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Population dynamics of brown shrimp (Crangon crangon) in the Belgian coastal waters*

2. Predation mortality

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Abstract.

The fish species, present in the Belgian coastal waters, are classified according to their abundance and according to their food preference for postlarval shrimp (*Crangon crangon*).
The presumed importance of the various fish species as predators of shrimp is deduced from this classification. The abundance and biomass of the most important predators are estimated. The results of quantitative stomach analyses on these species lead to the calculation of their daily shrimp rations. The combination of the data on abundance and biomass of the predators with the data on their daily food uptake results into estimates of the yearly predation mortality of postlarval shrimp.

Résumé.

Les espèces de poissons, présentes dans les eaux côtières belges, sont classées selon leur abondance et selon leur préférence alimentaire pour les crevettes postlarvaires (*Crangon crangon*).
L'importance présumée des différentes espèces de poissons comme prédateurs de crevettes est déduite de cette classification. L'abondance et la biomasse des plus importants prédateurs sont estimées. Les résultats d'analyses quantitatives sur la nourriture de ces espèces mène à la calculation de leurs rations journalières en crevettes. La combinaison des données sur l'abondance et la biomasse des poissons prédateurs avec les données sur leur ingestion journalière aboutit à une estimation de la mortalité annuelle de crevettes postlarvaires due à la prédation.

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1. Introduction.

Predation is considered as one of the most important causes of mortality among brown shrimp (Crangon crangon) (TIEWS, 1965, 1975 ; SCHUMACHER and TIEWS, 1976 and others). This contribution deals with predation-mortality of postlarval shrimp in the Belgian coastal waters, during the period 07.1973-06.1976 ; a study which was performed in the context of investigations on the population-dynamics of shrimp (see also C.M. 1980/K : 32). The aim of this study was to estimate the yearly predation-mortality of Crangon caused by demersal fishes.

2. Evaluation of shrimp predators.

During the period 07.1973-06.1976 about 60 different fish species were observed within the Belgian coastal area (up to 10 miles offshore)(table 1). These species were grouped according to their abundance on the one hand and according to their food preference for postlarval Crangon on the other hand. This classification permitted a reliable evaluation of the importance of each species as a predator of shrimp. The predators which are abundant enough and which prey regularly enough on shrimp to cause a substantial mortality were subject to a detailed quantitative study on predation.

The average densities observed during the spring and autumn sampling surveys on 30 stations along the entire coast, were used as an index for the abundance of each fish species. Corrections for the sampling efficiency of the gear were not introduced at this stage of the investigations. Pomatoschistus species (6934 individuals/10^5 m^2 on averge) appeared to be the most abundant fish species, followed by Limanda limanda (415/10^5 m^2), Sprattus sprattus (346/10^5 m^2), Agonus cataphractus (334/10^5 m^2), Solea solea (288/10^5 m^2), Trisopterus luscus (268/10^5 m^2), Callionymus lyra (194/10^5 m^2) and Odontogadus merlangus (128/10^5 m^2). The average densities of the other species were below 100 individuals/10^5 m^2. The fishes were classified into five abundance categories, namely rare (average density below 1/10^5 m^2), rather rare (1-10/10^5 m^2), rather abundant (10-100/10^5 m^2), abundant (100-1000/10^5 m^2) and very abundant (more than 1000/10^5 m^2)(table 1).

The food preference of the fishes for postlarval shrimp was deduced from bibliographic data (a complete list of references can be found in REDANT, 1978). The fish species were grouped into four semi-quantitative predation categories, namely not or only occasionally feeding on shrimp, sometimes feeding on shrimp, frequently feeding on shrimp and predominantly feeding on shrimp (table 1). During the evaluation of the bibliographic data several factors were taken into consideration : the origin, size-range and numbers of fishes analysed and the type of analyses (qualitative, semi-quantitative or quantitative data on food composition). For some, especially rare species no data on the food composition could be found.

The above mentioned classifications result into a grouping of the fish species in an abundance/food-preference diagram (table 1). Species close to the left-hand top corner of the diagram are negligible as predators of postlarval shrimp because (1) they are rare or rather rare and (2) they do not or only sporadically feed on shrimp. Species close to the right-hand bottom corner of the diagram can be expected to be important shrimp predators because (1) they are abundant or very abundant and (2) they feed frequently or predominantly on shrimp. It is obvious that the quantitative analysis of predation was started with the latter, i.e. Pomatoschistus species, Odontogadus merlangus, Trisopterus luscus, Agonus cataphractus, Trigla species, Ciliata mustela, Liparis liparis and Gadus morhua. The food composition of the three gurnards Trigla lucerna, T. gurnardus and T. cuculus show such a high degree of ressemblance that they were considered as one species (T. species).

3. Abundance and biomass of predators.

Predation-mortality of postlarval shrimp, caused by any predator, can be computed from (1) the density (abundance or biomass) of the predator and (2) the amount of shrimp eaten by the predator per unit of time (see sections 4 and 5).

3.1. Sampling methods.

The estimates of abundance and biomass of the shrimp predators are based on the results of monthly and half-yearly sampling surveys in the coastal waters. Detailed information on the sampling methods can be found in C.M. 1980/K : 32. The laboratory analyses of the fish samples included measurements of individual length and countings and weighings of the total numbers of fishes per species.

3.2. Estimates of abundance and biomass.

The calculations of the yearly average abundance and biomass of each shrimp predator were performed in analogy to these for brown shrimp. A description of those methods is also given in C.M. 1980/K : 32.

During the calculations gross corrections factors for the efficiency of the sampling gear were introduced. Scientific data on the catchability and selectivity of shrimp trawls for other organisms than shrimp are rather scarce (BOHL, 1963 ; DE GROOT, 1973 ; VAN DEN BROUCKE, 1975 ; JOHANNESSEN, 1976). For some, especially commercial fish species useful information could be gathered from the literature. For most, especially non-commercial species, the correction factors were established in analogy to the correction factors cited in the literature for commercial or non-commercial fishes. These extrapolations were made, taking into account the similarities or differences in size, physionomy and behaviour between the respective fish species.

Pomatoschistus is the most abundant shrimp predator in the coastal area, followed by Odontogadus, Agonus, Trisopterus, Trigla, Liparis, Gadus and Ciliata (table 2). Odontogadus has the greatest biomass, followed by Trisopterus, Pomatoschistus, Gadus, Trigla, Agonus, Liparis and Ciliata (table 2).

Their seasonal occurrence in the Belgian coastal waters can be summarized as follows. Gadus, Pomatoschistus, Agonus and Liparis are most abundant or exclusively present during autumn and winter. Odontogadus is observed year-round but its biomass tends to a maximum during autumn and winter. Trigla occurs almost exclusively during summer. The same applies to some extent to Trisopterus but this species is still locally abundant during autumn. Ciliata is observed year-round in small numbers. From this it clearly appears that the predation on postlarval shrimp is heaviest in the second half-year, i.e. during the period of highest density of postlarval shrimp.

4. Stomach analyses.

Although the food of many fish species is described extensively in the literature, only few publications deal with the quantitative composition of fish food. Most investigations are only qualitative or semi-quantitative (e.g. giving incidence frequencies of preys only). For this reason quantitative stomach analyses were performed on the shrimp predators, except on Pomatoschistus, in order to quantify the importance of postlarval shrimp in their food. The literature on Pomatoschistus (KUHL, 1961, 1964) contained enough information on its food composition and prey size to enable us to make a reliable estimation of the predation-mortality caused by this species.

4.1. Methods.

The fishes used for the stomach analyses were all collected during daytime. Sampling was spread over the year as representatively as possible, taking into account the seasonal variations in abundance and in length composition of the fish populations. In total about 6000 specimens were examined (table 3).

The fishes were analysed the day they were captured. When this was impossible they were temporarily preserved in a deep freezer (- 25 °C). Each fish was measured and weighed. Afterwards its stomach content was isolated, weighed and preserved in a 5 % formaline solution. Fishes with regurgitated, partly digested food in their oral cavity or oesophagus were rejected. Fishes with empty stomachs, but without indications of regurgitation, however were not omitted. In analogy with many authors these empty stomachs were considered as a normal feature of the seasonal or daily feeding periodicity of the fishes (RAE, 1956, 1967 ; WAGNER, 1959 ; DE GROOT, 1964 ; ARNTZ, 1971, 1974 ; THYSSEN et al. 1974 and others). In all species the percentage of fishes with empty stomachs was below 5 %.

After at least two weeks the preserved stomach contents were analysed on shrimp. Meanwhile the Caridea got their typical pink colour, which made them - even the smallest debris - easily recognizable among the other food particles. The Caridea were isolated, determined, counted and weighed. The intact or broken Crangon crangon were measured : either total length (L_{cc}), either carapax-length (CL) or - width (CW). In the latter case the total length was calculated using the formulas :

$$L_{cc} = 6.267\ CW + 4.372$$
(r = 0.998)
(number of observations n = 1200)

and

$$L_{cc} = 4.394\ CL + 2.755$$
(r = 0.998)

4.2. Results.

For each length class and for each fish species the following parameters were computed from the stomach analyses : incidence frequency of Caridea and of Crangon crangon in the stomachs (IF_c and IF_{cc}), mean number of Caridea and of Crangon crangon per stomach (N_c and N_{cc}), mean body weight of fishes (W_f), mean weight of stomach content (W_s), mean weight of Caridea and of Crangon crangon per stomach (W_c and W_{cc}) and also the relations between these parameters (e.g. W_c/W_s, W_{cc}/W_s, W_{cc}/W_c, ...). Only the most important findings are discussed in this report (table 3).

4.2.1. Incidence frequency and mean number of shrimps per stomach.

Caridea were very frequently observed in the stomachs of Trigla, Gadus and Liparis. Slighly more than 50 % of the stomachs of Trisopterus, Ciliata and Odontogadus contained Caridea. Agonus showed the lowest incidence frequency of Caridea (table 3). The incidence frequencies of Crangon crangon were, according to the fish species, 10 to 20 % lower than those of Caridea (table 3).

The mean number of Caridea and of Crangon crangon per stomach were highest in Trigla, followed by Gadus, Liparis, Cilata, Trisopterus, Odontogadus and Agonus. In most cases nearly all the Caridea in the stomachs were Crangon crangon. Other shrimp species only rarely occurred in the food of fishes. Exception however must be made for Hippolyte varians which was observed regularly, especially in Agonus (incidence frequency 9.1 %, mean number per stomach 0.34) and in Liparis (incidence frequency 12.1 %, mean number per stomach 0.23).

4.2.2. Weight of shrimps in the stomachs.

The relative contribution of Caridea and of Crangon crangon to the stomach contents, respectively $W_c/W_s \cdot 100$ % and $W_{cc}/W_s \cdot 100$ %, was highest in Trigla (72.9 and 72.4 %), followed by Liparis (56.1 and 54.3 %), Gadus (41.6 and 41.3 %), Trisopterus (41.6 and 40.1 %), Ciliata (28.8 and 28.4 %), Odontogadus (27.3 and 27.0 %)and Agonus (22.8 and 15.5 %). In all species, except Agonus, postlarval brown shrimp represents at least 25 % of the food of the fishes (table 3).

4.2.3. Length distribution of shrimps in the stomachs.

The percentage of brown shrimps whose total length could be measured or calculated (from carapax measurements) varied between 30 and 45 %, according to the predator species. The majority of these shrimps was smaller than 45 mm. Larger shrimps were observed almost exlusively in larger specimens of Odontogadus, Trisopterus, Gadus and Trigla (figure 1).

The maximum length of the shrimps in the stomachs increases in all fish species with increasing body size of the fishes. In the largest predators (Odontogadus, Trisopterus, Gadus and Trigla) the relation between maximum size of shrimp eaten and length of fish reaches an optimum, corresponding to the maximum shrimp size which still abundantly occurs in the population. In the smaller predators such an optimum was not observed (figure 2). On the other hand even the stomachs of the largest fishes (e.g. Odontogadus and Gadus up to 27 cm and Trisopterus up to 24 cm) still contained shrimps as small as 18 mm. These observations show that, although larger fishes also feed on adult shrimp, predation mainly will affect the stock of small, juvenile shrimp.

5. Daily shrimp ration of fishes.

The quantities of postlarval Crangon eaten daily by its predators were expressed in numbers of shrimps and in weight units of shrimp. The computations of the daily rations were based on (1) the results of the stomach analyses and (2) bibliographic data on digestion time and daily food uptake of fishes.

5.1. Daily ration in numbers.

The numbers of Crangon consumed daily by its predators (C_{cc}) were calculated from the mean number of shrimps per stomach (N_{cc}) and from the average digestion time of shrimps (D) :

$$C_{cc} = N_{cc}/D$$

Digestion or gastric evacuation in fishes depends upon the fish species, fish size, size of the meal, biochemical composition of the meal, temperature and experimental conditions (WAGNER, 1959 ; BREGNBALLE, 1961 ; KIONKA and WINDELL, 1962 ; MOLNAR and TOLG, 1962 ; PANDIAN, 1967a, b ; KIRAYA, 1969 ; WINDELL et al., 1969 ; TYLER, 1970 ; KIONKA and WINDELL, 1972 ; SWENSON and SMITH, 1973 ; JONES, 1974 ; RESHETNIKOV et al., 1974 ; KAPOOR et al. 1975 and others). A critical evaluation of the bibliographic data resulted in an estimation of the average digestion time of Crangon, taking into consideration the water temperature in the Belgian coastal waters and the fact that Crangon has a hardly digestable exoskeleton. The digestion time of shrimp in the stomachs of its predators (D) was assumed to be on average 3 days, with a minimum and maximum of 2 and 4 days. In similar investigations on the predation mortality of brown shrimp in the German Bight the

same average digestion time was used (TIEWS, 1965, 1975).

For each predator species three values of the daily shrimp ration, expressed in numbers of shrimps, were calculated, corresponding to the minimum, average and maximum value of the digestion time (table 4).

5.2. Daily ration in weight units.

The simplest way to calculate the daily food ration, or daily ration of any food component, expressed in weight units (C_d), is by Daan's formula, originally designed for cod (DAAN, 1973) :

$$C_d = 2 \cdot W_s/D$$

W_s = mean weight of stomach content,
D = digestion time.

This formula can be used on the condition that gastric evacuation is described by a linear function, no feeding takes place during stomach depletion and stomach analyses are spread homogeneously over 24 hours.

The curves describing gastric evacuation or depletion however differ greatly from one fish species to another : they may be exponential, logaritmic or linear (PANDIAN, 1967a ; HERTING and WITT, 1968 ; KITCHELL and WINDELL, 1968 ; KARIYA and TAKAHASHI, 1969 ; BRETT and HIGGS, 1970 ; TYLER, 1970 ; DAAN, 1973 ; KAPOOR et al. 1975 and others). For a same species, viz. Gadus morhua, different curves have been published (TYLER, 1970 ; DAAN, 1973).

Bibliographic data on the question whether fishes feed or not while they still have food in their stomachs are also contradictory, even when the same fish species is considered (WILSON, 1937 ; HEMPEL, 1964 ; KARIYA and TAKAHASHI, 1969 ; TYLER, 1970 ; KUHL, 1973 ; DAAN, 1973 ; ARNTZ, 1974 ; JONES, 1974 and others).

The exact determination of the mean weight of stomachs in the population (W_s) implies some supplementary difficulties. After capture, during the stay of the fishes in the trawl and on deck, and after death, digestion slowly proceeds, until all the digestive enzymes are used up (i.e. the post mortem digestion) (EGGERS, 1977). Consequently the observed mean weight of the stomachs is an underestimate of their real mean weight in vivo.

It is clear that Daan's formula, which is subject to very strict conditions, cannot be extrapolated (in its original form) to any other fish species. Such an extrapolation in fact would imply a serious risk of under - or over - estimating the daily shrimp rations of most predators. For this reason Daan's method was abandonned and an indirect method was introduced to estimate the quantities of Crangon eaten daily by its predators (C_{cc}) :

$$C_{cc}\ (\%) = C_d\ (\%) \cdot W_{cc}/W_s$$

C_d = daily food rate in % of body weight,

W_{cc}/W_s = relative contribution of brown shrimp to the stomach contents.

In this formula the daily shrimp ration (C_{cc}) is expressed as a percentage of the body weight of the fishes. The values of W_{cc}/W_s are produced by the stomach analyses ; the values of the daily food rations C_d were derived from the literature. The above formula is valid under the assumption that the stomach composition perfectly reflects the food composition.

The food uptake of fishes depends upon their energy requirements (PHILIPS, 1972) and is influenced by fish species, size, age, activity, physiological condition, composition of the food and environmental conditions (BALDWIN, 1956 ; HUNT, 1960 ; PANDIAN, 1967a, 1970 ; BRETT et al., 1969 ; MULLER, 1969 ; LIPSKAYA et al., 1972 ; DAAN, 1973 ; SWENSON and SMITH, 1973 ; ARNTZ, 1974 ; UZARS, 1975 ; MURAI and ANDREWS, 1976 ; ZALACHOWSKI et al., 1976 and others). The following general values for the daily food ration, expressed as a percentage of body weight, were deduced from the literature : larval and first postlarval stages 40-10 %, juveniles 10-2.0 % and adults 2.0-0.5 %. The variations due to activity, physiological condition and environmental temperature are included within these ranges.

For each predator two values of the daily shrimp ration were calculated, corresponding to the minimum and maximum value of the daily food ration (table 4). A daily food rate ranging from 2.0-10 % was used for those species of which only juveniles were observed in the coastal waters (i.e. Odontogadus and Gadus). For the others, whose coastal populations comprise adults as well as juveniles, a range of 1.0-10 % was used.

The daily shrimp rations of Pomatoschistus, on which no stomach analyses were performed (see section 4), were calculated from (1) the mean number of shrimps per stomach (KUHL, 1961, 1964), (2) the mean weight of these shrimps and (3) the mean weight of the fishes (table 4).

6. Predation mortality of postlarval shrimp.

The average yearly predation mortality of postlarval Crangon, expressed in numbers of shrimps, was calculated from the average yearly abundance of its predators and the mean daily shrimp rations (in numbers) of these predators. For each predator species three values were calculated, corresponding to the minimum, mean and maximum value of the daily shrimp ration (table 5).

Pomatoschistus caused, on average, the greatest predation mortality of postlarval shrimp (77.0 % of the total predation mortality), followed by Odontogadus, Trisopterus, Trigla, Agonus, Liparis, Gadus and Ciliata. Total predation mortality during the period 07.1973 - 06.1976 amounted to 14.12 ± 5.66 Crangon/m^2/year on average (table 5). The real value of predation mortality probably is higher than this estimate, which, in fact, only refers to mortality caused by the most important vertebrate predators and which does not yet include estimates for the invertebrate or less important vertebrate predators.

The average yearly predation mortality of shrimp, expressed in weight units, was computed from the average yearly biomass of the predators and their daily shrimp rations (in % of body weight). For each species two values were calculated, corresponding to the minimum and maximum value of the daily shrimp ration (table 5).

Odontogadus is on average the most important predator (53.4-66.6 % of the total predation mortality), followed by Trisopterus, Trigla, Gadus, Liparis, Pomatoschistus, Agonus and Ciliata. Total predation mortality during the period 07.1973-06.1976 was minimally 126 ± 40 and maximally 789 ± 236 mg C/m^2/year (table 5).
The results of these investigations were incorporated into the quantitative consumption-production-model for postlarval brown shrimp (see C.M. 1980/ K : 32).

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Table 1 - Synoptic diagram of the importance of the fish species in the Belgian coastal waters as predators of portlarval Crangon crangon.

Abundance / Food preference	Rare	Rather rare	Rather abundant	Abundant	Very abundant
Food unknown	03 29 06 32 27	-	-	-	-
Not or only occasionally feeding on brown shrimp	01 25 04 31 09 34 10 35 12 46 14 48 19 51 24 56	22 26 33	07 23 36	08 52-juv.	-
Sometimes feeding on brown shrimp	15 50 20 55 30	11 28 53	54	47 57	-
Frequently feeding on brown shrimp	02	13 18-adu.	52-adu.	-	37
Predominantly feeding on brown shrimp	38 42 40 45 41 49	05 18-juv.	21 39 44	16 17 43	-

numbers refer to species in faunistic list : see overleaf

all abundance data refer to the period 07.1973-06.1976

PETROMYZONES

01 Lampetra fluviatilis (L.)

ELASMOBRANCHII

02 Galeorhinus galeus (L.)
03 Mustelus mustelus (L.)
04 Scyliorhinus canicula (L.)
05 Raja clavata L.
06 Dasyatis pastinaca (L.)

TELEOSTOMI

07 Clupea harengus L.
08 Sprattus sprattus (L.)
09 Alosa alosa (L.)
10 Alosa fallax (Lacépède)
11 Engraulis encrasicholus (L.)
12 Salmo trutta L.
13 Anguilla anguilla (L.)
14 Belone belone (L.)
15 Pollachius pollachius (L.)
16 Odontogadus merlangus (L.)
17 Trisopterus luscus (L.)
18 Gadus morhua L.
19 Merluccius merluccius (L.)
20 Enchelyopus cimbrius (L.)
21 Ciliata mustela (L.)
22 Gasterosteus aculeatus L.
23 Syngnathus species
24 Zeus faber L.
25 Mugil labrosus Risso
26 Atherina presbyter Cuvier
27 Morone lagrax (L.)
28 Trachurus trachurus (L.)
29 Spondyliosoma cantharus (L.)
30 Mullus surmulletus L.
31 Trachinus vipera Cuvier
32 Blennius gattorugine Brünnich
33 Ammodytes laceolatus (le Sauvage)
34 Ammodytes lancea Yarrell
35 Gymnammodytes semisquamatus Jourdain
36 Aphia minuta (Risso)
37 Pomatoschistus species
38 Trigla gurnardus L.
39 Trigla lucerna L.
40 Trigla cuculus L.
41 Myxocephalus scorpius (L.)
42 Taurulus bubalis (Euphrasen)
43 Agonus cataphractus (L.)
44 Liparis liparis (L.)
45 Liparis montagui Donovan
46 Cyclopterus lumpus L.
47 Callionymus species
48 Scomber scombrus L.
49 Arnoglossus laterna (Walbaum)
50 Scophthalmus maximus (L.)
51 Scophthalmus rhombus (L.)
52 Limanda limanda (L.)
53 Platichthys flesus (L.)
54 Pleuronectes platessa L.
55 Microstomus kitt (Walbaum)
56 Buglossidium luteum (Risso)
57 Solea solea (L.)

Table 2 - Abundance and biomass of shrimp predators in the Belgian coastal waters.

Predator species	Abundance $n/10^4\ m^2$	Biomass $g\ ww/10^4\ m^2$
Odontogadus merlangus	98.1 ± 79.3	7392 ± 3206
Trisopterus luscus	47.3 ± 21.1	2886 ± 1753
Gadus morhua	1.6 ± 0.4	436 ± 115
Ciliata mustela	1.4 ± 1.0	36 ± 17
Pomatoschistus species	4461.0 ± 2264.0	1490 ± 782
Trigla species	8.8 ± 4.9	425 ± 72
Agonus cataphractus	48.4 ± 35.6	148 ± 78
Liparis liparis	4.0 ± 2.3	86 ± 67

all figures refer to the period 07.1973-06.1976

Table 3 - Most important results of the stomach analyses on shrimp predators.

	Parameter	Odontogadus merlangus	Trisopterus luscus	Gadus morhua	Ciliata mustela	Trigla species	Agonus cataphractus (a)	Liparis liparis
	Number of fishes analysed	2219	1235	790	326	320	1059	257
IF_c	Incidence frequency of *Caridea*	53.7	58.0	85.9	58.0	86.6	32.9	84.4
IF_{cc}	Incidence frequency of *Crangon*	44.3	45.8	74.8	47.6	67.8	10.4	63.0
N_c	Mean number of *Caridea* per stomach	1.26	1.64	3.38	1.70	3.89	0.77	3.19
N_{cc}	Mean number of *Crangon* per stomach	1.24	1.54	3.33	1.65	3.82	0.43	2.94
W_s	Mean weight of stomach (grammes)	1.68 ± 2.15	1.03 ± 1.07	3.39 ± 3.84	1.32 ± 1.60	1.47 ± 1.44	0.070 ± 0.082	1.43 ± 1.76
W_c	Mean weight of *Caridea* in the stomachs (grammes)	0.46 ± 0.88	0.43 ± 0.65	1.41 ± 1.80	0.38 ± 0.60	1.07 ± 1.16	0.016 ± 0.056	0.80 ± 1.02
W_{cc}	Mean weight of *Crangon* in the stomachs (grammes)	0.45 ± 0.85	0.41 ± 0.61	1.40 ± 1.81	0.37 ± 0.59	1.06 ± 1.18	0.011 ± 0.045	0.78 ± 1.04

a : after GABRIELS (1977)

Table 4 - Daily shrimp rations of demersal predators.

Predator species	Daily ration in number of shrimps per fish			Daily ration in percent of fish body weight	
	mean	minimum	maximum	minimum	maximum
Odontogadus merlangus	0.41	0.31	0.62	0.54 %	2.70 %
Trisopterus luscus	0.51	0.38	0.77	0.40 %	4.01 %
Gadus morhua	1.11	0.83	1.67	0.83 %	4.13 %
Ciliata mustela	0.55	0.41	0.82	0.28 %	2.84 %
Pomatoschistus species	0.07	0.05	0.10	0.07 %	0.14 %
Trigla species	1.28	0.96	1.91	0.72 %	7.24 %
Agonus cataphractus	0.14	0.11	0.21	0.16 %	1.55 %
Liparis liparis	0.98	0.74	1.47	0.54 %	5.43 %

Table 5 - Predation mortality of postlarval Crangon crangon caused by demersal fishes.

Predator species	n/m²/year			mg C/m²/year	
	mean	minimum	maximum	minimum	maximum
Odontogadus merlangus	1.48 ± 1.20	1.11 ± 0.90	2.22 ± 1.80	84.2 ± 36.5	421.1 ± 182.6
Trisopterus luscus	0.89 ± 0.40	0.66 ± 0.30	1.33 ± 0.59	24.4 ± 14.8	244.2 ± 148.3
Gadus morhua	0.06 ± 0.02	0.05 ± 0.01	0.10 ± 0.02	7.6 ± 2.0	38.0 ± 10.0
Ciliata mustela	0.03 ± 0.02	0.02 ± 0.02	0.04 ± 0.03	0.2 ± 0.1	2.2 ± 1.0
Pomatoschistus species	10.86 ± 5.51	8.14 ± 4.13	16.28 ± 8.26	2.1 ± 1.1	4.2 ± 2.2
Trigla species	0.41 ± 0.23	0.31 ± 0.17	0.61 ± 0.34	6.5 ± 1.1	64.9 ± 11.0
Agonus cataphractus	0.25 ± 0.19	0.19 ± 0.14	0.38 ± 0.28	0.5 ± 0.3	4.8 ± 2.6
Liparis liparis	0.14 ± 0.08	0.11 ± 0.06	0.22 ± 0.12	1.0 ± 0.8	9.9 ± 7.7
Total	14.12 ± 5.66	10.59 ± 4.24	21.18 ± 8.49	126.5 ± 39.5	789.3 ± 235.9

all figures refer to the period 07.1973-06.1976

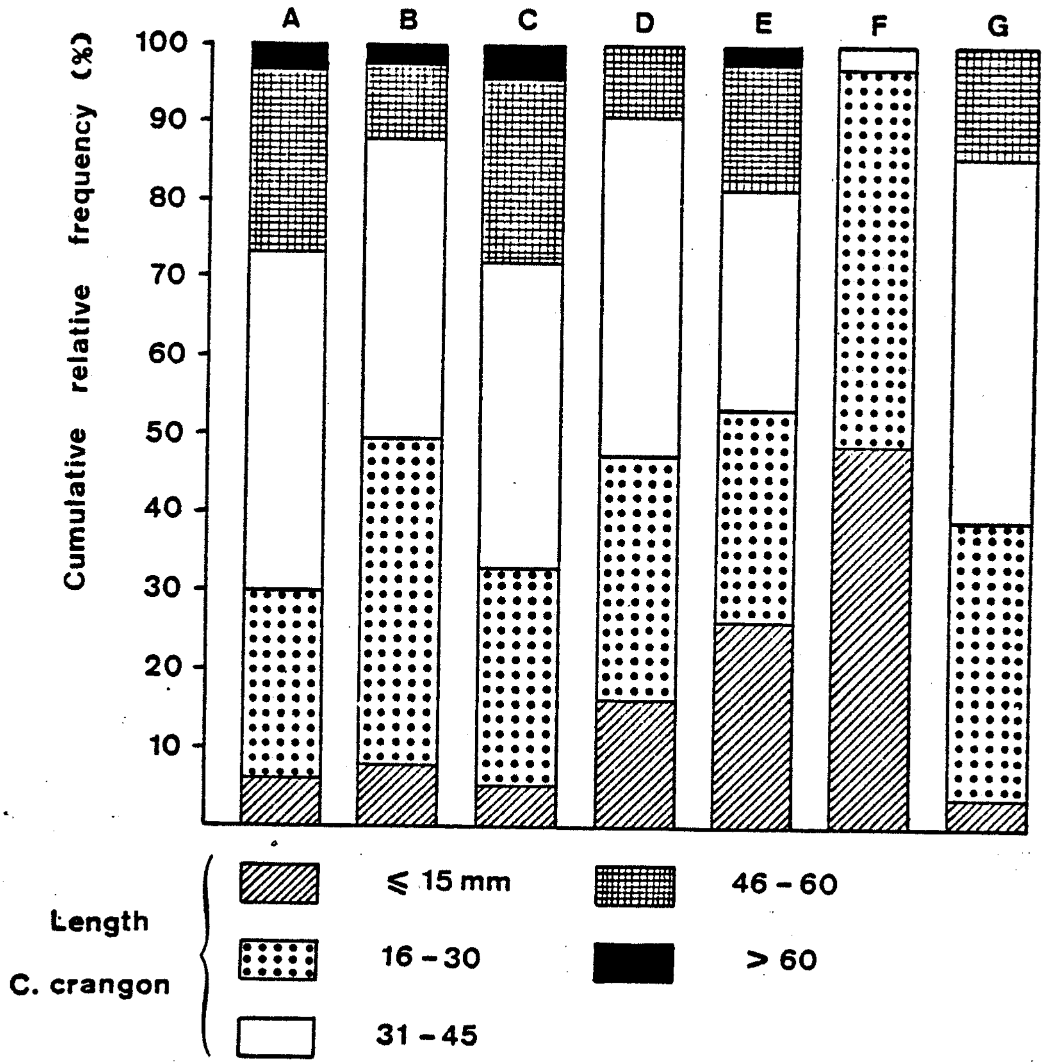

Figure 1 - Cumulative relative frequency distribution of length classes of shrimp in the stomachs of
A : Odontogadus merlangus,
B : Trisopterus luscus,
C : Gadus morhua,
D : Ciliata mustela,
E : Trigla species,
F : Agonus cataphractus,
G : Liparis liparis.

Data on Agonus after GABRIELS (1977).

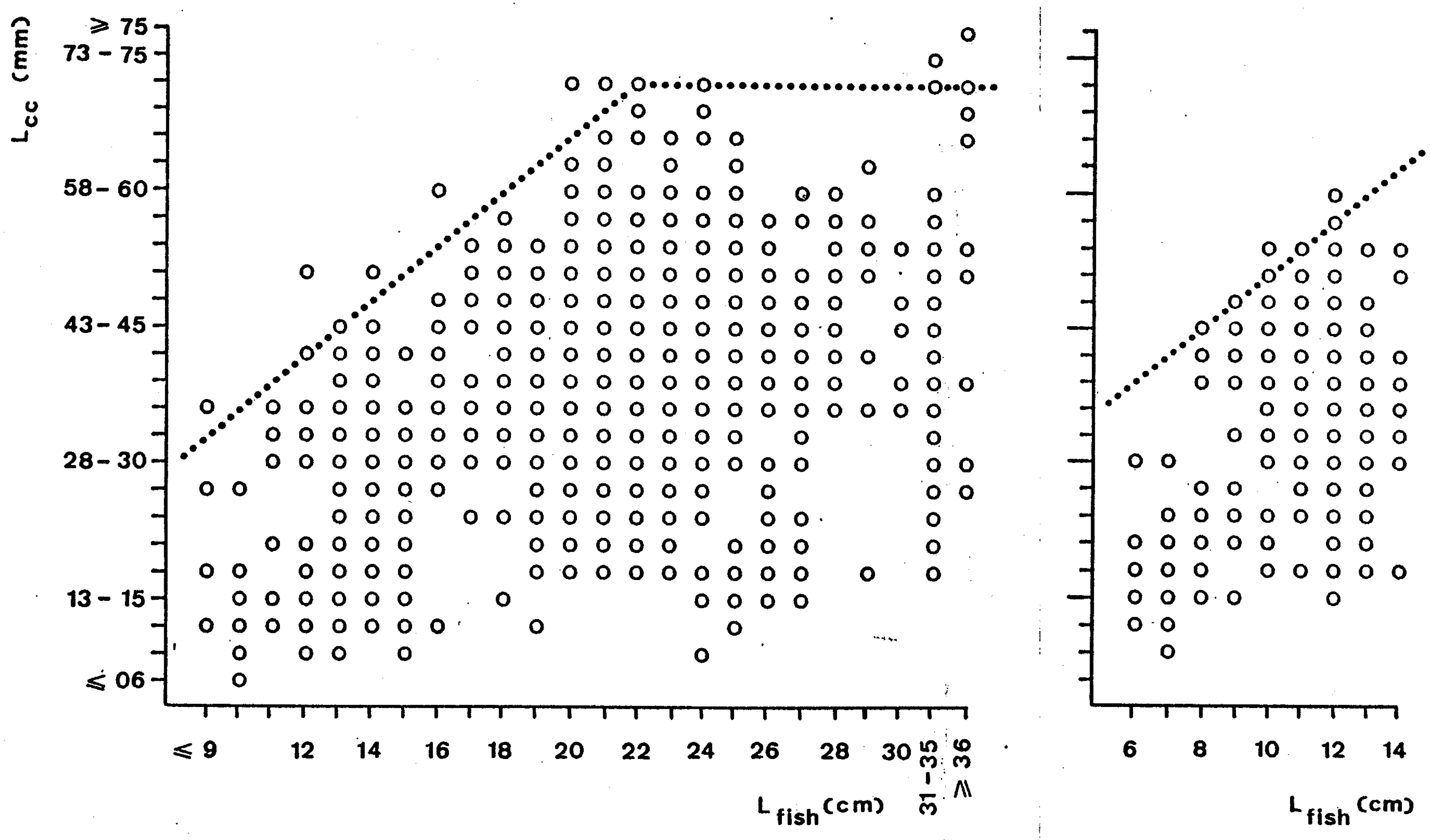

Figure 2 - Length distribution of shrimps in the stomachs of a large predator (Odontogadus merlangus, left) and in the stomachs of a small predator (Liparis liparis, right) in relation to the size of the predators.