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The daily feeding dynamics in various length groups
of the Barents Sea capelin during the feeding period

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ABSTRACT

A total of 700 capelin stomachs collected during the feeding period in August 1989 by 24-h fishery were analyzed for each 3-cm length groups. The number of prey categories consumed by the Barents sea capelin showed a tendency to increase with increasing fish length up to 12 cm. *Calanus finmarchicus* was the major contributor in the diet (66.39%) of length group 6–8.9 cm. Capelin in length group 9–11.9 cm had mainly fed on *Calanus finmarchicus* (33.53%), *Parathemisto abyssorum* (14.54%) and *Thysanoessa raschii* (28.04%) while the two species, *Thysanoessa inermis* and *Thysanoessa raschii* occupied 95.2% of the stomach contents weight in length group 12–14.9 cm. The evening peaks in feeding occurred approximately for all length groups and the feeding was at minimum during the midday. The daily ration during the first half of August is estimated between 1.47% and 2.0% of fish body weight. Accordingly, these data gives about 4116 tonnes as the daily consumption of zooplankton by capelin stock at the Goose Bank area.

INTRODUCTION

Capelin *Mallotus villosus* is one of the most important predators on zooplankton organisms in the Barents Sea and it has been shown to play a major role in the ecosystem during their feeding migration to the northern part of the Barents Sea (Panassenko and Soboleva, 1980; Panassenko and Nesterova, 1983, Hassel, 1984, 1986; Panassenko, 1989; Skjoldal and Rey, 1989). Furthermore, Hassel et al. (1991) reported that when capelin will consume 10% of its body weight per day, the zooplankton will be depleted in only 3–4 days where the capelin is heavily concentrated.

The heat content of the water masses exerts a significant influence on the feeding migration routes. During the warm years the immature part of the population is distributed in the northeastern area while in cold years the capelin stock mainly found at the western and the northwestern parts of the Barents Sea (Panassenko and Soboleva, 1980).

The development of the capelin stock during 1972–1989 was dramatic and the driving forces were stock interactions (Bogstad and Tjelmeland, 1990), operating under strong influence of physical environmental variability, particularly on the climatic scale (Skjoldal and Rey, 1989). The capelin stock development can only be understood in a multispecies context (Bogstad and Tjelmeland, 1990), and

hence the consumption rate have to be estimated for a larger number of species in the ecosystem.

The objective of the present study, is to determine the diel feeding pattern of various length groups, estimates gastric evacuation rate based on field data from the observed decline in stomach fullness during part of the diel cycle and estimate a total stock consumption during the first half of August.

MATERIAL AND METHODS

The data on capelin stomach contents was obtained from a joint Norwegian-Soviet fish stomachs data base. Capelin stomachs were collected during the 9–11 August 1989 by bottom trawl on board a Soviet vessel with one hour tows made every 4 hour at the same geographical position (7051N and 4456E) at a depth 106–110m. Capelin in length 6–15 cm were selected for further analysis. Table 1 summarizes number of the stomachs by 3–cm length groups collected during 24–h fishery. Figure 1. shows the geographical position of the many days station from where the capelin stomachs were collected.

Table 1. Number of the stomachs in each length group by time from 9/8–11/8–1989.

length groups	9/8					10/8					11/8			total
	7:00	12:20	16:00	20:00	23:20	4:00	8:00	11:45	16:40	20:00	00:00	4:00	7:20	
6-8.9cm	15	15	16	15	1	6	12	15	13	17	3	8	9	145
9-11.9cm	19	22	24	23	12	5	22	32	41	37	18	21	11	287
12-14.9cm	1	22	21	24	17	22	6	15	28	22	22	19	-	219

15-17.9cm	-	1	1	-	3	2	-	-	3	11	7	3	-	31
total	35	60	62	62	33	35	40	62	85	87	50	51	20	

RESULTS AND DISCUSSION

The number of prey categories consumed by the Barents Sea capelin showed a tendency to increase with increasing fish length up to 12 cm: 49 different prey categories have been recorded in length group 6–8.9 cm and 63 in 9–11.9 cm while only 36 prey categories are found in the larger size group 12–14.9 cm. Three preys were considered as important component of the capelin diet, *Calanus* spp., *Parathemisto* and *Thysanoessa*. They either occurred in a high percentage of the total diet or with high frequency and number. *Calanus finmarchicus* was the major contributor in the diet (66.39%W) of length group 6–8.9 cm. Capelin in size group 9–11.9 had mainly fed on *Calanus finmarchicus* (33.53%W), *Parathemisto abyssorum* (14.54 %W) and *Thysanoessa raschii* (28.04%W) while the two species, *Thysanoessa inermis* and *Thysannoessa raschii* occupied 95.23% of the stomach weight in length group 12–14.9 cm. (Table 2, 3 and 4).

Table 2. Diet compositions of length group 6–8.9 cm of capelin during 9/8–11/8–1989.

TAXA	SIZE-CM	MGRAMS/ PREDATOR	WEIGHT %
Gastropoda	.02-.029	.00	.00
	.03-.039	.00	.00
	.04-.049	.00	.00
	.1-.14	.00	.00
Bivalvia	.02-.029	.02	1.86
	.03-.039	.04	.35
<i>Calanus glacialis</i>	.06-.069	.04	.35
	.4-.49	.09	.81
	.5-.69	.06	.58

<i>Calanus finmarchicus</i>	.15-.19	.06	.58
	.2-.24	1.71	15.58
	.25-.29	1.78	16.28
	.3-.39	3.68	33.60
	.4-.49	.37	3.37
	indet	.04	.35
<i>Microcalanus pygmaeus</i>	.06-.069	.09	.81
	.07-.079	.01	.12
	.08-.089	.00	.00
<i>Pseudocalanus elongatus</i>	.08-.089	.09	.81
	.1-.14	.08	.70
	.15-.19	.27	2.44
	.2-.24	.01	.12
<i>Metridia longa</i>	.1-.14	.00	.00
	.15-.19	.00	.00
	.2-.24	.51	4.65
	.25-.29	.00	.00
	.3-.39	.01	.12
<i>Acartia</i>	.1-.14	.00	.00
<i>Microsetella norvegicus</i>	.06-.069	.00	.00
<i>Oncaea borealis</i>	.05-.059	.00	.00
<i>Oithona similis</i>	.06-.069	.03	.23
	.07-.079	.01	.12
	.08-.089	.00	.00
<i>Oithona atlantica</i>	.06-.069	.00	.00
	.07-.079	.00	.00
	.1-.14	.01	.12
<i>Parathemisto abyssorum</i>	.25-.29	.01	.12
	.5-.69	.09	.81
	.7-.99	.09	.81
<i>Euphausiidae</i>	.06-.069	.00	.00
	.08-.089	.00	.00
	.09-.099	.00	.00
	.1-.14	.18	1.63
	.15-.19	.00	.00

Decapoda	.3-.39	.03	.23
Oikopleura	.3-.39	.02	.14
Oikopleura labradoriensis	.1-.14	.00	.00
	.2-.24	1.34	12.18
Indeterminatus	egg	.01	.13

PREY SIZE

Prey size distribution based on stomach contents analysis of three length groups seems to change with length of the fish. Prey in size less than one cm consist of 100% of prey size distribution in the stomachs of fish less than 9 cm, while in length groups 9–11.9 cm and 12–14.9 cm, the same prey size contributed 82% and 58%, respectively. The possible explanation of consuming smaller prey items in length groups 6–8.9 : 1) fish in this size group are unable to capture the larger size of the same prey due to their swimming speed. 2) the larger size of the same prey are scarce. 3) prey size is the function of the mouth size. When capelin in total length reached 9–11.9 cm, food preference shifted only slightly to the larger preys (Table 3). This shift did not appear as a response to changes in prey availability since the abundance of the same prey taxa and size in stomachs increases in larger size group (12–14.9). Other studies on diet compositions of the Barents Sea capelin have indicated that selection of prey species and prey size seems to change with the length of the fish (Lund, 1981; Hassel, 1984; Panasenko, 1984).

Table 3. Diet compositions of length group 9–11.9 cm of capelin during 9/8–11/8–1989.

Gastropoda	.03-.039	.04	.15
	.06-.069	.00	.00
	.1-.14	.00	.00
Clione limacina	indet	1.47	5.25
Bivalvia	.02-.029	.03	.11
	.03-.039	.03	.11
	.06-.069	.00	.00
Copepoda	.03-.039	.00	.00
Calanus glacialis	.4-.49	.48	1.70
	.5-.69	.34	1.20

<i>Calanus finmarchicus</i>	.02-.029	.04	.13
	.1-.14	.00	.00
	.15-.19	.01	.02
	.2-.24	1.62	5.78
	.25-.29	2.20	7.85
	.3-.39	4.63	16.55
	.4-.49	.79	2.81
	.5-.69	.10	.37
	indet	.01	.02
<i>Microcalanus pygmaeus</i>	.06-.069	.00	.00
	.07-.079	.01	.02
<i>Pseudocalanus elongatus</i>	.08-.089	.00	.00
	.1-.14	.06	.22
	.15-.19	.14	.50
<i>Metridia longa</i>	.15-.19	.01	.02
	.2-.24	.62	2.22
	.25-.29	.07	.24
	.3-.39	.04	.15
<i>Microsetella norvegica</i>	.03-.039	.00	.00
<i>Oncaea borealis</i>	.1-.14	.00	.00
<i>Oithona similis</i>	.06-.069	.01	.02
	.07-.079	.00	.00
<i>Oithona atlantica</i>	.07-.079	.00	.00
	.1-.14	.01	.02
<i>Parathemisto abyssorum</i>	.06-.069	.06	.23
	.2-.24	.01	.03
	.25-.29	.01	.05
	.3-.39	.07	.25
	.5-.69	.44	1.59
	.7-.99	.85	3.05
	1-1.4	2.01	7.17
	1.5-1.9	.78	2.17

Euphausiidae	.02-.029	.00	.00
	.06-.069	.01	.04
	.08-.089	.00	.00
	.1-.14	.00	.00
	.15-.19	.00	.00
	.2-.24	.00	.00
Thysanoessa inermis	indet	1.04	3.71
Thysanoessa raschii	.3-.39	1.46	5.21
	1.-1.4	.53	1.90
	1.5-1.9	1.39	4.96
	2.-2.4	.62	2.20
	2.5-2.9	2.08	7.43
	3.-3.9	1.77	6.32
Echinodermata	.03-.039	.00	.00
Asteriidae	.04-.049	.00	.00
Oikopleura	.2-.24	.34	1.21
	.3-.39	.46	1.65
	.5-.69	.12	.43
Oikopleura labradoriensis	.05-.059	.02	.07
	.4-.49	1.15	4.12
Indeterminatus	-	.04	.15

Diet analysis shows a critical length group between 12–14.9 cm within which a slight reduction in the number of preys consumed was recorded while prey size increased. The switch in feeding strategy of capelin in this length group was most likely related to the transition stage between mature and immature fish since maturation of individual is known to be length dependent, rather than age dependent in the Barents Sea Capelin (Forberg and Tjelmeland, 1984) and maturity starts when capelin reaches 12 cm, especially for females (Gjøsæter pers. com.).

Table 4. Diet compositions of length group 12–14.9 cm during 9/8–11/8–1989.

TAXA	SIZE-CM	MGRAMS/ PREDATOR	WEIGHT %
<i>Calanus glacialis</i>	.4-.49	.07	.04
<i>Calanus finmarchicus</i>	.2-.24	.11	.07
	.25-.29	.32	.19
	.3-.39	1.11	.68
	.4-.49	.08	.05
	.5-.69	.03	.02
	indet	.03	.02
<i>Microcalanus pygmaeus</i>	.06-.069	.00	.00
<i>Pseudocalanus elongatus</i>	.1-.14	.00	.00
<i>Metridia longa</i>	.2-.24	.03	.02
	.3-.39	.01	.00
<i>Oithona similis</i>	.06-.069	.00	.00
	.07-.079	.00	.00
<i>Parathemisto abyssorum</i>	.4-.49	.08	.05
	.5-.69	.54	.33
	.7-.99	1.01	.62
	1.-1.4	.25	.15
	1.5-1.9	1.91	1.16
	2.5-2.9	.49	.30
<i>Thysanoessa inermis</i>	.25-.29	.55	.33
	.5-.69	3.87	2.36
	1.5-1.9	1.18	.72
	2.-2.4	8.44	5.14
	2.5-2.9	63.43	38.64
	3.-3.9	37.15	22.63
<i>Thysanoessa raschii</i>	.2-.24	.37	.22
	1.-1.4	.14	.08
	1.5-1.9	.81	.50
	2.-2.4	5.51	3.35
	2.5-2.9	24.34	14.82
	3.-3.9	10.58	6.44

Ophiurida	.01-.019	.00	.00
Oikopleura	.2-.24	.03	.02
	.4-.49	.35	.22
Oikopleura labradoriensis	.15-.19	.03	.02
Lumpenus	3.-3.9	1.31	.80

LENGTH-WEIGHT RELATIONSHIP

Log-transformation of length —weight relationship of the Barents Sea capelin showed increase in the slope of the regression line for fish bellow 12 cm (Fig. 2). This relationship has the following form for fish length between 6–11.9 cm and 12–17.9 cm, respectively:

$$W = 0.00092L^{3.6928} \quad (1)$$

F1,277=4650, P>.0001;S.E slope=.0541

$$W = 0.00371L^{3.1604} \quad (2)$$

F1,250=853.61, P>.0001;S.E.slope=.1081

Commonly the growth stanzas in fish are separated by a change in a body form which shows up in the length-weight relationship (Ricker,1975). The two growth stanzas may reflecte an increase in a gross conversion efficiency in a capelin smaller size compared to the larger fish and indicate that the proportion of the total food energy available for growth is slightly higher in smaller fish. Niimi (1981) found that the gross conversion efficiency decrease with increasing fish weight because the body surface area of the fish increases only as 0.6–0.7 power of body weight.

Biphasic growth patterns can also arise, if the sample were biased towards the number of females within the length interval since the capelin growth is higher in males than in females (Gjøsæter, 1984). The length —weight relationship was analysed for each sex for capelin above and bellow 12 cm. Table bellow summarizes the relationship for females which indicate that the slope of the relationship in the smaller fish is substancially higher than in the larger fish (Fig. 3):

length groups	n	slope	S.E slope	intercept	P>
6-11.9	232	3.6708	0.05869	0.000963	.0001
12-17.9	188	3.15867	0.12429	0.00370	.0001

GASTRIC EVACUATION RATE

The amount of food in the stomach at any time (t) of a nonfeeding period follows an exponential decay function (Elliot and Persson, 1978):

$$S_t = S_0 \exp^{-rt} \quad (3)$$

The equation for S_t can be used to estimate r if it assumed that capelin do not feed during nonfeeding period. The best exponential curve was fitted with a non linear regression (Fig. 4), all regression lines were forced through t=0, $S_t=S_0$. Estimated regression parameters were run by SAS using non linear least square regression of the type $y=B_0 \text{Exp}(-B_1*x)$. Text table below summarizes the regression for capelin length group 6–17.9 cm.

Source	DF	Sum of Squares	Mean Square
Regression	2	2.4930	1.2465
Residual	2	.0072	.0036
Uncorrected total	4	2.5002	
Parameter	Estimate	Std.error	95% Conf.interval
B ₀	1.2395	.05749	.9921-1.4869
B ₁	0.1037	.01037	.05907-.1483

DAILY FOOD CONSUMPTION:

Two approaches were applied to the capelin stomachs contents to estimate the daily ration:

1.The calculation of daily consumption follows the formula (Elliot and Pearson,1978):

$$C_t = \frac{(S_t - S_0 e^{-rt})rt}{1 - e^{-rt}} \quad (4)$$

where C_t =the consumption of food by fish over the time interval T_o to T_t , S_t and S_o = the amount of food in the stomach at time T_t and T_o , r =exponential gastric evacuation rate. C_t calculated for each time interval and then summed to give the total daily ration (Durbin et. al., 1983).

2.The total daily ration calculated as:

$$C_t = 24rS \quad (5)$$

Where S equals the mean stomach contents weight over 24-h (Elliot and Persson, 1978). This model assumes that during 24-h period the food ingested is equal to the amount of food passed through the stomach (Doble and Eggers, 1978).

DIEL FEEDING PATTERN:

Maximum stomach filling occurred between 16:00 and 23:20 approximately for all length groups (Fig. 5A and 5B). The daily level of the food intake during that period was higher than that observed during the first half of the day, and the feeding was at minimum during the midday (12:00). The evening peak in feeding during August has also been reported by Panasenko (1984, 1989), and the reason is thought to be due to the prey behaviour. According to Panasenko (1984), Copepoda, Euphausiacea and Hyperiididae in that period of the year formed dense concentration at the deeper layer and thier vertical migration were poorly pronounced. Two daily peaks of feeding activity from May to August was reported for capelin in the estuary and Western Gulf of St. Lawrence (Vesin et. al., 1981). In the Southern part of Bering Sea capelin has a single peak during the afternoon hours during winter (Naumenko, 1986).

The capelin daily ration based on the present investigation provided an evidence of low predation pressure on the zooplankton community at the Goose Bank area. The above data questions whether the Goose Bank is an ideal feeding ground compared to the Northern area. Hassel (1986) reported that the index of stomach fullness increased markedly towards the northern limit of capelin distribution. However, a high index of stomach fullness reflects the feeding activity of the fish population (Lilly, 1989) and do not necessarily indicate a high consumption rate, since gastric evacuation rate is a function of temperature. Digestion, being a physiological process, accelerates with rising temperature (Ney, 1990). One would assume a low daily ration in fish distributed in the area dominated by Arctic water.

Polar cod and capelin have a similar annual rhythm of feeding and in the period of maximum feeding (July, August) they are feeding in the same area (Panassenko and Soboleva, 1980). A high food similarity and the magnitude of competition on Euphausiids from the same area (Goose Bank) were very high (Panassenko and Soboleva, 1980). Our data on diet compositions of polar cod sampled from the same area (Ajiad and Gjørseter, 1990) revealed that in the length group 8–10.9cm, Copepoda and Euphausiidae were the major dietary components (36.7% and 47.84% of the total stomach weight). This data clearly demonstrated that the polar cod in this length interval are sharing the same prey taxa (Copepoda) with capelin 6–8.9cm, while with capelin in length 9–11.9 and 12–14.9 cm (Table 2, 3 and 4), the two species are preying upon Copepoda and Euphausiidae. Another possible interaction between capelin and polar cod is predation on polar cod larvae by capelin, especially the young year classes (Skjoldal and Rey, 1989). No single incidence confirms this interaction during the present investigation. The only one fish species recorded in capelin stomachs (length group 12–14.9) was from the genus *Lumpenus*. A key question in trophic interrelation between capelin and polar cod is to what extent the food competition is more important between the two species than a competition between different length groups of the same species.

The estimated total capelin biomass based on acoustic survey during September-October 1989 in the same area (Gjørseter, pers.com.) was about 280 000 tonnes for capelin in the length between 8–16.9 cm. By applying the estimates of the daily ration to capelin biomass, these data gives about 4116 tonnes of daily consumption of zooplankton by capelin in the Goose Bank area.

Length group-cm	n	day, time	mean length-cm	mean fish weight gr.	mean stomach fullness %	consumption %BW	consumption 24h %BW	
6-17.9		9/8-89						
	35	07:00	9.194	3.72	0.553			
	60	12:20	10.95	7.97	0.556	0.8075		
	62	16:00	11.09	7.89	1.052			
	62	20:00	10.97	8.1	0.985			
	33	23:20	12.68	12.6	1.262	0.6671		
			10/8-89				total=	2.009
	35	04:00	12.51	11.88	0.7105	1.4746		
	40	08:00	10.31	6.277	0.4907			
	62	11:45	10.36	5.917	0.402			
	85	16:40	11.04	7.275	1.062			
	87	20:00	11.47	9.219	0.589	1.048		
	50	24:00	12.75	12.47	0.5806			
			11/8-89					1.699
51	04:00	11.62	9.12	0.318				
20	07:20	9.47	4.32	0.278				

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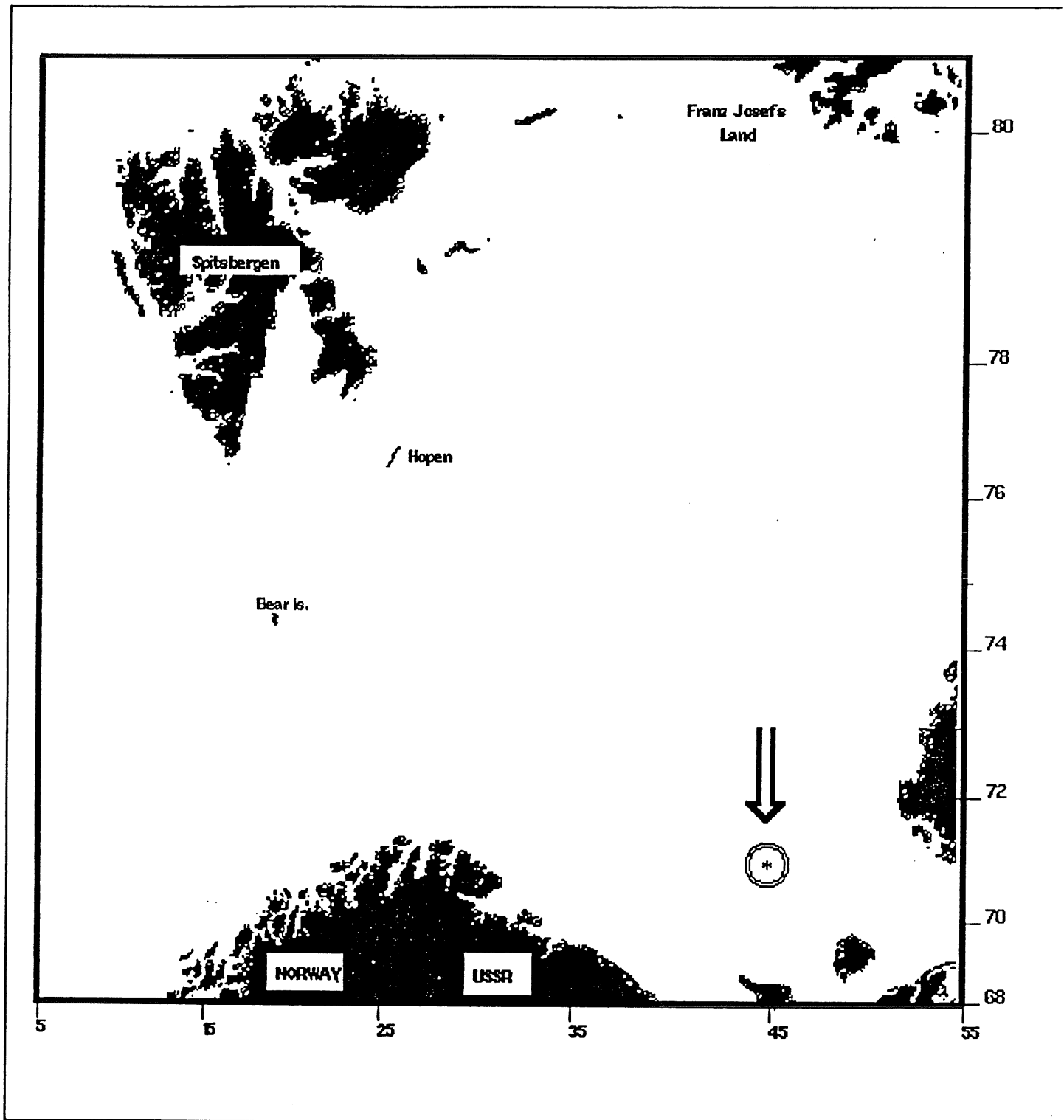


Fig.1

Figure 2

length – weight relationship
length group 06-17.9cm, Males and Females

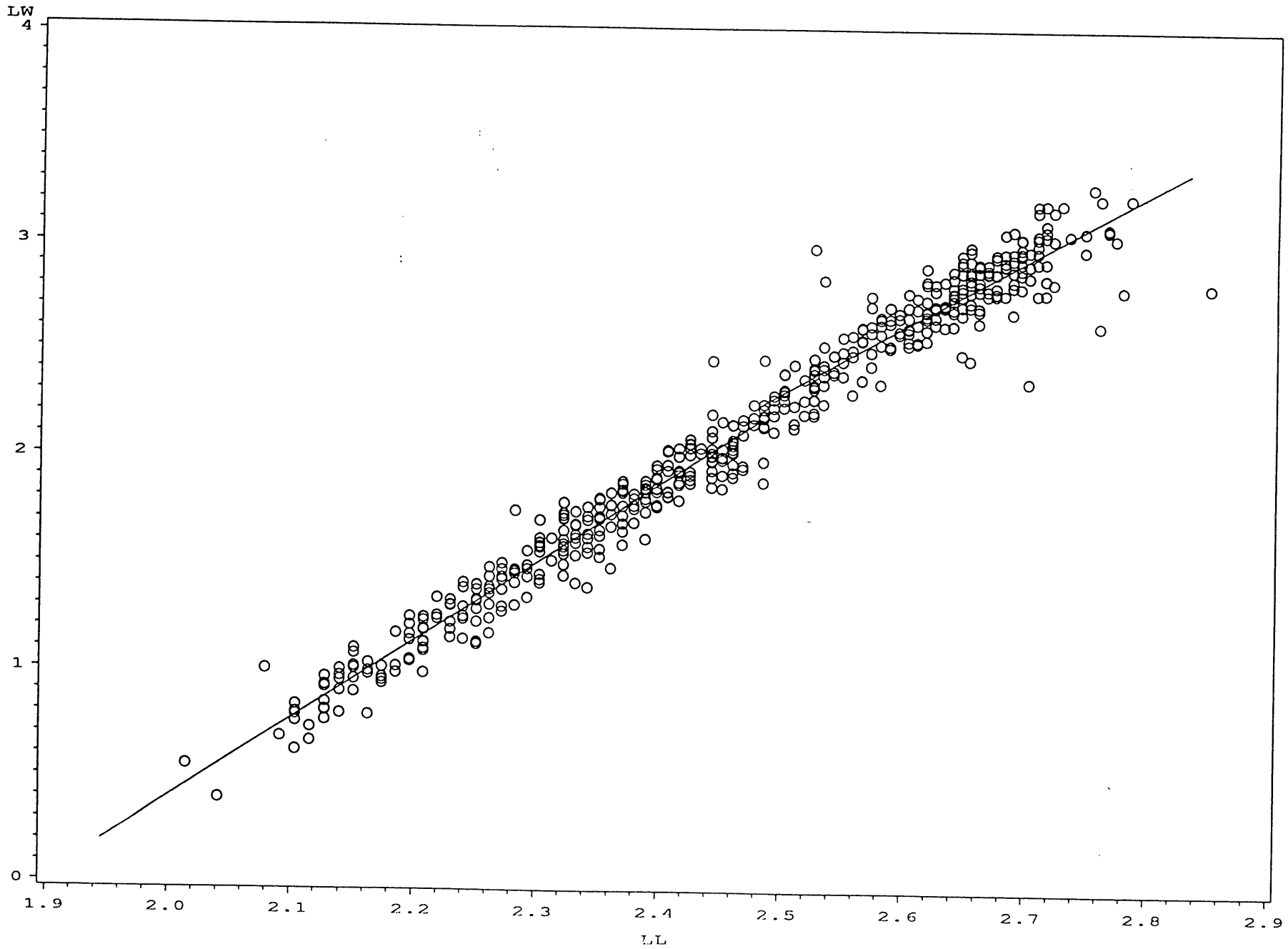
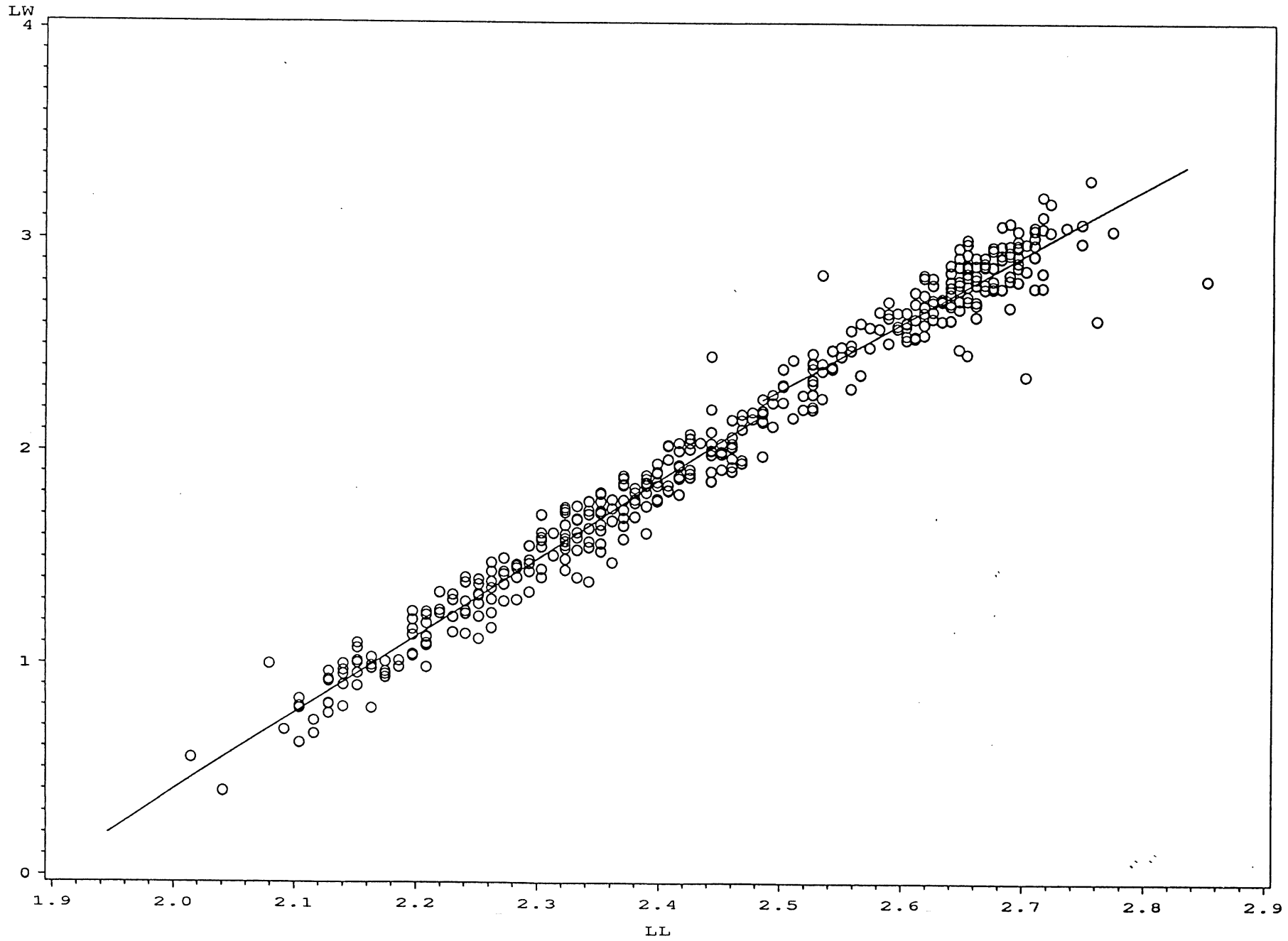


Figure 3

length - weight relationship
length group 06-17.9cm, Female



Gastric evacuation for capelin 6-17.9cm
(star=predicated, square=observed)

Fig.4.

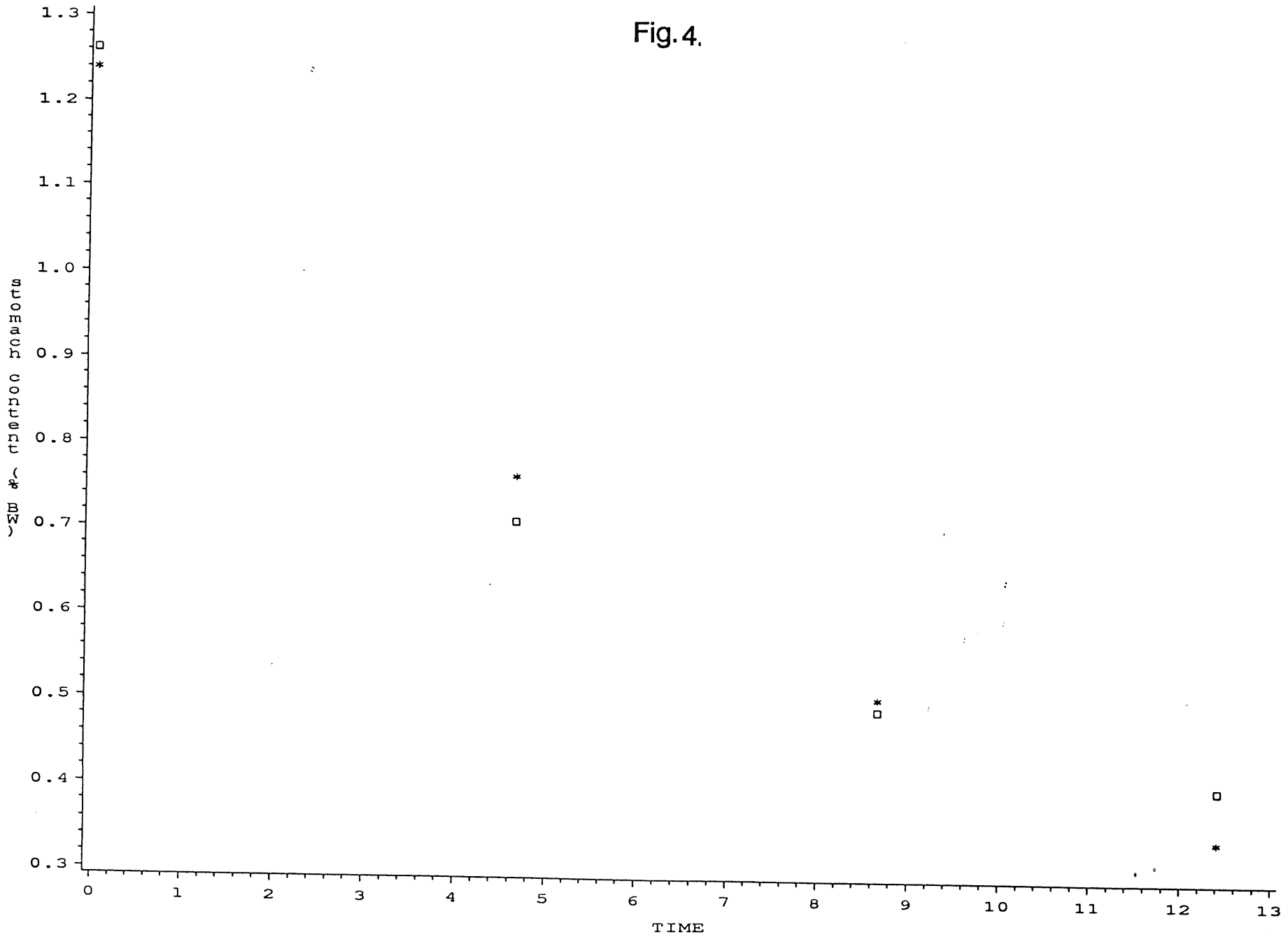


Fig.5a – Length group 06 – 14.9 cm

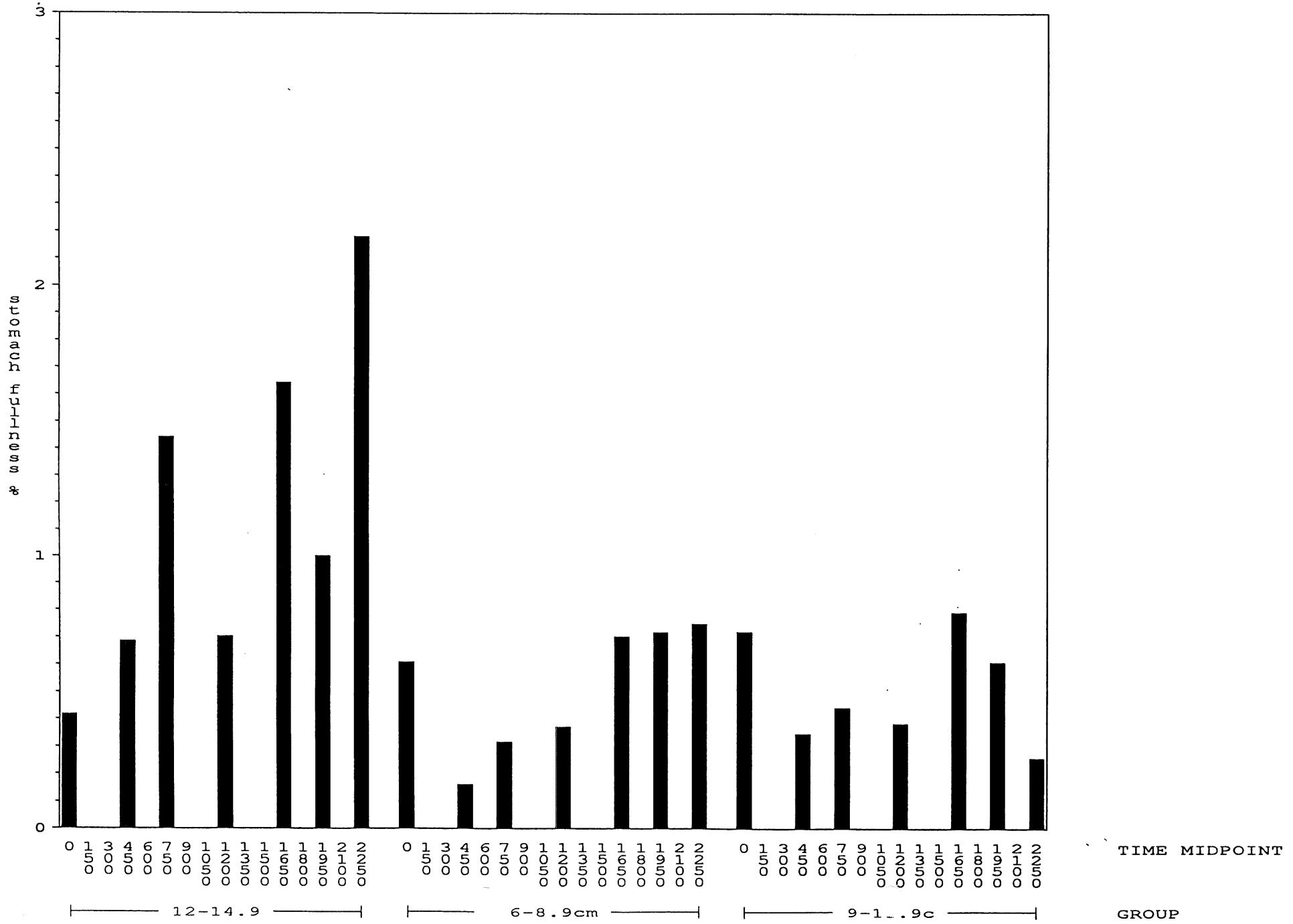


Fig.5b – Length group 06–17.9 cm

