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To cite this article: S. Montanini, M. Stagioni, E. Benni & M. Vallisneri (2017) Feeding strategy and ontogenetic changes in diet of gurnards (Teleostea: Scorpaeniformes: Triglidae) from the Adriatic Sea, The European Zoological Journal, 84:1, 356-367, DOI: 10.1080/24750263.2017.1335357

To link to this article: http://dx.doi.org/10.1080/24750263.2017.1335357

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Published online: 28 Jun 2017.

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Feeding strategy and ontogenetic changes in diet of gurnards (Teleostea: Scorpaeniformes: Triglidae) from the Adriatic Sea

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(Received 10 December 2016; accepted 19 May 2017)

Abstract
A multi-specific approach in fish diet studies provides insight into the complexity of trophic interactions in marine communities. The feeding habits of three gurnard species, Aspitrigla cuculus, Chelidonichthys lucerna and Eutrigla gurnardus (Scorpaeniformes: Triglidae), from the north-middle Adriatic Sea were studied to evaluate prey-resource partitioning amongst species and within species, comparing juveniles’ and adults’ diet for each gurnard species. A total of 1818 specimens (390 A. cuculus, 973 C. lucerna, 455 E. gurnardus) were collected by bottom trawling and they were assigned to size classes (juveniles or adults) on the basis of macroscopic evaluation of the gonads. Stomach contents were analysed. A common dietary preference for Crustacea was found in all species and size classes considered. Nevertheless, gurnards showed distinct feeding behaviour: C. lucerna and E. gurnardus were generalist-opportunistic predators, showing a varied diet based on epi-benthic, bentho-pelagic and necto-benthic preys belonging to different taxa such as Teleostei and Mollusca, while A. cuculus may be considered a specialist feeder, feeding almost exclusively on necto-benthic invertebrates. Morisita’s index calculated for critical size classes (juveniles and adults) pointed out differences. At the inter-specific level, possible dietary competition between A. cuculus and E. gurnardus were generalist-opportunistic predators, showing a varied diet based on epi-benthic, bentho-pelagic and necto-benthic preys belonging to different taxa such as Teleostei and Mollusca, while A. cuculus may be considered a specialist feeder, feeding almost exclusively on necto-benthic invertebrates. Morisita’s index calculated for critical size classes (juveniles and adults) pointed out differences. At the inter-specific level, possible dietary competition between A. cuculus and E. gurnardus were generalist-opportunistic predators, showing a varied diet based on epi-benthic, bentho-pelagic and necto-benthic preys belonging to different taxa such as Teleostei and Mollusca, while A. cuculus may be considered a specialist feeder, feeding almost exclusively on necto-benthic invertebrates. Morisita’s index calculated for critical size classes (juveniles and adults) pointed out differences. At the inter-specific level, possible dietary competition between A. cuculus and E. gurnardus were generalist-opportunistic predators, showing a varied diet based on epi-benthic, bentho-pelagic and necto-benthic preys belonging to different taxa such as Teleostei and Mollusca, while A. cuculus may be considered a specialist feeder, feeding almost exclusively on necto-benthic invertebrates.

Keywords: Aspitrigla cuculus, Chelidonichthys lucerna, Eutrigla gurnardus, feeding strategy, resource partitioning

Introduction
Trophic relationships are fundamental to understanding biological interactions in animal communities (Carrassón & Cartes 2002). Strategies used by related groups of animals in exploiting resources are of continuing interest in ecological studies. Many of the behaviour patterns and morphological adaptations of fish species have evolved in relation to the capture of food, in addition to the requirements of reproduction and avoidance of predation (Labropoulou & Eleftheriou 1997).

Gurnard species (Scorpaeniformes: Triglidae) are demersal fishes that inhabit the continental and insular shelves of tropical and temperate seas to depths of 500 m, and are found on sandy, muddy or rubble substrates (Fischer et al. 1987). There are seven different species in the north-middle Adriatic Sea (42–45°N, 13–15°E), showing differences related to biometric features as well as ecological ones such as diet, spawning period and depth distribution (Tsimenides et al. 1992; Colloca et al. 1994; Vallisneri et al. 2010). During their early life cycle they go through a pelagic phase, while during their demersal stage changes in their ecological behaviour are associated with the onset of sexual maturity (Vallisneri et al. 2012), the tendency to migrate to greater depths and a change in diet with a wider trophic
Diet overlap among Mediterranean gurnards

spectrum (Colloca et al. 1994; Montanini et al. 2010). Gurnards use the free radii of their pectoral fins to search for prey on sedimentary beds (Whitehead et al. 1989). *Aspitrigla cuculus* (Linnaeus, 1758), *Chelidonichthys lucerna* (Linnaeus, 1758) and *Eutrigla gurnardus* (Linnaeus, 1758) are included in the list of reference species of the MEDITS project (International Bottom Trawl Surveys in the Mediterranean) and are the subject of a new Memorandum of Understanding (MOU) from the International Council for the Exploration of the North Sea (ICES 2006) in order to investigate biological parameters for stock assessment purposes. In fact, subsequent to the decline in traditionally exploited fish stock, Triglidae have been considered new emerging species by trawlers (Boudaya et al. 2008–2009). The sampling site was in the GFCM-GSA 17 area (Northern and Central Adriatic Sea) and covered a surface area of 59,400 km² from the Gulf of Trieste (45°40′N, 13°37′E) to the Tremiti Islands (42°08′N, 15°16′E) at depths of between 12 and 252 m. Samples were taken on a seasonal basis (summer and autumn–winter) between 2005 and 2009 as part of several national and international oceanographic bottom trawl surveys, namely MEDITS (summer surveys) and GRUND (Assessment of Italian Demersal Resources – autumn/winter surveys). The sampling gear included an experimental bottom trawl featuring four panels and a mesh cod-end size of 20 mm (stretched mesh) for the MEDITS, while a 40 mm cod-end was used for the GRUND surveys (Fiorentini et al. 1999).

All previous studies on the diet of the three species reported that crustaceans were the most abundant preys, but these studies were undertaken on separated populations (Valiani 1934; Froglia 1976; Montanini et al. 2010; Stagioni et al. 2012). No study has taken into account diet in terms of niche overlap, resource partitioning and ontogenetic diet shift as a possible important contributing factor to the segregation of gurnard species in the studied area. Resource partitioning allows fish species to avoid inter- and intraspecific competition, influencing the number of individuals that can coexist in the same area. Resource partitioning may occur by segregation from one of the three main resource axes: food, space and time, where trophic separation explains most of the mechanisms that allow coexistence among closely related species (Schuckel et al. 2012).

The aim of this study was to compare trophic relationships among three gurnard species in the Adriatic Sea, northern Mediterranean. Our specific goal was to investigate whether prey-resource partitioning or potential competition occurs among these species.

### Materials and methods

#### Sampling

The sampling site was in the GFCM-GSA 17 area (Northern and Central Adriatic Sea) and covered a surface area of 59,400 km² from the Gulf of Trieste (45°40′N, 13°37′E) to the Tremiti Islands (42°08′N, 15°16′E) at depths of between 12 and 252 m. Samples were taken on a seasonal basis (summer and autumn–winter) between 2005 and 2009 as part of several national and international oceanographic bottom trawl surveys, namely MEDITS (summer surveys) and GRUND (Assessment of Italian Demersal Resources – autumn/winter surveys). The sampling gear included an experimental bottom trawl featuring four panels and a mesh cod-end size of 20 mm (stretched mesh) for the MEDITS, while a 40 mm cod-end was used for the GRUND surveys (Fiorentini et al. 1999).

#### Data analyses

A total of 1818 gurnards (390 *Aspitrigla cuculus*, 973 *Chelidonichthys lucerna* and 455 *Eutrigla gurnardus*) were collected (Table I). Specimens from each trawl were measured to the nearest mm (total length = TL) and weighed to the nearest 0.1 g. The sex was defined following four categories: male, female, undetermined (impossible to determine by eye) and not determined (the individual was not examined). The gonadal maturity levels were defined according to the code of sexual maturity used in the European MEDITS project (MEDITS 2007). Fish lengths were classified into two size groups according to the above maturity scale: juveniles (individuals corresponding to stages 0 and 1) and adults (individuals corresponding to stages from 2a to 4b). Juvenile to adult transition size was marked off at 110 mm for *A. cuculus*, 180 mm for *C. lucerna* and 100 mm for *E. gurnardus*.

Samples were dissected and stomachs were removed and preserved in 70% ethanol for analysis.

|                | *Aspitrigla cuculus* | *Chelidonichthys lucerna* | *Eutrigla gurnardus* |
|----------------|----------------------|---------------------------|----------------------|
|                | Juveniles            | Adults                    | Juveniles            | Adults                    | Juveniles            | Adults                    |
| No. of fish examined | 118                  | 272                       | 325                  | 648                       | 138                  | 317                       |
| TL max (mm)     | 113                  | 262                       | 214                  | 415                       | 102                  | 264                       |
| W max (g)       | 12.7                 | 181                       | 95                   | 651                       | 9                    | 166                       |
| Depth range (m) | 55.25–176.5          | 82.3–246                  | 13.55–94.05          | 12.4–232                  | 37.15–170            | 37.15–181.5               |

*Notes: Juvenile: individuals corresponding to stages 0 and 1; adult: individuals corresponding to stages 2a to 4b; TL = total length; W = weight.*
of stomach contents. Gut contents were analysed with a stereoscopic microscope identifying each prey to the lowest taxonomic level possible by using specialised keys. Prey types were counted (Np) and weighed (Wp) after removal of excess moisture.

Statistical analyses

Depth distribution of the specimens belonging to the three species was analysed by Pearson’s Chi-squared test in order to test the significance of the relationship between size classes and depth. Differences in species niche depth were compared using a Kruskal–Wallis one-way analysis of variance (ANOVA) on ranks and a post hoc all pairwise multiple comparison procedure using Dunn’s method.

Diets were expressed as percentage abundance (Cn%) by prey item for each dietary category, percentage by weight (Cw%) and percentage by frequency of occurrence (F%), being understood as the proportion of non-empty stomachs containing a given prey item or category. According to N'Da (1992), prey items are considered dominant when Cn% > 50%; secondary prey have values of Cn% ranging from 10% – 50%; and accidental prey are defined as Cn% < 10%. The main food items were identified using the index of relative importance (IRI):

\[
IRI_i = \frac{F\%(Cn\% + Cw\%)}{100}
\]

and the modified form

\[
IRI_i = \frac{IRI_i}{\sum IRI_i} \times 100
\]

These indexes were calculated for each prey category and used in diet comparisons (Pinkas et al. 1971; Cortés 1997). Data was sorted on the basis of the decreasing value of IRI%.

The ontogenetic shift in the diet was explored using a hierarchical cluster analysis based on numerical abundance Bray–Curtis dissimilarity (Clarke & Warwick 1994). Data was transformed by Wisconsin double standardisation (square root transformation) and then analysed by non-metric multidimensional scaling (nMDS) in relation to size class and depth. Regression fit goodness (Stress S) was determined on the basis of the sum of squared differences between ordination-based distances and predicted distances. Low Stress S values indicated goodness of fit.

For the analysis of trophic niche breadth, the normalised version of the Leivins (Bi) index (Hurlbert 1978) was used:

\[
Bi = 1/n - 1 \left\{ \frac{1}{\sum p_{ij}^2} - 1 \right\},
\]

where \( p_{ij} \) is the proportion of prey \( j \) in the diet of predator \( i \), and \( n \) is the number of prey categories. \( B_i \) was expressed on a scale from 0 to 1.0 (with a low value indicating a specialist predator with a diet dominated by few prey items, and a high value indicating a generalist predator) and calculated for each size class.

Species diversity in prey number was calculated using the Shannon–Wiener index (\( H' \)) and the evenness measure of the Shannon–Wiener function (\( J' \)) (Colwell & Futuyma 1979). The Shannon–Wiener formula was expressed as:

\[
H' = -\sum p_i \log p_i,
\]

where \( p_i \) is the proportion of individuals found in or using resource \( j \). A high \( H' \) value indicates feeding on a wider spectrum of prey-items. As Shannon–Wiener measures may range from 0 to \( \infty \), an evenness measure (\( J' \)) was calculated so as to standardise \( H' \) on a 0 to 1 scale:

\[
J' = H' / \log n,
\]

where \( n \) is the total number of possible resource states. A high \( J' \) indicates a specimen feeding on a relatively larger number of a few main prey types (Shouzeng 1995).

The simplified Morisita index (\( C_H \)) proposed by Horn (1966) was used to investigate intra- and interspecific niche overlap among size classes and species. This index ranges from 0 (no resource used in common) to 1.0 (full overlap), with values > 0.6 being considered to be indicative of a biologically significant overlap (Pusey & Bradshaw 1996). Morisita’s measure was expressed as:

\[
C_H = 2\sum p_{ij}p_{ik}/(\sum p_{ij}^2 + \sum p_{ik}^2).
\]

where \( p_{ij} \) is the corresponding proportion of resource \( i \) in the total resource used by species \( j \), and \( p_{ik} \) is the corresponding proportion of resource \( i \) in the total resource used by species \( k \).

Multivariate analysis was conducted using the R software version 3.3.2 (R Core Team 2016) base and the Vegan package for community ecology.

Results

Biological and ecological parameters

Biological and ecological parameters of Aspitrigla cuculus, Chelidonichthys lucerna and Eutrigla gurnardus are summarised in Table I. Significant differences were found in distribution by depth (Pearson’s Chi-squared test with Yates’ continuity correction: \( \chi^2 \)-
squared = 84.9339, df = 1, p-value < 0.001). More precisely, these significant differences were found by comparing all possible size-class pairs according to the post-hoc Dunn test (p-value < 0.001) in species niche depth (Kruskal-Wallis test; p-value < 0.001) both among species (inter-specific differences) and between juveniles and adults within the same species (intra-specific differences). *Aspitrigla cuculus* was generally encountered at greater depths, while *C. lucerna* was more common at shallow depths near the coast. For all three gurnard species, juveniles were found at shallower waters than adults, which consistently migrate to deeper depths.

**Diet composition**

Dietary analysis of the main taxa preyed by the three species examined is summarised in Table II. Examination of the collected specimens did not reveal any sign of regurgitation. Sixteen food items were identified in the diet of *A. cuculus* and classified into four main categories: Crustacea, Teleostei, Mollusca and Echinodermata. Almost the entire diet of this species was based on crustaceans (%Cn = 93.88; %Cw = 91.15; %IRI = 98.26), while other taxa were classified as accessory prey. Sixty different preys belonging to five main groups (Crustacea, Teleostei, Mollusca, Anellida and Bryozoa) were identified in the stomachs of *C. lucerna*. Crustaceans were the most abundant in number and weight with a high IRI value (%Cn = 90.0; %Cw = 58.11; %IRI = 96.7). Teleostei were considered secondary prey in the diet of *C. lucerna*, with a significant contribution in terms of weight and frequency of occurrence (%Cw = 40.12; %F = 31.35). Molluscs, annelids and bryozoa were recorded as accidental prey. Thirty-four categories of prey items were identified in the stomachs of *E. gurnardus* and classified into five main groups: Crustacea, Teleostei, Mollusca, Nematoda and Echinodermata. For *E. gurnardus* also, the diet consisted essentially of crustaceans (%Cn = 93.65; %W = 61.25; %IRI = 98.5).

The diet of both juveniles and adults of all species was mainly composed of crustaceans. *Lophogaster typicus* (*Lophogastrida*) was the most abundant and preferred prey for both ontogenetic groups of *A. cuculus* (%IRI = 97.08 juveniles; %IRI = 97.81 adults) and *E. gurnardus* (%IRI = 64.31 juveniles; %IRI = 47.46 adults). *Liocarcinus* sp. (*Decapoda: Brachyura*), *Solenocera membranacea* (*Decapoda: Macrura–Natantia*) and *Acanthomysis longicornis* (*Mysida*) occurred quite frequently in the diet of juveniles of *E. gurnardus*, but were replaced in the diet of the adults by *Goneplax rhomboides* (*Decapoda: Brachyura*).
Philocheras sp. (Decapoda: Macrura–Natantia) was the dominant prey (%IRI = 79.99) of juveniles of C. lucerna, while G. rhomboides (%IRI = 80.63) was the dominant prey of adults of C. lucerna.

Teleostei were considered secondary preys (Table II). Seventeen different species of bony fish preys were found in the diet of adults of C. lucerna (%Cn = 16.86); anchovy Engraulis encrasicolus (%Cw = 12.98) and gobid Gobius niger (%Cw = 10.29) contributed well in terms of weight.

Full details of diet, with juveniles and adults considered separately for each species, are given in the Appendix.

**Inter-/intra-specific variation in diet**

Inter-specific nMDS analysis highlights three different groups, each within the same species: juveniles and adults of each species were grouped together, reflecting specific feeding behaviour (Figure 1). This trend was further borne out by the nMDS analysis of the size–depth relationship; in fact, same-species clusters were basically found also by this type of analysis (Figure 2).

Inter-and intra-specific feeding differences are reported in Table III. Although stomach contents generally showed a high number of different prey items and a relatively wide spectrum, the niche breadth ($B'$ values) reached low levels in all the size–species groups. In terms of prey species diversity, juveniles of E. gurnardus showed the highest values ($H' = 2.24$ and $J'' = 0.79$), quite similar to those found for the adults of E. gurnardus ($H' = 2.09$ and $J'' = 0.62$) and for adults of C. lucerna ($H' = 2.26$ and $J'' = 0.56$). For the other ontogenetic groups (juveniles and adults of A.culus and juveniles of C. lucerna), low species diversity values were recorded ($H' < 1.50$; $J'' < 0.60$).

Intra-specific feeding competition was considered between juveniles and adults of A.culus and E. gurnardus. In fact, as may be seen in Table IV, Morisita index values were high in both species (C = 0.991 for A.culus, and C = 0.843 for E. gurnardus). By contrast, very low intra-specific competition levels were recorded for C. lucerna (C = 0.186). Low levels of inter-specific competition show the trophic niche of C. lucerna to be different from that of A.culus and E. gurnardus (C range = 0.249–0.589) (Table IV).

**Discussion**

**Inter-/intra-specific variation in depth**

The study focuses on the role of fish size and depth distribution in food resource partitioning of gurnards.
Aspitrigla cuculus, Chelidonichthys lucerna and Eutrigla gurnardus from the Adriatic Sea. Inter-specifically, the narrowest bathymetric distribution, mostly above 100 m, was reported for A. cuculus, while the greatest relative abundance was recorded for C. lucerna at between 0 and 50 m. Intra-specifically, a species-specific distribution pattern associated with nursery-recruitment patterns and fish size was found for each gurnard species, according to Colloca et al. (1994), Manfredi et al. (2013). A spatial separation between juveniles and adults was observed for the three gurnard species, with adults tending to be sampled at greater depths than juveniles; although significant in all cases, juvenile–adult spatial separation was most pronounced for C. lucerna. In fact, C. lucerna shows a consistent nursery area along the coast with younger individuals more frequently found in shallow waters, while adults are dispersed more towards offshore sites, according to the literature (Froglia 1976; Papaconstantinou 1983; Tsimenides et al. 1992; Colloca et al. 1994; Serena et al. 1998; Boudaya et al. 2008).

Inter-specific variation in diet

Our data suggests that the three species show a crustacivorous feeding behaviour; however, they appear to have distinct feeding preferences according to the literature (Colloca et al. 1994; Morte et al. 1997; Montanini et al. 2010; Lopez-Lopez et al. 2011; Stagioni et al. 2012). Lophogaster typicus (Lophogastrida) represents the most abundant and preferred prey for both A. cuculus and for E. gurnardus, though not for C. lucerna. Four crustacean species were found in the stomachs of gurnard species of all size classes considered: Goneplax rhomboides, Liocarcinus sp., Alpheus glaber and Selenocera membracae. These crustaceans are in fact among the most common prey items for both fish and other decapod crustaceans in the muddy bottom communities of the lower continental shelf and upper slope of the western Mediterranean Sea (Rufino et al. 2006).

Aspitrigla cuculus, which feeds almost exclusively on necto-benthic invertebrates, may be considered a “specialist feeder”, in line with the literature (Colloca et al. 1994, 2010; Morte et al. 1997). In contrast, C. lucerna, which feeds mostly on epibenthic crustacea and nectobenthic teleost fish; and E. gurnardus which feeds on a mixed diet of epibenthic, bentho-pelagic and nectobenthic preys may both be considered “opportunistic predators”, according to the literature (Colloca et al. 1994, 2010; Morte et al. 1997; Montanini et al. 2010). These characteristics, allowing them to be able to feed opportunistically, would be typical for fish such as C. lucerna and E. gurnardus that live principally in nearshore waters where the relative abundance of the different prey types varies with temperature and habitat type (Schafer et al. 2002).

A possible diet competition was recorded between A. cuculus and E. gurnardus (C > 0.65) only, while C. lucerna showed food resource partitioning. However, our data suggests that prey item distribution, predator size range and depth distribution are the main variables affecting trophic niche breadth and, hence, the relative differences encountered among the gurnards species. Therefore, the three species inhabit overlapping geographic areas, but may occupy different depth ranges and microhabitats within their shared distribution.

Intra-specific variation in diet

At critical sizes of sexual maturity (Vallisneri et al. 1997) for the diet of each ontogenetic group (juvenile and adult) of Aspitrigla cuculus, Chelidonichthys lucerna and Eutrigla gurnardus.

| A. cuculus | C. lucerna | E. gurnardus |
|------------|------------|-------------|
| **Bi** | **H'** | **J'** | **Bi** | **H'** | **J'** | **Bi** | **H'** | **J'** |
| Juveniles | 0.14 | 1.04 | 0.53 | 0.06 | 1.20 | 0.38 | 0.36 | 2.24 | 0.79 |
| Adults | 0.03 | 0.77 | 0.28 | 0.07 | 2.26 | 0.56 | 0.15 | 2.09 | 0.62 |

Table III. Levins index ($B_0$), Shannon–Wiener index ($H'$), and evenness measure ($J'$) for the diet of each ontogenetic group (juvenile and adult) of Aspitrigla cuculus, Chelidonichthys lucerna and Eutrigla gurnardus.

Table IV. Morisita’s index of dietary overlap for each ontogenetic group (juvenile and adult) of Aspitrigla cuculus, Chelidonichthys lucerna and Eutrigla gurnardus.

| AspJuv | AspAdu | CheJuv | CheAdu | EutJuv | EutAdu |
|--------|--------|--------|--------|--------|--------|
| AspJuv | 1      |        |        |        |        |
| AspAdu | 0.982** | 1      |        |        |        |
| CheJuv | 0.020  | 0.008  | 1      |        |        |
| CheAdu | 0.086  | 0.077  | 0.174  | 1      |        |
| EutJuv | 0.686* | 0.596  | 0.172  | 0.291  | 1      |
| EutAdu | 0.696* | 0.647* | 0.230  | 0.589  | 0.835** | 1   |

AspJuv = juveniles of A. cuculus ≤ 110 mm; AspAdu = adults of A. cuculus > 110 mm.
CheJuv = juveniles of C. lucerna ≤ 180 mm; CheAdu = adults of C. lucerna > 180 mm.
EutJuv = juveniles of E. gurnardus ≤ 100 mm; EutAdu = adults of E. gurnardus > 100 mm.

** = intra-specific overlap; * = inter-specific overlap.
(110 mm for _A. cuculus_; 180 mm for _C. lucerna_; 100 for _E. gurnardus_), the gurnard species migrate to greater depths and change dietary habits, increasing the variety of food items eaten, according to the literature for other Mediterranean areas (Moreno-Amich 1992; Colloca et al. 1994; Boudaya et al. 2008). The trophic niches occupied were different in spatial distribution but not in terms of prey-item composition. In fact, the predominant prey of the three species (for juveniles and adults), consisted of Crustacea.

An ontogenetic dietary shift found for all species examined indicated that the number of prey items in the gut increased with increasing predator body size. Ontogenetic dietary shifts are often explained as a reflection of the changing abilities of fish; essentially, as fish grow they become more proficient at handling larger prey, which are more profitable. Increasing prey size usually leads to taxonomic changes in the diet. Migratory patterns associated with reproduction and feeding patterns have also been reported for gurnards, and the occupation of new niches may result in differences in diet (Papaconstantinou 1983; Colloca et al. 1994). The demersal migration undertaken by adults allows them to feed on a larger variety of prey species (more than twice the number found in the diet of juveniles). The higher number of different items consumed by adult as compared to juvenile individuals does not, however, correspond to a higher diversity index. In fact, this index value is high only in the case of _C. lucerna_, while in the case of _E. gurnardus_ and _A. cuculus_ diversity values are greater in juveniles, a finding that highlights species-specific differences. This result suggests that individual specialisation may occur within a predator population, lending support to Bolnick et al.’s conclusion (2007) that the more generalized the population, the higher the level of individual specialization, as also reported in the case of the opportunistic feeding behaviour observed for _E. gurnardus_ from the North Sea (Weinert et al. 2010). The low niche-breadth index value (\(B^s\)) showed that juvenile and adult gurnard diet was characterised by a preference for few species. _Aspittigla cuculus_ displayed low values for both niche-breadth and prey species diversity (\(H^p\) and \(J^p\)), while for adults of _C. lucerna_ and _E. gurnardus_ low niche breadth did not match with prey species diversity. These species may be considered generalist-opportunistic, even if they prey on preferred species.

No high values for intra-specific juvenile–adult difference in the trophic niche overlap index (C) were observed for _A. cuculus_ or _E. gurnardus_, indicating that both size groups feed on similar preys. In contrast, a low value for the trophic niche overlap index is reported for _C. lucerna_, showing different trophic niches colonised during growth.

These findings suggest habitat partitioning mainly at the inter-specific level, and trophic segregation/competition at the intra-specific level, in line with studies on Atlantic gurnards (Lopez-Lopez et al. 2011). According to Amorim et al. (2004), smaller _E. gurnardus_ compete for food by contest tactics whereas larger specimens predominantly scramble for food, probably because their larger body size affords them an advantage in locating, capturing and handling prey. Food resource availability depends not only on prey abundance, but also on the interaction of other factors, including prey size, micro-distribution, capture success and speed of movement.

**Conclusion**

In brief, our data suggest, at the inter-specific level, the possibility that _A. cuculus_ and _E. gurnardus_ may compete for the same prey resources while _C. lucerna_ showed food resource partitioning, but it should be considered that _A. cuculus_ is a “specialist predator” in contrast to _E. gurnardus_ and _C. lucerna_ which are “generalist-opportunistic predators”. At the intra-specific level, our data suggest a high dietary overlap between juveniles and adults of _A. cuculus_ and between juveniles and adults of _E. gurnardus_, while we found resource partitioning between juveniles and adults of _C. lucerna_ that change from preying on crustaceans to a piscivorus diet. However, according to Schafer et al. (2002), various factors including depth and micro-habitat can influence the distribution and composition of prey items; thus, even the most fine-scale habitat partitioning may reduce inter- and intra-specific competition through differential niche utilisation.

In conclusion, the existence of “fish strategies” tending to partition food resources and feeding areas are essential in minimising the effects of possible competition for the most desirable prey and for the co-existence of the species, and therefore they should be considered in developing adequate fishery management practices.

**Acknowledgements**

We are grateful to Prof. Corrado Piccinetti, working for the Laboratory of Marine Biology and Fisheries of the University of Bologna, who organised haul fish sampling in the study area and made this research possible.
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## Appendix

### Diet overlap among Mediterranean gurnards

| Species                        | Aspitrigla cuculus | Chlidonichthys lucerna | Eutrigla gurnardus |
|-------------------------------|-------------------|------------------------|--------------------|
|                               | %Cn   | %Cw   | %IRI | %Cn   | %Cw   | %IRI | %Cn   | %Cw   | %IRI | %Cn   | %Cw   | %IRI |
| CRUSTACEA                     |       |       |      |       |       |      |       |       |      |       |       |      |
| Lophogastrida                 | 97.62 | 96.35 | 99.12 | 92.61 | 90.51 | 97.92 | 78.03 | 56.15 | 83.38 | 99.52 | 78.03 | 56.15 |
| Lophogaster typicus           | 62.96 | 74.11 | 97.08 | 83.64 | 68.95 | 97.81 | 0.22  | 0.03  | <0.01 | 21.7  | 47.6  | 16.17 |
| Decapoda                      |       |       |      |       |       |      |       |       |      |       |       |      |
| Gonioplectronicidae           | 31.48 | 26.18 | 20.06 | 24.56 | 43.81 | 21.64 | 98.21 | 96.65 | 99.91 | 82.38 | 75.87 | 95.76 |
| Philocheras bipinnatus        | 72.34 | 74.11 | 97.08 | 83.64 | 68.95 | 97.81 | 0.29  | 0.03  | 0.01  | 21.7  | 47.6  | 16.17 |
| Liocarcinus depurator         | 31.48 | 26.18 | 20.06 | 24.56 | 43.81 | 21.64 | 98.21 | 96.65 | 99.91 | 82.38 | 75.87 | 95.76 |
| Liocarcinus sp.               | 61.21 | 16.51 | 79.99 | 4.59  | 0.16  | 0.63  | 0.27  | 0.04  | 0.01  | 13.87 | 13.72 | 8.08  |
| Philocheras echinulatus       |       |       |      |       |       |      |       |       |      |       |       |      |
| Philocheras trispinosus       | 2.13  | 1.81  | 0.11  | 1.15  | 2.00  | 0.06  | 4.4   | 16.62 | 1.75  | 11.59 | 20.91 | 7.34  |
| Squilla mantis                |       |       |      |       |       |      |       |       |      |       |       |      |
| Corystes casiridilus          |       |       |      |       |       |      |       |       |      |       |       |      |
| Munida sp.                    |       |       |      |       |       |      |       |       |      |       |       |      |
| Pontopilia sp.                |       |       |      |       |       |      |       |       |      |       |       |      |
| Pontophila spinosus           |       |       |      |       |       |      |       |       |      |       |       |      |
| Callinassia sp.               |       |       |      |       |       |      |       |       |      |       |       |      |
| Jaxea nocturna                |       |       |      |       |       |      |       |       |      |       |       |      |
| Philocheras echinulatus       |       |       |      |       |       |      |       |       |      |       |       |      |
| Philocheras trispinosus       | 2.13  | 7.94  | 0.35  | 0.46  | 0.58  | 0.01  | 0.03  | 0.04  | <0.01 | 0.11  | 0.05  | <0.01 |
| Ebalia sp.                    |       |       |      |       |       |      |       |       |      |       |       |      |
| Ebalia granulosa              |       |       |      |       |       |      |       |       |      |       |       |      |
| Chlorotocus crassicornis      | 2.13  | 8.14  | 0.36  | 0.46  | 1.08  | 0.01  | 0.11  | 0.05  | <0.01 | 0.27  | 0.47  | <0.01 |
| Plecostoma sp.                |       |       |      |       |       |      |       |       |      |       |       |      |
| Prionoidea denticulata        |       |       |      |       |       |      |       |       |      |       |       |      |
| Macroopus tuberculatus        |       |       |      |       |       |      |       |       |      |       |       |      |
| Liocarcinus maculatus         |       |       |      |       |       |      |       |       |      |       |       |      |
| Liocarcinus cornutus           |       |       |      |       |       |      |       |       |      |       |       |      |
| Liocarcinus vernalis          |       |       |      |       |       |      |       |       |      |       |       |      |
| Galathea intermedia           |       |       |      |       |       |      |       |       |      |       |       |      |
| Galathea dispersa             |       |       |      |       |       |      |       |       |      |       |       |      |
| Galathea sp.                  |       |       |      |       |       |      |       |       |      |       |       |      |
| Gonioplectronicidae           |       |       |      |       |       |      |       |       |      |       |       |      |
| Gonioplectronicidae           |       |       |      |       |       |      |       |       |      |       |       |      |
| (Continued)                   |       |       |      |       |       |      |       |       |      |       |       |      |
|                         | Aspitrigla cuculus |                         | Chlidonichthys lucerna |                         | Eutrigla gurnardus |                         |
|-------------------------|-------------------|-------------------------|------------------------|------------------------|-------------------|------------------------|
|                         | %Cn | %Cw | %IRI | %Cn | %Cw | %IRI | %Cn | %Cw | %IRI | %Cn | %Cw | %IRI | %Cn | %Cw | %IRI | %Cn | %Cw | %IRI |
| Brachynotus sp.         |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Pisidia sp.             |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Pisidia longimana       |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Parapeneaus longirostris|     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Penaeus kerathurus       |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Pachygrapsus marmoratus |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Processa medica          |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Mysida                  |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Acanthomysis longicornis|     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Gastroacaeus sanctus     |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Gastroacaeus sp.         |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Stomatopoda             |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Spulla mantis           |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Isopoda                 |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Tanaidaceae             |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Euphausiacea             |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Meganyctiphanes norvegica|     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Amphipoda               |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Ampelisca sp.           |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Leucothoe sp.           |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Cumacea                 |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| TELEOSTEI               |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Clupeiformes            |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Euphausiidae            |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Perciformes             |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Gobius niger            |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Lesueurigobius friesi   |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Cepola rubescens        |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Lesueurigobius suerii   |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Callionymus sp.         |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Gobius sp.              |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Clupeonelius sp.        |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Delenentoops squamosus   |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Pomatoschistus minutus   |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Serranus hepatus        |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Callionymus nico        |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Gadiformes              |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Trisopterus minutus     |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Merlangius merlangus    |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |
| Merluccius merluccius   |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |     |     |      |

(Continued)
(Continued).

|                     | Aspitrigla cuculus | Chelidonichthys lucerna | Eutrigla gurnardus |
|---------------------|---------------------|-------------------------|---------------------|
|                     | Juveniles | Adults | Juveniles | Adults | Juveniles | Adults | Juveniles | Adults | Juveniles | Adults | Juveniles | Adults |
| %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI | %Cn %Cw %IRI |
| **Gaidropsarus biscayensis** | – – – | 0.03 0.99 < 0.01 | 0.17 0.09 < 0.01 | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Pleuronectiformes** | – – – | 0.05 0.74 < 0.01 | 0.27 1.41 < 0.01 | – – – | – – – | – – – | – – – | – – – | 1.04 11.8 0.14 | – – – | – – – |
| **Arnoglossus laterna** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Microchirus variagatus** | – – – | 0.03 0.33 < 0.01 | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **MOLLUSCA** | – – – | 1.08 0.34 0.03 | 4.18 0.6 0.57 | 1.1 0.49 0.06 | 2.95 0.45 0.31 | – – – | – – – | – – – | – – – | – – – | – – – |
| **Gaidropsarus biscayensis** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Pleuronectiformes** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **MOLLUSCA** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Gaidropsarus biscayensis** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Pleuronectiformes** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **MOLLUSCA** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Gaidropsarus biscayensis** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Pleuronectiformes** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **MOLLUSCA** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Gaidropsarus biscayensis** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Pleuronectiformes** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **MOLLUSCA** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Gaidropsarus biscayensis** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Pleuronectiformes** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **MOLLUSCA** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Gaidropsarus biscayensis** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |
| **Pleuronectiformes** | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – | – – – |

**Diet overlap among Mediterranean gurnards**