

Feeding habits, seasonal and ontogenetic diet shift of blacktail comber, *Serranus atricauda* (Pisces: Serranidae), from the Azores, north-eastern Atlantic

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Abstract

The stomach contents of 422 *Serranus atricauda*, sampled between June 1993 and September 1994 in the Azores (north-eastern Atlantic), were examined. Fishes and crustaceans were the main contents with gastropods, bivalves and salps uncommon. Mysids (*Siriella jaltensis*) and *Tripterygion delaisi* were the most frequent prey items followed by *Capros aper*, *Parablennius* spp., *Alpheus* spp. and *Xantho* sp. The type and quantity of food ingested changed over season. *S. atricauda* are generalists that can feed opportunistically on alternative prey. They are diurnal predators. Ontogenetic differences were found in the diet composition and feeding activity within the range of sizes studied. There was a significant positive relation between mean prey width and predator size. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Stomach contents; Blacktail comber; *Serranus atricauda*; Seasonal changes; Diel patterns; Ontogenetic changes

1. Introduction

Serranids are carnivorous fishes that live near the bottom in littoral and sub-littoral zones of tropical and temperate seas. They play an important role in coastal marine ecosystems where they are active predators of a number of fishes, crustaceans and cephalopods (Heemstra and Randall, 1993; Tuset et al., 1996; Labropoulou and Eleftheriou, 1997; Barreiros and Santos, 1998). Blacktail comber, *Serranus atricauda* (Günther, 1874), is a serranid fish that lives on rocky bottoms, from the shallow subtidal down to about 90 m depth. Its distribution extends from the Bay of

Biscay (north-eastern Atlantic) southward to Mauritania and around the Azores, Madeira and Canaries archipelagos, the Mediterranean coast of Morocco, Algeria, southern Spain, and occasionally southern France (Tortonese, 1986). Blacktail comber is a hermaphrodite, which in the Azores matures at about 250 mm total length (TL) and spawns from July to September (Lourinho, 1998). Maturation length corresponds to about 4 years of age (Costa, 1997).

Around the Azores there is considerable recreational and semi-subsistence fishing with rod and line or handline from the shore and close inshore from small boats, as well as considerable use of coastal nets and spear-fishing activity (Santos et al., 1995). Blacktail comber is one of the serranids targeted by these fisheries. In spite of its relative abundance and importance to fisheries, information on the biology and

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ecology of this species is not available. This study was undertaken to provide information on the feeding ecology of blacktail comber. The basic components of the diet as well as seasonal, diel and size related variability in feeding behaviour were examined.

2. Material and methods

2.1. Sampling

Blacktail comber was sampled around Faial and Pico islands, in the central group of the archipelago of the Azores (north-eastern Atlantic). A total of 422 fish were collected between June 1993 and September 1994, between 5 and 25 m depth. The individuals were collected by spear gun to eliminate the regurgitation of stomach contents caused by stress and the evagination of the stomachs that occurs when individuals are caught by hook. Disrupted stomachs were discarded. The TL of the 422 fishes ranged from 15 to 46 cm.

In the laboratory, immediately after capture, the fishes were measured (TL) and weighed. The digestive tract was removed and the stomach fullness recorded using a semi-quantitative scale. The weight of the stomach contents was obtained by subtracting the weight of the empty stomach from the total stomach weight. Stomach contents were fixed in 4% buffered formalin and preserved in 70% alcohol.

Stomach contents were identified to the lowest possible taxon. In order to minimise the underestimation of small and soft prey, utmost care was given to the identification of even small fragments. Prey items were weighed to the nearest 0.01 g after removing the surface water, and when undigested items were found, their lengths were measured according to each group standard measure.

2.2. Diet analysis

The cumulative trophic diversity (Hurtubia, 1973), measured by the Shannon index (as $H' = -\sum P_i \log P_i$, where P_i is the proportion of individuals in the i th species), was calculated to determine if sample size was adequate. The percent of empty stomachs and stomach content weight, as a percent of fish body weight (repletion index — RI), was used to evaluate

the feeding activity of fish. For diet analysis, the percent frequency of occurrence (%FO), percent of numerical abundance (%N) and percent of total weight (%W) of prey categories were calculated (see Hyslop (1980)).

Seasonal changes in the diet and in feeding activity were analysed by partitioning the time covered into five periods: June–August 1993 ($n=123$); September–November 1993 ($n=78$); December 1993–February 1994 ($n=39$); March–May 1994 ($n=93$) and June–August 1994 ($n=89$). Diel feeding periodicity was examined only for June–August 1994 (because of the differences in photoperiod) and was assessed by calculating the RI. The data were grouped in seven periods: 6–8 h ($n=6$); 9–11 h ($n=13$); 11–13 h ($n=14$); 14–16 h ($n=13$); 17–19 h ($n=18$); 20–22 h ($n=12$); 23–01 h ($n=13$). Ontogenetic variation in diet was examined by grouping fish lengths in five size classes (mm, TL): 150–199 ($n=27$); 200–249 ($n=165$); 250–299 ($n=134$); 300–349 ($n=61$) and 350–460 ($n=35$). Predator–prey size relation was examined using the predator size classes described above and prey width. This last measure is known to be superior to prey length for defining size relation in trophic dynamics analysis (Pearre, 1986). Predator–prey size relations were tested by simple linear regression between mean prey width and predator size (Zar, 1996).

3. Results

3.1. Diet composition

The curve of cumulative trophic diversity converges to an asymptote at 70–80 stomachs suggesting that the number of individuals analysed was sufficient to describe the diet of blacktail comber in Azorean waters.

From the 259 stomachs with contents, 1819 prey belonging to five groups (fish, crustaceans, bivalves, gastropods, thaliaceans) were identified (Table 1). Fish and crustaceans were the most important groups. The former dominated by weight, the latter by number. The food of blacktail comber consisted of at least 47 different species (Table 1). The mysids, *Siriella jaltensis* (%FO=26.0), and the small benthic fish, *Trip-terygion delaisi* (%FO=22.9), were the most frequent prey items. Other fish prey found included *Capros*

Table 1

Number (*n*), percent of number (%*N*) and weight (%*W*), occurrence (*O*) and percent of frequency of occurrence (%*FO*) calculated for each prey item in the diet of *S. atricauda*

Prey items	<i>n</i>	% <i>N</i>	% <i>W</i>	<i>O</i>	% <i>FO</i>
Algae	1	0.1	0.0	1	0.4
Sipuncula	1	0.1	0.1	1	0.4
Gastropoda					
<i>Haliotis coccinea</i>	8	0.4	1.8	8	3.1
<i>Calliostoma</i> sp.	2	0.1	0.0	1	0.4
<i>Alvania</i> sp.	1	0.1	0.0	1	0.4
<i>Columbella adansoni</i>	1	0.1	0.2	1	0.4
<i>Diacria trispinosa</i>	1	0.1	0.0	1	0.4
Bivalvia					
<i>Chlamys</i> sp.	1	0.1	0.0	1	0.4
<i>Mantellum hians</i>	7	0.4	0.1	6	2.3
<i>Mantellum</i> sp.	5	0.3	0.0	4	1.5
Crustacea					
Natantia					
<i>Pandalina brevirostris</i>	1	0.1	0.2	1	0.4
<i>Athanas nitescens</i>	1	0.1	0.0	1	0.4
<i>Alpheus dentipes</i>	18	1.0	0.5	13	5.0
<i>Alpheus macrocheles</i>	3	0.2	0.4	3	1.2
<i>Alpheus</i> spp.	6	0.3	0.2	5	1.9
Unidentified Penaeidae	1	0.1	0.0	1	0.4
Unidentified Caridae	1	0.1	0.0	1	0.4
Unidentified Natantia	12	0.7	0.2	12	4.6
Reptantia					
<i>Scyllarus arctus</i>	3	0.2	0.6	3	1.1
<i>Dardanus arrosor</i>	1	0.1	0.5	1	0.4
<i>Galathea squamifera</i>	8	0.4	1.1	8	3.1
<i>Galathea</i> sp.	3	0.2	0.5	3	1.1
<i>Dromia marmorea</i>	1	0.1	0.3	1	0.4
<i>Inachus leptochirus</i>	1	0.1	0.0	2	0.8
<i>Achaeus cranchii</i>	1	0.1	0.0	1	0.4
<i>Acanthonyx lunulatus</i>	5	0.3	0.5	4	1.5
<i>Pisa nodipes</i>	1	0.1	0.1	1	0.4
<i>Macropipus depurator</i>	1	0.1	0.5	1	0.4
<i>Pilumnus vilosissimus</i>	6	0.3	2.9	5	1.9
<i>Pilumnus</i> sp.	1	0.1	0.3	1	0.4
<i>Xantho incisus</i>	9	0.5	2.9	9	3.4
<i>Xantho</i> sp.	6	0.3	0.6	6	2.3
<i>Pachygrapsus maurus</i>	7	0.4	1.6	6	2.3
<i>Pachygrapsus</i> sp.	2	0.1	0.1	2	0.8
<i>Percnon gibbesi</i>	7	0.4	3.9	7	2.7
Unidentified Brachyura	8	0.4	0.5	8	3.1
Unidentified Decapoda	1	0.1	0.0	1	0.4
Mysidacea					
<i>Siriella jaltensis</i>	1158	63.7	1.1	68	26.0
Isopoda					
Flabelifera	7	0.4	0.0	5	1.9
Amphipoda					
Gammaridae	34	1.9	0.1	8	3.1
Unidentified Crustacea	11	0.6	0.3	10	3.8

Table 1 (Continued)

Prey items	<i>n</i>	% <i>N</i>	% <i>W</i>	<i>O</i>	% <i>FO</i>
Thaliacea					
<i>Salpa</i> sp.	59	3.2	1.1	9	3.4
Pisces					
<i>Gaidropsarus guttatus</i>	2	0.1	0.4	2	0.8
<i>Capros aper</i>	36	2.0	20.7	17	6.5
<i>Scorpaena maderensis</i>	3	0.2	8.5	3	1.2
<i>Mullus surmuletus</i>	3	0.2	0.0	1	0.4
<i>Coris julis</i>	2	0.1	5.2	2	0.8
<i>Tripterygion delaisi</i>	132	7.3	5.7	60	22.9
<i>Coryphoblennius galerita</i>	2	0.1	0.2	2	0.8
<i>Lipophrys pholis</i>	1	0.1	0.3	1	0.4
<i>Lipophrys trigloides</i>	1	0.1	0.2	1	0.4
<i>Ophioblennius atlanticus</i>	1	0.1	5.4	1	0.4
<i>Parablennius incognitus</i>	14	0.8	1.3	13	5.0
<i>Parablennius ruber</i>	15	0.8	8.4	14	5.3
<i>Diplecogaster bimaculata</i>	5	0.3	0.2	5	1.9
Unidentified <i>Gobiesocidae</i>	2	0.1	0.1	2	0.8
<i>Sphoeroides marmoratus</i>	1	0.1	0.1	1	0.4
Unidentified Pisces	184	9.9	19.9	114	43.5
Stomach with contents	260				

aper (%FO=6.5), *Parablennius ruber* (%FO=5.3) and *P. incognitus* (%FO=5.0). The most frequent decapods found included the reptantians *Xantho incisus* (%FO=3.4), *Galathea squamifera* (%FO=3.1), *Percnon gibbesi* (%FO=2.7), and the natant *Alpheus dentipes* (%FO=5.0). Salps were a numerous prey but occurred in a small number of stomachs (%FO=3.4). Amphipods, isopods, gastropods and bivalves were uncommon.

3.2. Seasonal changes in diet and in feeding activity

Feeding activity, as indicated by the number of empty stomachs (Fig. 1), varied over the year. Percent of empty stomachs was highest for December–February (59.0%) and lowest for June–August 1993 and June–August 1994 (31.5 and 22.5%, respectively). RI also varied over season but showed somewhat different trends, being highest for March–May and lowest for June–August 1993, June–August 1994 and December 1993–February 1994 (Fig. 1).

In terms of seasonal diet composition (Table 2), mysids were very frequent in June–August, both in 1993 (%FO=27.1) and 1994 (%FO=30.4), and infrequent in all other periods. During these periods, crustaceans dominated the diet by number and fish

by weight. In the other three periods, fish dominated the diet by number, weight and frequency of occurrence, whereas crustaceans, mainly decapods, were the second most important group. The fish species, *T. delaisi*, were the most frequent prey from June 1993 to February 1994 (%FO>25). The frequency of occurrence of this prey item were lower in the other two periods (%FO<10). Salps (%FO=15.4) and the fish species, *C. aper* (%FO=28.9), were only frequent from March to May. All the other prey items showed similar occurrences in all periods.

3.3. Diel pattern of feeding activity

Feeding activity varied throughout the day (Fig. 2). Values of RI increased gradually after sunrise (about 7 h), peaked at about 15 h, then declined throughout the afternoon and evening until just prior to midnight.

3.4. Ontogenetic changes

Percentage of empty stomachs increased with fish size, being about 30% for individuals with less than 300 mm, and about 50% for fish with more than 300 mm (Fig. 3). Mean RI also increased with fish size, from 0.6 (150–199 mm) to 1.1 (350–460 mm).

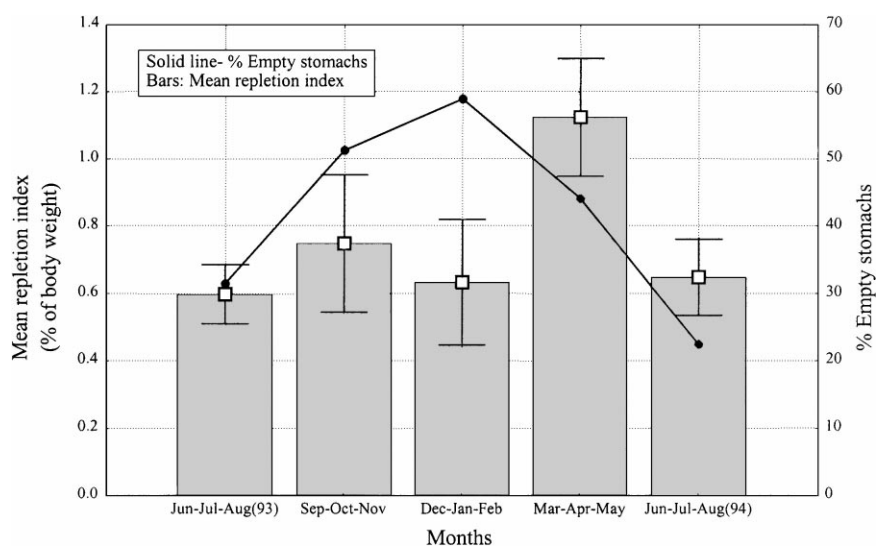


Fig. 1. Repletion index over one year. Error bars show standard error of means.

Table 2

Percentages of the frequency of occurrence (%FO) by season and predator size (mm)

Prey items	Season					Predator length class (mm)				
	JJA ^a 1993	SON ^b 1993	DJF ^c 1993/1994	MAM ^d 1994	JJA 1994	150–199	200–249	250–299	300–349	>350
Algae	0.0	2.6	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Sipuncula	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Gastropoda										
<i>Haliotis coccinea</i>	3.5	2.6	6.3	3.9	1.5	0.0	1.9	3.2	11.1	0.0
<i>Calliostoma</i> sp.	0.0	0.0	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0
<i>Alvania</i> sp.	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
<i>Columbella adansoni</i>	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	5.9
<i>Diacria trispinosa</i>	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	5.9
Bivalvia										
<i>Chlamys</i> sp.	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	5.9
<i>Mantellum hians</i>	3.5	0.0	0.0	0.0	4.4	5.3	0.0	4.3	3.7	0.0
<i>Mantellum</i> sp.	1.2	0.0	0.0	1.9	1.5	0.0	0.9	1.1	7.4	0.0
Crustacea										
Natantia										
<i>Pandalina brevirostris</i>	0.0	0.0	0.0	1.9	0.0	0.0	0.9	0.0	0.0	0.0
<i>Athanas nitescens</i>	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
<i>Alpheus dentipes</i>	5.9	5.3	6.3	3.9	2.9	0.0	7.5	3.2	7.4	0.0
<i>Alpheus macrocheles</i>	2.4	0.0	0.0	1.9	0.0	5.3	0.9	1.1	0.0	0.0
<i>Alpheus</i> spp.	3.5	0.0	0.0	3.9	0.0	0.0	3.7	1.1	0.0	0.0
Unidentified Penaeidae	1.2	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Unidentified Caridae	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Unidentified Natantia	8.2	3.3	0.0	3.9	1.5	21.1	5.6	1.1	3.7	0.0
Reptantia										
<i>Scyllarus arctus</i>	0.0	5.3	0.0	1.9	0.0	0.0	0.9	1.1	3.7	0.0
<i>Dardanus arrosor</i>	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	5.9

Table 2 (Continued)

Prey items	Season					Predator length class (mm)				
	JJA ^a 1993	SON ^b 1993	DJF ^c 1993/1994	MAM ^d 1994	JJA 1994	150–199	200–249	250–299	300–349	>350
<i>Galathea squamifera</i>	2.4	0.0	12.5	5.8	1.5	0.0	1.9	3.2	11.1	0.0
<i>Galathea</i> sp.	0.0	0.0	0.0	5.8	0.0	0.0	1.9	0.0	3.7	0.0
<i>Dromia marmorea</i>	0.0	0.0	6.3	0.0	0.0	0.0	0.0	1.1	0.0	0.0
<i>Inachus leptochirus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
<i>Achaeus cranchii</i>	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
<i>Acanthonyx lunulatus</i>	3.5	0.0	0.0	0.0	1.5	5.3	1.9	1.1	0.0	0.0
<i>Pisa nodipes</i>	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
<i>Macropipus depurator</i>	0.0	2.6	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
<i>Pilumnus vilosissimus</i>	1.2	0.0	0.0	0.0	5.8	0.0	0.0	1.1	11.1	5.9
<i>Pilumnus</i> sp.	0.0	2.6	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
<i>Xantho incisus</i>	3.5	2.6	0.0	3.9	4.4	0.0	3.7	2.2	3.7	11.8
<i>Xantho</i> sp.	4.7	0.0	0.0	0.0	2.9	5.3	0.9	2.2	7.4	0.0
<i>Pachygrapsus maurus</i>	4.7	0.0	0.0	0.0	2.9	0.0	1.9	4.3	0.0	0.0
<i>Pachygrapsus</i> sp.	0.0	0.0	0.0	1.9	1.5	0.0	0.0	2.2	0.0	0.0
<i>Percnon gibbesi</i>	1.2	7.9	0.0	0.0	4.4	0.0	0.9	4.3	7.4	0.0
Unidentified Brachyura	3.5	5.3	6.3	1.9	1.5	0.0	4.7	3.2	0.0	0.0
Unidentified Decapoda	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Mysidacea										
<i>Siriella jaltensis</i>	27.1	5.3	6.3	3.9	30.4	42.1	24.3	15.1	3.7	0.0
Isopoda										
Flabellifera	3.5	0.0	0.0	1.9	1.5	5.3	1.9	1.1	3.7	0.0
Amphipoda										
Gammaridae	5.9	2.6	0.0	0.0	2.9	10.5	3.7	1.1	3.7	0.0
Unidentified Crustacea	2.4	2.6	0.0	5.8	5.8	5.3	4.7	2.2	3.7	5.9
Thaliacea										
<i>Salpa</i> sp.	1.2	0.0	0.0	15.4	0.0	0.0	2.8	4.3	3.7	5.9
Pisces										
<i>Gaidropsarus guttatus</i>	0.0	0.0	0.0	0.0	2.9	0.0	0.9	1.1	0.0	0.0
<i>Capros aper</i>	0.0	2.6	6.3	28.9	0.0	0.0	1.9	6.5	14.8	29.4
<i>Scorpaena maderensis</i>	2.4	0.0	0.0	1.9	0.0	0.0	0.0	2.2	0.0	5.9
<i>Mullus surmuletus</i>	1.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
<i>Coris julis</i>	1.2	0.0	0.0	0.0	1.5	0.0	0.0	1.1	3.7	0.0
<i>Tripterygion delaisi</i>	32.9	42.1	25.0	9.6	8.7	42.1	27.1	18.3	18.5	5.9
<i>Coryphoblennius galerita</i>	1.2	0.0	0.0	0.0	1.5	0.0	0.9	1.1	0.0	0.0
<i>Lipophrys pholis</i>	0.0	0.0	0.0	0.0	1.5	0.0	0.0	1.1	0.0	0.0
<i>Lipophrys trigloides</i>	0.0	0.0	0.0	0.0	1.5	0.0	0.0	1.1	0.0	0.0
<i>Ophioblennius atlanticus</i>	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	3.7	0.0
<i>Parablennius incognitus</i>	7.1	2.6	6.3	0.0	7.3	5.3	5.6	5.4	0.0	5.9
<i>Parablennius ruber</i>	1.2	5.3	12.5	5.8	8.7	0.0	3.7	7.5	0.0	17.6
<i>Diplecogaster bimaculata</i>	0.0	0.0	0.0	7.7	0.0	0.0	2.8	1.1	3.7	0.0
Unidentified <i>Gobiesocidae</i>	1.2	0.0	0.0	1.9	0.0	0.0	0.0	2.2	0.0	0.0
<i>Sphoeroides marmoratus</i>	0.0	2.6	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Unidentified Pisces	37.7	57.9	37.5	40.4	44.9	31.6	41.1	49.5	37.0	47.1
Stomach with contents	85	38	16	52	69	19	104	93	27	17

^a JJA: June–July–August.^b SON: September–October–November.^c DJF: December–January–February.^d MAM: March–April–May.

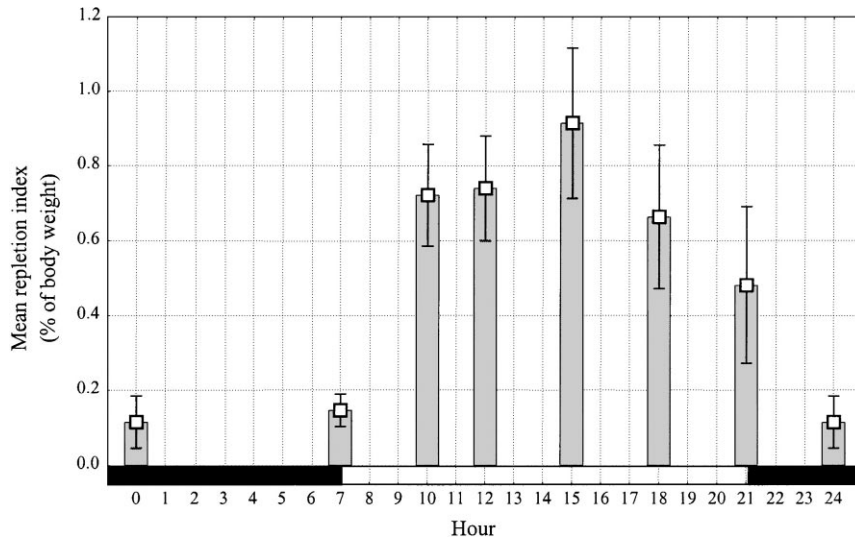


Fig. 2. Diel feeding activity as determined from changes in the mean repletion index. Open and solid portions of horizontal bars represent light and dark hours during the sampling period. Error bars show standard error of means.

Diet composition was relatively homogeneous among size groups, with fish and crustaceans composing most of the total food (Table 2). However, the consumption of some prey items vary with fish size. The consumption of the fish prey, *T. delaisi*, the amphipods, the mysids and the reptantians, *Acanthonyx lunulatus*, apparently decreased with blacktail

comber size. An apparent increase in consumption of the fish prey, *C. aper*, the salps and the reptantians, *G. squamifera*, was observed with increasing fish length.

Prey width data were plotted against total length of blacktail comber (Fig. 4). The lower limit of prey width remained at almost the same level, but the upper

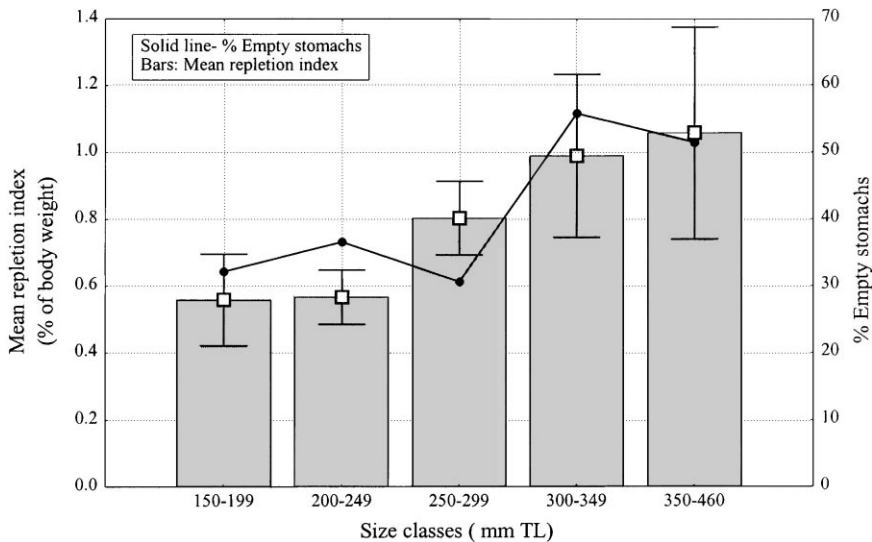


Fig. 3. Values calculated for mean repletion index for different size classes. Error bars show standard error of means.

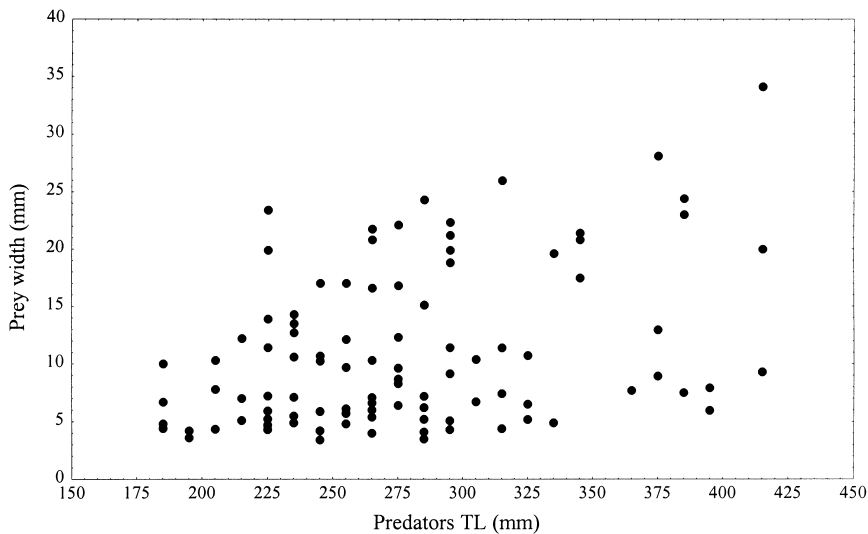


Fig. 4. Scatter-plot expressing the relationship between prey width ($n=126$) and total length (TL) of *S. atricauda*.

limit increased with fish size, with an overall prey width range of 3.4–34.1 mm. Mean prey width increased as the fish grew with a significant positive linear relation between mean prey width and predator's TL ($r^2=0.71$; $P<0.001$).

4. Discussion

This study indicates that blacktail comber of the Azores feed primarily on benthic and epibenthic organisms like fishes, particularly *T. delaisi*, mysids and crustacean decapods. Similar results were reported for congeneric species like *S. scriba* from the Gulf of Palermo (Italy, Mediterranean Sea) by Arculeo et al. (1993), and *S. cabrilla* from the Canary Island (Spain, central East Atlantic) by Tuset et al. (1996). The high diversity of prey items found in the stomachs suggests that the blacktail comber is a generalist predator. The occurrence of *Scorpaena maderensis*, a carnivorous fish, in the stomach points to the high trophic position of blacktail comber in the rocky littoral food web.

Blacktail comber shows seasonal differences in diet composition. The observed selection for some prey items coincides with an increased abundance of these groups in the environment, as reported by Raymont (1983) to the mysids, by Ménard et al. (1994) to salps,

and by Borges (pers. comm., IPIMAR, Lisboa, Portugal) to *C. aper*. Blacktail comber responds to seasonal changes in food availability, which reflects the opportunistic behaviour and the trophic adaptability of this predator.

The mean RI showed significant changes during the year, being high from March to May and low from December to February. However, there is no apparent relation between feeding activity and reproduction or water temperature, suggesting that the observed variation of the RI throughout the year may reflect the type of prey ingested, more than any biotic or abiotic factor.

Blacktail comber is a diurnal predator, influenced by light intensity. Diel feeding activity increased gradually after sunrise (about 07 h), peaked after mid-day (about 15 h) and then declined throughout the afternoon and evening until just prior to midnight. According to Eggers (1977) this is a typical behaviour of size-selective predators that rely on visual cues.

Ontogenetic differences on feeding activity and diet composition were observed for fishes ranging in length from 150 to 460 mm TL. As the blacktail comber grows, the consumption of several small prey items, like amphipods, mysids (when available) and the fish species *T. delaisi* decrease, while the consumption of larger prey, like *C. aper* (when available) or *G. squamifera*, increase. Thus, ontogenetic differ-

ences on diet composition may reflect a size preference for larger prey as the predator grows. On the other hand, the small blacktail comber feeds mainly on cryptic and benthic species (*T. delaisi*), while larger blacktail comber preys also on benthopelagic and pelagic species (*C. aper*, salps and the pelagic gastropod, *Diacria trispinosa*). Nevertheless, this simplified description suggests that younger individuals depend mainly on bottom species, while larger blacktail comber can also prey at the water column on benthopelagic species. The amount of food ingested, as shown by the RI, also increases with fish size. This suggests that larger individuals consumed heavier prey, thus maximising the energetic gain relative to capture effort. The range of prey size increased with fish body size. While the upper bound increased with predator size, the minimum prey size remained constant. Similar results were described for several fish species (e.g. Ware, 1972) and may indicate that large predators can utilise all of the resources, ranging from smaller food items to larger prey, thus giving them a competitive advantage (Brooks and Dodson, 1965).

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