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LIFE HISTORY, FOOD CONSUMPTION AND RESOURCE PARTITIONING IN TWO SYMPATRIC GOBIES POMATOSCHISTUS MINUTUS AND P.LOZANOI IN THE BELGIAN COASTAL WATERS

by

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ABSTRACT

Gobies were obtained monthly from the bycatch of a commercial shrimp trawler operating in the shallow waters (less than 20 m depth) of the Westdiep area, Southern Bight of the North Sea, from May through December 1984. Pomatoschistus lozanoi juveniles appear later than P.minutus juveniles, indicating a temporal segregation of reproduction. Yearly average density of P.minutus is about twice that of P.lozanoi. Food consumption by the two species amounts to 1-2 g AFDW/m^2/year. Stomach analysis of several hundred gobies shows that P.minutus is a food generalist that obtains most of its food from the benthos and epibenthos. P.lozanoi is a more specialised feeder, strongly dependant on the hyperbenthos, on mysidacea in particular. The absence of a food niche shift in P.lozanoi when no P.minutus are present suggests that present-day competition is unimportant in shaping the food niche segregation observed.

1. INTRODUCTION

The search for interspecific competition is a fashionable pursuit for ecologists (Schoener 1983). The number of studies claiming to demonstrate competition is influenced by scientific editors, referees and the behaviour of scientists in general (Connell 1983).

Competition as the main factor that determines the distribution, abundance and resource use of species in natural communities is directly related to the Darwinian theory of evolution (Darwin, 1859).

The impossibility of indefinite coexistence of two or more species limited by the same resource was first modeled mathematically by Volterra (1928). The competitive exclusion principle (Hardin, 1960) states that n species cannot coexist on fewer than n resources or in fewer than n niches. The principle is in a sense tautological: if it is valid we will be unable to demonstrate competition in coexisting species (Slobodkin 1961), so ecologists may well be hunting the ghost of competition past (Connell 1980).

Armstrong & McGehee (1980) have shown that systems can be constructed where n species coexist on $k<n$ resources or limiting factors. Important aspects of their model are non-linearity of the functional response and relaxation of fixed density assumptions. The species can then coexist because of internally generated cyclic behaviour. This makes competitive exclusion less probable in ecosystems with important seasonal cycles. Wiens (1977) presents some evidence from a variable environment where competition seems to be temporally sporadic and impotent.

Pomatoschistus species are the most abundant fish in the Belgian coastal waters and are an important food source for several commercial demersal fish species, notably *Gadus morhua* and *Merlangius merlangus* (Redant 1977).

Data on life history, density, biomass and food consumption of two sympatric gobies of the genus *Pomatoschistus* collected in the shallow coastal waters of the Southern Bight of the North Sea are presented here.

The data are analysed with special emphasis on food niche segregation. Field evidence for present-day competition is examined.

2. MATERIALS AND METHODS

Approximately monthly samples were obtained from the bycatch of a commercial shrimp trawler "O62" operating in the Westdiep-Trapegeer area off Nieuwpoort (Fig 1) from May 1984 through December 1984. During the exceptionally cold months of early 1985 no samples were taken because most fish and shrimp moved to deeper areas out of reach of the small trawlers. In April 1985 fish were obtained from the Spring Survey of the Fisheries Research Institute Ostend with the vessel "Broodwinner". The sampling stations 16, 17, 19, 23, 24 and 91 (Fig 1) are situated in the shrimp fisheries area normally visited by the O62. Gobies from these sampling stations were pooled to yield a sample similar to the O62 samples. In June and August 1985 samples were again available from the O62. In September 1985 fish were obtained from the same sampling stations in another survey with the Fisheries Research Institute (Table 1). Both vessels are beam trawlers. The O62 has two 7 meter beams, the Broodwinner has two 6 meter beams. Both are equiped with standard commercial shrimp nets with an 18 mm stretched mesh in the cod end. Trawl speeds are 2 to 3 knots.

On board all fish are immediately anaesthesized in a Benzocaine (Ethylamino-4-benzoate) solution in sea water to prevent regurgitation of stomach contents. Within 15 minutes after capture the fish are preserved in neutralised formaldehyde 7% final concentration.

At least three months after capture, to allow for shrinkage to stabilize, all gobies are identified and measured to the nearest mm. All lengths are standard lengths, measured from the tip of the mouth to the base of the tail fin. A linear regression analysis was performed on a December subsample of *Pomatoschistus lozanoi* to determine the relationship standard length-total length.

If a sufficient number of fish of the same 5 mm size class of both species was present in the same trawl from nightly samples from the Trapegeer area (51 07'40'' NB, 02 30'40''OL to 51 08'40 NB, 02 34'20 OL), thirty fish from each species were selected at random from that size class for stomach analysis.

On May 17, 1984 fishing was only done at daytime and numbers of *Pomatoschistus minutus* were so low that *P.minutus* and *P.lozanoi* from all trawls were pooled. On July 20, 1984 samples were obtained during the day and in the following night. Because no overlapping size classes were found, *Pomatoschistus minutus* were again pooled from all trawls and *Pomatoschistus lozanoi* of size classes comparable to the August and September samples were taken from a nightly trawl in the Trapegeer area. All other O62 samples are night samples, all Broodwinner samples are daytime samples. From relative densities in the different samples, taking hours of trawling into account, and average monthly densities per 1000 m2 from Redant (1978), approximate densities for 1984 can be estimated (Table 1). Efficiency of the net was assumed to be 25% for all size classes.

Average biomass per m2 for 1984 was calculated using the Total Ash Free Dry Weight (TW) of the median of every 5 mm size class from length to TW regressions for *Pomatoschistus minutus* and *P.lozanoi* in Table 2. It is assumed that the yearly average does not differ substantially from the average based on May to December monthly averages.

As gobies do not have a functional sphincter at the gastrointestinal junction the food items in the entire gastrointestinal tract, excluding the rectum, are examined under a dissecting microscope. Every food item in the gastrointestinal tract (hereafter refered to as "stomach") is identified, if possible and reasonably practical to species level. Hydroidea, phytal material and detritus are not regarded as prey. All food items, except calanoids and harpacticoids are measured to the nearest .1 mm using a drawing mirror and curvimeter. If prey are incomplete , loose parts that have a linear relationship with total length e.g. a carapax or a telson are measured, so that conversion to Ash Free Dry Weights (AFDW) is possible. If a prey item is partly in the rectum a subjective estimate is made of what proportion remains in the "stomach", and only that proportion is counted for percentage AFDW calculations.

Length to AFDW relationships of prey are derived from various sources (Table 2). For *Pomatoschistus minutus*, *P.lozanoi* and bivalve siphons relationships are determined from our own samples (Figs 2,3,4 and Table 2). Undigested bivalve siphons are obtained from the esophagus of fish. A subjective technique is used to estimate the AFDW of the tentacle crowns of *Lanice conchilega*. If these are present their volume is compared "de visu" to a volume of undigested tentacles from the esophagus of a fish of the same size class and sampling date. Comparison of the AFDW of some esophagus samples with their estimated volume shows the "de visu" method to be reasonably accurate if crude designations like double, half, a third or a fourth are used. Luckily the epidermis of Lanice seems to resist digestion rather well, therefore bulk of the tentacles (and body size for entire animals) in the stomach may resemble original bulk quite closely. Errant polychaetes are not always eaten whole so using body width as a measure of body length is dubious. We try to make an educated guess of the original size of the fragment by estimating the number of segments, measuring the AFDW of the fragment as present in the stomach, measuring jaws or other undigested parts, etc... Still, polychaete importance is probably underestimated by this technique.

Other soft bodied animals like oligochaeta and nemertineans, though not rare in the ecosystem, were never found in the stomachs. This may be an artifact. Nematode consumption is certainly underestimated because of rapid digestion (Hofsten et al. 1983). Over 90 % of the nematodes encountered in the stomachs are *Mesacanthion spec.* a 2-3 mm long Enoplid.

This does not reflect its predominance in the ecosystem, but the fact that its cuticula has three thick layers probably slows digestion (M.Vincx, pers.comm.).

For some food categories we assigned an AFDW independent of length (Table 2). Most of these food items, except the chaetognaths, are very small and the influence of even a very wrong AFDW will be marginal. For the chaetognath *Sagitta* a length to Dry Weight regression is stated in Feigenbaum (1979). Unfortunately he does not state the relationship between the size of the undigestable grasping spines and the total body length. We chose an intermediate value from his regression and, although we measured different sizes of grasping spines, allocated .500 mg AFDW to every chaetognath. This corresponds to a *Sagitta* of about 15 mm.

Another problem is the possibility that food items in the stomachs of prey species are mistaken for food items taken by the fish. In crustaceans the carapax is usually so well preserved that food remains stay contained. In chaetognaths on the contrary the body wall is rapidly digested and prey items are scattered in between those of the fish. No attempt is made to distinguish between e.g. calanoids consumed by the fish and those primarily consumed by the chaetognaths. Conceivably a correction for this bias is possible if the average number of calanoids per chaetognath is known.

Stomach analysis data should always give a measure of the relative importance of different prey items and a measure of the bulk of the food present in the stomach. Results must allow comparison with other areas, other species or other seasons, therefore they must be objective and expressed in convertible units (Berg 1979). The Points method and Frequency of Occurrence method, still widely used, must be considered obsolete. Percentage AFDW is calculated in this study. Bulk of food present in the stomach was measured by drying the examined stomach contents at 120 C for 2 hours. It is expressed as Fullness Index (FI = Dry Weight of stomach content * 100 / TW).

Individual Total Weight (TW) is the sum of Somatic Weight (SW) and Gonad Weight (subsequently GW). Somatic Weight is determined by drying individual fish for 5 days at 60 C and subsequently incinerating the dried remains at 550 C for 2 hours, the difference between Dry Weight and Ash Weight is the Ash Free Dry Weight. Ash Free Dry Weights can be converted to caloric content. The complete digestive tube is added to the fish after stomach analysis and before drying so that it is included in SW and TW measurements.

All sizes are in mm, all weights in mg unless otherwise stated.

Niche overlap is measured by calculating Renkonen's index (Renkonen 1938).

3. RESULTS

3.1. Identification.

Of 12725 gobies of the *Pomatoschistus minutus* complex (Webb 1980) examined, 9398 (74%) are *Pomatoschistus minutus*, 3327 (26%) are *Pomatoschistus lozanoi*. Other *Pomatoschistus species* encountered are *Pomatoschistus pictus* and *Pomatoschistus microps*. These are very rare (less than 20 each) and will not be dealt with here.

With some experience the identification of gobies of the *P.minutus* complex is not difficult. Webb (1980) cites three important differences: the number of vertical c-rows of papillae on the jaw (higher in Pomatoschistus minutus, but with an overlap in number), the fact that the 2nd and 4th c-rows descend beyond the horizontal d-line in *Pomatoschistus lozanoi* and the difference in vertebral number (though also with an overlap). We have found many gobies with the 4th c-row continuing under the d that were clearly *Pomatoschistus minutus* according to a variety of other criteria: size, pigmentation, number of vertical rows etc.... With the same criteria we found many *Pomatoschistus lozanoi* that do not have a 4th c-row continuing below d.

3.2. Life history.

Length-frequency distribution of the 1984 and 1985 samples are shown in Fig 5 for *Pomatoschistus minutus* and in Fig 6 for *P.lozanoi*. It must be stressed that sample sizes depicted are not directly related to densities: different numbers of trawls of different duration are pooled per sampling date. To reduce this bias length-frequency is converted to length-percentage frequency distribution (Figs 7 and 8). Thirty fish is taken to be the minimal size for a length-percentage frequency distribution to be meaningful.

In spring *Pomatoschistus minutus* 1+ adults are ready to spawn as demonstrated by nuptial colours and high GSI. By June they become extremely rare. Most *P.minutus* have probably spawned by then and are dead or dying. In July the 0+ juveniles recruit into the net, having attained a body length of about 30 mm. Growth is extremely rapid as by the end of September a sizeable proportion of the population attains adult length. Recruitment continues through October as seen by the slight decrease of average length in an increasing population of rapid growers (Table 3). In 1985 there is a similar pattern, with the recruits of the fall of 1984 spawning and dying in spring and early summer.

Pomatoschistus lozanoi is much more abundant in late spring than *P.minutus*. The population consists of 1+ adults with little or no nuptial colouring. There seems to be virtually no somatic growth (constant mean length with no change in density) but gonads are developing. Adult size averages less than in Pomatoschistus minutus. By July nuptial colouring is very pronounced.

In August the first juveniles recruit into the net, a sizeable population of 1+ adults is still present. By the end of September virtually all 1+ have disappeared and population buildup begins. A large proportion of the *Pomatoschistus lozanoi* population seems to pass the winter at subadult length. The 1985 data confirm this general pattern.

The relationship found for conversion of standard length to total length is: TL = 1.089 + 1.157 * SL.

(n=96, r2=.99) (Fig 9).

3.3. Density, biomass and food consumption.

Estimated yearly average density is 80 *Pomatoschistus minutus* per 1000 m2 and 40 *P.lozanoi* per 1000 m2 (Table 1). This represents 33.19 mg and 8.45 mg AFDW per meter square, for *Pomatoschistus minutus* and *P.lozanoi* respectively. With an 8.6% of body weight daily consumption, calculated by Andersen (1984) for *Pomatoschistus microps*, this amounts to 969 mg AFDW /m2/yr for *Pomatoschistus minutus* and 247 mg AFDW /m2/yr for *P.lozanoi*.

3.4. The food of *Pomatoschistus minutus*.

Data from the stomach analyses of 419 *P.minutus* are summarized in Table 4. A survey of food categories that provide at least 10% of AFDW for a certain size class at any one time may give some insight into the feeding of *Pomatoschistus minutus*. Siphons of bivalves are responsible for the bulk of energy derived from molluscs. Errant polychaetes are only important if a large *Nephtys* or *Sthenelais boa* is eaten, this is rather infrequent. Sedentary polychaetes, mostly *Lanice*, and some *Pectinaria* are very important, except in September. This is probably not a seasonal effect of some sort but an artifact of the trawl just missing the fields of *Lanice*: in a later trawl of the same night only a few meters deeper down on the slope of the Trapegeer most *P minutus* did eat *Lanice* (Hamerlynck, unpubl. data). Calanoid copepods are important in autumn, especially for the smaller size classes. There is a huge peak in the abundance of *Temora longicornis* at that time (Polk et al. 1975). Caridean decapods are also very important. In spring nearly 50% of caridean bulk is provided by *Pontophilus trispinosus*, later in the year nearly 100% by *Crangon crangon*. Mysids are frequently consumed and have high individual AFDW, most are *Schistomysis spec.*. *Pariambus typicus* is very important in July and August, this seems to be an effect of the presence of larger animals: mean AFDW of consumed *Pariambus* is .031 mg in August (n=277) and .015 mg in September (n=1584). No fish other than *Pomatoschistus* species were found in goby stomachs. Partial digestion makes identification very difficult. However, the life history data suggest that predation is on juvenile *P.lozanoi* in September, and that cannibalism (in May) is less important. Table 6 lists all food items found in *Pomatoschistus minutus* and *P.lozanoi*.

3.5. The food of *Pomatoschistus lozanoi*.

Data from the stomach analyses of 306 *Pomatoschistus lozanoi* are summarized in Table 5 . When a similar survey of the data as in *P.minutus* is done the importance of *Lanice* in August, and its near absence in the other months is striking. The importance of calanoids is rather similar to that in *P.minutus* in September, but *P.lozanoi* is also predating strongly on the spring peak. Mysids are almost always the most important food, except in May when gammaridean amphipods are more prominent.As in *P.minutus* predation on the juveniles of the other species is more important than cannibalism.

3.6. Changes in the predation with fish size.

There are obvious qualitative and quantitative changes in the importance of different food categories with increasing fish length for *Pomatoschistus minutus* (Fig 10). The range of lengths of *P.lozanoi* investigated is still rather limited, but the data do suggest that changes in the predation with increased length are less pronounced than in *P.minutus* (Fig 11).

3.7. Food niche segregation.

Niche overlap is measured by: $Cxy = 1-1/2(\sum^{i}|p_{xi} - p_{yi}|)$ (Renkonen 1938).

Its calculation for similar size classes of both fish per sampling date shows quite strong overlap (.44 to .72) in the food niche of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* (Table 6). It is most pronounced in the smaller size classes (35-39 mm) and is stronger in October than in September. The consumption of some 17-25% (AFDW) by *P.minutus* of *Lanice conchilega* in October does not compensate for the large overlap of *Schistomysis spiritus* and *Temora longicornis* consumption.

Niche breadth indices were not calculated, because standardization is not without problems (Colwell & Futuyma 1971). A simple count of food categories found exclusively in *Pomatoschistus minutus* stomachs (n=44), food categories common to both species (n=42) and those found exclusively in *P.lozanoi* stomachs (n=6) does indicate that *P.minutus* is more of a generalist, and that *P.lozanoi* is more of a specialist (Table 6).

To demonstrate the nature of the difference in food niche all prey items were lumped into three categories: benthic, epibenthic and hyperbenthic-pelagic (Table 8). Calculations of cumulated percentage AFDW of these categories per sampling date are shown in Table 9. It is clear that the *Pomatoschistus lozanoi* population extracts a more substantial proportion of its energy from the water column in comparison to the *P.minutus* population in all but one month. The result of August seems completely aberrant.

4. DISCUSSION

4.1. Identification.

In the laboratory viable larvae have been produced by hybridisation of *Pomatoschistus minutus* with *P.lozanoi* (Fonds 1973) and individuals have been found in nature with morphological and biochemical characteristics intermediate between those of *Pomatoschistus minutus* and *P.lozanoi* (Swedmark 1968, Fonds 1973, Wallis & Beardmore 1980, Webb 1980). Individuals with intermediate morphological characteristics are extremely rare in our study. This may be explained by our criterion for deciding in favour of one species or the other. Our rule is: if the 2nd vertical c-row continues under d the fish is a *Pomatoschistus lozanoi*, if it does not, it is a *P.minutus*.

4.2. Life history.

Our life history data are similar to the results of other studies that distinguish *Pomatoschistus minutus* from *P.lozanoi* (Fonds 1973, Wallis & Beardmore 1984, Claridge et al. 1985). The precise mechanisms of reproductive isolation and of temporal segregation of reproduction are still unknown. There may be direct competition for nest sites, a resource that can be monopolisized. We have few data on gonad ripening but it seems that in early spring *Pomatoschistus minutus* is ready to spawn, while an important part of the *P.lozanoi* population has to channel some of its energy into somatic growth before ripening of the gonads starts.

4.2. Density, biomass and food consumption.

Admittedly our estimated densities may be wrong. If so they are probably underestimates. In a detailed study of a shallow sandy beach using a fine mesh net we found an average density of 71 *Pomatoschistus minutus* and 393 *P.lozanoi* per 1000 m2 (Hamerlynck, unpubl.data).

If densities are reasonably accurate the consumption of nearly 1 g AFDW per m2 per year for Pomatoschistus minutus and of .25 g AFDW per m2 per year for P.lozanoi is very high for animals of such low biomass. Pihl (1985) calculated consumption of mobile epifauna in a shallow bay in western Sweden. *For Pomatoschistus minutus* he found a consumption of 1 g AFDW per m2 per year for a production of .24 g per m2 per year. The finding of exactly the same consumption figure does not mean it is correct. Their study area is rather different from ours: it is a shallow bay of less than one meter depth. It is only visited by *P.minutus* juveniles in summer and autumn (Pihl & Rosenberg 1982). Evans (1983, 1984) working in a similar bay estimates consumption by *P.minutus* to be .4 g AFDW per m2 per year. He uses an ingestion of 3% of body weight per day from Healey (1972). This just shows the uncertainty of a figure like 1 g AFDW per m2 per year, it can easily be 50 % higher or lower, depending on the parameters chosen for calculation.

The impact of this predation on the fauna is also difficult to assess. Experiments with inclusion (Berge & Hesthagen 1981) and exclusion (Berge & Valderhaug 1983) of *P.microps* suggest that predation impact is small: only in the exclusion experiments a slight increase in ostracods and amhipods was seen. In most other experimental studies epifauna is claimed to regulate infauna (reviewed by Peterson 1979).

Most authors agree that the Atlantic-Mediterranean gobies of the genus *Pomatoschistus* are not food limited but predator controlled (Healey 1971, Evans 1983, Miller 1984).

4.3. Food niche segregation.

The result of niche overlap calculation seems in accordance with the strong food niche overlap (.80 to .86) found between *Pomatoschistus minutus* and *P.microps* in October and November in Gulmarsvik, a shallow bay on the Swedish west coast (Pihl 1985).

This does not mean that there is competition: during the autumn peak of the zooplancton food may not be a limiting resource. Renkonen's index is simple to calculate, but that does not reduce the difficulties of interpretation. On the contrary its use is strongly critisized because it ignores variation in resource state abundance (Hurlbert 1978). It is also inappropriate in that it is not expressed in units that are relevant for a discussion of competition, resource relationships and the like. It is just an index and certainly no proof of competition as mistakingly asserted by Thorman (1982). The calculation of a more sophisticated index that takes frequency of interspecific encounter and directionality into account is not feasible because we lack data on prey abundance.

The suggestion made by Hamerlynck et al. (1985) that the Pomatoschistus lozanoi and P.minutus occupy more or less separate food niches in the coastal waters of the Southern Bight is confirmed by this study. Fonds (1973) did not find a difference in frequency of occurrence of different prey items between P.minutus and P.lozanoi from the North Sea, however he did find that in the Waddenzee stomachs of P.minutus contained more often harpacticoid copepods and polychaetes, and that stomachs of P.lozanoi contained more often mysids. Frequency of occurrence is a very crude measure of prey importance because it is not related to a measure that can be converted into energy content. Thus one harpacticoid in every stomach is equivalent to 1000 harpacticoids in every stomach. A more sophisticated analysis might have given the same results for the North Sea as found in our study. Claridge et al. (1985) find no differences in percentage weight composition of the food of *Pomatoschistus minutus* and *P.lozanoi* from the inner Severn. The diet of both species consisted almost entirely of *Gammarus salinus* and *Neomysis integer* in all seasons. Possibly prey diversity so high up the estuary is very low and little or no bivalves and polychaetes are available.

Support to the hypothesis (Hamerlynck et al. 1985) that differences in the pattern of the sensory papillae are of adaptive significance to the observed feeding patterns is given by Gibson & Ezzi (1981): *Pomatoschistus norvegicus* which has a pattern similar to *P.lozanoi* is also feeding primarily on mysids and calanoids.

4.4. Spatial segregation.

Food niche segregation of the kind described here implies vertical spatial segregation between the species with *Pomatoschistus minutus* confined to the bottom and *P.lozanoi* cruising at some distance from the bottom in the water column.

Though not analysed in detail here there is a strong indication of some horizontal spatial segregation between the species. In spite of large numbers of fish collected and considerable size overlap of both populations (Figs 5 and 6) only one overlapping size class is found in October and none are found in December in any single trawl. The fact that this segregation seems stronger when population size increases may be an effect of competition. An alternative hypothesis is that horizontal segregation is directed by the abundance of preferred prey.

4.5. Competition.

Interspecific competition may be defined as follows: with two species sharing at least one common resource the presence of species A has a negative influence on fitness in species B. Proof of this effect requires field experiments: species have to be transplanted and/or enclosed without ill effects, they must be stocked at different densities when alone (to assess intraspecific competition) and when together in close to ambient conditions (Conell 1983). Competition is often inferred from indirect evidence like retarded growth because fitness is too difficult to measure directly (e.g. Werner & Hall 1976).

In a recent review of field experiments Schoener (1983) emphasises that little or no studies were done on food competition in marine vertebrate carnivores. The coastal zone of the North Sea with its frequent storms, low transparency, high current speeds and large tidal amplitude is not very amenable to experimental studies. Thus another approach is warranted.

Hutchinson (1958) distinguishes between fundamental and realized niche. The fundamental or "pre-competitive" niche is larger than the actual or realized niche of a population in a certain environment. Actual niche is expanded in the absence of competitors to fundamental niche and vice versa. Thus observations of niche shifts in the presence and absence of competitors are seen as strong indicators of competition.

The temporal segregation of spawning combined with the annuality of *Pomatoschistus species* creates a situation where adults of one species are present and adults of the other species are lacking because the 1+ have died and the 0+ are still too small to compete. This is precisely what we observed in the beginning of July 1984 (compare Figs 5 and 6).

Stomach analysis data for adult *Pomatoschistus lozanoi* in July do not reveal a major niche shift in the absence of its supposed competitor. This suggests absence of active present-day competition. Of course temporal effects of fluctuation in prey abundance may make niche widening impossible. This is improbable because the very small *P.minutus* present eat *Pariambus typicus* of sizes apparently still profitable to 60-64 mm adults (data of September). Alternatively *Pomatoschistus minutus* may still be present but catchability is reduced by spawning activities (Miller 1984). The territorial bottom dwelling spawners may be even more agressive than usual, keeping *P.lozanoi* confined to the water column.

The strong niche shift towards benthic feeding by adult *Pomatoschistus lozanoi* in August in the presence of 0+ *P.minutus* of the same length class may be a belated response to the disappearence of 1+ *P.minutus*, if gobies need a lot of time to adapt to a new situation. This is highly improbable in annual fishes adapted to a very dynamic ecosystem. Moreover data from laboratory experiments (Edlund & Magnhagen 1981, Magnhagen & Wiederholm 1982) show an immediate niche shift response in *Pomatoschistus minutus* and *P.microps*. When alone both species eat similar amounts of *Corophium* and chironomids. When together *P.microps* switches to *Corophium* and its feeding rate is reduced.

Another hypothesis is that *Pomatoschistus lozanoi* is confined to the bottom in August because of spawning activities at that time, e.g. it can not go feeding in the water column without ruining its chances for successful reproduction.

If competition there is, it is likely to be stronger in the smaller size classes when *Pomatoschistus minutus* are still dependent on hyperbenthic-pelagic prey for a sizeable proportion of their diet.

5. CONCLUSIONS

Pomatoschistus species are versatile microcarnivores that consume large amounts of food. They derive their energy from secondary consumers in the water column, from the meiobenthos and from secondary and tertiary consumers in the benthos, epibenthos and hyperbenthos. The data suggest that the small mobile epifauna plays an important role in the food web of the shallow coastal waters inshore of the Flemish Banks (Southern Bight of the North Sea) .

The lack of niche shift in *Pomatoschistus lozanoi* in July suggests present-day competition to be unimportant in explaining food niche segregation between *P.minutus* and *P.lozanoi*, but alternative explanations can be found. The mechanisms directing the complex pattern of temporal, spatial and food niche segregation in the two species of *Pomatoschistus* can only be elucidated by field and laboratory experiments with adequate controls for prey abundance variability and for effects of spawning behaviour.

The function and adaptive significance of the species diagnostic papillary pattern in the feeding ecology of gobies requires further investigation. The morphology of the 2nd vertical c-row of papillae is a reliable criterion for the separation of *Pomatoschistus lozanoi* from *P.minutus*.

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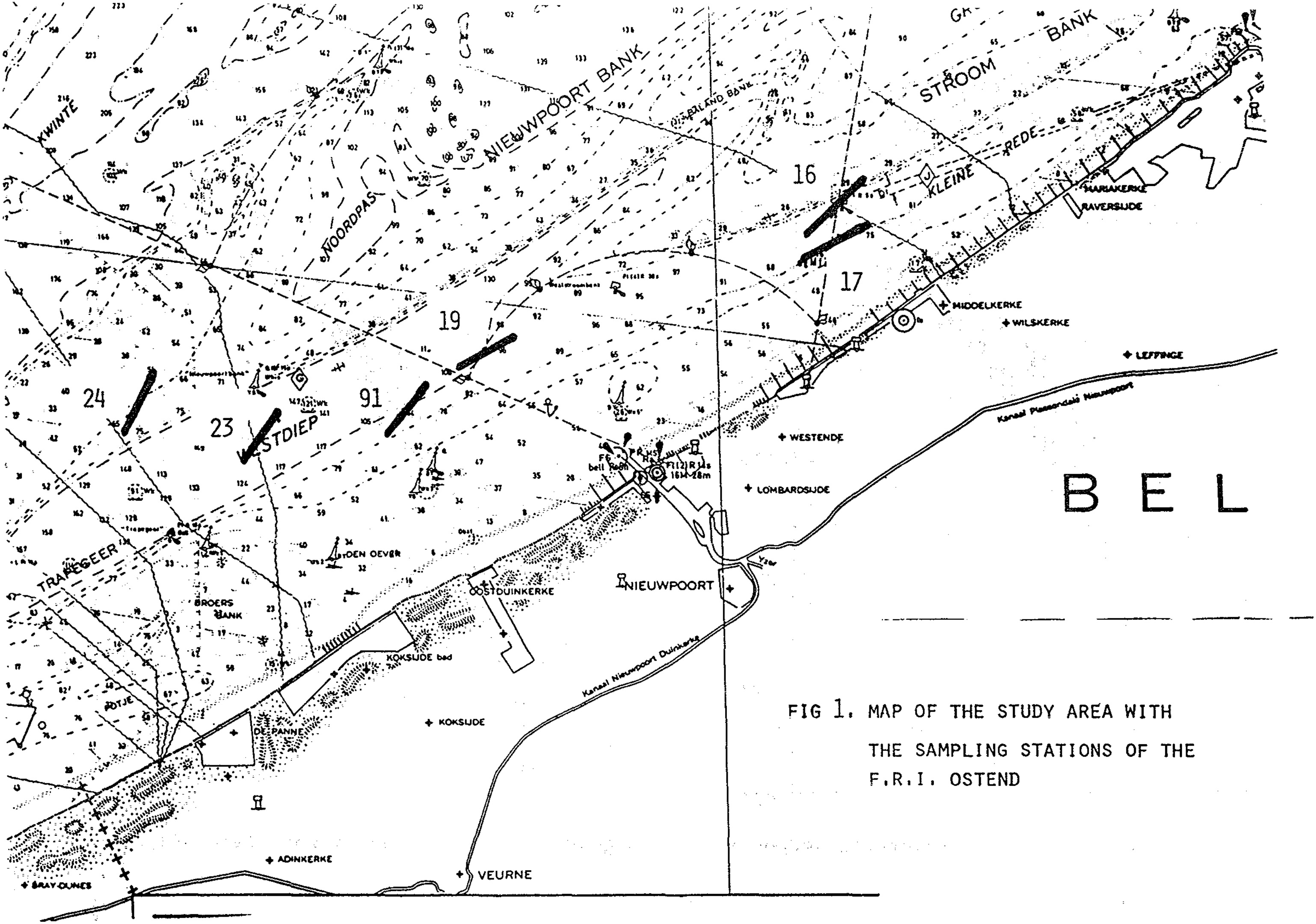

FIG 1. MAP OF THE STUDY AREA WITH THE SAMPLING STATIONS OF THE F.R.I. OSTEND

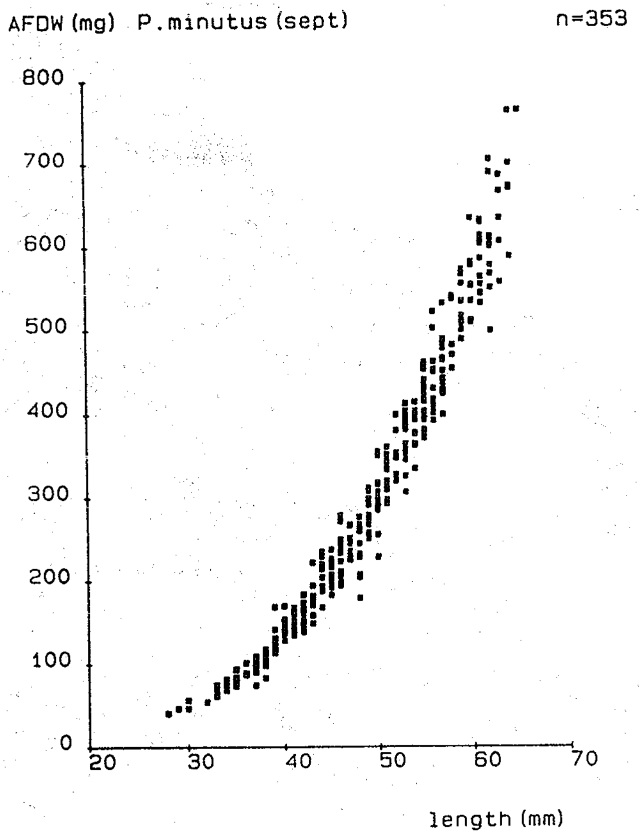

FIG 2. RELATIONSHIP STANDARD LENGTH TO AFDW
POMATOSCHISTUS MINUTUS

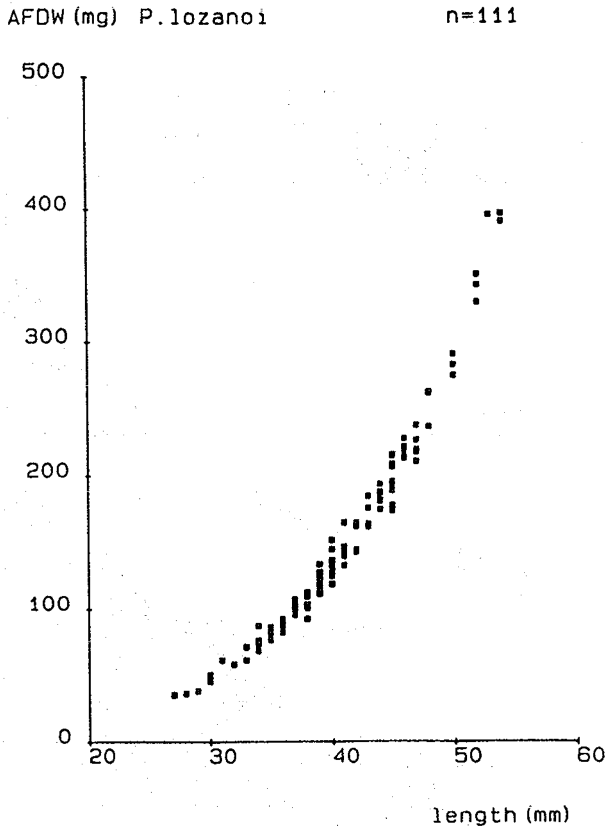

FIG 3. RELATIONSHIP STANDARD LENGTH TO AFDW
POMATOSCHISTUS LOZANOI

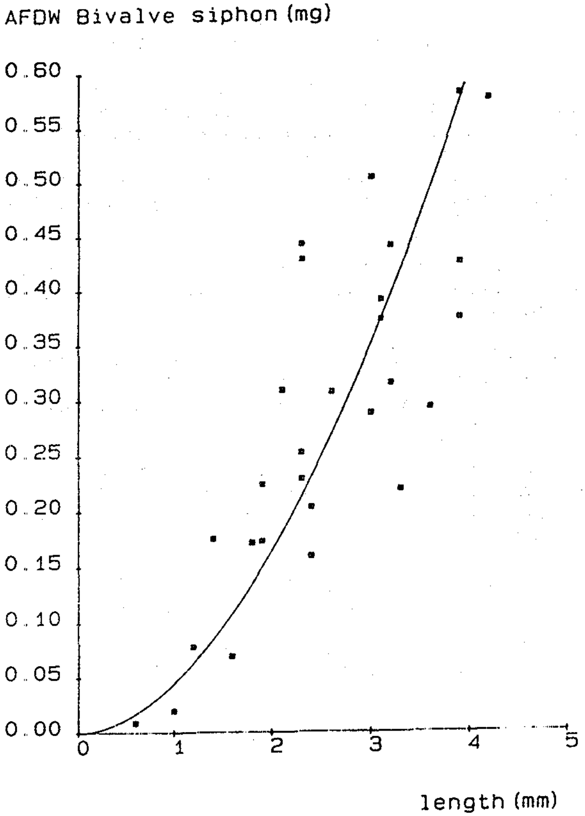

FIG 4. RELATIONSHIP BIVALVE SIPHON LENGTH TO BIVALVE SIPHON AFDW

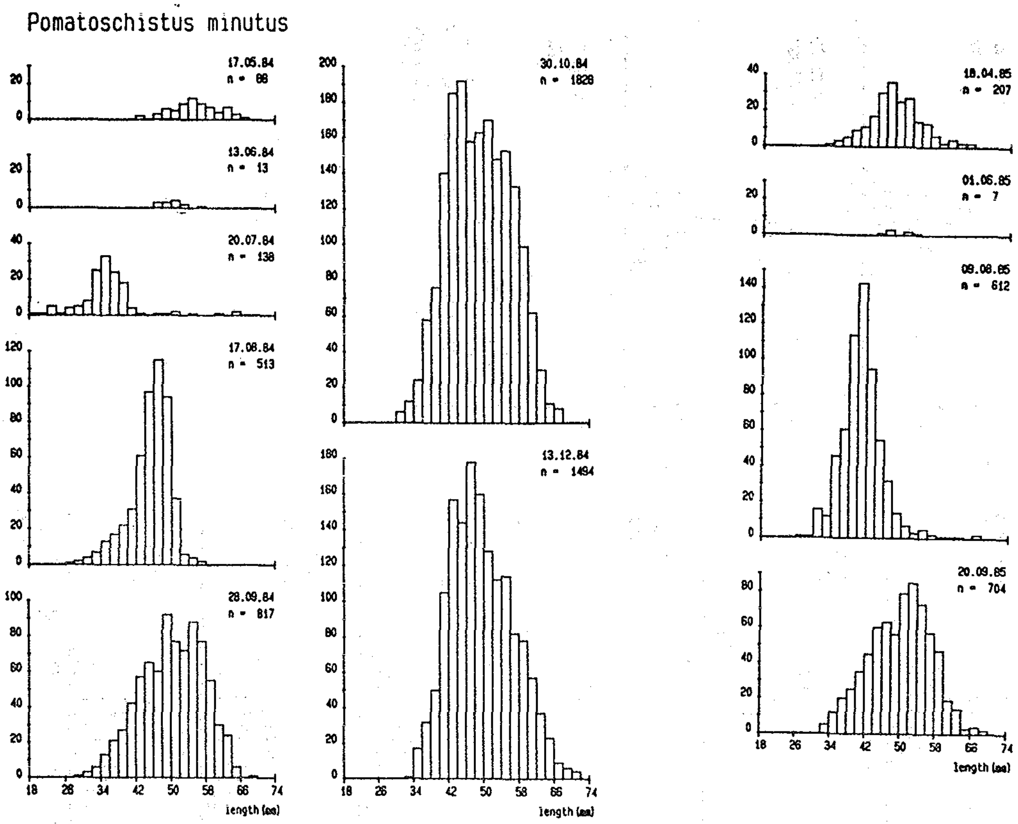

FIG 5. LENGTH-FREQUENCY DISTRIBUTIONS POMATOSCHISTUS MINUTUS

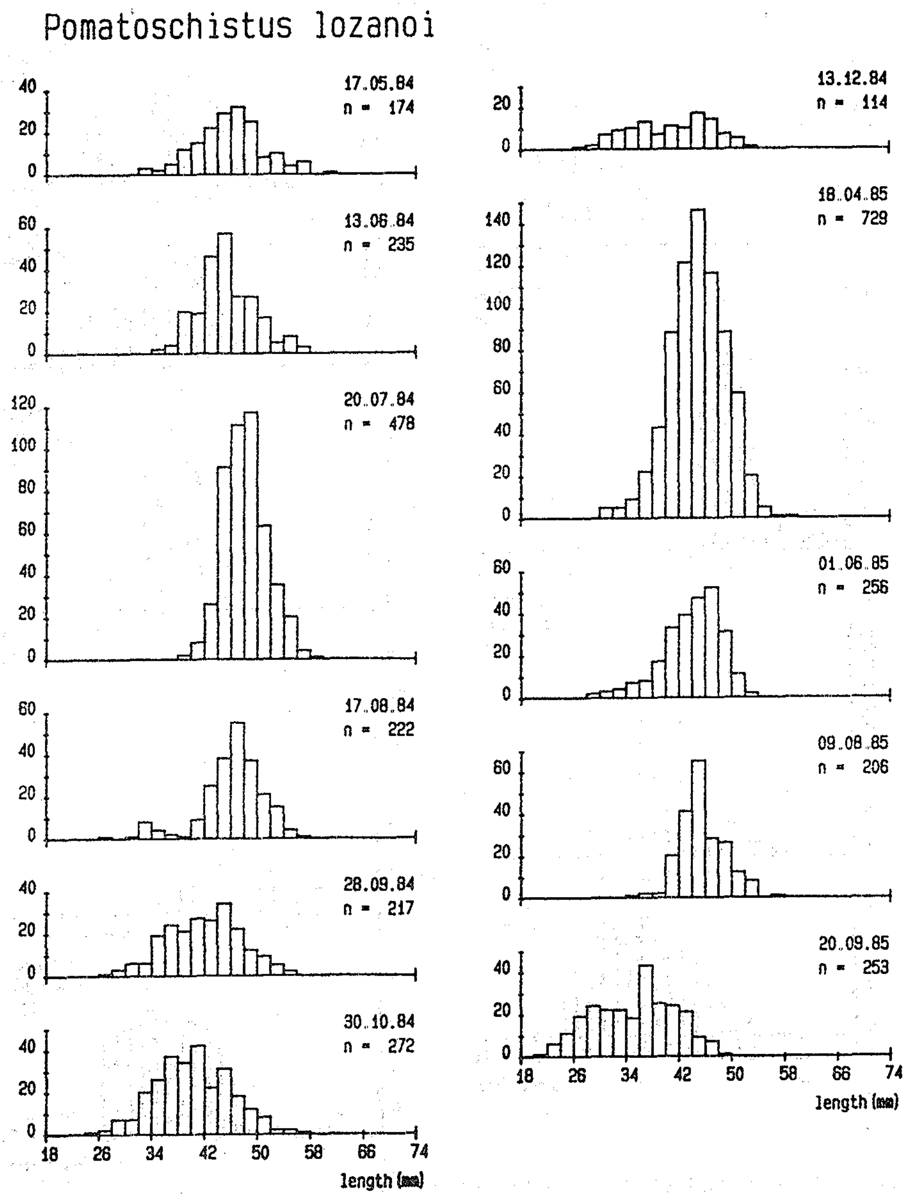

FIG 6. LENGTH-FREQUENCY DISTRIBUTIONS POMATOSCHISTUS LOZANOI

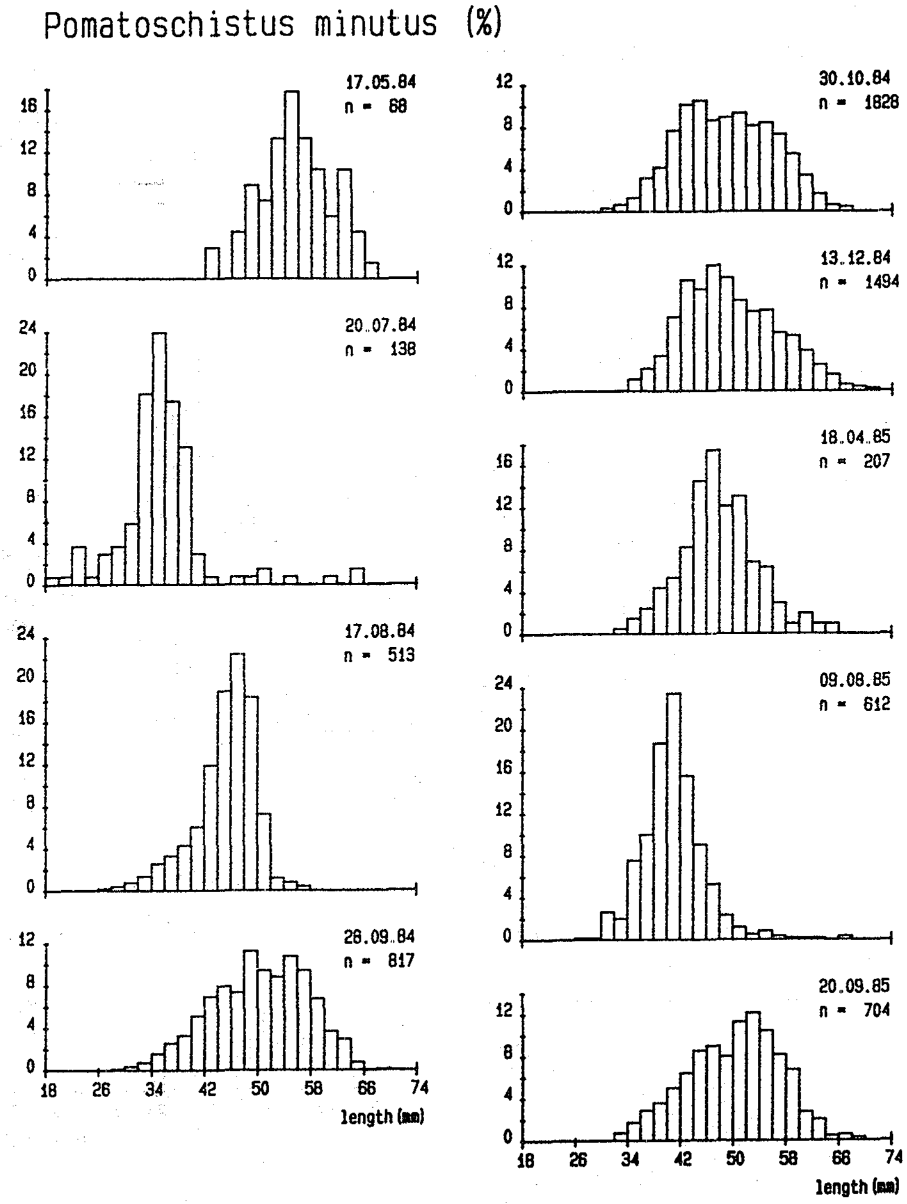

FIG 7. LENGTH-PERCENTAGE FREQUENCIES POMATOSCHISTUS MINUTUS

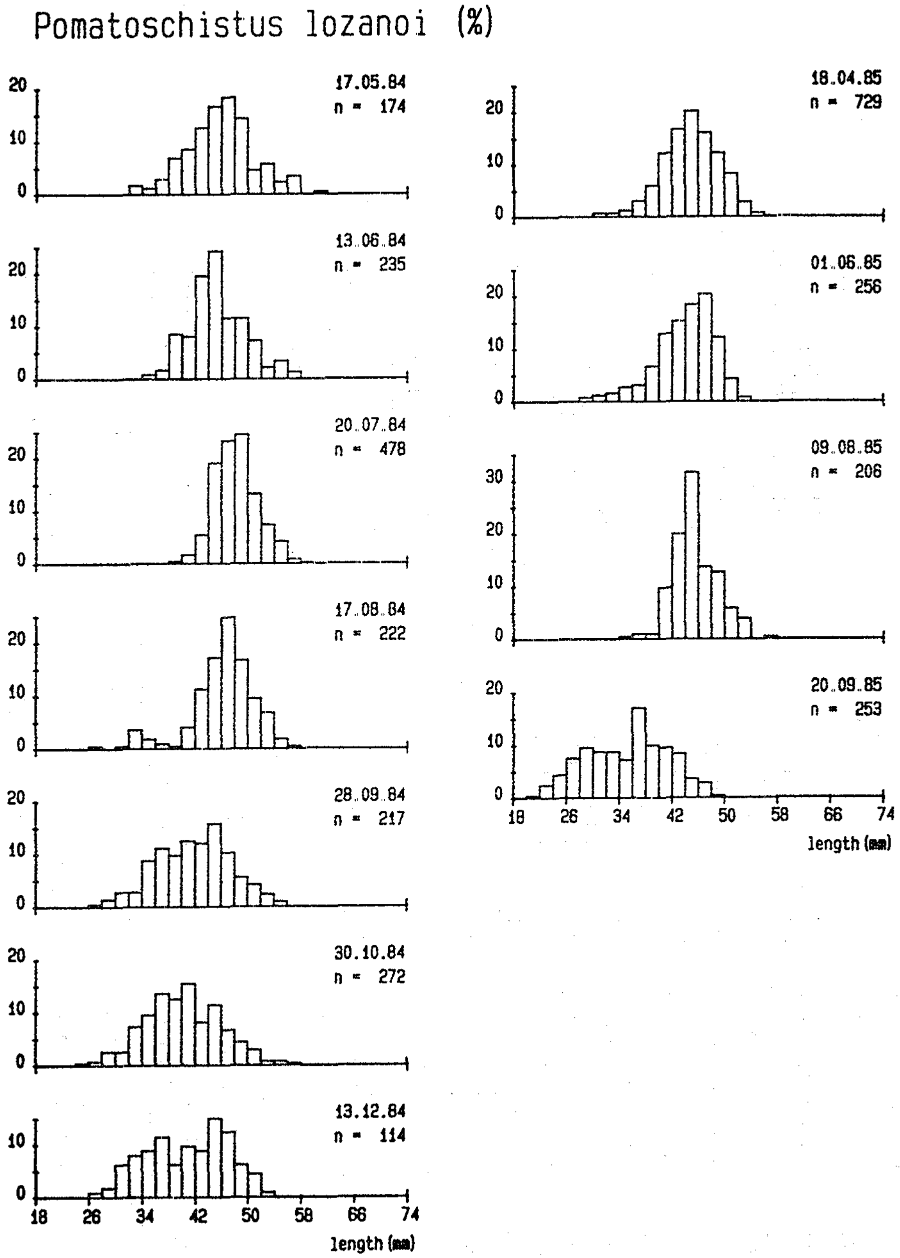

FIG 8. LENGTH-PERCENTAGE FREQUENCIES POMATOSCHISTUS LOZANOI

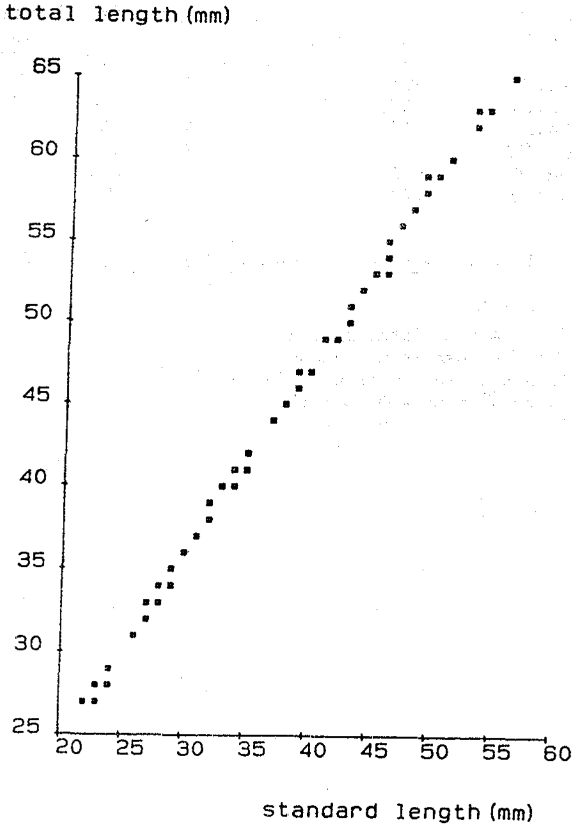

FIG 9. RELATIONSHIP STANDARD LENGTH TO TOTAL LENGTH
POMATOSCHISTUS LOZANOI

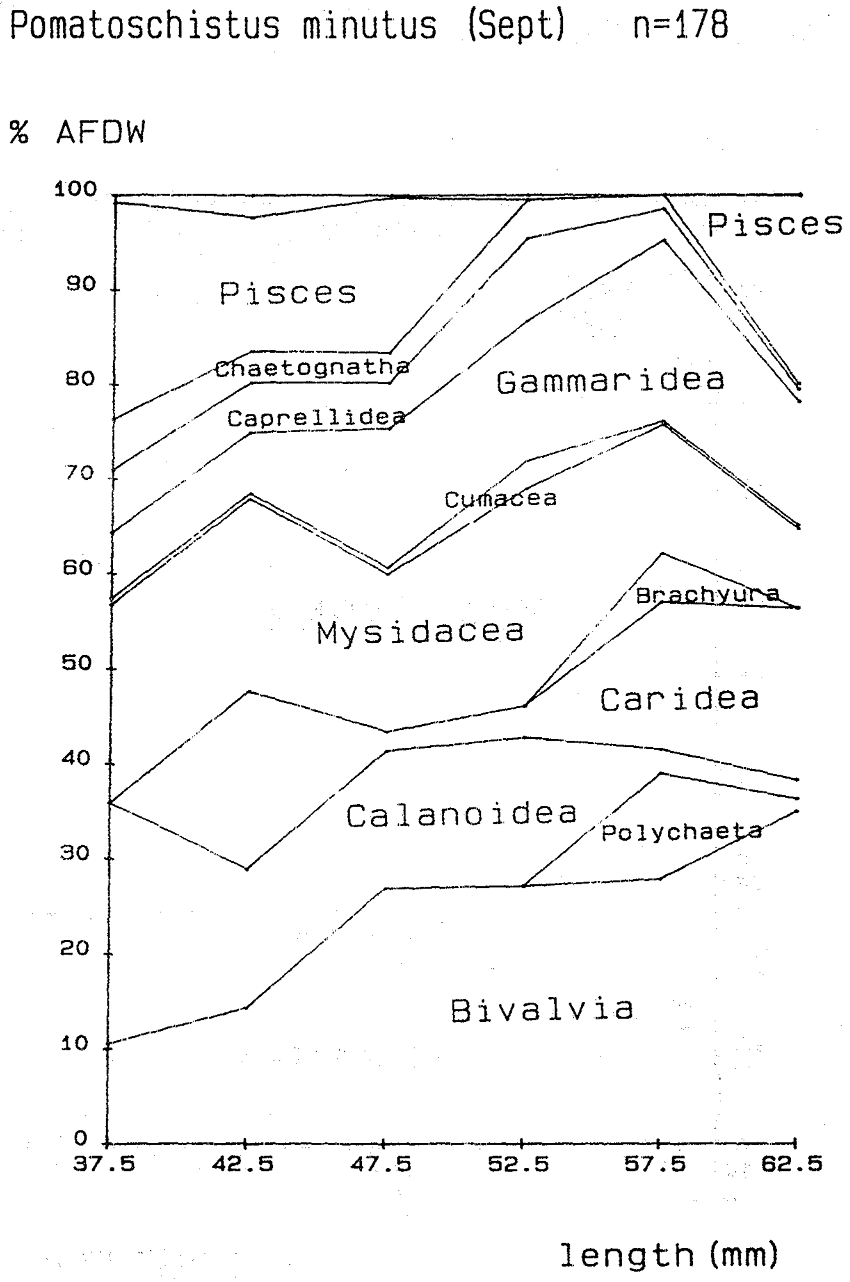

FIG 10. FOOD COMPOSITION IN PERCENTAGE AFDW FOR DIFFERENT SIZE CLASSES OF POMATOSCHISTUS MINUTUS

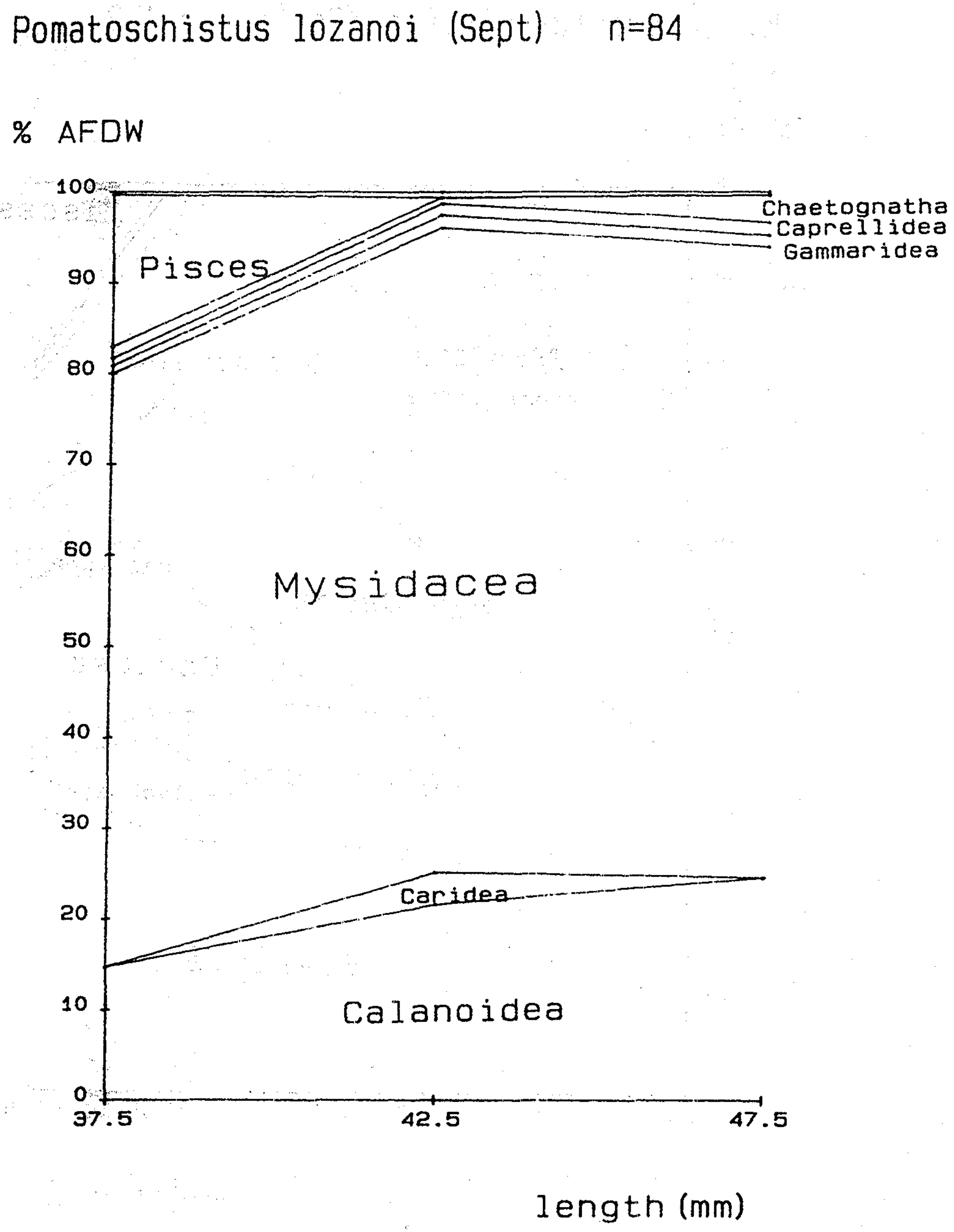

FIG 11. FOOD COMPOSITION IN PERCENTAGE AFDW FOR DIFFERENT SIZE CLASSES OF POMATOSCHISTUS LOZANOI

Ship	Date	PM:n=	dens	biom	*	PL:n=	dens	biom
062	17.05.84	68	6	2,6	*	174	40	7,3
062	13.06.84	13	3	1,3	*	235	40	8,2
062	20.07.84	138	15	1,6	*	479	40	15,1
062	17.08.84	513	100	21,7	*	222	50	11,3
062	28.09.84	817	175	57,0	*	217	25	4,2
062	30.10.84	1828	250	75,8	*	432	75	7,0
062	13.12.84	1494	250	72,4	*	114	30	6,2
BRW	18.04.85	202			*	730		
062	01.06.85	7			*	256		
062	09.08.85	612			*	206		
BRW	20.09.85	706			*	262		

TABLE 1. SAMPLING DATES, NUMBERS PER SPECIES, DENSITY AND BIOMASS

PM= Pomatoschistus minutus
PL= Pomatoschistus lozanoi
Densities in number per 1000 m^2
Biomass in mg AFDW per m^2

ASH FREE DRY WEIGHTS OF PREY SPECIES

Nematods: width * length 2 /1600000 = fresh weight
AFDW = 15% of fresh weight
source: Andrassy 1956

Bivalvia: ln AFDW = -4.052 + 2.817 ln length
source: Govaere 1978
siphons: log AFDW = 1.876 + .043 log length
n = 29; r = .80

Polychaeta:
Sthenelais boa: ln AFDW = -4.389 + 1.785 ln length
Eteone spec.: ln AFDW = -5.717 + 1.530 ln length
Anaitides spec.: ln AFDW = -5.882 + 1.674 ln length
Nephtys spec.: ln AFDW = -7.139 + 2.489 ln length
Polychaeta errantia indet cfr. Anaitides
source: Govaere 1978
Nereis spec.: log body weight = 3.3 * log jaw length + 1.57
source: Olive & Garwood 1981
Spionidae: ln AFDW = -6.030 + 1.831 ln length
Capitella capitata: ln AFDW = -6.354 + 2.051 ln length
Pectinaria koreni: ln AFDW = -6.918 + 2.689 ln length
Lanice conchilega: ln AFDW = -6.918 + 2.181 ln length
source: Govaere 1978
Sabellinae indet. cfr. Lanice

Calanoidea: .016 mg assigned value

Harpacticoids:
Longipedia minor, Canuella perplexa, Halectinosoma sarsi, Thompsonula hyaenae: .004 mg assigned value
all others: .002 mg assigned value
copepodites: 1/3 adult weight
source: R. Herman pers. comm.

Cirripedia: AFDW of an amphipod of the same length as the cirri, assigned value.
Cypris:.014 mg assigned value

Caridea: log AFDW = log .00046 + 3.321 log length
source: van Lissa 1977
zoea: .01 mg assigned value

Brachyura: log wet weight = -3.961 + 3.160 log carapaxbreadth; AFDW = 20% wet weight
source: Borremans 1982
Portunidae zoe: .01 mg assigned value
Portunidae megalopa: .015 mg assigned value

Mysidacea: ln AFDW = -4.422 + 1.924 ln length
source: Govaere 1978

Cumacea: ln AFDW = -6.078 + 2.525 ln length
source: Govaere 1978

Isopoda: cfr. amphipoda

Amphipoda:
Bathyporeia spec.: ln AFDW = -8.674 + 4.563 ln length
all others: ln AFDW = -6.958 + 3.225 ln length
source: Govaere 1978

Chaetognatha: .5 mg assigned value from Feigenbaum 1979

Pisces: total weights = somatic weight + gonad weight
Pomatoschistus minutus: log AFDW = -3.40976 + 3.460 log length; n = 191; r = .98
Pomatoschistus lozanoi: log AFDW = -3.40566 + 3.448 log length; n = 113; r = .97
Pomatoschistus spec. cfr P. minutus

TABLE 2. LENGTH TO AFDW RELATIONSHIPS
OF PREY SPECIES

P.minutus	Mean	Stand.Dev.	n
May 1984	55,3	5,31	68
June 1984	50,2	2,85	13
July 1984			
Yearcl. 0+	33,8	4,27	130
Yearcl. 1+	55,1	6,96	8
Aug 1984	44,7	4,57	513
Sept 1984	49,7	7,14	817
Oct 1984	48,5	7,10	1828
Dec 1984	49,1	7,13	1494
Apr 1985	47,4	5,86	207
June 1985	48,0	2,65	7
Aug 1985	40,5	4,78	612
Sept 1985	49,6	6,97	704

P.lozanoi	Mean	Stand.Dev.	n
May 1984	45,3	5,10	174
June 1984	44,8	4,29	235
July 1984	47,4	3,25	478
Aug 1984			
Yearcl. 0+	33,3	2,59	17
Yearcl. 1+	46,8	3,28	205
Sept 1984	41,4	5,61	217
Oct 1984	39,7	5,66	272
Dec 1984	40,4	6,02	114
Apr 1985	44,4	4,30	729
June 1985	43,6	4,45	256
Aug 1985	45,1	3,38	206
Sept 1985	34,7	6,14	253

TABLE 3. MEAN LENGTHS OF POMATOSCHISTUS MINUTUS AND P.LOZANOI PER SAMPLING DATE

P.minutus	Nem.	Biv.	P.E.	P.S.	Cal.	Harp.	Cirr.	Car.	Bra.	Mys.	Cum.	Iso.	Gam.	Cap.	Chae.	Pisc.	AFDW(mg)
MAY 1984																	
l 50-54 n=19	0,0	6,0	9,1	28,4	3,0			25,5		0,2	0,2		27,7	0,0	0,5		111,1
l 55-59 n=18		11,0	0,9	36,2	6,0	0,0		10,7		4,9	1,3		19,4	1,2	2,3	5,4	66,7
JULY 1984																	
l 30-34 n=38	0,0	0,1	2,6	16,6	2,4	0,3		28,9	0,2	40,4	0,1		0,4	8,0			14,3
l 35-39 n=46		2,2	0,4	6,0	4,1	0,2			0,2	12,5	1,0		4,8	33,5			19,6
AUG. 1984																	
l 45-49 n=30	0,0	0,3	0,8	39,7		0,0			0,1	5,2			8,3	45,6			18,8
SEPT. 1984																	
l 35-39 n=29	0,0	10,5		0,4	25,3	0,4	0,1			20,9	0,7		6,9	6,4	5,4	22,9	55,9
l 40-44 n=30	0,0	15,3	0,0	0,1	15,8	0,5	0,0	18,2	0,0	20,2	0,6		6,5	5,3	3,3	14,2	75,8
l 45-49 n=30	0,0	26,9		0,1	14,5	0,2	0,0	2,0		16,5	0,7	0,0	14,7	4,8	3,2	16,4	78,2
l 50-54 n=30	0,0	27,1	0,0	0,3	15,7	0,1	0,0	3,3	0,0	22,9	2,9		14,8	8,7	4,1		72,8
l 55-59 n=30		27,8	11,0	0,2	2,5	0,0		15,5	5,1	13,6	0,4	0,0	19,1	3,3	1,4		104,4
l 60-64 n=29		35,0	1,2	0,1	2,0	0,0	0,0	18,1	0,0	8,3	0,4	0,1	13,0	1,3	0,6	19,9	169,1
OCT. 1984																	
l 35-39 n=30			0,1	16,6	14,3	0,0				63,3	0,3		2,2	2,1	1,2		43,1
l 40-44 n=30			0,3	24,8	8,4	0,0				56,2	0,5		3,0	2,6	4,1		49,1
l 45-49 n=30		0,3	12,9	18,7	4,0	0,0	0,0	11,3		45,7	0,1		2,2	2,7	2,2		89,8

TABLE 4. FOOD COMPOSITION IN % AFDW FOR POMATOSCHISTUS MINUTUS

Nem= nematodes; Biv= bivalves; P.E.= errant polychaetes; P.S.= sedentary polychaetes
Cal= calanoids; Harp.= harpacticoids; Car.= caridean decapods; Bra.= brachyurans
Mys.= mysids; Cum.= cumaceans; Iso.= isopods; Gam.= gammaridean amphipods
Cap.= caprellids; Chae= chaetognaths; Pisc.= Pisces.

P.lozanoi	Nem.	Biv.	P.E.	P.S.	Cal.	Harp.	Car.	Bra.	Mys.	Cum.	Iso.	Gam.	Cap.	Chae.	Pisc.	AFDW(mg)
MAY 1984																
l 45-49 n=30	0,0			0,7	21,1	0,0	1,9		11,4	0,2		23,8		2,5	40,8	78,9
l 50-54 n=21			8,1	0,5	15,7	0,0	9,5		12,5	0,2		52,4	0,9			42,2
JULY 1984																
l 40-44 n=30		0,0		2,7	0,3		2,9		69,4	0,1		0,5	0,2	0,6	23,3	83,7
l 45-49 n=30				0,7	0,3	0,0	7,0		49,0			0,2	0,1		42,7	93,7
AUG. 1984																
l 45-49 n=30				95,8	0,1	0,0						3,6	0,6			60,3
SEPT. 1984																
l 35-39 n=30					14,7	0,0	0,0	0,0	65,5	0,1	0,0	1,0	0,7	1,3	16,7	76,7
l 40-44 n=30		0,2		0,0	21,5	0,0	3,5		71,0	0,4	0,0	1,4	1,3	0,7		74,8
l 45-49 n=24		0,1			24,5	0,0		0,1	69,5	0,2	0,0	1,3	1,5	2,9		67,8
OCT. 1984																
l 35-39 n=30			0,6		7,1	0,0	1,5		88,5	0,3		0,1	0,0	2,0		102,6
l 40-44 n=30			0,1	0,[illegible]	2,7	0,0	0,3		94,8	0,1		0,0	0,1	1,3		114,0
l 45-49 n=21					2,5	0,0			97,2	0,1		0,2	0,0			127,8

TABLE 5. FOOD COMPOSITION IN % AFDW FOR POMATOSCHISTUS LOZANOI

Nem.= nematodes; Biv.= bivalves; P.E.= errant polychaetes; P.S.= sedentary polychaetes
Cal.= calanoids; Harp.= harpacticoids; Car.= caridean decapods; Bra.= Brachyurans
Mys.= mysids; Cum.= cumaceans; Iso.= isopods; Gam.= gammaridean amphipods
Cap.= caprellids; Chae.= chaetognaths; Pisc= Pisces.

TABLE 6. SYSTEMATIC LIST OF FOOD ORGANISMS IN STOMACHS

	P.min	P.loz
Phylum NEMATODA		
Sabatieria hilarula (De Man, 1922)	+	-
Mesacanthion spec.	+	-
Enoplidae spec.	+	+
Leptolaimidae spec.	+	-
Nematoda spec.	+	-
Phylum MOLLUSCA		
Cl.Bivalvia		
Cerastoderma edule (Linnaeus, 1758)	+	-
Abra alba (Wood, 1802)	+	-
Tellina fabula (Gronovius, 1781)	+	-
Spisula spec.	+	-
Bivalvia indet.	+	+
Bivalvia siphons	+	+
Phylum ANNELIDA		
Cl.Polychaeta		
O.Errantia		
Sthenelais boa (Johnston, 1839)	+	-
Eteona spec.	-	+
Anaitides mucosa (Oersted, 1843)	+	-
Anaitides groenlandica (Oersted, 1842)	+	-
Anaitides spec.	+	-
Nereis spec.	+	-
Nephtys hombergii (Savigny, 1818)	+	+
Nephtys spec.	+	-
Polychaeta Errantia indet.	+	-
O.Sedentaria		
Spionidae spec.	+	-
Capitella capitata (Fabricius, 1780)	+	-
Pectinaria koreni (Malmgren, 1865)	+	-
Lanice conchilega (Pallas, 1766)	+	+
Lanice tentacle crowns	+	+
Sabellinae indet.	+	-
Phylum ARTHROPODA		
Subph.Crustacea		
Cl.Ostracoda		
Ostracoda indet.	+	+
Cl.Copepoda		
O.Calanoidea		
Temora longicornis (Muller, 1792)	+	+
Centropages hamatus (Lilljeborg, 1853)	+	+
Calanoidea indet.	+	+

	P.min	P.loz
O.Harpacticoidea		
Longipedia minor (T.& A. Scott, 1893)	+	-
Canuella perplexa (T.& A. Scott, 1893)	+	-
Halectinosoma propinquum (T.& A.Scott, 1894)	+	-
Halectinosoma sarsi (Boeck, 1872)	+	-
Pseudobradya beduina (Monard, 1935)	+	-
Euterpina acutifrons (Dana, 1884)	+	+
Microarthridion littorale (Poppe, 1881)	+	+
Thompsonula hyaenae (I.C. Thompson, 1889)	+	+
Harpacticus littoralis (Sars, 1910)	+	-
Tisbe furcata (Baird, 1837)	+	+
Tisbe spec.	+	+
Altheuta interrupta (Goodsir, 1845)	+	+
Dactylopodia tisboides (Claus, 1863)	+	-
Dactylopodia vulgaris (Sars, 1905)	+	+
Ameira parvula (Claus, 1866)	+	-
Cl.Cirripedia		
Cirripedia indet. cirri	+	-
Cl.Malacostraca		
O.Decapoda		
InfraO.Caridea		
Hippolyte varians (Leach, 1814)	+	+
Crangon crangon (Linnaeus, 1758)	+	+
Pontophilus trispinosus (Hailstone, 1838)	+	+
Caridea zoe	+	+
InfraO.Brachyura		
Carcinus maenas (Linnaeus, 1758)	+	-
Liocarcinus spec.	+	-
Portunidae zoe	+	+
Portunidae megalopa	+	+
O.Mysidacea		
Gastrosaccus spinifer (Goes, 1864)	+	+
Schistomysis spiritus (Norman, 1860)	+	+
Schistomysis spec.	+	+
Mesopodopsis slabberi (van Beneden, 1861)	+	-
O.Cumacea		
Cumopsis goodsiri (van Beneden, 1861)	+	-
Pseudocuma longicornis (Bate, 1858)	+	+
Diastylis rathkei (Kroyer, 1841)	+	-
Diastylis lucifera (Kroyer, 1841)	+	+
Diastylis spec.	+	+

	P.min	P.loz
O. Isopoda		
Eurydice pulchra (Sars, 1899)	+	+
Idotea linearis (Bate & Westwood, 1868)	+	-
O. Amphipoda		
SubO. Gammaroidea		
Orchomene nana (Kroyer, 1864)	-	+
Amphilochus neapolitanus (Della Valle, 1893)	+	-
Stenothoe marina (Bate, 1856)	+	-
Gammarus crinicornis (Stock, 1966)	+	+
Gammarus spec.	+	+
Maera grossimana (Montagu, 1808)	+	-
Melita obtusata (Montagu, 1813)	+	-
Bathyporeia elegans (Watkin, 1938)	+	+
Bathyporeia guilliamsoniana (Bate, 1856)	-	+
Bathyporeia spec.	+	+
Urothoe poseidonis (Reibisch 1905)	+	-
Perioculodes longimanus (Bate & Westwood, 1868)	-	+
Calliopius laeviusculus (Kroyer, 1838)	+	-
Pontocrates arenarius (Bate, 1858)	+	+
Atylus falcatus (Metzger, 1871)	+	-
Atylus swammerdami (Milne-Edwards, 1830)	+	+
Ampithoe rubricata (Montagu, 1808)	-	+
Aora typica (Kroyer, 1845)	+	-
Gammaropsis nitida (Stimpson, 1853)	-	+
Microprotopus maculatus (Norman, 1867)	+	+
Jassa falcata (Montagu, 1808)	+	-
SubO. Caprellidea		
Pariambus typicus (Stebbing, 1888)	+	+
Subph. Uniramia		
Cl. Insecta		
Diptera indet.	+	-
Phylum CHAETOGNATHA		
Sagitta spec.	+	+
Phylum CHORDATA		
Cl. Pisces		
Pomatoschistus minutus (Pallas, 1770)	+	+
Pomatoschistus lozanoi (De Buen, 1923)	+	+
Pomatoschistus spec.	+	+

	Oxy
Aug 40-44mm	0,44
Sept 35-39mm	0,56
Sept 40-44mm	0,44
Sept 45-49mm	0,38
Oct 35-39mm	0,72
Oct 40-44mm	0,62
Oct 45-49mm	0,49

TABLE 7. RENKONEN SIMILARITIES FOOD POMATOSCHISTUS MINUTUS-LOZANOI

BENTHIC PREY	EPIBENTHIC PREY	HYPERBENTHIC-PELAGIC PREY
NEMATODA	POLYCHAETA ERRANTIA	CALANOIDEA
BIVALVIA	EPIBENTHIC HARPACTICOIDA	PELAGIC HARPACTICOIDEA
POLYCHAETA SEDENTARIA	CARIDEA	MYSIDACEA
OSTRACODA	CUMACEA	PELAGIC ISOPODA
CIRRIPEDIA	GAMMAROIDEA	CHAETOGNATHA
BRACHYURA	EPIBENTHIC ISOPODA	PISCES
CAPRELLIDEA		

TABLE 8. PREY CATEGORIES CONVERSION TO FOOD NICHE CATEGORIES

P.minutus	BENTHIC	EPIBENTH	HYPERBENTH PELAGIC
May 50-59mm n= 37	40	51	9
July 30-39mm n= 84	54	18	28
Aug 45-49mm n= 30	86	9	5
Sept 35-49mm n= 89	24	18	58
Sept 35-64mm n= 178	32	28	40
Oct 35-49mm n=90	23	15	63

P.lozanoi	BENTHIC	EPIBENTH	HYPERBENTH PELAGIC
May 45-54 mm n= 51	1	41	57
July 40-49mm n=60	2	5	93
Aug 45-49mm n= 30	96	4	0
Sept 35-49mm n= 84	1	3	96
Oct 35-49mm n= 81	0	1	99

TABLE 9. PERCENTAGE ASH FREE DRY WEIGHTS OF PREY IN FOOD NICHE CATEGORIES