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EFFECTS OF REPRODUCTIVE FACTORS ON INTERRELATIONSHIPS BETWEEN THREE DEEP WATER SHARKS FROM NORTHERN TUNISIA (CENTRAL MEDITERRANEAN)

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ABSTRACT

Three deep water sharks are known to occur in the waters off the northern Tunisian coast: the blackmouth cat-shark *Galeus melastomus* (Rafinesque, 1810), the gulper shark *Centrophorus granulosus* (Schneider, 1801) and the velvet belly *Etmopterus spinax* (Linnaeus, 1758). They all inhabit similar biotopes. Competition for food may be inferred among the three squalid species, but sufficient food is available in these areas. Moreover, morphological characteristics, such as size at first sexual maturity, maximal size, fecundity and reproductive mode, viviparity and oviparity, are different for each species. These characteristics considerably reduce the inferred competition for food in the area between the three species. They allow the three sympatric deep-water sharks to live and reproduce off northern Tunisia.

Key-words: deep water sharks, *Etmopterus spinax*, *Galeus melastomus*, *Centrophorus granulosus*, prey composition, biological factors, interrelationships, northern Tunisia, Mediterranean

EFFETTI DI FATTORI RIPRODUTTIVI SU INTERRELAZIONI TRA TRE SPECIE DI SQUALI DI ACQUE PROFONDE IN TUNISIA SETTENTRIONALE (MEDITERRANEO CENTRALE)

SINTESI

Tre specie di squali di acque profonde sono note al largo della costa settentrionale della Tunisia: il boccanera *Galeus melastomus* (Rafinesque, 1810), il centroforo *Centrophorus granulosus* (Schneider, 1801) ed il moretto *Etmopterus spinax* (Linnaeus, 1758), che occupano biotopi simili. Si può pertanto supporre una competizione per il nutrimento tra le tre specie di squalidi, benché in tali aree sia disponibile una quantità sufficiente di cibo. Inoltre, caratteri morfologici quali la taglia alla prima maturità sessuale, la taglia massima, la fecondità e la modalità di riproduzione, ovipara e vivipara, sono differenti per tali specie. Questi caratteri riducono ulteriormente la possibile competizione per il nutrimento nell'area fra queste tre specie, permettendo loro di vivere e riprodursi nelle acque al largo della Tunisia settentrionale.

Parole chiave: squali di acque profonde, *Etmopterus spinax*, *Galeus melastomus*, *Centrophorus granulosus*, composizione delle prede, fattori biologici, interrelazioni, Tunisia settentrionale, Mediterraneo

INTRODUCTION

According to Quignard & Capapé (1971), Capapé (1989) and Bradaï (2000), three deep water sharks are known to occur off the northern Tunisian coast (Fig. 1): the blackmouth catshark *Galeus melastomus* (Rafinesque, 1810), the gulper shark *Centrophorus granulosus* (Schneider, 1801) and the velvet belly *Etmopterus spinax* (Linnaeus, 1758).

They are usually caught at depths exceeding 400 m with quite unfavourable abiotic parameters and not very high biological diversity, and involve an interspecific competition pressure especially with regard to the three sympatric deep water sharks, active predators and voracious feeders as other elasmobranch species (Capapé, 1976).

Nevertheless, commercial and scientific trawlings conducted in deep waters off the northern Tunisia have shown that the three shark species are concomitantly captured together in relative abundance. Moreover, for each species, juvenile and adult males and females have been collected. Adult females bearing encapsulated eggs or embryos and different stages of development have also been examined. These records suggest that the three sympatric species are probably able to live and reproduce in the same area, although interspecific competition pressure is probably inferred and cannot be totally neglected.

In order to answer this question, two separate analyses were conducted.

The first analysis was to compare prey composition of the diet in *E. spinax*, *G. melastomus* and *C. granulosus*. Diet composition of *G. melastomus* and *C. granulosus* from off the northern Tunisian coast had been previously studied (Capapé & Zaouali, 1976; Capapé, 1985). However, little is known about food and feeding habits of *E. spinax* from the area and only general data were provided (Capapé, 1975). Further observations allow to

expand upon the previous data. In the present work, we first of all present a conventional content analysis (qualitative) of *E. spinax* from the northern Tunisian coast and examine the role of seasonal, sexual and ontogenic factors on its diet, which are compared with those of its two sympatric species.

The second analysis was to compare some aspects of the reproductive biology of sharks, which had been previously studied for the blackmouth catshark (Capapé & Zaouali, 1977; Tursi *et al.*, 1993), the gulper shark (Capapé, 1985; Golani & Pisanty, 2000) and the velvet belly (Hickling, 1963; Vacchi & Orsi Relini, 1979; Kabasakal & Unkal, 1999; Capapé *et al.*, 2001; De Madalena & Piscitelli, 2001), and to explain their role in the interrelationships between the three sympatric deep water sharks captured off northern Tunisia.

MATERIAL AND METHODS

Velvet bellies were collected by means of trawlings on the Bank of Esquerquis (northern Tunisia) and off the northern coast of Tunisia between 1978 and 1990. Of the 120 captured specimens, 43 males (27 juveniles and 16 adults) and 77 females (63 juveniles and 14 adults) were recorded. Digestive tracts were removed and examined for food items.

Two qualitative parameters were used to analyse stomach contents:

- percent of occurrence (PO) indicating the percent of stomachs with food items or with remains of food items (Tab. 1);

- frequency index of zoological group preys (FI) indicating the number of times a zoological group is found in stomach contents related to the total number of full stomach contents examined (Tab. 2).

Food items were identified at generic and specific levels when possible. Zoological groups found in *E. spinax* stomach contents are listed in Table 3.

Tab. 1: Percent of occurrence of food items in stomach contents of *Etmopterus spinax* for sex, category and season.

Tab. 1: Delež polnih želodcev morskih psov vrste *Etmopterus spinax* glede na spol, starostno kategorijo in sezono.

Sex	Males						Females						General total
Category	Juveniles			Adults			Juveniles			Adults			
Season	Sum	Win	Annual total	Sum	Win	Annual total	Sum	Win	Annual total	Sum	Win	Annual total	
Stomachs examined	14	13	27	9	7	16	32	31	63	12	2	14	120
Stomachs with food	12	10	22	7	6	13	26	27	53	10	2	12	100
Percent of occurrence	86	77	81	77	86	81	81	87	84	83	100	86	83

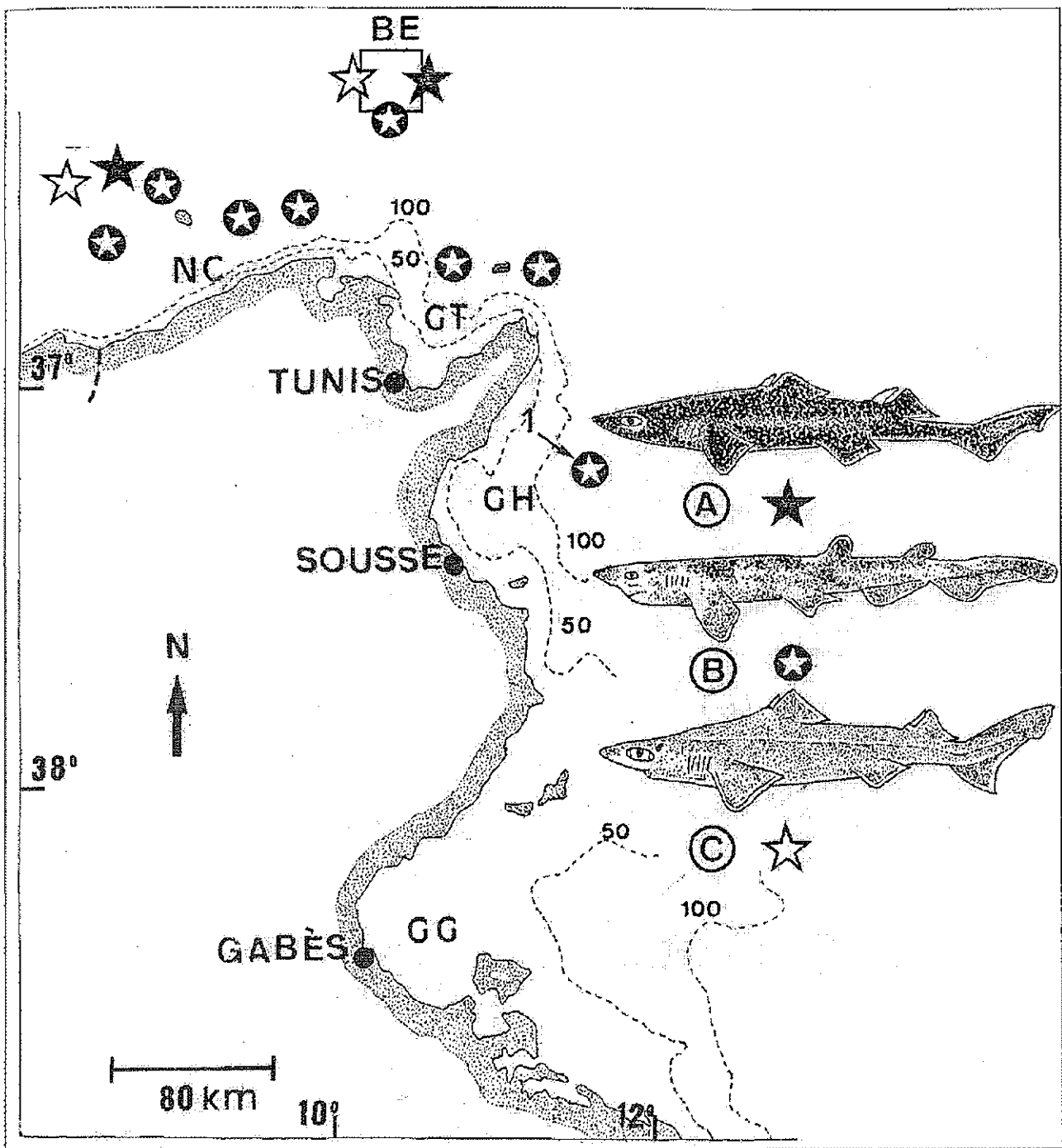


Fig. 1: Geographic distribution along the coast of Tunisia of (A) *Etmopterus spinax*, (B) *Galeus melastomus* and (C) *Centrophorus granulosus*. BE: Bank of Esquerquis, GG: Gulf of Gabès, GH: Gulf of Hammamet, GT: Gulf of Tunis, NC: Northern Coast. Arrow 1 points at the site of *G. melastomus* recorded for the first time in GH (see Bradai *et al.*, 2000).

Sl. 1: Geografska razširjenost obravnavanih morskih psov vzdolž tunizijske obale: (A) *Etmopterus spinax*, (B) *Galeus melastomus* in (C) *Centrophorus granulosus*. BE: Banc des Esquerquis, GG: Gabeški zaliv, GH: Hammameški zaliv, GT: Tuniški zaliv, NC: severna obala. Puščica 1 kaže na lokaliteto v Hammameškem zalivu, kjer je bil prvič zabeležen *G. melastomus* (glej Bradai *et al.*, 2000).

Males and females, with juveniles and adults among them, are examined separately. The specimens larger than the size at first sexual maturity, which is reached by velvet bellies in Tunisian waters at about 350 mm and 380 mm TL by males and females, respectively, were considered as adults (Capapé et al., 2001).

The specimens were grouped into seasonal categories corresponding to the period of the year when the trawling surveys were made: summer (Sum), from June to September and winter (Win), from December to February.

Tests for significance were assessed for t-test ($p < 0.01$).

RESULTS

Twenty stomachs were empty and the mean value of percent of occurrence (PO) was 83. The PO of juvenile and adult males and females had high value from 77 to 87 (Tab. 1). However, seasonal variation is not clearly evident except in juvenile males.

Crustaceans, cephalopods and teleosts were the most important preys and their occurrence in the stomach contents showed seasonal variation. Annelids and elasmobranchs were poorly represented (Tab. 2).

The crustacean species were best represented, of the seven identified species *Aristeus antennatus* (9), *Pontophilus spinosus* (9) and *Plesionika martia* (12) were most often recorded in the stomach contents. Three cephalopod species were identified, *Sepia elegans* (5), *Sepietta oweniana* (11) and *Sepiola* sp. (2) and of the six teleost species identified, *Ichtyococcus ovalis* (9), *Myctophum punctatum*, *Gadiculus argenteus* (5) were most frequently consumed by *E. spinax* (Tab. 3).

Some annelid worms, crustaceans, cephalopods and teleosts were unidentified, as they were represented by remains of food.

Moreover, two elasmobranch species were identified. Small specimens and three egg-capsules of *G. melastomus*, but also two *E. spinax* newborns with remains of an internal vitellin vesicle and umbilical scar were present in stomach contents.

Tab. 2: Frequency index (FI) of zoological groups ingested by *Etmopterus spinax* for sex, category and season.

Tab. 2: Frekvenčni indeks (FI) posameznih skupin živali glede na spol, starostno kategorijo in sezono, ki jih je plenil morski pes *Etmopterus spinax*.

Sex	Males						Females						General total
Category	Non-adults			Adults			Non-adults			Adults			
Season	Sum	Win	Annual total	Sum	Win	Annual total	Sum	Win	Annual total	Sum	Win	Annual total	
Crustaceans	8* (0.66)	8 (0.61)	16 (0.73)	1 (0.14)	0	1 (0.08)	20 (0.77)	16 (0.59)	36 (0.68)	2 (0.2)	0	2 (0.16)	55 (0.55)
Cephalopods	2 (0.16)	5 (0.23)	7 (0.32)	2 (0.28)	0	2 (0.16)	4 (0.15)	6 (0.22)	10 (0.19)	2 (0.20)	0	2 (0.16)	21 (0.21)
Teleosts	4 (0.33)	2 (0.15)	6 (0.27)	6 (0.86)	4 (0.57)	10 (0.77)	4 (0.15)	5 (0.18)	9 (0.17)	6 (0.6)	2 (1.0)	8 (0.66)	33 (0.33)
Other groups	1 (0.08)	0	1 (0.04)	1 (0.14)	2 (0.28)	3 (0.23)	0	1 (0.04)	1 (0.02)	2 (0.2)	0	2 (0.16)	10 (0.10)

* number of times a prey belonging to a zoological group is ingested

DISCUSSION

The mean value of percent of occurrence (83, see Table 1) indicates that *E. spinax* is an active predator and voracious as other elasmobranch species and agrees with McPherson (1980). However, only five zoological items were reported from *E. spinax* stomach contents and for each of them few species were recorded. This suggests that the species is rather opportunist and feeds on the most abundant food items available in their environment; the velvet bellies being restricted to deep bottoms where biological environment does not present a high diversity. The variation of frequency incidence among zoological items in juveniles and adults suggests a change in food and feeding habits and prey selectivity in *E. spinax* according to the category of specimens

(Tab. 2). For instance, the adults ingested more cephalopods and teleosts than the juveniles. This may be due to the fact that larger specimens were more active predators and experienced feeders. Moreover, depth segregation with sex and size cannot be neglected. With regard to this point, Orsi Relini & Würtz (1977) wrote: "The young of *Etmopterus spinax* have also been observed on epybathyal bottoms (about 450 m) in late spring, whilst the adults are observable in varying numbers at 500 meters, throughout the year."

Our observations of *E. spinax* agree with previous papers referring to items ingested but they differ at specific level. This difference could be related to the available species between the areas and depths involved.

Tab. 3: List of prey species identified in stomachs contents of *Etmopterus spinax*.Tab. 3: Seznam vrst plena, določenih v želodcih morskega psa *Etmopterus spinax*.

Sex	Males				Females				Total
Category	Juveniles		Adults		Juveniles		Adults		
Season	Sum	Win	Sum	Win	Sum	Win	Sum	Win	
Stomachs examined	14	13	9	7	32	31	12	2	120
Annelids									
unidentified	1					1	1		3
Crustaceans									
<i>Aristeus antennatus</i>	1				6	2			9
<i>Chlorotocus crassicornis</i>	1				2	2			5
<i>Plesionika heterocarpus</i>	1	1			1	2			5
<i>P. martia</i>	2		1		2	1			6
<i>P. edwardsii</i>				1	2	1			4
<i>Pontophilus spinosus</i>		2			3	3	1		9
<i>Goneplax rhomboides</i>		2		1	3	3			9
unidentified	3	3			1	2	1		10
Cephalopods									
<i>Sepia elegans</i>	1		1		2	1			5
<i>Sepiola</i> sp.			1				1		2
<i>Sepietta oweniana</i>	1	3	1			5	1		11
unidentified		2			2				4
Elasmobranchs									
<i>Galeus melastomus</i>				2		1	2		5
<i>Etmopterus spinax</i>			1				1		2
Teleosts									
<i>Ichtyococcus ovatus</i>	2	1		2	1	1	2		9
<i>Myctophum punctatum</i>	2			1	1		2		6
<i>Gadiculus argenteus</i>			2		2		1		5
<i>Phycis phycis</i>			1		1				2
<i>Hoplosthetus mediterraneus</i>			1			1			2
<i>Callynimum</i> sp.			1			1			2
unidentified	1	1	1	1		2	1	2	9

Wheeler (1969) reported Euphausiacea, crustaceans and bony fishes of the genus *Micromesistius* in stomachs contents of specimens from British waters. In Italian seas, according to Bini (1967), the species feeds on cephalopod molluscs and small decapod crustaceans. Capapé (1975) found some unidentifiable teleosts in stomach contents of some *E. spinax* caught off the Tunisian coast. Orsi Relini & Würtz (1977) analysed and compared stomach contents of the velvet belly and the blackmouth catshark from the Ligurian Sea. They wrote that "*E. spinax* feeds in the pelagic zone above all on large size preys; its food specially seems to be orientated towards nektonic cephalopods." McPherson (1980) noted that prey composition in *E. spinax* usually consists on fishes, cephalopods, Euphausiacea and crustacean decapods in the western Mediterranean. Kabasakal & Unsal (1999) examined stomach contents of five specimens caught in the north-eastern Aegean Sea, two of which were empty, while the others contained remains

of decapod crustaceans, cephalopods and teleosts.

Tab. 4: Comparisons of annual percent of occurrence (PO) between *Etmopterus spinax*, *Centrophorus granulosus* and *Galeus melastomus* for each category

Tab. 4: Primerjava števila polnih želodcev (PO; letni delež v %) globokomorskih vrst morskih psov *Etmopterus spinax*, *Centrophorus granulosus* in *Galeus melastomus* glede na starostno kategorijo.

Category Species	Non-adults		Adults		Average annual PO
	n	PO	n	PO	
<i>Etmopterus spinax</i>	90	82.5	30	83.5	83.0
<i>Centrophorus granulosus</i>	81	89.0	68	79.0	84.0
<i>Galeus melastomus</i>	276	80.4	166	79.6	80.0

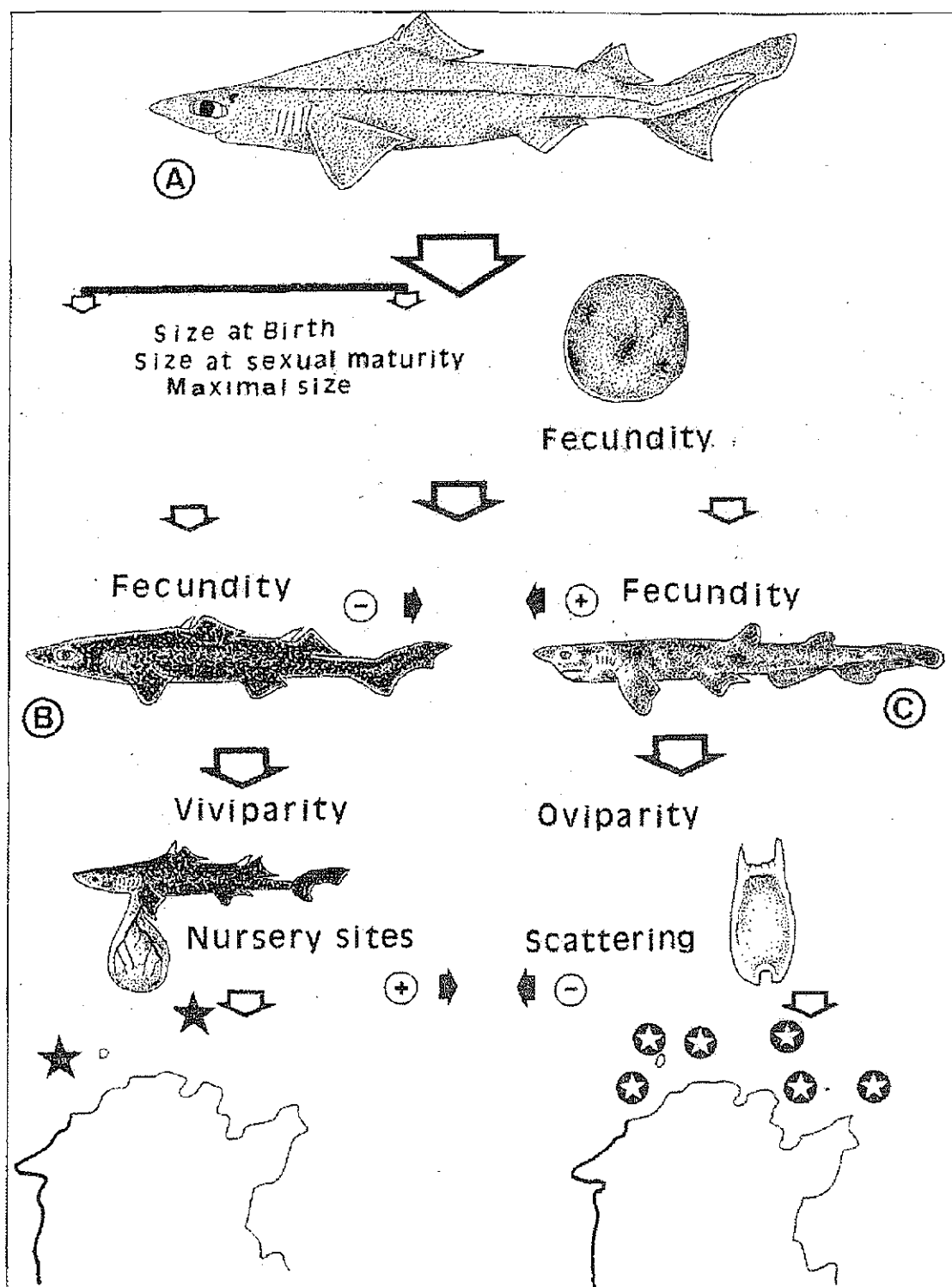


Fig. 2: Interspecific competition among (A) *Centrophorus granulosus*, (B) *Etmopterus spinax* and (C) *Galeus melastomus*, involving factors which increase (+) or reduce (-) the demographic pressure exerted by one species on another (partially redrawn from Capapé, 1989).

Sl. 2: Tekmovanje med vrstami (A) *Centrophorus granulosus*, (B) *Etmopterus spinax* in (C) *Galeus melastomus*, z dejavniki, ki povečujejo (+) ali zmanjšujejo (-) demografske pritiske, ki jih ustvarja ena vrsta na drugo (delno prirejeno po Capapé, 1989).

The elasmobranch occurrence in stomach contents of some Tunisian velvet bellies had probably accidental significance: they could be ingested during trawling. On the other hand, they could be the result of a competition pressure for food items. Records of elasmobranchs as prey items are usually reported in diet of elasmobranch species (Bigelow & Schroeder, 1948; Stevens & Lyle, 1989; Waller & Baranes, 1994). Moreover, the record of *E. spinax* in stomach contents of our sample species probably suggests a case of cannibalism in elasmobranchs, nevertheless different of oophagy and/or adelphophagy described in other sharks (Springer, 1948; Gilmore, 1983; Gilmore et al., 1983).

During trawling surveys in deep areas off the Tunisian northern coast, two other deep-sea shark species, *G. melastomus* and *C. granulosus*, are concomitantly caught together with *E. spinax*. They probably inhabit the same or closed niches and competition for food between them could be inferred. For each shark, mean annual PO of the three sharks had high values, and were not significantly different ($p > 0.01$, Tab. 4). These high values suggest that they are active feeders, as well as that an important availability in food occurred in their respective habitats.

However, *E. spinax*, *C. granulosus* and *G. melastomus* feed on crustaceans, cephalopods and teleosts (Tab. 5), but crustaceans were mainly consumed by *E. spinax*, cephalopods by *G. melastomus* and teleosts by *C. granulosus*.

Moreover, of the 78 prey species numbered in stomach contents of *E. spinax*, *C. granulosus* and *G. melastomus*, only eight species were recorded in common. Intraspecific competition for food and consequently niche overlap for diet seem to be considerably reduced.

Referring to Golani & Galil (1991) and his own observations on the diet of the striped red mullet from the eastern central Adriatic, Dulčić (2002) wrote: "Food specialisation and dietary breadth are a result of evolutionary development of unique feeding behaviour, mor-

phology and mouth structure, which interact with the size, distribution and abundance characteristics of certain types of the available benthic fauna."

To explain the overlap of diet niches for the three deep-water sharks from the western Mediterranean, *G. melastomus*, *E. spinax* and *Dalatias licha*, McPherson (1980) used theoretical model based on mathematic parameters.

We have used only some biological parameters of the three sharks, which are summarized in Table 6 as size at birth, size at sexual maturity, maximal size, reproductive mode and fecundity. Their roles on interrelationships are generated as a model plotted in figure 2.

The gulper shark matures at a larger size and has a larger maximal size than its sympatric sharks and, consequently, it consumed larger preys than *E. spinax* and *G. melastomus* were able to do. A competition for food could be inferred between juvenile *C. granulosus* and adult *E. spinax* and *G. melastomus*, but this opinion needs confirmation: a spatial segregation occurs between sexes and categories of specimens in elasmobranch species (Waller & Baranes, 1994). Mouth width is smaller in *E. spinax* and *G. melastomus* than in *C. granulosus*, and teeth counts and teeth shape are very different between the three species (Ledoux, 1970; Capapé & Ben Brahim, 1984). Moreover, the fecundity of the first species seems to be the lowest ever recorded in an elasmobranch species whatever the area (Sarà, 1968; Capapé, 1985; Mellinger, 1989; Golani & Pisanty, 2000; Guallart & Vicent, 2001). Its recruitment is poor, lesser than this of both *E. spinax* and *G. melastomus*. It expelled its foetuses, generally a single specimen per litter (Capapé, 1985; Guallart & Vicent, 2001) in nursery sites restricted at the level of the Bank of Esquerquis (northern Tunisia) as this was the case of *E. spinax* according to Capapé et al. (2001), but size at birth is very different for each species (Tab. 6) and competition pressure for food is reduced between them with regard to neonates and juveniles.

Tab. 5: Comparison of frequency indexes (FI) and number of species-preys (n) belonging to different prey items ingested by *Etmopterus spinax*, *Centrophorus granulosus* and *Galeus melastomus*.

Tab. 5: Primerjava frekvenčnih indeksov (FI) in števila vrst plena (n) posameznih skupin živali, ki so jih uplenile tri vrste morskih psov *Etmopterus spinax*, *Centrophorus granulosus* in *Galeus melastomus*.

Prey item	Crustaceans		Cephalopods		Teleosts		Other groups		Total
Species	FI	n	FI	n	FI	n	FI	n	n
<i>Etmopterus spinax</i>	0.55	7	0.21	3	0.33	6	0.10	3	19
<i>Centrophorus granulosus</i>	0.21	6	0.13	3	0.74	11	0.09	3	23
<i>Galeus melastomus</i>	0.44	11	0.44	5	0.53	13	0.08	7	36

Tab. 6: Biometric measurements and reproductive data for *Etmopterus spinax*, *Centrophorus granulosus* and *Galeus melastomus*.**Tab. 6: Biometrični in razmnoževalni podatki za tri vrste morskih psov *Etmopterus spinax*, *Centrophorus granulosus* in *Galeus melastomus*.**

Species	Size at first maturity (mm)	Maximal size (mm)	Reproductive mode	Reproductive cycle period (months)	Fecundity	Authors
<i>Etmopterus spinax</i>	350-380	460	viviparous	24	5-17 / 2 years	Capapé <i>et al.</i> (2001)
<i>Centrophorus granulosus</i>	800-900	960-1280	viviparous	24	1 / 2 years	Capapé (1985)
<i>Galeus melastomus</i>	420	550-560	oviparous	?	15-25 / one year	Capapé & Zaouali (1977)

On the other hand, size at sexual maturity and maximal size do not show important differences between *E. spinax* and *G. melastomus* (Tab. 6). Moreover, the first is a viviparous species and the second an oviparous one. The deposition sites of egg capsules of the blackmouth catshark are widely distributed throughout the waters off northern Tunisia as well as scyliorhinid species from other marine areas (Capapé, 1977; Able & Flesher, 1991; Capapé *et al.*, 1991). Consequently, the discovery of egg-cases in *E. spinax* stomach contents could not affect the blackmouth cat shark populations. Barrul & Mate (2001) reported records of yolks sacks embryos of the small spotted catshark *Scyliorhinus canicula* in stomach contents of the angular roughshark *Oxynotus centrina*. They gave similar opinion as Cox & Koob (1993) who reported that predation of shark egg-case by marine animals is rather rare. However, a competition for food could be inferred between adults of *E. spinax* and *G. melastomus*. Nevertheless, the preference

of *E. spinax* for crustaceans and the cephalopod preference of *G. melastomus* considerably reduce this inter-specific competition between the adults of both species in the area. These observations allow to state that the three deep water sharks are able to live and reproduce off northern Tunisia.

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UČINKI REPRODUKCIJSKIH DEJAVNIKOV NA MEDSEBOJNE ODNOSI MED TREMI VRSTAMI GLOBOKOMORSKIH PSOVI V OBALNIH VODAH TUNIZIJE

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POVZETEK

V obalnih vodah Tunizije se pojavljajo tri globokomorske vrste morskih psov: *Galeus melastomus* (Rafinesque, 1810), *Centrophorus granulosus* (Schneider, 1801) in *Etmopterus spinax* (Linnaeus, 1758), ki vsi naseljujejo podobne biotope. Med vrstami tu in tam poteka tekmovalstvo za hrano, pa čeprav je v teh vodah ravno ne manjka. Sicer pa je

med njimi zaznati različne morfološke značilnosti, kot na primer velikost, doseženo ob njihovi spolni zrelosti, maksimalna dolžina, plodnost in način razmnoževanja, živorodnost in jajcerodnost. In prav te značilnosti v veliki meri zmanjšujejo tekmovalnost teh treh vrst za hrano in dovoljujejo, da ti simpatrični globokomorski psi živijo in se razmnožujejo v tuniškimi obalnih vodah.

Ključne besede: globokomorski psi, *Etmopterus spinax*, *Galeus melastomus*, *Centrophorus granulosus*, sestava plena, biološki dejavniki, medsebojni odnosi, severna Tunizija, Sredozemlje

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