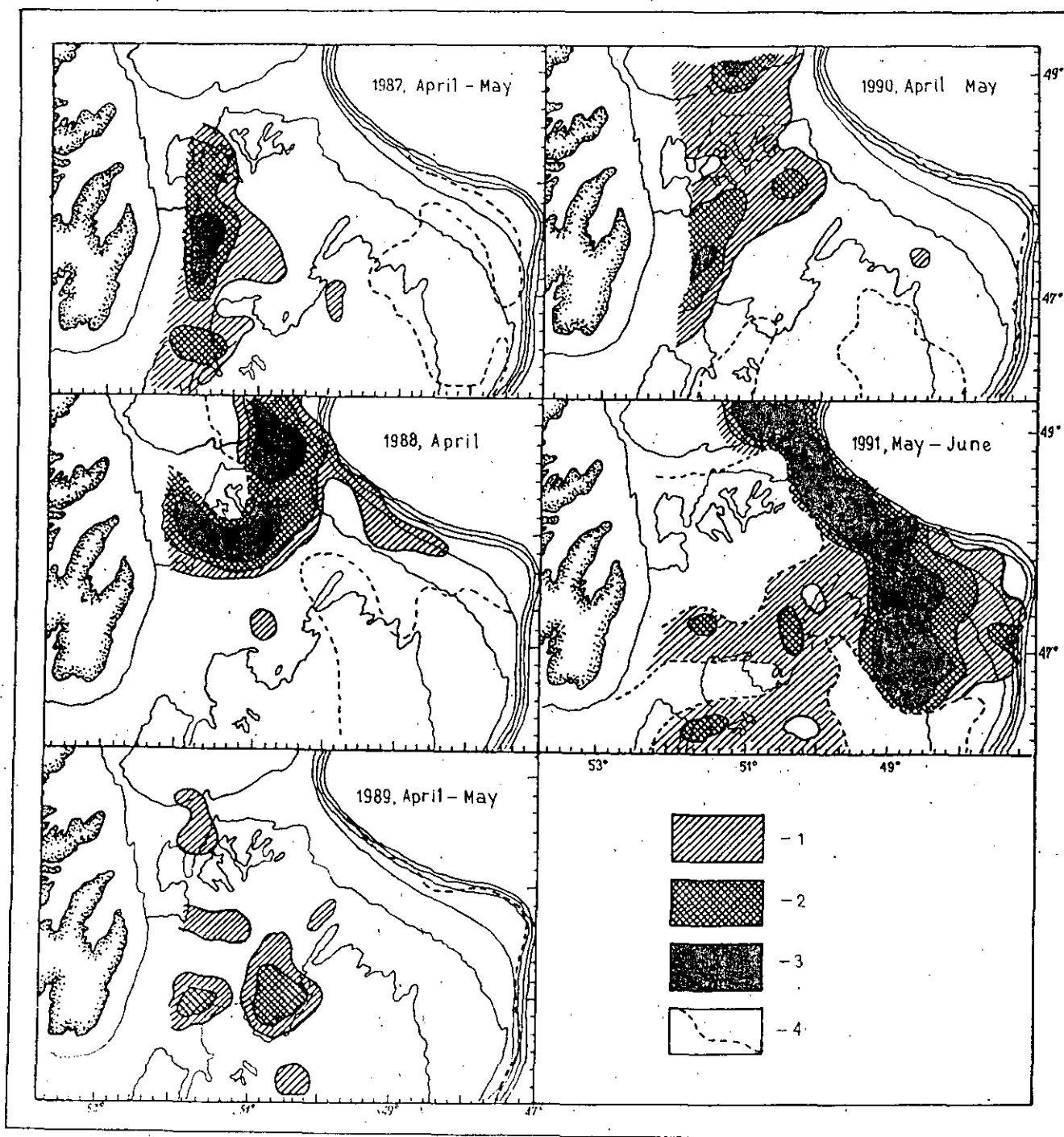


Fig. 4 Chart of principal feeding areas of cod on capelin. Intensity of capelin consumption: 1 - 25-50 kg/day/sq.mile; 2 - 51-100; 3 - over 100. 4 - boundaries of cod distribution areas.

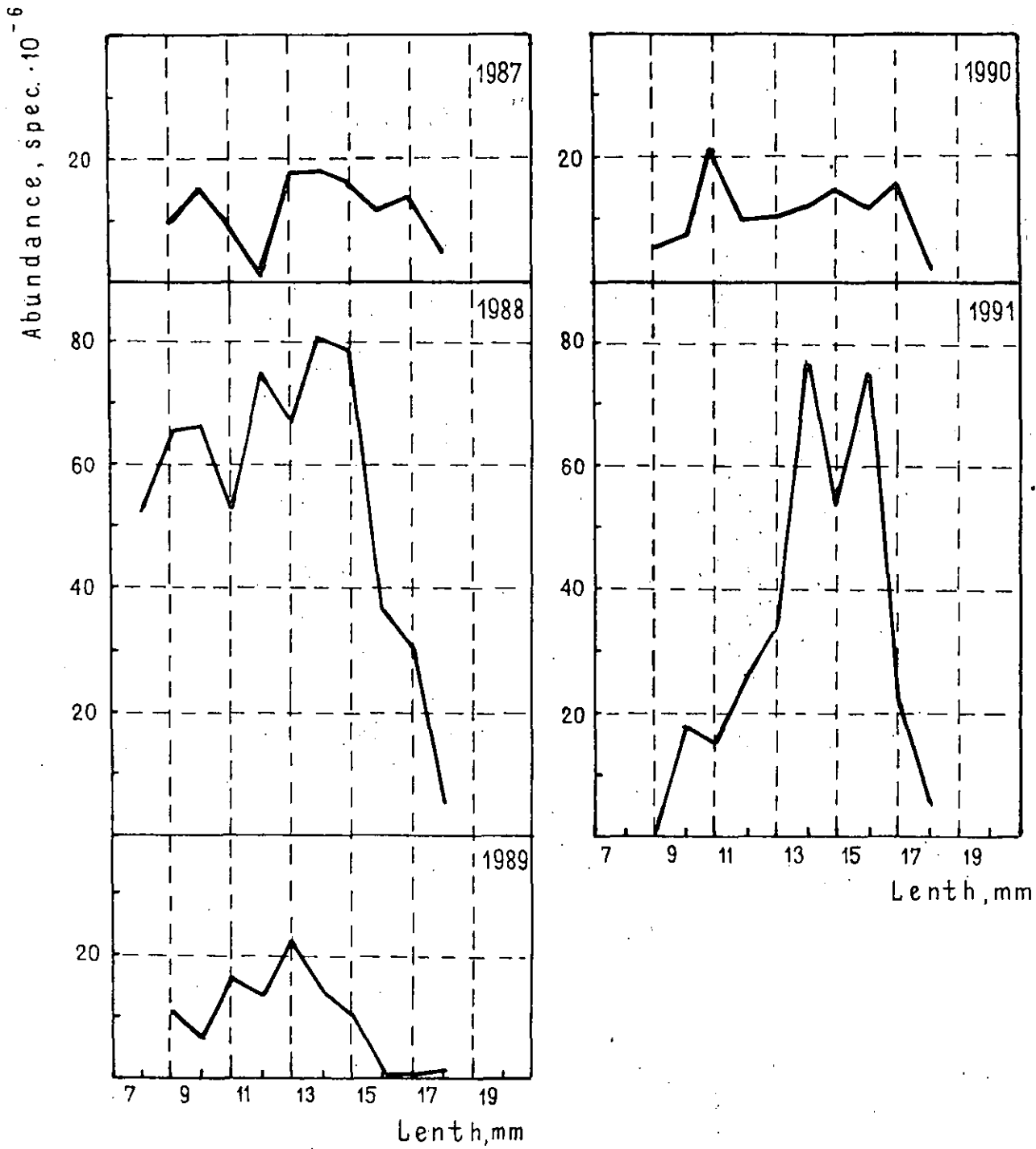


Fig. 5 Numbers of capelin at age in the cod diet in Div. 3L in 1987-1991.