*Mar. Life 1994 - Vol.* ***4*** *(2) : 45-57*

# Trophic ecology of gurnards (Pisces: Triglidae) in the Central Mediterranean Sea

## *Écologie trophique des grondins (Pisces : Triglidae) dans la mer Méditerranée centrale*

Francesco Colloca* , Gian Domenico Ardizzone**, Maria Flavia Gravina**
* Soc. Coop. Si.R.P.A.B., C.da Piano del Greco, 85050 Tito (PZ)
**Dipartimento di Biologia Animale e dell'Uomo, Università "La Sapienza", Viale dell'Università, 32 - 00185 Roma, Italy

***Key-words:*** *Triglidae, feeding habits, trophic overlap, depth distribution*

***Mots clés :*** *Triglidae, régime alimentaire, recouvrement trophique, distribution bathymétrique*

## *ABSTRACT*

*Colloca F., G.D. Ardizzone, M.F. Gravina, 1994 - Trophic ecology of gurnards (Pisces: Triglidae) in the Central Mediterranean Sea.* Mar. Life, **4** (2) : 45-57.

*In the Central Tyrrhenian Sea (Latium coasts) the most common gurnard species are* Trigla lucerna, Lepidotrigla cavillone, Aspitrigla cuculus *and* Aspitrigla obscura. *These fish species inhabit the soft bottoms down to 270 m of depth and show a wide depth range of overlap. The fish diet has been examined in relation to the sampling season and body size in order to examine the main ontogenetic changes and the food and feeding relationships between species. The four species showed similar feeding habits based upon groups of benthic organisms with close ecological features. Fish body size and depth distribution were the main factors affecting the kind and size of prey ingested, and consequently the levels of trophic overlap among the gurnard species. During growth, the fish diet changed with the capture of bigger sized prey and with the replacement of food categories or bathymetric migration. These changes in diet and feeding habits increased when gurnards reached a critical size. Trophic partitioning does not appear to play an important role in resource use among gurnards. Evidence of food partitioning was only apparent for some size classes with high levels of spatial overlap in the study area. The bathymetric distribution of gurnards was consequently the most important mechanism allowing coexistence of the four gurnard stocks examined.*

## *RÉSUMÉ*

*Colloca F., G.D. Ardizzone, M.F. Gravina, 1994 - [Écologie trophique des grondins (Pisces : Triglidae) dans la mer Méditerranée].* Mar. Life, **4** (2) : 45-57.

*Dans la mer Tyrrhénienne centrale (Côte de Latium), les espèces les plus communes de grondins sont* Trigla lucerna, Lepidotrigla cavillone, Aspitrigla cuculus *et* Aspitrigla obscura. *Ces espèces de poisson habitent les fonds meubles jusqu'à 270 m de profondeur et montrent un fort recouvrement de leur spectre alimentaire. Le régime alimentaire des poissons a été étudié en fonction de la saison d'échantillonnage et selon leur taille pour examiner les principaux changements ontogéniques et les relations alimentaires entre espèces. Les quatre espèces montrent des habitudes alimentaires semblables basées sur des groupes d'organismes benthiques présentant des caractéristiques écologiques voisines. La taille des poissons et leur distribution bathymétrique sont les principaux facteurs qui influencent le type et la dimension des proies ingérées et, par conséquent, les niveaux de recouvrement de l'alimentation parmi les espèces étudiées. Pendant la croissance, le régime des poissons change, soit par la capture de proies plus grandes et le remplacement de catégories alimentaires, soit par leur migration bathymétrique. Cette évolution alimentaire devient rapide quand les grondins arrivent à une dimension critique. La séparation de l'alimentation ne joue pas un rôle important dans l'utilisation des ressources parmi les grondins. Une séparation trophique a été observée uniquement pour quelques classes de taille qui présentent une forte superposition spatiale. La distribution bathymétrique des grondins apparaît comme le mécanisme le plus important qui permet la coexistence des quatre stocks de grondins examinés.*

# INTRODUCTION

The gurnards or searobins are marine nectobenthonic fishes found mainly in tropical and temperate seas. In the Mediterranean Sea and in N-E Atlantic Ocean, 5 genera and 8 species occur (Hureau, 1986). During recent years, there have been several studies of the biology of the species. Papaconstantinou ( 1981, 1982a, 1982b, 1983, 1984, 1985) investigated the stock structure, reproductive biology, growth and depth distribution of gurnards in Greek Seas; Priol (1932) and Baron (1985a, 1985b) studied the biology of the species living along the French Mediterranean coasts and Brittany coasts respectively.

The few studies that have focused on the diet of the gurnards in the Mediterranean Sea (Reys, 1960; Froglia, 1976; Labarta, 1977; Moreno and Matallanas, 1983) reported a common pattern of feeding habits in the species. According to Ross (1977), who studied the gurnard species of the Gulf of Mexico, *"they are a part of a feeding guild of demersal fishes which utilize primarly epibenthic and infaunal invertebrates"*. In the past few years, there has been an increase in research on nectobenthonic and benthonic marine fish communities (Hacunda, 1981; Targett, 1981; Gladfelter and Johnson, 1983; Bell and Harmelin-Vivien, 1983; Laroche and Idelhaj, 1988), and many of the recent studies on fish communities have focused on increasing our understanding of the mechanisms allowing the coexistence of fish species. For the Mediterranean Sea, where knowledge on this question is sketchy, an important study is that by Macpherson (1981) who examined food and habitat overlap among demersal fishes on Spanish soft-bottoms between 200 and 800 m. In this fish community, diet is the most important factor contributing to the segregation of fish species. Other works have described resource partitioning among scorpaenid fishes (Harmelin-Vivien *et al.*, 1989) and goatfish (Golani and Galil, 1991) in seagrass beds and soft bottom respectively.

As Pike *et al.* (1977) noted, trophic structures are an essential ingredient of community stability. Thus predation, as determined by the foraging behaviour of all animals in a community, is the key feature of the community structure.

Among fishes, continuous growth implies continuous change with size of their food and habitat use patterns. Hence it can be argued that fish species simultaneously occupy several niches (Werner and Gilliam, 1984; Ross, 1986). According to Werner and Gilliam (1984), it seems reasonable to hypothesize that niche shift occurs in order to maximize absolute growth rates or surplus energy at each size. The change in feeding patterns during growth can be rapid (Tyler, 1972) and it can be related to particular phases of the biological cycle (Ross, 1978). In fish assemblages, generally strongly size-structured, a variety of interactions may potentially occur between different life history stages of species (Ross, 1986). It is, therefore, interesting to investigate whether there are critical stages in the competition for the utilization of food resources or a continuum modulation of relationships which occurs during the ontogenic development of the species (Harmelin-Vivien *et al.*, 1989).

The purpose of the present study is to examine the diet and feeding relationships between four triglid species in the Central Tyrrhenian Sea: *Trigla lucerna, Lepidotrigla cavillone, Aspitrigla cuculus, Aspitrigla obscura*. The specific objectives are: 1- to investigate their feeding habits; 2- to examine how predator species are distributed along the resource axis of location, food type and food size.

# MATERIAL AND METHOD

### Study area and sampling design

Demersal fish samples were collected in the Central Tyrrhenian Sea (Western Italy).

The area examined of 1.476 square nautical miles was subdivided into depth zones (strata). The depth strata were separated by the 50, 100, 200, 450, 700 meter isobaths. Each stratum was subdivided into 3 square nautical mile areas, several of which were randomly chosen for investigation (stratified random sampling design).

Two research cruises were carried out each year in 1985, 1986, 1987 in the months of May and September, for a total of 164 hauls. The duration of each haul was of one hour and the Italian type trawl-net employed had a code mesh-size of 24 mm (stretched size).

### Fish and data analysis

For each research cruise the gurnards collected were identified and counted, and standard length (S.L.) and weight were measured to the nearest 0.5 cm and 1 g respectively for each specimen. The relative abundance of 1 cm S.L. size groups of each searobin species for every 25 m depth interval was considered. Stomach contents only were analyzed to study the diet in order to reduce errors resulting from the differential digestion rates of the prey along the digestive tract (Berg, 1979). For each fish dissected stomach contents were blotted dry with absorbent paper, and the total wet weight was recorded to the nearest 0.001 g. A binocular microscope was used to analyze stomach contents and dietary components were identified at the species level whenever possible. The prey was sorted by taxa from each 10 mm size class of gurnards and a random sample of each prey was measured to the nearest 0.5 mm along the axis of the greatest dimension. A criterion for the minimum sample size (t) was established by plotting the cumulative number of prey category, found in one fish species, against a randomly pooled number of stomachs (K). The minimum number of stomachs necessary was estimated as the point at which the curve levelled out (Hurtubia, 1973). All comparisons were based on sample with K > t. The importance of the different food types in the diet of each species was calculated in terms of: the percentage frequency of occurrence (F) of a given food type in the number of stomachs examined which contained food; the percentage number (CN) of a given food type in the total number of food types consumed; the mean number of individuals per stomach in each food category (A) (Hyslop, 1980). The fishes collected were divided into size classes according to the season in order to analyze the main changes of the diet in relation to the recruitment and growth processes. The main differences in the diet during fish growth were expressed by means of the average number of prey per stomach (Nm), average wet weight of stomach contents (Wm), frequency of occurrences of food type and prey size. To provide information on length at first sexual maturity the shortest 1-cm length group in which more than 50 % of the sample was sexually mature (Elder, 1976) was identified for females of *Aspitrigla cuculus, A. obscura* and *L. cavillone.* To evaluate the similarity of the depth distribution and diet among the fish size classes, the Two Way Indicator Species Analysis (Twin Span), was carried out (Hill, 1979). Depth distribution similarities were investigated using the percentage of abundance of each gurnard size class collected every 25 m of depth. Comparisons of size classes by prey kind were made using the following taxa : Mysidae, *Lophogaster typicus*, Amphipoda, Decapoda natantia, Decapoda reptantia, Megalopae larvae, Cephalopoda, Teleostea (The mysid *Lophogaster typicus* was considered as a separate taxon due to the fact that its dimension was significatively greater than that of the other mysid species preyed by gurnards). Prey size similarities among the gurnard size classes were based on 2 mm intervals of prey sizes for prey less than 5 mm and on 5 mm for prey larger than 10 mm.

The Factorial Analysis of Correspondence (Benzécri *et al.*, 1973) was carried out on prey frequency of occurrence data (taxa are listed in Table II) in order to evaluate the pattern of the diet of each gurnard species and to stress the main factors affecting trophic resource, partitioning among the triglid stocks examined.

## RESULTS

During the six research cruises carried out 3509 individuals were collected: 311 of *T. lucerna,* 294 of *A. cuculus,* 164 of *A. obscura* e 2740 of *L. cavillone.*

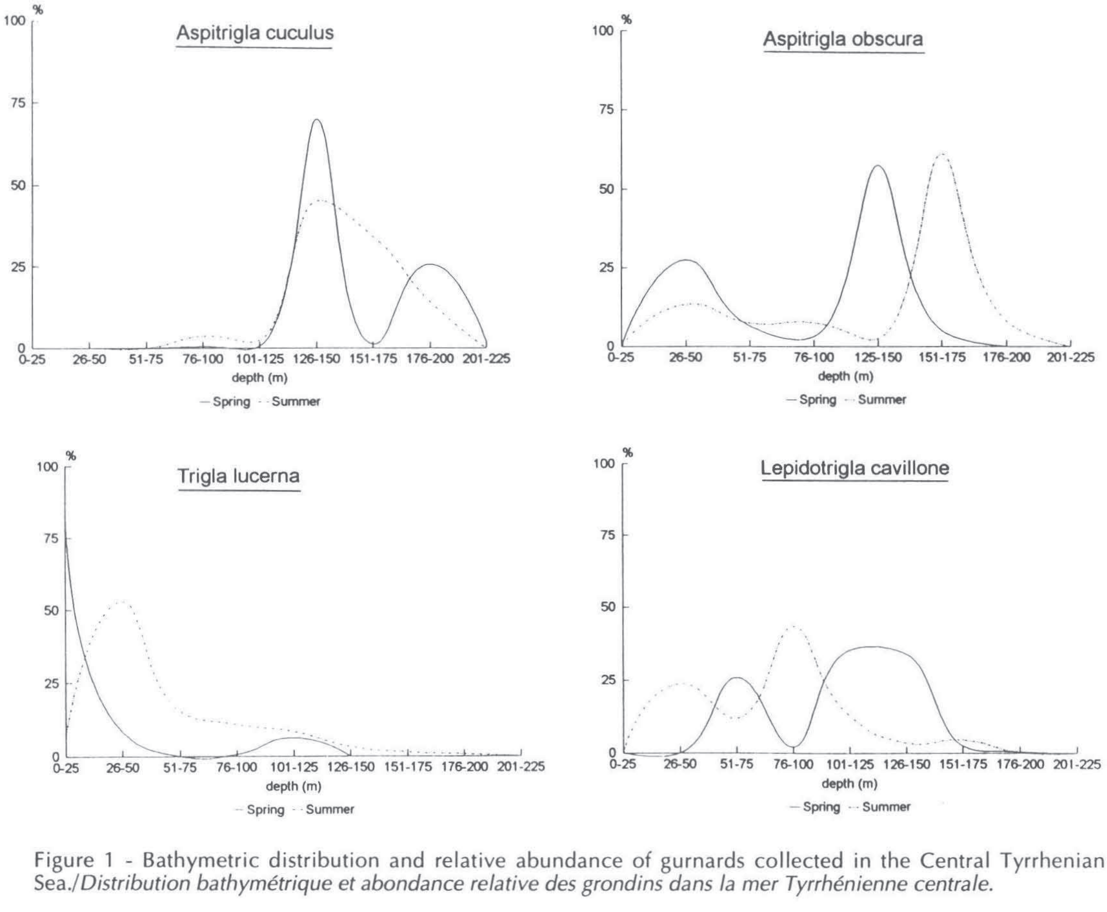


Figure 1 - Bathymetric distribution and relative abundance of gurnards collected in the Central Tyrrhenian Sea./*Distribution bathymétrique et abondance relative des grondins dans la mer Tyrrhénienne centrale.*

## Depth distribution

All the species sampled had a wide depth distribution except for *A. cuculus* which exhibits a certain degree of habitat restriction in the study area (Figure 1). Down to 150 m depth, *L. cavillone* showed the greatest relative abundance, whereas the most abundant searobin between 150 and 200 m was *A. cuculus*. *A. obscura* was collected widely between 20-170 m. *T. lucerna* was the coastal species most abundant in spring time within the 25 m isobath, rarely found deeper than 100 m. Each stock sampled showed a different seasonal depth range linked to the dynamics of its stock structure (Figures 1, 2). A significant positive relationship between increasing size and increasing depth of capture was found for all the species (*T. lucerna* r = 0.62, n = 127, P = 0.0001; *L. cavillone* r = 0.4, n = 112, P = 0.0003; *A. obscura* r = 0.76, n = 38, P = 0.0001) except for *A. cuculus* in spring time. In the study area nursery grounds of *T. lucerna* and *L. cavillone* were identified in shallow depths: inshore soft bottoms around 10 and 30-40 m respectively.

## Feeding habits

421 specimens of *T. lucerna*, *A. cuculus*, *A. obscura* and *L. cavillone* were sampled for the study of feeding habits (Table I). The Triglidae studied fed on crustaceans, fishes and cephalopods and their diet was found to vary both in composition and frequency of occurrence of the main food categories according to the season (Table II).

## Seasonal diet variation

The sampled stock of *T. lucerna* was composed basically of juveniles born the same year (Figure 2). In spring, they fed mainly on the crustacean *Gastrosaccus sanctus* (F = 81, CN = 76.7), the most abundant prey per stomach (A = 9.2), on *Liocarcinus vernalis* (F = 35.1, CN = 4.9) and on *Philocheras monacanthus* (F = 35.1, CN = 8.0). In summer, a clear diversification of the food preferences to larger size prey was observed in relation with the size and growth of juveniles which also have a wider depth range. Mysids became less abundant (F = 7.2, CN = 8.0) owing to a wider predation on brachyurans (F = 51.5, CN = 33.1), such as *Goneplax rhomboides* (F = 31.2, CN = 11.8) and *Liocarcinus pusillus* (F = 12.2, CN = 8.8), and fishes such as *Callyonimus risso* (F = 20.7) and Gobiidae (F = 9.9) (Table II).

*L. cavillone* is a crustacean feeder (F = 100), mysids representing over 90 % by number of its prey in spring time: the most important prey was *Gastrosaccus normani or/and G. spinosus* (F = 71, Cn = 62.4) and *Lophogaster typicus* (F = 63.3, CN = 22.6). In summer, the juveniles of the same year (4-5 cm S.L.) appeared on the coastal soft bottom. The trophic niche of the species was wider due to the juvenile predation upon new food items. In addition to mysids this species ingested amphipods (F = 68.0, CN = 25.1) belonging to the Oedicerotidae (*Westvoodilla rectirostris* (F = 32.0, CN = 9.6) and *Monoculodes sp.* (F = 14.3, CN = 3.0), Crangonidae shrimps (F = 42, CN = 10.6) and megalops larvae (F = 39.3, CN = 16.9) (Table II). The size of

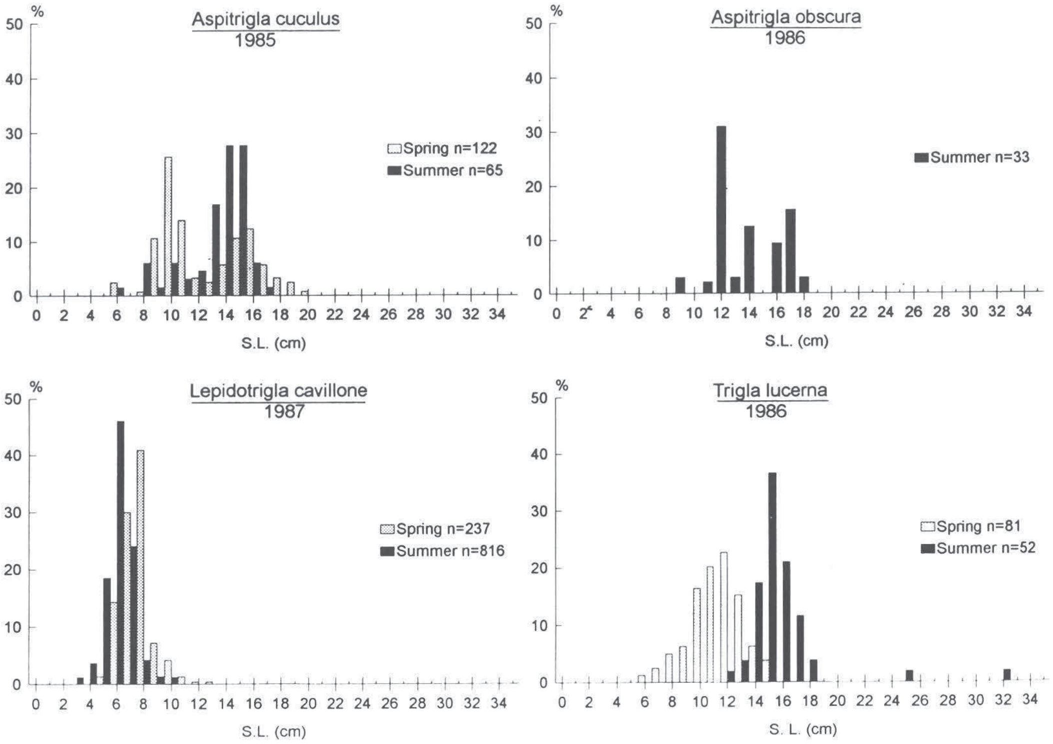


Figure 2 - Seasonal length frequency distribution of four gurnard species./*Distribution saisonnière des fréquences de longueur de quatre espèces de grondins.*

Table I - Data on Central Mediterranean gurnards examined in this study in Spring (Sp) and Summer (Su)./*Données sur les grondins étudiés au printemps et en été en mer Méditerranée centrale.*

| | *T. LUCERNA* | | *L. CAVILLONE* | | *A. CUCULUS* | | *A. OBSCURA* |
|---|---|---|---|---|---|---|---|
| | Sp | Su | Sp | Su | Sp | Su | Su |
| N° of fish examined | 43 | 92 | 80 | 61 | 26 | 44 | 75 |
| % of empty stomachs | 9,3 | 7,4 | 11,8 | 16,3 | 26,9 | 18,4 | 8 |
| Mean number of prey per stomach | 8,13 | 4,16 | 7,03 | 9,7 | 9,3 | 4,05 | 8,1 |
| Mean weigth of stomach content | 0,34 | 0,88 | 0,16 | 0,095 | 0,44 | 1,14 | 0,48 |
| Size range (S.L. cm) | 6-24.5 | | 4-10 | | 8.5-19.5 | | 11-18 |
| Depth range in the study area | 8-180 | | 36-194 | | 115-230 | | 20-165 |

prey decreased in relation with the reduction of the stomach content weight and the increase of the mean number of prey per stomach (Table I).

*A. cuculus* fed mainly on mysids and cephalopods. Feeding habits exhibited only slight seasonal variation regarding the principal prey. *Lophogaster typicus* (F > 60) and the Cephalopods Sepiolidae (F > 30) were the main prey in the two seasons. Shrimps decreased in importance in summer, *Leptomysis gracilis* was preyed in spring time with a low occurrence (F = 15.7) but with a higher number of specimens per stomach (A = 30.3) (Table II ). Juveniles were present in the two seasons with different relative abundances. Adults and juveniles did not show a clear spatial separation.

The feeding habits of *A. obscura* were considered only in summer because of the low number of specimens caught in spring time. The diet of this gurnard was more diversified than the diet of the other three studied species. Among the 24 different taxa found, the main prey were the decapods natantia (F = 72.6, CN = 18.6) and reptantia (F = 46.2, CN = 23.4) belonging to the Crangonidae (*Philocheras bispinosus, Pontocaris cathapracta)* and Portunidae (*Liocarcinus pusillus)* and mysids of the *Gastrosaccus* and *Lophogaster* genera (Table II).

### Diet variation with size

With the increase in size each searobin species showed a reduction of average prey number (Nm) and an increasing in stomach content weight (Wm) and prey size (Tables III and IV). Fish size showed a highly significant correlation with Wm (*T. lucerna* r = 0.60, n = 102, P = 0.0001; *L. cavillone* r = 0.25, n = 106, P = 0.0009; *A. obscura* r = 0.65, n = 38, P = 0.0001) and a negative and significant correlation with Nm (*T. lucerna* r = -0.31, n = 127, P = 0.0004; *L. cavillone* r = -0.31, n = 112, P = 0.0009; *A. obscura* r = -0.48, n = 62, P = 0.0001; *A. cuculus* r = -0.29, n = 46, P = 0.05 ). The mysids contributed most to the average number of prey per stomach (*T. lucerna* r = 0.97, n = 41, P = 0.0001; *L. cavillone* r = 0.74, n = 81, P = 0.0001; *A. cuculus* r = 0.96, n = 16, P = 0.0001; *A. obscura* r = 0.48, n = 10, P = 0.0001). Table III shows a decrease in the occurrence of mysids with size growth except for *L. cavillone* in whose diet mysids were fundamental in every size class. This pattern also occurred in amphipods and in megalopae larvae, preyed upon by smaller size classes of *L. cavillone* and *A. obscura* (Table IIIb-c). The increase in size of *L. cavillone* corresponded to higher predation of *L. typicus* (Table IIIb). A significant correlation between the depth of fish capture and the frequency of occurrence of *L. typicus* (r = 0.67. n = 18. P = 0.002) showed that this finding was due to the fish migration in relation with the fish growth.

An abrupt diet change with size occurred in *T. lucerna, A. obscura* and *L. cavillone* (Table IIIa-b-c). In the first species, the change occurred between 14 and 16 cm S.L. with a consistent increase in Wm and a decrease in Nm. The diet of *A. obscura* changed over 13 cm S.L. because of an increase in predation of *L. typicus* and cephalopods with regard to the amphipods, megalops and crabs (Table IIIc). A change in food habits of *L. cavillone* occurred between 6 and 7.9 cm S.L.: the 50 % growth of Wm was in correlation with the increasing occurrence of *L. typicus* and shrimps and with the decrease of megalops and amphipods (Table IIIb). The dietary pattern of *A. cuculus* was characterized by the high increase in the mean prey size and the decrease in Nm in the fishes over 15 cm S.L. (Table IIId ). The average standard deviation in prey size generally increased with fish size (Table IV ). This implies that with growth, gurnards could consume larger prey but they continued to capture smaller-sized prey (Figure 3). The mean number of prey species per stomach was generally less than three (Table IV).

Depth migration of gurnards linked to the increase in body size brought about the replacement of prey species by other congeneric species showing similar size and ecological features. For example, we observed a replacement of *Gastrosaccus sanctus* by *Gastrosaccus sp., Liocarcinus vernalis* by *L. pusillus, Philocheras monacanthus* by *P. bispinosus, Callyonimus risso* by *C. maculatus.*

### Trophic and spatial partitioning

The interrelationships among fish size classes were analyzed according both to depth distribution

Table II - Seasonal diet of four gurnard stocks in the Central Tyrrhenian Sea. F, % frequency of occurrence of prey; CN, % of total prey number ; A, mean numerical abundance of prey per stomach. * marks the taxa used in the F.A.C./*Régime alimentaire saisonnier de quatre stocks de grondins en mer Tyrrhénienne centrale. F, pourcentage d'occurrence des proies, CN, pourcentage du nombre total de proies ; A, abondance numérique moyenne des proies par estomac. * montre les taxa utilisés pour la A.F.C.*

| | | *T. LUCERNA* | | | | | | *L. CAVILLONE* | | | | | | *A. CUCULUS* | | | | | | *A. OBSCURA* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | SPRING | | | SUMMER | | | SPRING | | | SUMMER | | | SPRING | | | SUMMER | | | SUMMER | | |
| | | F % | CN % | A | F % | CN % | A | F % | CN % | A | F % | CN % | A | F % | CN % | A | F % | CN % | A | F % | CN % | A |
| | **CRUSTACEA** | 97,4 | 95,8 | 9,9 | 70,6 | 64,3 | 3,0 | 100,0 | 100,0 | 7,0 | 100,0 | 99,6 | 9,6 | 89,4 | 94,8 | 6,5 | 86,1 | 76,6 | 4,8 | 96,0 | 98,8 | 8,1 |
| | Ostracoda n.i. | | | | | | | | | | | | | | | | | | | 6,7 | 2,7 | 4,0 |
| | Copepoda n.i. | | | | | | | 1,0 | 0,2 | 1,0 | 2,4 | 2,5 | 1,0 | | | | | | | | | |
| | Mysidacea | 81,0 | 76,7 | 9,2 | 7,2 | 8,0 | 3,9 | 98,0 | 93,1 | 7,8 | 83,4 | 44,3 | 5,3 | 84,2 | 88,0 | 9,6 | 66,6 | 68,8 | 4,4 | 43,1 | 49,4 | 12,0 |
| * | Gastrosaccus sanctus | 81,0 | 76,7 | 9,2 | | | | | | | 18,7 | 5,2 | 2,6 | | | | | | | | | |
| * | Gastrosaccus sp. | | | | 6,4 | 7,4 | 4,6 | 71,0 | 62,4 | 5,3 | 55,6 | 34,0 | 5,9 | | | | 11,1 | 7,1 | 2,7 | 29,4 | 42,7 | 9,2 |
| * | Anchialina agilis | | | | | | | 2,6 | 2,2 | 2,1 | 7,7 | 0,9 | 1,2 | | | | 2,7 | 0,7 | 1,0 | | | |
| * | Siriella clausi | | | | | | | 1,0 | 0,2 | 1,0 | | | | | | | | | | | | |
| * | Siriella norvegica | | | | | | | 1,0 | 0,2 | 1,0 | | | | | | | | | | | | |
| * | Erythrops microps | | | | | | | 1,0 | 0,2 | 1,0 | | | | | | | | | | | | |
| * | Leptomysis gracilis | | | | | | | | | | | | | 15,7 | 51,7 | 30,3 | | | | 0,4 | 0,5 | 13,0 |
| * | Leptomysis sp. | | | | | | | | | | | | | | | | 2,7 | 1,3 | 2,0 | | | |
| * | Lophogaster typicus | | | | 2,1 | 0,6 | 1,0 | 63,3 | 22,6 | 2,2 | 5,5 | 0,6 | 1,0 | 68,0 | 28,0 | 3,9 | 63,8 | 52,9 | 3,5 | 11,5 | 4,2 | 3,9 |
| | Mysidacea n.i. | | | | | | | | 5,4 | | | 4,6 | | | 7,2 | | | 6,8 | | | 2,0 | |
| | Amphipoda | 10,8 | 1,2 | 1,5 | 2,3 | 1,1 | 1,4 | 6,2 | 4,4 | 4,3 | 68,0 | 25,1 | 3,6 | | | | | | | 24,0 | 4,0 | 1,7 |
| * | Westvoodilla rectirostris | | | | | | 2,0 | 1,3 | 4,0 | 32,0 | 9,6 | 3,6 | | | | | | | 3,1 | | 0,6 | 2,0 |
| * | Monoculodes sp. | | | | | | | 1,0 | 1,2 | 7,0 | 14,3 | 3,0 | 2,0 | | | | | | | 1,5 | 0,1 | 1,0 |
| | Oedicerotidae n.i. | | | | | | | 2,3 | 1,7 | 5,0 | | 3,4 | | | | | | | | | 0,7 | |
| * | Lyssianassa plumosa | | | | | | | | | | | | | | | | | | | | | |
| | Lyssianassidae n. i. | 2,7 | 0,3 | 1,0 | | | | | | | | | | | | | | | | | | |
| * | Ampelisca spinipes | 2,7 | 0,3 | 1,0 | | | | | | | | | | | | | | | | | | |
| * | Urothoe sp. | | | | | | | | | | | | | | | | | | | 6,1 | 1,8 | 3,0 |
| * | Corophidae sp. | | | | | | | | | | | | | | | | | | | 1,5 | 0,1 | 1,0 |
| * | Pleustidae n.i. | | | | | | | | | | 1,2 | 0,3 | 2,0 | | | | | | | | | |
| * | Leucothoidae n.i. | | | | | | | | | | 1,2 | 0,4 | 3,0 | | | | | | | | | |
| * | Hyperidae n.i. | | | | 1,1 | 0,7 | 2,0 | | | | | | | | | | | | | | | |
| * | Caprellidae n.i. | | | | | | | | | | 1,2 | 0,1 | 1,0 | | | | | | | | | |
| | Amphipoda n.i | | 0,6 | | | 0,4 | | | | | | | | | | | | | | | 0,7 | |
| * | Cumacea n.i. | 2,7 | 0,3 | 1,0 | 1,2 | 1,7 | 5,0 | | | | 2,4 | 0,3 | 1,5 | | | | | | | | | |
| * | Tanaidacea n.i. | 2,7 | 0,5 | 2,0 | 1,0 | 0,3 | 1,0 | | | | 2,5 | 0,8 | 3,0 | | | | | | | 6,4 | 0,6 | 1,0 |
| | Isopoda n.i. | 5,4 | 0,5 | 1,0 | 1,2 | 0,3 | 1,0 | | | | | | | | | | | | | | | |
| * | Anilocra frontalis | 5,4 | 0,5 | 1,0 | 1,2 | 0,3 | 1,0 | | | | | | | | | | | | | | | |
| | Decapoda Natantia | 37,8 | 8,8 | 2,3 | 31,3 | 19,7 | 2,1 | 15,4 | 2,0 | 1,4 | 42,0 | 10,6 | 2,6 | 42,0 | 6,8 | 1,5 | 19,4 | 6,5 | 1,4 | 72,6 | 18,6 | 2,8 |
| * | Philocheras bispinosus | | | | 6,3 | 3,2 | 1,8 | 4,2 | 1,2 | 1,7 | | | | | | | | | | 39,4 | 10,2 | 2,5 |
| * | Philocheras monacanthus | 35,1 | 8,0 | 2,2 | 5,7 | 6,0 | 3,4 | | | | 10,0 | 2,4 | 2,3 | | | | | | | 9,5 | 2,8 | 3,1 |
| * | Philocheras sculptus | | | | | | | 2,9 | 0,5 | 1,0 | | | | | | | | | | | | |
| * | Philocheras echinulatus | | | | | | | | | | | | | | | | | | | 0,4 | 0,0 | 1,0 |
| * | Crangon crangon | | | | | | | 1,0 | 0,3 | 2,0 | | | | | | | | | | | | |
| * | Pontocaris cathapracta | | | | 3,5 | 1,1 | 1,0 | | | | | | | | | | | | | 14,3 | 2,4 | 2,0 |
| * | Pontocaris lacazei | | | | 1,1 | 0,3 | 1,0 | | | | | | | | | | | | | | | |
| | Crangonidae n.i. | | | | | 0,6 | | | | | | 0,4 | | 3,2 | 0,5 | 1,6 | | | | | | |
| * | Alpheus glaber | | | | 5,7 | 3,5 | 1,8 | | | | | | | 22,2 | 1,1 | 1,0 | | | | | | |
| * | Parapeneus longirostris | | | | 3,3 | 1,6 | 1,6 | | | | | | | | | | 5,5 | 3,2 | 2,5 | | | |
| * | Solenocera membranacea | | | | | | | | | | | | | | | | | | | 0,8 | 0,1 | 1,5 |
| * | Chlorotocus crassicornis | | | | | | | | | | | | | | | | 5,5 | 1,9 | 1,5 | | | |
| * | Processa sp. | | | | | | | | | | 2,6 | 0,3 | 1,0 | | | | | | | | | |
| * | Decapoda Natantia n.i. | | 0,5 | | | 4,8 | | | | | | 7,5 | | | 1,3 | | | 1,3 | | | 3,1 | |
| * | Decapoda Reptantia | 46,0 | 7,8 | 1,6 | 51,5 | 33,1 | 2,1 | | | | 44,4 | 19,0 | 4,0 | | | | 5,5 | 1,3 | 1,0 | 46,2 | 23,4 | 6,9 |
| * | Liocarcinus vernalis | 35,1 | 4,9 | 1,4 | 3,5 | 2,8 | 2,6 | | | | | | | | | | | | | | | |
| * | Liocarcinus pusillus | 5,4 | 0,6 | 1,1 | 12,2 | 8,8 | 2,4 | | | | 12,7 | 1,6 | 1,2 | | | | 2,7 | 0,7 | 1,0 | 36,7 | 12,6 | 4,6 |
| * | Macropipus zariquei | 5,4 | 0,6 | 1,1 | 1,6 | 0,3 | 2,0 | | | | | | | | | | | | | | | |
| | Portunidae n.i. | | | | | 3,3 | | | | | | | | | | | | | | | | |
| * | Goneplax rhomboides | | | | 31,2 | 11,8 | 1,2 | | | | | | | | | | | | | | | |
| * | Ebalia deshayesi | | | | | | | | | | | | | | | | 2,7 | 0,7 | 1,0 | 1,5 | 0,1 | 1,0 |
| * | Galathea intermedia | | | | 7,0 | 4,3 | 2,0 | | | | | | | | | | | | | 3,1 | 0,3 | 1,0 |
| * | Ethusa mascarone | | | | | | | | | | | | | | | | | | | 11,0 | 6,9 | 6,7 |
| * | Dorippe lanata | | | | 1,1 | 0,7 | 2,0 | | | | | | | | | | | | | | | |
| * | Paguridae n.i. | | | | 3,3 | 1,0 | 1,0 | | | | 1,8 | 0,2 | 1,0 | | | | | | | | 0,1 | |
| * | Megalopae larvae | | | | | | | | | | 39,3 | 16,9 | 4,7 | | | | | | | 12,7 | 2,6 | 2,2 |
| | Decapoda reptantia n.i. | | 1,5 | | | | | | | | | 0,4 | | | | | | | | | 0,6 | |
| | **MOLLUSCA** | 21,6 | 2,5 | 1,1 | 19,7 | 5,7 | 1,3 | | | | 2,4 | 0,3 | 1,0 | | | | 32,7 | 9,7 | 1,0 | 10,0 | 1,0 | 1,0 |
| | Gastropoda | 2,7 | 0,3 | 1,0 | 2,1 | 0,5 | 1,0 | | | | 1,2 | 0,1 | 1,0 | | | | | | | | | |
| * | Euspira nitida | | | | | | | | | | 1,2 | 0,1 | 1,0 | | | | | | | | | |
| * | Turbonilla rufa | 2,7 | 0,3 | 1,0 | | | | | | | | | | | | | | | | | | |
| | Bivalvia | 21,6 | 2,2 | 1,0 | 8,7 | 1,0 | 1,0 | | | | 1,2 | 0,1 | 1,0 | | | | 2,7 | 0,7 | 1,0 | 8,8 | 0,8 | 1,0 |
| * | Mactra corallina | 13,5 | 1,4 | 1,0 | | | | | | | | | | | | | | | | | | |
| * | Similpecten symilis | | | | | | | | | | | | | | | | | | | 1,6 | 0,1 | 1,0 |
| * | Corbula gibba | | | | 0,3 | 0,3 | 1,0 | | | | | | | | | | | | | 6,4 | 0,6 | 1,0 |
| * | Cuspidaria abbreviata | | | | | | | | | | | | | | | | | | | 0,4 | 0,0 | 1,0 |
| * | Myrtea spinifera | | | | 0,3 | 0,3 | 1,0 | | | | | | | | | | | | | | | |
| * | Tapes decussatus | | | | 0,3 | 0,3 | 1,0 | | | | | | | | | | | | | | | |
| * | Venus ovata | | | | | | | | | | 1,2 | 0,1 | 1,0 | | | | | | | | | |
| * | Tellina sp. | 2,7 | 0,3 | 1,1 | | | | | | | | | | | | | | | | | | |
| | Bivalvia n.i | | | | | | | | | | | | | | | | | | | | 0,0 | |
| | Cephalopoda | | | | 9,7 | 4,2 | 1,4 | | | | | | | 31,0 | 4,5 | 1,3 | 30,0 | 9,0 | 1,0 | 1,7 | 0,2 | 1,0 |
| * | Sepia officinalis | | | | 1,2 | 0,3 | 1,0 | | | | | | | | | | | | | | | |
| * | Sepiolidae n.i. | | | | 9,7 | 3,7 | 1,4 | | | | | | | 31,0 | 4,5 | 1,3 | 30,0 | 9,0 | 1,0 | 1,7 | 0,2 | 1,0 |
| | **TELEOSTEA** | | | | 56,0 | 27,9 | 1,6 | | | | | | | | | | 27,0 | 9,0 | 1,1 | 3,5 | 0,9 | 1,0 |
| * | Callyonimus maculatus | | | | 31,0 | 1,0 | 1,8 | | | | | | | | | | 25,0 | 8,4 | 1,0 | 0,8 | 0,0 | 1,0 |
| * | Callyonimus risso | | | | 20,7 | 10,5 | 1,4 | | | | | | | | | | | | | 1,5 | 0,7 | 1,0 |
| * | Gobidae n.i. | | | | 9,9 | 6,1 | 2,0 | | | | | | | | | | | | | | | |
| | Teleostea n.i. | | | | | 10,9 | | | | | | | | | | | | 0,6 | | | 0,2 | |

and to trophic resources along the food niche axis of prey size and type (cf. Schoener, 1974). The Twin Span analysis of depth distribution of each gurnard size class revealed three distinct groups (Figure 4a): 1- shallow shelf size group corresponding to the juveniles of *T. lucerna* in their coastal nursery; 2- middle shelf size group which includes juveniles of the year of *T. lucerna* at the end of the summer growth, juveniles and adults of *L. cavillone* up to 9 cm S.L. and specimens of *A. obscura* less than 14 cm S.L.; 3- deep shelf group including the *A. cuculus* stock and the adults of *A. obscura* and *L. cavillone*.

The Twin Span carried out on frequency of occurrence of prey types distinguishes two main groups (Figure 4b). The first (A) includes the smallest individuals of *T. lucerna, A. obscura* and *L. cavillone*, the specimens of *L. cavillone* being separated from all others. The second group (B) is formed by the stock of *A. cuculus*, adults of *L. cavillone* between 7 and 9 cm S.L., and the largest individuals of *A. obscura* (S.L. > 13 cm) and

Table III - Diet changes with size of four gurnard species in the Central Tyrrhenian Sea. Nm , mean prey number per stomach; Wm, mean weight of stomach content; percentage of occurrence of the main prey categories: Mis (Mysidae), L. typ (*L. typicus*), Amph (Amphipodae), D. Nat. (Decapoda Natantia), D. Rep. (Decapoda Reptantia), Meg (Megalopae larvae), Ceph (Cephalopoda), Tel (Teleostea).
*Changements de régime alimentaire de quatre espèces de grondins en mer Tyrrhénienne centrale. Nm, nombre moyen de proies par estomac ; Wm, poids moyen des contenus stomacaux ; pourcentage d'occurrence des principales catégories de proies : Mis (Mysidae), L. typ (L. typicus), Amph (Amphipodae), D. Nat. (Decapoda Natantia), D. Rep. (Decapoda Reptantia), Meg (Megalopae larvae), Ceph (Cephalopoda), Tel (Teleostea).*

(a)

*TRIGLA LUCERNA*

| | | | | % OCCURRENCE | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| SIZE CLASS S.L. (cm) | N° | Wm | Nm | Mis | L. typ | Amph | D. Nat | D. Rep | Ceph | Tel |
| 6 - 8,9 | 11 | 0,20 | 8,20 | 72,70 | 0,00 | 9,00 | 9,00 | 54,50 | 0,00 | 0,00 |
| 9 - 10,9 | 18 | 0,26 | 9,94 | 66,60 | 0,00 | 11,10 | 66,60 | 50,00 | 0,00 | 22,20 |
| 11 - 13,9 | 41 | 0,34 | 5,07 | 26,80 | 0,00 | 4,80 | 24,40 | 56,10 | 4,80 | 51,20 |
| 14 - 15,9 | 32 | 0,80 | 3,14 | 3,10 | 0,00 | 0,00 | 31,20 | 50,00 | 12,50 | 53,10 |
| 16 - 18,9 | 15 | 1,20 | 3,40 | 6,60 | 0,00 | 0,00 | 53,30 | 86,60 | 13,30 | 26,60 |
| 19 - 24 | 8 | 2,10 | 3,50 | 12,50 | 37,50 | 0,00 | 37,50 | 50,00 | 0,00 | 50,00 |

(b)

*LEPIDOTRIGLA CAVILLONE*

| | | | | % OCCURRENCE | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| SIZE CLASS S.L. (cm) | N° | Wm | Nm | Mis | L. typ | Amph | D. Nat | D. Rep | Meg |
| 4 - 4,9 | 13 | 0,08 | 7,75 | 61,50 | 0,00 | 53,80 | 30,70 | 15,40 | 61,50 |
| 5 - 5,9 | 15 | 0,06 | 10,00 | 73,30 | 7,60 | 73,30 | 20,00 | 6,60 | 66,60 |
| 6 - 6,9 | 35 | 0,14 | 11,80 | 77,10 | 22,80 | 45,70 | 28,50 | 11,40 | 22,80 |
| 7 - 7,9 | 15 | 0,15 | 4,30 | 85,70 | 57,10 | 7,10 | 57,10 | 0,00 | 7,10 |
| 8 - 8,9 | 25 | 0,155 | 5,00 | 59,10 | 68,10 | 4,50 | 68,20 | 60,00 | 0,00 |
| 9 - 9,9 | 18 | 0,174 | 6,10 | 92,80 | 85,70 | 28,60 | 85,70 | 14,20 | 0,00 |

(c)

*ASPITRIGLA OBSCURA*

| | | | | % OCCURRENCE | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| SIZE CLASS S.L. (cm) | N° | Wm | Nm | Mis | L. typ | Amph | D. Nat | D. Rep | Meg | Ceph | Tel |
| 11 - 11,9 | 11 | 0,20 | 17,00 | 45,40 | 9,00 | 36,30 | 63,60 | 63,60 | 36,30 | 0,00 | 18,20 |
| 12 - 12,9 | 15 | 0,20 | 11,70 | 20,00 | 6,60 | 33,30 | 66,60 | 66,60 | 26,60 | 0,00 | 0,00 |
| 13 - 13,9 | 12 | 0,56 | 6,60 | 16,60 | 58,30 | 8,30 | 16,60 | 16,60 | 0,00 | 8,30 | 16,60 |
| 14 - 15,9 | 22 | 0,95 | 3,30 | 27,20 | 54,50 | 0,00 | 40,90 | 0,00 | 0,00 | 13,60 | 4,50 |
| 16 - 17,9 | 8 | 0,93 | 7,00 | 25,00 | 75,00 | 0,00 | 25,00 | 0,00 | 0,00 | 12,50 | 12,50 |

(d)

*ASPITRIGLA CUCULUS*

| | | | | % OCCURRENCE | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| SIZE CLASS S.L. (cm) | N° | Wm | Nm | Mis | L. typ | D. Nat | D. Rep | Ceph | Tel |
| 8 - 11,9 | 12 | 0,317 | 10,20 | 54,50 | 81,80 | 36,30 | 0,00 | 18,20 | 0,00 |
| 12 - 14,9 | 20 | 0,48 | 6,00 | 16,60 | 38,90 | 27,70 | 11,00 | 27,70 | 33,30 |
| 15 - 18 | 11 | 0,44 | 2,80 | 36,40 | 72,70 | 27,20 | 0,00 | 45,40 | 0,00 |

*T. lucerna* (S.L. > 11 cm). This latter species forms a separate cluster with the *A. obscura* of 13-13.9 cm S.L.

The prey-size relationships among gurnard size classes were examined using the length-frequency distribution of prey items (Figure 3). The Twin Span analysis, carried out utilizing the frequency of occurrence of prey size groups, distinguished two distinct groups (L and R) (Figure 4c). group includes the individuals of *T. lucerna* and *A. obscura* less than 11 cm and 14 cm S.L. respectively, and the stock of *L. cavillone*, except for individuals over 9-10 cm S.L. The fishes belonging to this group based their diet on small prey less than 15 mm. The R group comprises the bigger specimens of *A. cuculus* (S.L > 12 cm) with to the adults of *A. obscura* (S.L. > 14 cm) and the *T. lucerna* between 19 and 24 cm S.L. The younger individuals of *A. cuculus* (8-11.9 cm S.L.), and the individuals of *L. cavillone* of 9-9,9 cm S.L. form a separate cluster with the intermediate size class of *T. lucerna*. The R gurnard size classes mainly utilized prey over 15 mm length.

Table IV - Variation of feeding diversity with size of four gurnard species : mean and standard deviation of prey size and of number of prey species per stomach. / *Évolution de la diversité trophique avec la taille de quatre espèces de grondins : moyenne et déviation standard de la taille des proies et du nombre de proies par estomac.*

| | | Prey size | | Prey species per stomach | |
|---|---|---|---|---|---|
| | S.L. (cm) | Mean | S. D. | Mean | S. D. |
| *T. LUCERNA* | 6-8.9 | 7,39 | 2,00 | 2,28 | 0,47 |
| | 9-10.9 | 7.66 | 2,41 | 2,22 | 1,26 |
| | 11-13.9 | 10,36 | 5.61 | 2,05 | 1,18 |
| | 14-15.9 | 13.85 | 7,10 | 2,03 | 0,95 |
| | 16-18.9 | 11.71 | 7,00 | 2,58 | 1,5 |
| | 19 - 24 | 18,28 | 11,48 | 2,87 | 1,1 |
| *L. CAVILLONE* | 4-4.9 | 4,30 | 1,86 | 2,87 | 1,46 |
| | 5-5.9 | 5,02 | 1,92 | 2,93 | 1,44 |
| | 6-6.9 | 5,30 | 1,87 | 2,87 | 1,45 |
| | 7-7.9 | 7,84 | 2,80 | 1,86 | 0,99 |
| | 8-8.9 | 9,94 | 4,00 | 1,54 | 0,59 |
| | 9-9.9 | 9,83 | 5,80 | 2,26 | 1,2 |
| *A. OBSCURA* | 11-11.9 | 5,50 | 3,00 | 3,90 | 1,80 |
| | 12-12.9 | 5,03 | 2,80 | 3,00 | 1,65 |
| | 13-13.9 | 7,85 | 4,00 | 1,80 | 1,20 |
| | 14-15.9 | 14,10 | 4,61 | 1,60 | 0,92 |
| | >16 | 15,40 | 3,83 | 1,30 | 0,50 |
| *A. CUCULUS* | 8-11.9 | 10,20 | 4,43 | 2,07 | 0,95 |
| | 12-14.9 | 12,64 | 7,41 | 1,90 | 0,80 |
| | 15-18.9 | 20,35 | 6,80 | 1,70 | 0,60 |

In the prey-size predation pattern, other morphological characteristics, such as mouth dimensions, played an important role, as the interspecific association of gurnards of different body size showed (Figure 4c). The 20 fish size classes formed two distinct feeding groups relative to the utilization of the trophic resources (prey size and type) as the comparison of the clusters showed: the size classes belonging to the A cluster were present mainly in the L group whereas those of the B group basically

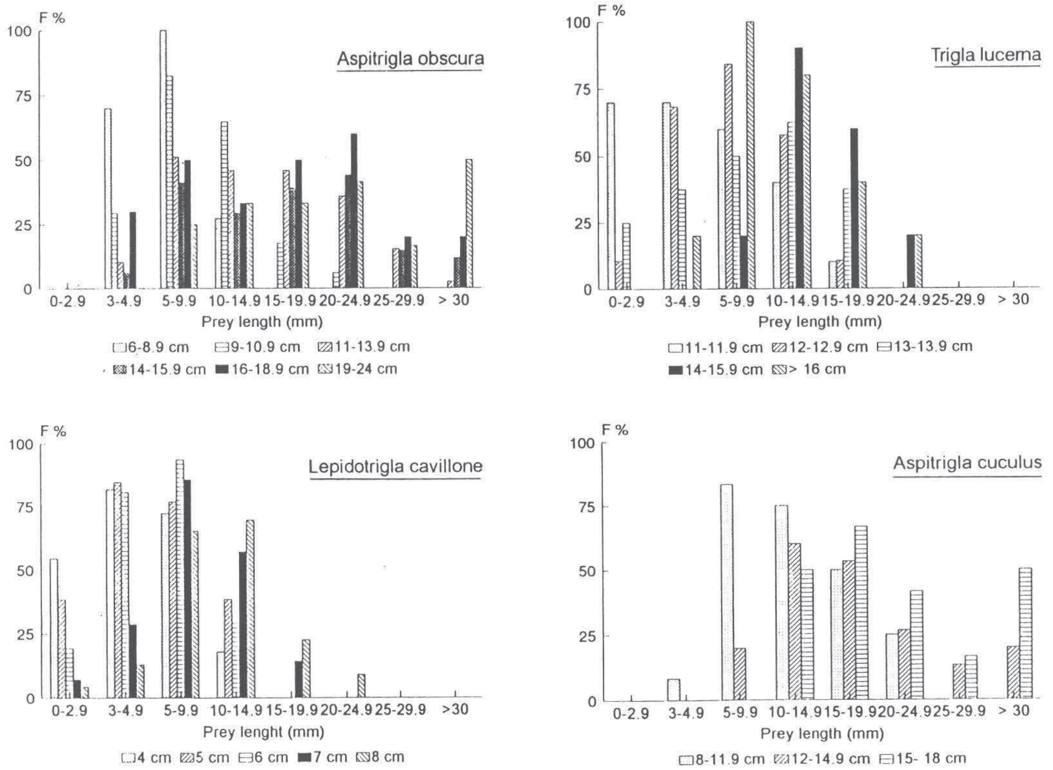
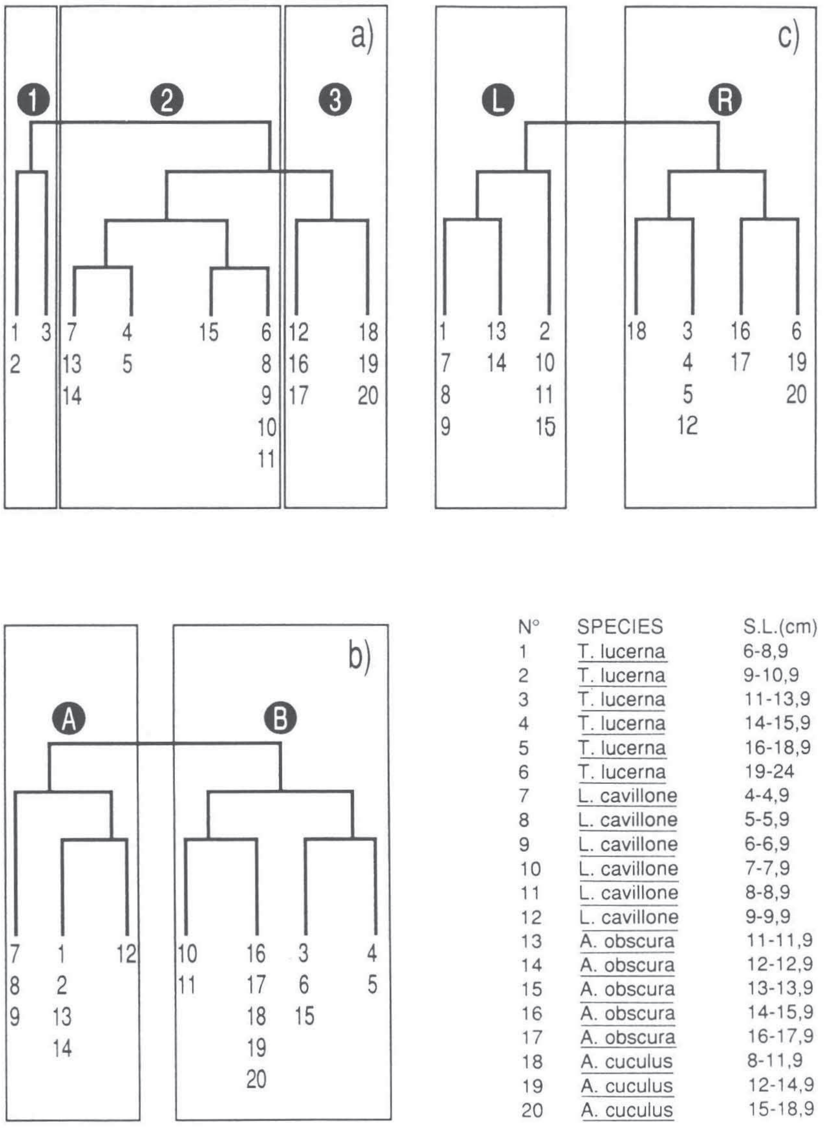


Figure 3 - Frequency of occurrence of prey size classes for the studied gurnards./*Fréquence de présence des classes de taille de proies pour les grondins examinés.*



| N° | SPECIES | S.L.(cm) |
|---|---|---|
| 1 | T. lucerna | 6-8,9 |
| 2 | T. lucerna | 9-10,9 |
| 3 | T. lucerna | 11-13,9 |
| 4 | T. lucerna | 14-15,9 |
| 5 | T. lucerna | 16-18,9 |
| 6 | T. lucerna | 19-24 |
| 7 | L. cavillone | 4-4,9 |
| 8 | L. cavillone | 5-5,9 |
| 9 | L. cavillone | 6-6,9 |
| 10 | L. cavillone | 7-7,9 |
| 11 | L. cavillone | 8-8,9 |
| 12 | L. cavillone | 9-9,9 |
| 13 | A. obscura | 11-11,9 |
| 14 | A. obscura | 12-12,9 |
| 15 | A. obscura | 13-13,9 |
| 16 | A. obscura | 14-15,9 |
| 17 | A. obscura | 16-17,9 |
| 18 | A. cuculus | 8-11,9 |
| 19 | A. cuculus | 12-14,9 |
| 20 | A. cuculus | 15-18,9 |

Figure 4 - Cluster analysis (Twin Span Analysis) of bathymetric and trophic similarity of four gurnard stocks in the Central Tyrrhenian Sea based on: a- relative abundance of each gurnard size class considered according to depth; b- frequency of occurrence of prey type for gurnard size classes; c- percentage occurrence of prey size groups for gurnard size classes.
*Analyse de la similitude bathymétrique et trophique de quatre stocks de grondins dans le mer Tyrrhénienne centrale basée sur : a) pourcentage d'abondance relative par classe de taille des grondins considérés en fonction de la profondeur ; b) pourcentage d'occurrence des catégories de proies pour les classes de taille des grondins ; c) pourcentage d'occurrence des classes de taille de proies pour les classes de taille des grondins.*

occupied the R cluster (Figure 4b-c). The AL group includes the juveniles of *T. lucerna, L. cavillone,* and *A. obscura* on coastal and medium shelf bottoms ; the BR group was formed by the stock of *A. cuculus,* the adults of *A. obscura* and of *L. cavillone* and specimens of *T. lucerna* over 11 cm S.L. living on bottoms between 100 and 200 m depth. The *T. lucerna* over 11 cm S.L., though living at low or medium depths, belonged to the feeding mode BR which indicated an evident trophic isolation of the species.

In interspecific comparisons, divergences in feeding habits were observed only for the size classes showing a wide spatial overlap, such as between the larger size classes of *A. obscura* and *L. cavillone;* between the juveniles of these species and *T. lucerna* of 14 and 19 cm S.L., between the larger specimens of *T. lucerna* and *L. cavillone* of 7-8.9 cm S.L. Other size classes, such as the adults of *A. obscura* and the *A. cuculus* over 12 cm S.L. did not show strong differences in food and habitat utilization (Figure 4).

The ordination model obtained by the Factorial Analysis of Correspondence is shown in Figure 5. The first two axes accounted for 51,1 % of the total variance (29,7 for F1 and 21,4 for F2). Along F1 the point of *T. lucerna* in spring time is in opposite position to the points of *A. cuculus* with the other fish species' points in intermediate position. In-shore prey species points such as *M. corallina* and *G. sanctus* are in opposite position to off-shore prey (Sepiolidae, *C. maculatus* and *L. typicus*). Along F2 the points of *L. cavillone* and *T. lucerna* in summer time are located at the opposite poles. The small-sized prey species *W. rectirostris* and *Monoculodes sp.* characterize the positive pole while the large-sized prey species, *G. rhomboides,* Gobidae and juveniles of *S. officinalis* are located at the negative pole.

Therefore depth distribution and body size resulted as the fundamental factors affecting trophic relationships among the examined gurnard stocks.

## DISCUSSION AND CONCLUSION

In the Central Tyrrhenian Sea, four gurnard species inhabit soft bottoms down to 270 m: *Trigla*

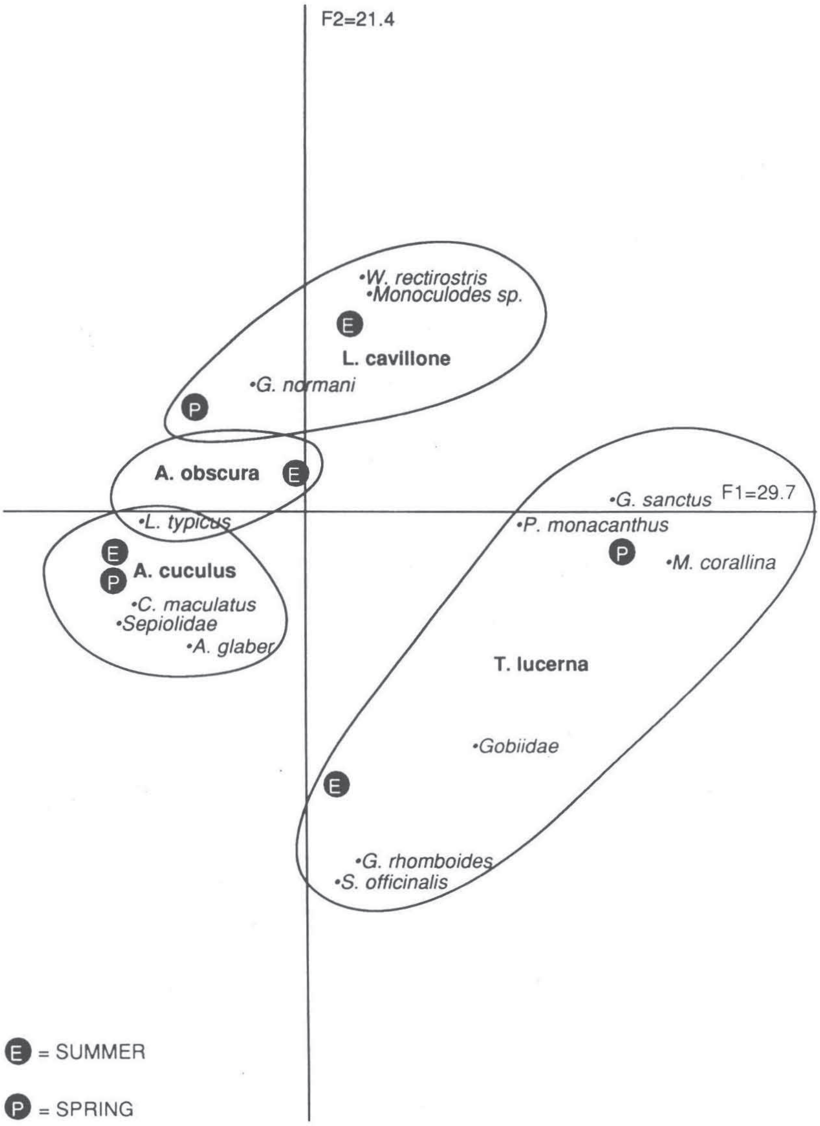


Figure 5 - Ordination model of the Factorial Analysis of Correspondence (F.A.C.). The figure shows gurnard stocks in the two sampling season and the prey items with the highest contribution to the axis./*Figure 5 - Résultat de l'Analyse Factorielle des Correspondances (AFC). La figure montre les stocks de grondins pendant les deux saisons d'échantillonnage et les proies ayant les plus fortes contributions aux axes.*

*lucerna, Lepidotrigla cavillone, Aspitrigla cuculus* and *A. obscura.* Their depth range does not differ significantly from other Mediterranean fishing areas (Dieuzeide *et al.,* 1955; Collignon, 1968; Maurin, 1968; Rizzi and Bello, 1986 and Papaconstantinou, 1983). Every gurnard stock sampled showed a different seasonal bathymetric distribution linked to recruitment patterns and individual size growth. Spatial separation between juveniles and adults was quite pronounced except for *A. cuculus*: juveniles of the same year had a high relative abundance on bottoms shallower than 100 m while adults were more abundant between 100 and 200 m. Coastal nursery grounds of *T. lucerna* and *L. cavillone* were identified in spring and summer time respectively (Collignon, 1968; El-Hehyawi, 1974; Froglia, 1976; Papacostantinou, 1983). The depth migration of the juveniles during growth has been documented for *L. cavillone, A. obscura* and *T. lucerna.* Such behaviour is very common in fishes (Helfman, 1978) and particularly in searobin species (Meek, 1915; Lewis and Yerger, 1976; Richards *et al.*, 1979).

In this study area gurnard species showed a wide bathymetric overlap although they differed in their depth distributions and shared a common feeding pattern based on crustaceans and other epibenthic and infaunal animals. The most common crustaceans were mysids of the genera *Gastrosaccus* and *Lophogaster*, decapods of the family Portunidae and Crangonidae and the amphipods Oedicerotidae. While the gurnards' basic diet composition differed slightly compared to other geographical areas, conspicuous differences were observed in the frequency of the main preyed species.

*L. cavillone* fed mainly on mysids as observed in Greek Seas (Caragitsou and Papaconstantinou, 1990) and in the Northern Mediterranean Sea (Kartas, 1974; Moreno and Matallanas, 1983). *A. obscura, T. lucerna* e *A. cuculus* preyed upon crustaceans and to a lesser extent upon benthic fishes (Callyonimidae and Gobiidae) and Cephalopods Sepiolidae (Nouvel, 1950; Furnestin, 1958; Reys, 1960; Froglia, 1976; Labarta, 1977, Sorbe, 1981 ). The gurnard stocks, although utilizing similar trophic levels, showed a food partitioning pattern linked to the spatial distribution and body size of individuals as the in Twin Span and the Factorial Analysis of Correspondences demonstrated. This partitioning pattern was even more accentuated between *T. lucerna* and the other three gurnards species and between *A. cuculus* and *L. cavillone.*

Differences in body size and consequently in prey size may allow the coexistence of syntopic species. As Wilson (1975) stated, sympatry of two or more species with similar niches may be allowed by differences in growth rates which results in consumption of prey of different sizes. Several authors have shown a relationship between fish growth rate and mean prey length (Werner and Hall, 1974; Fox 1989). As observed in several benthic (Zander and Berg, 1984; Harmelin-Vivien, *et al.*,1989) and necto-benthonic Mediterranean fishes (Macpherson, 1981) body size of gurnards was the main factor determining the size and the kind of the prey ingested.

The increase in body size induced continuous diet change in a qualitative and quantitative way: mean weight of stomach contents and mean prey size increased while the mean number of items and of prey species per stomach decreased. The smaller sized prey (megalops larvae, amphipods, mysids) are replaced by larger sized prey (decapods, teleosts, cephalopods, *L. typicus*). Larger gurnards preyed with higher occurrence on the large prey but continued to take the smaller sized prey. Consequently predators of large prey occupied more of the resource axis of prey size than predators of small prey.

In this study the changes in food preference and feeding habits in gurnards have been proved to be rapid when fishes reach a critical size. In contrast to other Mediterranean fish species, such as scorpaenids, which showed gradual changes in food preference (Harmelin-Vivien *et al.*, 1989), the pattern observed here produces a strong resource partitioning among size classes. This intraspecific partitioning occurred in the study area as shown by the presence of two different feeding modes corresponding to the juveniles' and adults' feeding patterns. A rapid change in feeding habits was observed by Tyler (1972) among northern marine demersal fishes. The lengths at which feeding changes occur have been termed *"threshold lengths"* by Parker and Larkin (1959). According to Griffiths (1975) juvenile stages of several kinds of vertebrates take their prey in close proportion to their environmental occurrence. Although prey availability was not monitored, the juveniles of gurnards seemed to feed according to the abundance of the prey. The data suggest a switch in feeding strategy, during growth, to an energy maximizer in which predators feed in such a manner as to maximize their energy intake (Griffiths, 1975). The gurnards' threshold lengths at which the switch in feeding habits occurred corresponded to the length of the first sexual maturity of *L. cavillone, A. cuculus* and *A. obscura.* The energy requirement linked to gonadal development and breeding activity were hypothized to be the factor causing the switch in feeding behaviour of a triglid of the Gulf of Mexico (Ross, 1978). The onthogenic diet changes were also explained by the depth migration of juveniles of the year. For example the predation frequency of *L. typicus* was significantly correlated with the depth of fish capture. Schoener (1974) generalized that habitat separation is often more important than either prey separation or temporal separation in avoiding food resource overlap, as in the case of the gurnards.

A quite strong food partitioning pattern between juveniles and adults on a spatial and trophic basis was recorded for all the species studied. In interspecific coexistence among the stocks the observed correlation between depth distribution and diet demonstrated that trophic partitioning was generally not important for gurnards. The role of trophic partitioning was more significant when the spatial overlap was greater. Divergences in feeding habits were only observed for some size classes showing wide spatial overlap. Slight differences in depth distribution may allow the coexistence of fishes with similar feeding habits, as has been shown for adults of *A. cuculus* and *A. obscura*. As observed by Ross (1977) for a guild of gurnards of the west Florida coast, if spatial partitioning was highly effective, then the selection for trophic partitioning would be minimal. Consequently at low habitat overlap there was both low and high food overlap in prey size, an observation which was also confirmed in this study.

According to the optimal foraging theory that predicts a specialization in diet as the absolute abundance of preferred prey types increases (Pike *et al.*, 1977), the absence of substantial food partitioning among gurnards can be due to a low level of food resources in the study area. Pike *et al.* (1977) pointed out that if a variety of habitat patches with different food is available, patch utilization by two or more species may converge or diverge depending on the similarity of their responses to the declining food. However, several studies have demonstrated an increase in feeding niche overlap due to the opportunistic utilization of superabundant food resources by fishes (Macpherson, 1981; Targett, 1981; Delbeek and Williams, 1987). Macpherson (1981) noted that among some Mediterranean demersal fishes the epibenthic predators feed on prey items undergoing substantial seasonal fluctuation in abundance. The stability and uniformity of food resources can produce a strong segregation among sympatric correlated species (Margalef, 1977).

As has been noted out for many euriphagic fishes it may be hypothesized that the gurnards' diet is, in part, a reflection of prey availability. It is therefore possible that they may not have a preferred prey type. This could explain the geographical variation of gurnard diets in the occurrence of the main prey species. Yet the observed relationships among gurnards could also depend on food abundance, and the high dietary overlap between the two *Aspitrigla* species may occur when some food resources increase in abundance. Therefore, the high niche overlap can be interpreted as evidence both for and against competition, also according to Collwell and Futuyma (1971)

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*Reçu en février 1994 ; accepté en janvier 1995.*
*Received February 1994; accepted January 1995.*