

POPULATION CHARACTERISTICS OF THE CRAB *MONODAEUS COUCHII* (CRUSTACEA, BRACHYURA, XANTHIDAE) IN THE WESTERN MEDITERRANEAN

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Population characteristics of the crab Monodaeus couchii (Crustacea, Brachyura, Xanthidae) in the Western Mediterranean.— Some aspects of the biology of the bathyal crab *Monodaeus couchii* from the North Tyrrhenian Sea, Sardinian Channel and Catalan Sea (Western Mediterranean) have been studied. The occurrence depth range has been found to be of between 80 and 748 m. The sex-ratio was found to be highly biased towards males in the three study areas. The crabs are sexually dimorphic, adult males being larger than adult females. There appears to be seasonality in reproduction: ovigerous females were only collected in October, November and December. Puberty moult, as determined by morphological changes of the chelae, takes place in males within a size range of 11-16 mm carapace length. This species is heterochelic, with most males being right-handed. *M. couchii* is an opportunistic predator but seems to be also able of deposit feeding and scavenging.

Key words: Brachyura, Xanthidae, *Monodaeus*, Distribution, Population biology.

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INTRODUCTION

Monodaeus couchii (Couch, 1851) is a deep-water crab which inhabits muddy substrates on the outer shelf and continental slope. Its distribution area encompasses the

Mediterranean and Eastern Atlantic from Scotland southward to Angola (MANNING & HOLTHUIS, 1981; CLARK, 1986; INGLE, 1981). Published information on its biology is limited, especially because of its low densities and therefore scarce records. However, it

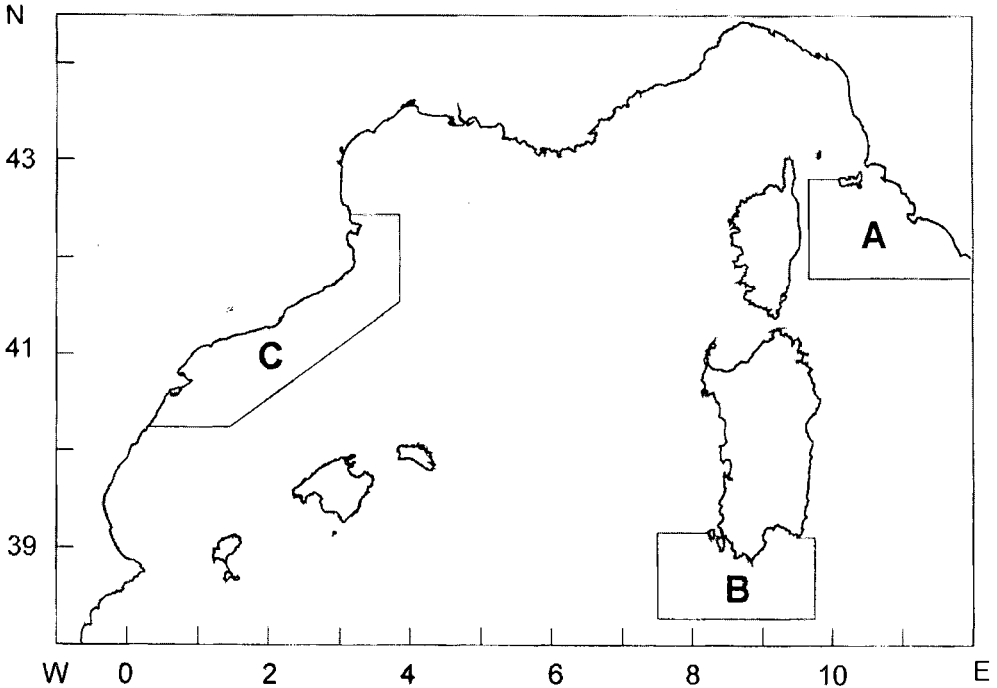


Fig. 1. Location of the three study areas in the western Mediterranean. A. Thyrrhenian Sea; B. Sardinian Channel; C. Catalan Sea.

Situación de las tres zonas de estudio en el Mediterráneo occidental. A. Mar Tirreno; B. Canal de Cerdeña; C. Mar Catalán.

is not a rare species, since it is preyed upon by many epibenthic species of the bathyal Mediterranean, such as the crabs *Geryon longipes* and *Paromola cuvieri* (RELINI & MORI, 1977; MORI, 1986), and the fishes *Chimaera monstrosa*, *Galeus melastomus*, *Phycis blennoides*, and *Conger conger* (VACCHI & RELINI, 1979; MACPHERSON, 1980; RELINI & FANCIULLI, 1981; MORI, 1982).

The present investigation was set out to analyse the main population characteristics of *Monodaeus couchii*, such as depth range of distribution, population structure, reproductive biology, morphometrics and diet from data collected on its populations from the Northern Tyrrhenian Sea, Sardinian Channel and Catalan Sea in the Western Mediterranean.

MATERIAL AND METHODS

Crabs were collected from three study areas: the North Thyrrhenian Sea between the islands of Elba and Giannutri, the Sardinian Channel between Sardinia and Tunisia, and the Catalan Sea off the coasts of Catalonia (fig. 1).

A total of 86 males and 19 females were collected from the Thyrrhenian Sea during six years of demersal trawl surveys (1985-86-87 and 1990-91-92) in the area lying between the islands of Elba and Giannutri. A total of 260 hauls were performed with a 20 mm mesh trawl net, within a depth range of 4-635 m. Samples were taken in all months of the year. In the Sardinian Channel a total of 50 females and 115 males were collected in

30 trawls from depths of between 400 and 550 m in June-December 1993 using 20 mm mesh size trawl nets. Data from the Catalan Sea were collected during two fishery research surveys with monthly samples performed between June 1981 and June 1983 and between November 1990 and November 1991 off the coasts of Catalonia. In 1981-83, a total of 185 trawls were completed in depths of between 3 and 871 m using bottom trawl nets of 20 mm mesh size equipped with a 9 mm mesh size covered codend. In 1990-91, 66 trawls were performed at depths comprised between 16 and 677 m. A total of 125 male and 49 female of *Monodaeus couchii* from this area were collected and examined.

Measurements were taken with vernier calipers to the nearest 0.1 mm. Data collected were: CL. Carapace length, from the frontal margin to the posterior edge of the carapace; CW. Carapace width, from tip to tip of the last anterolateral teeth; handedness; in right-handed individuals; RCRL. Crusher chela propodus length, right crusher length, from the ventral carpo-propodus junction to the tip of the chela and RCRH. Crusher chela propodus height, maximum height of the propodus at the level of the dactylar junction. A distinction was made in male crabs between those bearing a closed chela (juveniles) and those bearing an open chela (adults). Morphometric data were analyzed by calculating the linear regression of log CW, log RCRL and log RCRH on log CL (Model I). Allometry was determined by comparing the slope of the log-transformed regressions with the isometric slope of 1 using the Student's t-test. Histological examination of the vas deferens of three juvenile and five adult male crabs from the Thyrrenian Sea was performed to relate external morphology of the chelae with the onset of sexual maturity.

Natural diet was determined by foregut content analysis of 24 males from the Thyrrenian Sea and of 74 males and 33 fema-

les from the Sardinian Channel. All the crabs studied were collected in summer, during daytime, within a depth range of 400-500 m. Food items were scored using the percentage occurrence method (F%) as described by WILLIAMS (1981); in the samples from the Sardinian Channel the percentage number of a prey in relation to the total prey number (N%) was calculated for those prey items in which quantification was possible. Empty foreguts were omitted from all calculations. To test for differences in the proportional constitution of stomach contents of males and females from the Sardinian Channel, a chi-squared test was performed on the frequency of occurrence of the different prey categories (SIEGEL, 1956).

RESULTS

Bathymetric distribution

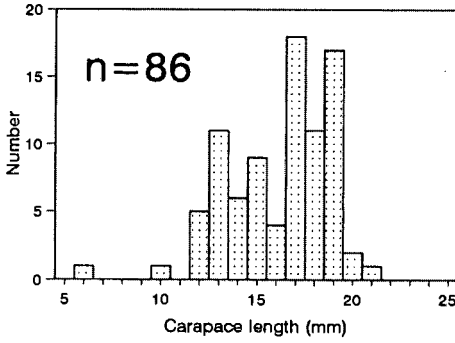
In the Northern Thyrrenian Sea, specimens of *Monodaeus couchii* were collected within a depth range of 80-635 m; the sampled depth range was 4-635 m. In the Sardinian Channel *M. couchii* occurred at depths of between 400 and 600 m; the sampled depth range was 100-600 m. The depth range of occurrence of *M. couchii* off the coasts of Catalonia was found to be 137-748 m; the sampled depth range was 3-871 m.

Size population structure and sex-ratio

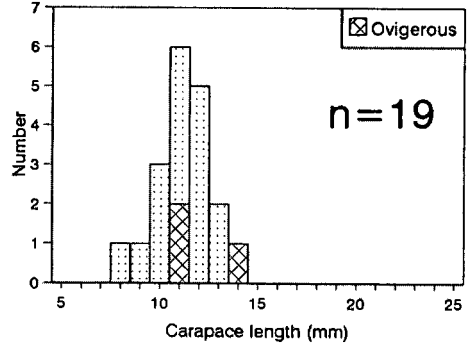
In the Thyrrenian Sea, the size of the individuals collected (86 males and 19 females) ranged between 5.5 and 21.2 mm CL for males and between 8.3 and 13.9 mm CL for females (fig. 2). Both juvenile and adult males occurred in the catches, while most of the females were adult individuals (the smallest ovigerous female sampled was 11 mm CL; see below). In the Sardinian Channel, male sizes ranged between 8.8 and 21.1 mm CL, and female sizes between 8.4 and

Thyrrhenian Sea

Males

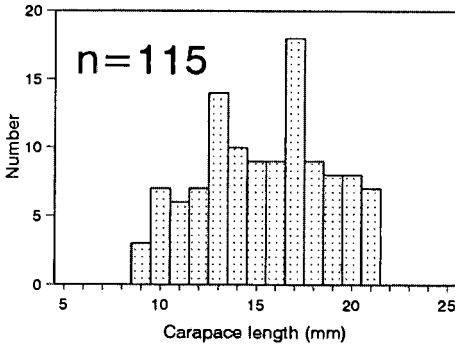


Females

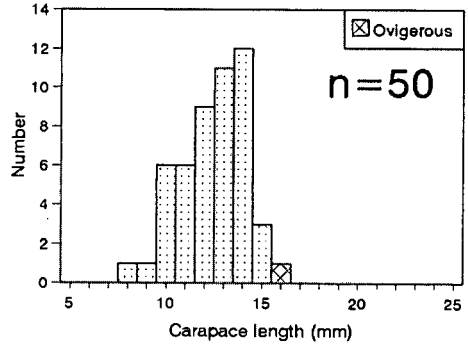


Sardinian Channel

Males

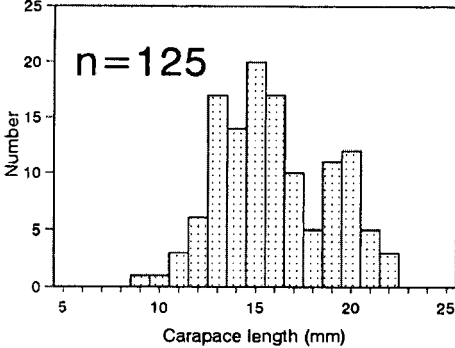


Females

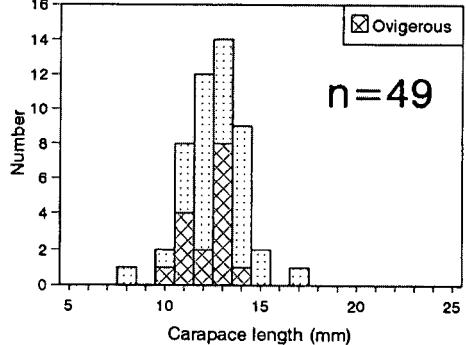


Catalan Sea

Males



Females



15.8 mm CL (fig. 2). In the Catalan Sea, sizes ranged between 9.4 and 22.0 mm CL for males, and between 8.0 and 16.6 mm CL for females (fig. 2). All crabs were captured within the codend. As in the Tyrrhenian Sea, most of the females captured were adult individuals (the smallest ovigerous female sampled was 10 mm CL; see below). In all the areas studied, the male population was markedly bimodal or polymodal, whereas the female population was clearly unimodal. The size range and the population structure were similar in the three populations studied.

The overall male:female sex-ratio found in the Tyrrhenian Sea was 4.5:1, in the Sardinian Channel, 2.3:1, and in the Catalan Sea, 2.6:1. In the three populations studied

males occurred more frequently in the catches than females. The sex-ratio at sizes larger than 15 mm CL was however clearly dominated by males.

Reproductive biology

Only three ovigerous females were collected in the Tyrrhenian Sea; they measured 10.8, 11.3 and 13.9 mm CL and were collected in October and November 1991, and December 1992 (fig. 2). Two out of three females collected in May-June 1992 had mature gonads of an orange colour. In the Catalan Sea, ovigerous females were only collected in three trawls performed in November 1990, and their sizes ranged between 10.3 and 13.6 mm CL (fig. 2); in November 1991, two

Table 1. Occurrence of a hydroid, living in epibiosis on the carapaces of *Monodaeus couchii*, and of a sacculinid parasite in the different study areas in the Western Mediterranean.

Presencia de un hidrozoo epibionte del caparazón de Monodaeus couchii y de un parásito saculinido en las distintas áreas de estudio en el Mediterráneo occidental.

	With hydroids		With parasite	
	%	n	%	n
Tyrrhenian Sea				
Adult males	55.6	27		
Juvenile males	21.4	28		
Total males	38.2	55	0.0	86
Adult females	40.0	15	0.0	19
Catalan Sea				
Males	6.2	32	4.0	125
Females	0.0	18	4.3	47
Sardinian Channel				
Males			3.5	115
Females			8.0	50
Overall				
Males			2.8	326
Females			5.2	116

Fig. 2. Size frequency distributions (CL, in 1 mm size classes) of male and female *Monodaeus couchii*.

Distribuciones de frecuencias de tallas (CL, en clases de talla de 1 mm) de machos y hembras de Monodaeus couchii.

out of six females had fully mature gonads of a violaceous colour. In the Sardinian Channel one ovigerous female of 15.5 mm CL was collected in December 1993, whereas 46% of the 39 females collected in June-July 1993 had yellow-orange developing ovaries and none had mature violaceous gonads.

Epizotes and parasites

The presence or absence of colonies of a hydroid epibiont on the carapace of the crabs was noted for a total of 55 males and 15 females in the Tyrrhenian Sea and for 32 males and 18 females in the Catalan Sea (table 1). This hydroid has been identified as *Opercularella panicula* (G. O. Sars, 1874). It was mainly located on the bases of the pereopods and on the lateral and posterior margins of the carapace. More than half the adult males examined in the Tyrrhenian Sea had hydroid colonies growing on them, while

a much smaller proportion of juvenile crabs carried epibionts (table 1). Only two of the male crabs examined in the Catalan Sea had colonies of this hydroid.

The occurrence of externae of a sacculinid parasite was noted in some of the crabs studied (table 1). No parasitized crabs were found in the Tyrrhenian Sea. The infestation prevalence was however low in the other populations studied (3.5-8.0%).

Handedness

The percentages of the different handedness types found in males and females in the three areas studied are shown in table 2. *Monodaeus couchii* is a heterochelous crab, with most individuals (around 88%) being right-handed, i.e. the right chela has a crusher morphology and the left, a cutter. The major chela (crusher) is different in shape from the minor one (cutter), and has large molariform teeth at the base of propodial claw.

Table 2. Percentage of crabs with one or both chelae missing, and of the different handedness types (right-handed (RH), left-handed (LH), and homochelous), in male and female *Monodaeus couchii* in the three study areas. Only individuals with both chelae present have been taken into account to study handedness.

Porcentajes de pérdida de quela y de tipos de lateralidad en machos y hembras de Monodaeus couchii de las tres áreas estudiadas: RH. Pinza robusta en la derecha; LH. Pinza robusta en la izquierda. Para el estudio de la lateralidad en las quelas sólo se han tomado en consideración aquellos individuos con las dos quelas presentes.

	RH	LH	Homochelous	%RH
Tyrrhenian Sea				
Males	54	4	1	91.5
Females	14	2	0	87.5
Catalan Sea				
Males	88	11	0	88.9
Females	31	8	0	79.5
Sardinian Channel				
Males	75	14	1	83.3
Females	38	0	1	97.4
Overall				
Males	217	29	2	87.5
Females	83	10	1	88.3

MorphometricsAll morphometric relationships were first studied by sex and area separately. Significant differences were only found between sexes, not between areas. Data were therefore grouped.

Table 3. Parameters of the potential regression equations ($y = a x^b$) in male and female *Monodaeus couchii* for carapace length (CL) and carapace width (CW) (in mm).

Parámetros de las ecuaciones potenciales de regresión entre la longitud de cefalotórax (CL) y la anchura de cefalotórax (CW) (en mm) en machos y hembras de Monodaeus couchii.

	Males	Females
a	0.3482	0.2752
b	1.016	1.055
r	0.9865	0.9705
n	252	117
Comparison		
H ₀	b = 1	b = 1
t	1.50	2.25
Significance	n. s.	p < 0.05
Allometric status	Isometry	Allometry (+)

The parameters of the relationship between carapace length (CL) and carapace width (CW) are shown in table 3. A significant positive allometry was found in carapace shape in females. Females would accordingly enlarge their body in width more than in length with size.

The relationship between carapace length and chelar propodus length and height has been studied in both sexes in right-handed individuals, i.e. those with a right crusher chela, in order to detect any possible change in allometry with size. The morphological change in cheliped shape between juvenile and adult crabs started at around 11 mm of carapace length; juvenile crabs, with closed chelae, were found up to a size of 16.0 mm CL, whereas crabs with open chela morphology ranged between 11.2 and 22.0 mm CL. Regressions were estimated separately for crabs with open and closed chelae (table 4). The histological examination of the vas deferens of juvenile and adult male crabs confirmed that this change in chela morphology coincided with

Table 4. Parameters of the potential regression equations ($y = a x^b$) between size (CL, in mm) and right chela propodus length (RCRL) and height (RCRH) in right-handed male and female *Monodaeus couchii*.

Parámetros de las ecuaciones potenciales de regresión entre la talla (CL, en mm) y la longitud (RCRL) y anchura (RCRH) del propodio de la quela derecha en machos y hembras de Monodaeus couchii con la quela derecha robusta.

	CL				t	Significance	Allometric Status
	a	b	r	n			
RCRL							
Males closed	-0.251	1.143	0.975	81	4.88	p < 0.001	Allometry (+++)
Males open	-0.589	1.281	0.963	139	9.18	p < 0.001	Allometry (+++)
Females	-0.292	1.127	0.953	80	3.12	p < 0.01	Allometry (++)
RCRH							
Males closed	-0.970	1.109	0.932	75	2.16	p < 0.05	Allometry (+)
Males open	-1.391	1.289	0.933	133	6.66	p < 0.001	Allometry (+++)
Females	-0.953	1.057	0.908	76	1.00	p > 0.05	Isometry

the onset of sexual maturity. No distinction was made in female crabs according to chela morphology.

Diet

The foregut contents of 24 male crabs from the Tyrrhenian Sea was investigated. Only nine of them were found to be empty. Of the remaining, three had full foreguts and 12 were at least one-fourth full. Bivalves were present in 60% of the samples examined, with gastropods, ophiuroids and peracarid Crustacea occurring less frequently (table 5).

The diet of crabs from the Sardinian Channel was examined in 74 males and 33 females, of which 16 males and 6 females had empty foreguts. There were no differences in diet composition between sexes ($\chi^2 = 6.4$; $p > 0.5$); data were therefore combined for both sexes. Crustaceans and polychaetes constituted the most important prey based both on presence/absence data and as number of prey (table 5).

DISCUSSION

The normal distribution depth range of *Monodaeus couchii* is comprised between around 60 m to at least 1300 m (ZARIQUIEY-ÁLVAREZ, 1968; MANNING & HOLTHUIS, 1981; INGLE, 1981). In the Mediterranean, the populations of *M. couchii* are found on muddy substrates on the outer shelf and, especially, on the upper and middle slope (MURA, 1987; ABELLÓ et al., 1988). However, some records have been reported at shallower depths in the Atlantic by INGLE (1981) and in the Mediterranean by PASTORE (1981), who reported this species at 7 m on *Modiolus* beds and at few centimeters on the seaweed *Cystoseira* spp., respectively.

Males clearly reach larger sizes than females (MURA, 1987; present results) and occurred more frequently in the samples in the three populations studied. This may be a characteristic of the population, but it may also be due in part to an artifact of trawl selectivity, since females are smaller than males and may escape more often the sampling gear. This size difference may help in any potential protective role of the male towards the female versus predators and male competitors during mating.

Spawning in the Western Mediterranean, according to present results, takes place in autumn-winter. No author has ever recorded ovigerous females of *Monodaeus couchii* in spring or summer in the Mediterranean. In the Atlantic, however, ovigerous females have been observed between April and June (INGLE, 1981). The scarcity of ovigerous females in the samples may be due to their remaining in their burrows during the egg-carrying period, thus being inaccessible to trawling, as seems to be the case of other deep-sea crabs such as *Geryon trispinosus* (ATTRILL et al., 1991).

The results regarding size at sexual maturity estimated from morphometric data in male *Monodaeus couchii* showed that maturity started within a size range of 11-16 mm CL. Morphology of the chelae in crabs is very important for a wide variety of behavioural interactions such as feeding habits, agonistic interactions and courtship behaviour (HARTNOLL, 1982; VANNINI & GHERARDI, 1988).

Monodaeus couchii can be considered as a right-handed species. Most xanthid crabs are known to be major predators of molluscs (VERMEIJ, 1977) and NG & TAN (1985) proposed that right-handedness may be related to the fact that almost all marine gastropod shells are dextral. However, the analysis of the feeding habits of *M. couchii* shows that it is not a specialized gastropod predator, but an opportunis-

Table 5. Diet of *Monodaeus couchii* from the Sardinian Channel ($\sigma^7 \sigma^7$ n = 58; ♀ ♀ n = 27) and Northern Tyrrhenian Sea ($\sigma^7 \sigma^7$ n = 15). F%. Percentage occurrence of a prey; N%. Percentage number of a prey.

Dieta de Monodaeus couchii en el Canal de Cerdeña ($\sigma^7 \sigma^7$ n = 58; ♀ ♀ n = 27) y norte del Mar Tirreno ($\sigma^7 \sigma^7$ n = 15). F%. Porcentaje de presencia de una presa; N%. Porcentaje en número de una presa.

	Sardinian Channel						N. Tyrrhenian Sea
	Males		Females		Total		Males
	F%	N%	F%	N%	F%	N%	F%
Crustacea							
Decapoda							
<i>Sergestes</i> sp.	1.7	4.3	3.7	4.3	2.3	4.3	
<i>Plesionika</i> sp.	3.4	4.3			2.3	2.9	
Natantia unidentified	1.7	2.2			1.2	1.4	
<i>Calocaris macandreae</i>	3.4	4.3	3.7	8.7	3.5	5.8	
<i>Ebalia</i> sp.	1.7	4.3			1.2	2.9	
unidentified	1.7	2.2			1.2	1.4	
Brachyura							6.6
Amphipoda							
<i>Lysianassa</i>	3.4	4.3	3.7	4.3	3.5	4.3	
unidentified	5.1	8.7	7.4	8.7	5.8	8.7	
Isopoda							
<i>Cirolana borealis</i>	3.4	4.3	3.7	4.3	3.5	4.3	
unidentified	8.6	10.9	11.1	17.4	9.4	13.0	
Cumacea							
<i>Leucon</i> sp.			3.7	4.3	1.2	1.4	
unidentified	3.4	4.3	3.7	4.3	3.5	4.3	
Copepoda							
unidentified	17.2	21.7	18.5	21.7	17.6	21.7	
Unidentified							13.3
Mollusca							
Bivalvia							60.0
<i>Nucula</i> sp.	1.7	2.2			1.2	1.4	
unidentified	1.7	2.2			1.2	1.4	
Gastropoda							13.3
Polychaeta							
Nephtyidae	3.4	4.3			2.3	2.9	
unidentified	12.1	15.2	11.1	13.0	11.8	14.5	6.6
Echinodermata							
Echinoidea	3.4				2.3		6.6
Crinoidea				3.7		1.2	
Ofiuroida							13.3
Porifera		1.7				1.2	
Foraminifera	12.1		7.4		10.6		26.6
Plastic		1.7				1.2	13.3
Sediment		3.4		18.5		8.2	
Marine Plants							
<i>Posidonia oceanica</i>	3.4				5.9		
Unidentified	5.2		7.4		2.3		26.6

tic predator. VANNINI & GHERARDI (1988) observed that the growth of the chelae of the xanthid crab *Eriphia smithi* did not differ between right and left-handed individuals, thus suggesting a possible genetic determination of handedness. In *Callinectes sapidus* (HAMILTON et al., 1976), *Nephrops norvegicus* (SARDA, 1983), and *Menippe mercenaria* (SIMONSON, 1985), handedness changes with age, i.e. the crabs may all begin life with a right crusher chela, but during their life cycle they can lose chelae and as a consequence there is a reversal of handedness. All our left-handed specimens were adult crabs, but, in agreement with ABELLÓ et al. (1990), a larger sample size of juvenile crabs is necessary to confirm a change with age.

A significant positive allometry was found in carapace shape in females, which would accordingly enlarge their body in width more than in length with size, a fact that may be related to an increase in carapace volume which would allow more space for ovaries to develop.

Monodaeus couchii in the Tyrrhenian Sea feeds mainly on bivalves and crustaceans, while in the Sardinian Channel the main prey are crustaceans and polychaetes. The differences in diet composition between the two Mediterranean populations may reflect differences in prey species availability in the two areas, especially for molluscs and other benthic organisms. A large part of identifiable food items in the foreguts of *M. couchii* of the two populations studied were organic particles. In deep-sea sediments a significant proportion of all organic particles consist of nanobiotal elements i.e. microorganisms between the size of bacteria and meiofauna (WATLING, 1989). This suggests that *M. couchii* can also act as a deposit feeder. Whether the microbial organisms are or are not a sufficient source of energy for macrobenthic populations is

still a subject open to discussion (CAMMEN, 1989). Deposit feeding probably represents an integration of the diet. Finally, the presence of unidentified organic debris confirmed that *M. couchii*, as many other crabs (WARNER, 1977), is also a scavenger. In conclusion, this species can be described, as many other species of bathyal crabs such as *Geryon longipes*, *Paromola cuvieri* and *Macropipus tuberculatus* (RELINI & MORI, 1977; MORI, 1986; ABELLÓ, 1989), as an opportunistic predator which is also able to switch between deposit and scavenger feeding.

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RESUMEN

Características poblacionales del cangrejo batial Monodaeus couchii (Crustacea, Brachyura, Xanthidae) en el Mediterráneo occidental.

Se han estudiado algunos aspectos de la biología del cangrejo *Monodaeus couchii* a partir de ejemplares capturados en el mar Tirreno, canal de Cerdeña y mar Catalán (Mediterráneo occidental) (fig. 1). El rango batimétrico de distribución abarcó profundidades comprendidas entre 80 y 748 m, abarcando parte de la plataforma continental y el talud superior y medio. Su presencia es no obstante más común en el talud continental. La proporción de sexos en las muestras se inclina claramente a favor de los machos en las tres áreas de estudio. La especie presenta dimorfismo sexual de tallas, alcanzando los machos tallas superiores a las de las hembras (fig. 2). Se detectó la presencia de hembras ovígeras en octubre, noviembre y diciembre. Se observó la presencia de un hidrozoo epibionte, así como de un parásito saculínido (tabla 1). La especie es heteroquérica, presentando la mayor parte de ejemplares la pinza robusta en la derecha (tabla 2).

Las hembras presentan una ligera alometría positiva en la forma del caparazón (tabla 3). La muda de pubertad, determinada por cambios morfológicos en las quelas, tiene lugar en los machos a una longitud de cefalotórax estimada alrededor de 11-16 mm (tabla 4). Su dieta está basada fundamentalmente en presas bentónicas y epibentónicas (bivalvos, gasterópodos, ofiuras, crustáceos peracáridos) (tabla 5). Se comporta como un depredador oportunístico capaz de actuar también como carroñero y sedimentívoro.

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