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A REVIEW OF THE FISHERIES BIOLOGY OF THE MANTIS SHRIMP,
Squilla mantis (L., 1758) (STOMATOPODA, SQUILLIDAE)
IN THE MEDITERRANEAN

BY

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ABSTRACT

Fisheries of *Squilla mantis* are found in the Mediterranean mostly in the vicinity of major river mouths. The life cycle of this species is well known: the spawning period is concentrated from winter to spring and planktonic larvae are found in summer, with the settlement of post-larvae occurring from the end of summer to mid-autumn. Recruitment to the fishery starts in late autumn, with full recruitment being reached between January and May. The population at sea consists of 3 year-classes and the life span is estimated at about 3 years. The mantis shrimp is a benthic species, strongly related to bottom sediments, as demonstrated by its burrowing behaviour and by the composition of its diet. The species shows also a territorial pattern of behaviour. A marked seasonality in the catches can be recognized, whereby catches are obtained mainly in the winter and spring months. The population structure varies seasonally due to the incorporation of recruits (winter-spring) and the disappearance of adults (summer-autumn). The fishery is mainly based on the exploitation of a single cohort constituted by the recruits of the previous year, and is highly recruitment-dependent. The levels of the catches have remained fairly constant in the 1990's due to the high resource turnover of the species. The facts that egg-bearing females do not exit their burrow during incubation, catchability is lower during day-time, and trawling is not permitted shallower than 50 m in the Mediterranean may protect this species from fishing.

RESUMEN

La pesca comercial de la galera, *Squilla mantis*, se desarrolla en el Mediterráneo en las proximidades de la desembocadura de los ríos más importantes. El ciclo de vida de esta especie se conoce bien: el periodo de puesta se concentra en invierno y primavera, y las larvas se encuentran en el plancton en verano. Las post-larvas se asientan en el fondo desde finales de verano a mediados de otoño. El reclutamiento a la pesquería empieza a finales de otoño y el reclutamiento completo

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se produce entre Enero y Mayo. La población en el mar consta de 3 clases anuales y la longevidad de esta especie se estima en 3 años. La galera es una especie bentónica, muy relacionada con el sedimento, como se demuestra por su comportamiento excavador y la composición de su dieta. Esta especie muestra también un territorialismo muy marcado. Se observa una fuerte estacionalidad en las capturas, que se producen principalmente en los meses de invierno y primavera. La estructura poblacional varía estacionalmente, debido a la incorporación de reclutas (invierno-primavera) y la desaparición de adultos (verano-otoño). La pesquería se basa principalmente en la explotación de una única cohorte constituida por los reclutas del año anterior y es altamente dependiente del reclutamiento. Los niveles de captura se han mantenido relativamente constantes en los años 1990 debido a la elevada tasa de renovación de la especie. La especie se encuentra relativamente protegida de la pesca debido a que las hembras no abandonan sus galerías durante la incubación, su capturabilidad es baja durante el día, y la pesca no está permitida en el Mediterráneo a profundidades inferiores a los 50 m.

INTRODUCTION

The spot-tail mantis shrimp, *Squilla mantis* (L., 1758) (fig. 1) is found in Mediterranean waters and in the adjacent Atlantic (fig. 2), where it has been reported from the Gulf of Cadiz and from the Canary Islands and Madeira, its southernmost distribution being Angola (Manning, 1977). Despite the information given in Holthuis (1987) or Do Chi (1975a), *S. mantis* is not present in European Atlantic waters other than in the Gulf of Cadiz: it is at present absent from Portugal (M. Cristo, pers. comm.), despite the three citations given in Nobre (1931). It is absent from Galicia and the Bay of Biscay (J. Freire and P. Noël, pers. comm.) and from the Atlantic coasts of France (P. Noël and J.-C. Sorbe, pers. comm.; Bourdon, 1965). Finally, it has not recently been reported from the British Islands (Allen, 1931; Mauchline, 1984; Hayward & Ryland, 1990), despite the citations reported in Leach (1815) and Bell (1853). It is found from sublittoral depths on sandy and muddy bottoms (>3 m, Abelló & Sardà, 1989) to around 150 m depth (Abelló et al., 2002), but occasionally deeper, to a maximum recorded depth of 367 m (Abelló et al., 2002).

This mantis shrimp is found in high densities in areas with suitable burrowing substrates (fine sand and sandy mud: Froglià, 1996; Atkinson et al., 1997), especially where the influence of river run-off is important. In the Mediterranean, it is very abundant on the continental shelves of the rivers Ebro, Rhone, Po, and Nile (Lewinsohn & Manning, 1980; Holthuis, 1987). It is a strongly sedentary species and the seasonal trends appearing in catch data series are not so much due to temporal changes in its distribution (limited migratory habits), as to its reproductive and burrowing behaviour, as linked to recruitment patterns.

Ten species of stomatopods are found in the Mediterranean and adjacent Atlantic waters (Froglià & Manning, 1989; De Ranieri & Mori, 1991; Abelló & Guerao (in press)). Among these, only *S. mantis* has economic importance, but a

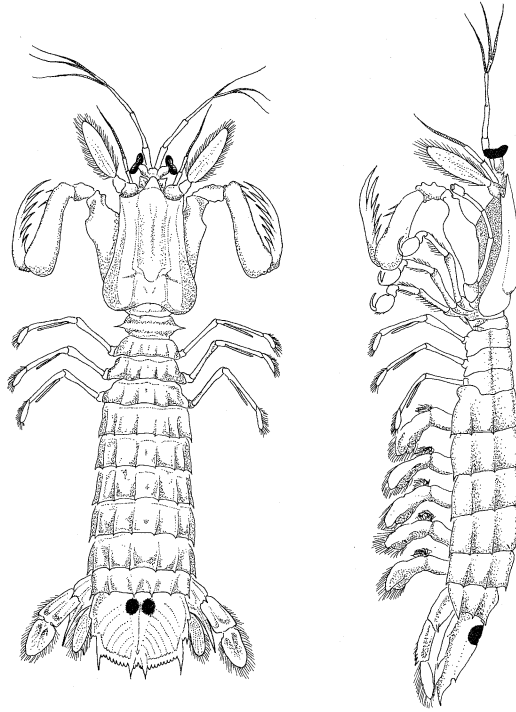


Fig. 1. Dorsal and lateral view of adult *Squilla mantis* (L., 1758) (original drawing by G. Guerao).

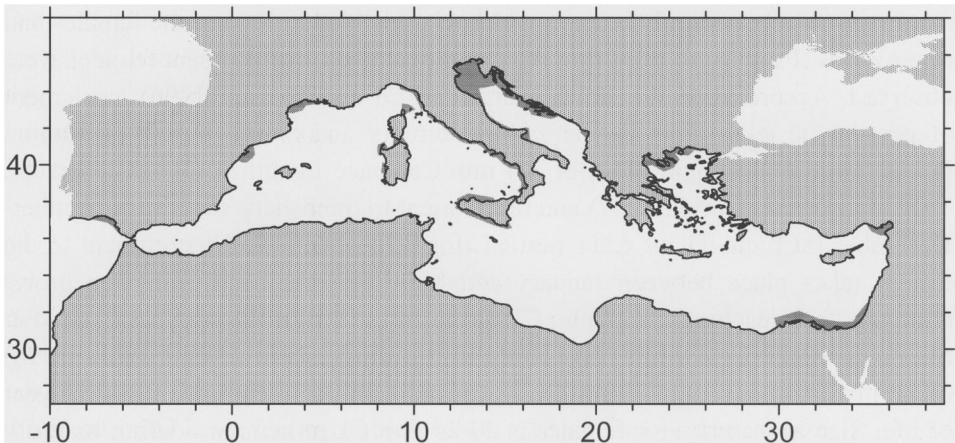


Fig. 2. Distribution area of *Squilla mantis* (L., 1758) in the Mediterranean Sea and adjacent Atlantic waters, black coastline. Darker shading denotes areas where *S. mantis* is found at high densities and is the object of commercial fisheries.

recent Lessepsian migrant, *Erugosquilla massavensis* (Kossmann, 1880), is fished commercially in the eastern Mediterranean (Holthuis, 1987). Galil & Zenetos (2002) point to possible competitive exclusion of *S. mantis* by *E. massavensis*: the former is fished commercially at 10-25 m depth in the western Mediterranean, while off the Israeli coast it is fished at 70-90 m.

LIFE HISTORY

Annual growth cycle and reproduction

The mating season occurs from winter to spring (January to June), when females have their cement glands active, although the activity of these glands may start as early as October (Do Chi, 1975a). The activity rate of the cement glands is at its maximum in January (100% in females of mature size) and decreases afterwards (Abelló & Sardà, 1989). Eggs are shed from April to June (Do Chi, 1975a). In spring and early summer, females incubate the eggs in their burrows. During incubation, females do not leave their burrows (Piccinetti & Piccinetti-Manfrin, 1970b; Do Chi, 1978). Larvae hatch between late spring and late summer (Piccinetti & Piccinetti-Manfrin, 1970b; Do Chi, 1978).

In the eastern Ligurian Sea, females with mature gonads were found from January to June, with a clear peak in April; this trend was also confirmed by the monthly development of the maturity stages (and further confirmed by the gonadosomatic index), that reached maximum values in March-April (fig. 3; M. Mori and P. Sartor, unpubl. data). In the central Adriatic, the peak of ovarian maturity was reported in February and March, when up to 80% of the females had ripe ovaries (Frogliia, 1996). From April to September, mainly spent females were observed. According to Abelló & Martín (1993) and Frogliia (1996), settlement of post-larvae takes place at the end of summer and the beginning of autumn (17-20 mm Total Length (TL), or 3-4 mm Carapace Length (CL)¹); Giesbrecht, 1910; Jacques & Thiriot, 1967) and recruitment to the fishery starts in November-December (at 6 cm TL or c. 11 mm CL for both sexes). Full recruitment to the fishery takes place between January and May. The mantis shrimp then grows relatively fast, reaching 25-27 mm CL at the end of the following year (Abelló & Martín, 1993) and growth is particularly fast in summer. However, Frogliia (1996) found that the cohort of 5-13 mm CL reaches 15 mm CL by the end of the first year of life. Size at maturity for females is 20-24 mm CL, when considering maturity

¹) Note that different authors give size data as either mm CL or cm TL. For consistency, we will report size as mm CL, using the allometric equation given by Abelló & Sardà (1989, retaken here in table I.e).

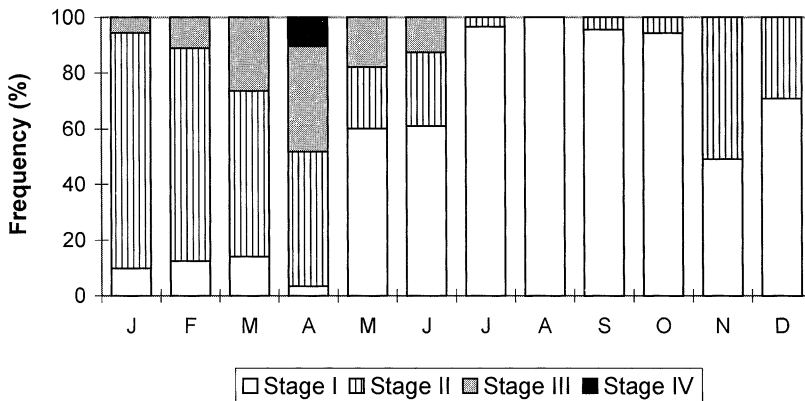


Fig. 3. Monthly development of maturity stages for females of *Squilla mantis* (L., 1758) in the eastern Ligurian Sea (M. Mori and P. Sartor, unpubl. data; maturity stages defined as in Frogliia, 1996, except Stage I: unripe + spent).

by the development of the cement glands (Piccinetti & Piccinetti-Manfrin, 1970b; Do Chi, 1975a; Abelló & Sardà, 1989; Frogliia, 1996), i.e., female *Squilla mantis* mature within 1 year of settlement to the bottom and spawn within their second year of life (Giovanardi & Piccinetti-Manfrin, 1984).

Abelló & Sardà (1989) found that the population is structured in 3 year classes in the Ebro delta area. The modes in each year class by sex are shown in table II. The maximum total length reported was 20 cm (40 mm CL, 39 mm CL in the Adriatic for both males and females; Frogliia, 1996). Do Chi (1975b) found a similar population structure in the northern Gulf of Lion (table II), the main difference being in the definition of the first mode, probably related to the different mesh sizes of the nets used in the two studies.

Do Chi (1975b) suggested a maximum life span of 3.5 years for *S. mantis*, with a maximum exploitation phase of 2 years. Other authors (Abelló & Martín, 1993; Righini & Bains, 1996) have found that the maximum sizes caught (37–40 mm CL) in the fishery would correspond to 3-year old individuals. The common size-range in the catch is, however, between 27 and 31 mm CL, i.e., the catch is based mostly on mature individuals. Do Chi (1975a) reported that *S. mantis* populations comprise one generation per year and each female spawns a single egg batch.

There is no clear distribution pattern of size by depth, although Abelló & Martín (1993) found that juveniles were more abundant in waters shallower than 30 m depth. Likewise, Piccinetti & Piccinetti-Manfrin (1971) reported a certain variability in catches by depth and season, and suggested that temperature may play a role in determining local migrations of *S. mantis* in search for “optimal” temperatures. This phenomenon has also been reported by Do Chi (1975b) and Lewinsohn & Manning (1980), but neither its importance to fisheries nor its causal mechanism have been thoroughly investigated.

TABLE I
Biological characteristics of *Squilla mantis* (L., 1758) by region

a. Size-weight relationship ¹⁾						
	Males		Females		Source	
	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>		
Ebro delta	0.0026	2.8305	0.0020	2.9026	Abelló & Sardà, 1989	
Gulf of Lion	0.0133	2.9700	0.0324	2.6200	Do Chi, 1975a	
Adriatic Sea	0.0116	3.0431	0.0138	2.9168	Giovanardi & Piccinetti-Manfrin, 1984	
Central Adriatic Sea	0.0014	3.0425	0.0014	3.0419	Frogliã, 1996	
Eastern Ligurian Sea	0.0356	2.6100	0.0526	2.4100	Righini & Baino, 1996	
b. Von Bertalanffy growth function ²⁾						
	Males		Females			
	<i>Lin</i> <i>f</i>	<i>k</i>	<i>Lin</i> <i>f</i>	<i>k</i>		
Ebro delta (mm CL)	40.0	1.6	39.0	1.3	Abelló & Martín, 1993	
Eastern Ligurian Sea (cm TL)	22.5	1.3	22.0	1.5	Righini & Baino, 1996	
Central Adriatic Sea (mm CL)	41.2	0.53	41.9	0.45	Frogliã, 1996	
c. Natural (<i>M</i>) and fishing (<i>F</i>) mortality						
	Males		Females			
	<i>M</i>	<i>F</i>	<i>M</i>	<i>F</i>		
Ebro delta	2.037	3.110	1.778	2.996	Abelló & Martín, 1993	
d. Various life cycle data						
	Size at 50% matur- ity (L ₅₀)	Age at matur- ity 1 yr after settle- ment	Egg incubation period Spring to early summer	Hatching season Summer	Longevity 1.5 yr after set- tlement	
Ebro delta						Abelló & Martín, 1993
Eastern Ligurian Sea			Late spring	Summer to early autumn		Righini & Baino, 1996
Central Adriatic Sea	14 cm TL					Piccinetti & Piccinetti- Manfrin, 1970b
e. Parameters of an allometric equation to convert CL to TL (<i>Y</i> = <i>aX^b</i>)						
	Males		Females			
	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>		
Ebro delta	0.7637	0.8937	0.6164	0.9523	Abelló & Sardà, 1989	

¹⁾ *a* and *b*, parameters of the size-weight relationship: $W = aL^b$, where *L* is the length and *W* is the weight of the animal.
²⁾ *Lin**f*, asymptotic length and *k*, growth rate, parameters of the Von Bertalanffy growth function: $L_t = Linf \cdot (1 - e^{-k \cdot t})$, where *t* is the age of the animal.

TABLE II

Modal size (mm CL) by age (cohort) in two populations of *Squilla mantis* (L., 1758) (cf. Abelló & Sardà, 1989; Do Chi, 1975b, recalculated from Froglià, 1996)

Age (cohort)	Catalan Sea		Gulf of Lion		Central Adriatic	
	Males	Females	Males	Females	Males	Females
0+	} 8.0	} 10.5			13.1	12.4
I			21.0	21.0	20.7	19.4
II	27.5	26.0	27.0	26.5	28.5	28.6
III	36.0	32.5	32.5	32.0	33.1	32.3

Habitat use and requirements by juveniles and adults

Squilla mantis is a burrowing species, associated with littoral soft bottoms where sediment is silty sand to sandy mud and very poorly sorted (Atkinson et al., 1997). De Biasi & Ferrero (1989) noted the strong intra-specific spatial competition of mantis shrimp in the pre-exploitation phase, as might be expected in a highly territorial species. Additionally, inter-specific competition (also noted by De Biasi & Ferrero, 1989) and the availability of suitable substrates for burrowing probably limit the total population size in this species. Other species competing for burrow space in the Adriatic are the thalassinid shrimp, *Upogebia tipica* (Nardo, 1868), the crab, *Brachynotus gemmellari* (Rizza, 1839), and the fish, *Gobius niger* L., 1758 (cf. Atkinson et al., 1998).

Froglià (1996) studied the burrowing behaviour of *S. mantis* in the Adriatic and provided descriptions of burrow morphology and building strategy, using in situ observations and burrow casts. *S. mantis* burrow casts revealed two openings, one larger than the other. The mean length (distance between the openings) was 4-5 times the total length of the occupant mantis shrimp. The alpheid shrimp, *Athanas amazone* Holthuis, 1951 was found as burrow associate in 5 out of 13 burrows.

Analysis of stomach contents provided evidence of a significant increase in the percentage of empty stomachs at day-time and a diel feeding rhythm, clearly related with *S. mantis*' night peaks of activity (see also below, Catchability). Piccinetti & Piccinetti-Manfrin (1970a) reported that *S. mantis* reared in the aquarium even refused to ingest food during the day. The main food items recorded in stomachs analysed by these authors were crustaceans, molluscs, and fishes, with a high percentage of empty stomachs and a strong seasonal variability in prey types. On the other hand, Froglià & Giannini (1989) found that the main food items in *S. mantis* stomachs were brachyurans (in particular the swimming crab, *Liocarcinus depurator* (L., 1758)), natantian decapods, polychaetes, benthic fishes, and bivalves. The diet of the mantis shrimp was also studied in the eastern Ligurian Sea (M. Mori and P. Sartor, unpubl. data): crustaceans (mainly the decapods

Liocarcinus sp., *Goneplax rhomboides* (L., 1758), *Pagurus* sp., and *Anapagurus* sp.), polychaetes, and benthic fishes, were the main prey all year round; in autumn and winter an important role in the diet was also played by benthic cephalopods. Additional food items were represented by bivalves, foraminiferans, and algae.

As already pointed out by Piccinetti & Piccinetti-Manfrin (1970a), this species may be an opportunistic predator and its diet reflects the local availability of food. Demestre et al. (2000) found that the mantis shrimp tends to aggregate with increasing trawl disturbance and is an opportunistic scavenger that feeds on dead animals after the passage of the trawl.

Population parameters

The parameters describing the population characteristics are shown in table I a-d. Due to the small number of stocks actually studied, it is difficult to make comparisons among the different population parameters by region. Males and females do not differ significantly in size, as reported for the Catalan Sea, the Adriatic, and the eastern Ligurian Sea (table Ia; M. Mori and P. Sartor, unpubl. data).

Reproduction

The onset of sexual maturity is at 20-24 mm CL for females, starting with the development of cement glands (Piccinetti & Piccinetti-Manfrin, 1970b; Do Chi, 1975a; Abelló & Sardà, 1989). After copulation, the female may store sperm for c. 2.5 months (Giesbrecht, 1910). Females lay eggs between late spring and summer. The female possesses cement glands in sternites 6-8, which secrete a sticky substance. The eggs are amassed by the anterior thoracopods with this sticky substance (Giesbrecht, 1910). Shedding takes approx. 4 hours, producing a capsule containing c. 50 000 eggs (Giesbrecht, 1910), gathered in a gelatinous mass up to 14 cm in diameter (Giovanardi & Piccinetti-Manfrin, 1984). The female incubates the egg mass in her burrow for c. 10 weeks (2.5 months) and does not feed while incubating (Giesbrecht, 1910). Analysis of oocytes by Froglià (1996) evidenced that, in some large females, two batches of oocytes were present, supporting the hypothesis that large females may have two successive clutches in the same spawning season (Ferrero et al., 1988).

Larval ecology

A pelagic larva (alima, pl. 1) hatches from the egg and a 10-stage planktonic development follows for c. 2-3 months (Giesbrecht, 1910; Piccinetti-Manfrin,



Plate 1. Alima larva of *Squilla mantis* (L., 1758) from the Adriatic (original photograph by A. Ligas).

1999). The larvae can be found in the plankton from June to November (Lo Bianco, 1909; Giesbrecht, 1910). Very few reports of *Squilla mantis* larvae exist in the literature: in the eastern Mediterranean, larvae have been found from June to November, with a peak abundance in August (Williamson, 1967; Lewinsohn & Manning, 1980; Özel & Koray, 1983). In the Adriatic Sea, pelagic larval stages of *S. mantis* were found from July to November (Steuer, 1911; Giovanardi & Piccinetti-Manfrin, 1984; Soro & Piccinetti-Manfrin, 1992). Jacques & Thiriot (1967) reported the presence of planktonic larvae from July to November (with a maximum in September) off Banyuls-sur-Mer in the Gulf of Lion.

The dynamics of *S. mantis* larvae have been studied in the Gulf of Cadiz by I. Sobrino and collaborators in a research project on ichthyoplankton sampling (I. Sobrino, pers. comm.). The sampling was conducted at monthly intervals at 7 stations ranging from 6 to 18 m depth. Larvae of *S. mantis* were present from June

to September, with a maximum abundance in July and August at the station located at 13.5 m depth.

FISHERY

Squilla mantis fisheries

Squilla mantis is commercially exploited primarily on the Mediterranean coasts of Italy, Spain, and, to a lesser extent, France, Egypt, and Israel (Piccinetti & Piccinetti-Manfrin, 1971; Do Chi, 1975b; Abelló & Sardà, 1989; Martín, 1991; Galil & Zenetos, 2002). The mantis shrimp is mainly caught by bottom trawl, although catches with trammel nets, gill nets, and baited traps also occur.

In the Mediterranean multi-species bottom trawl fishery, the mantis shrimp usually is an important by-catch of the fishing activity carried out on the continental shelf, from 30 to 80 m depth. The gear used is a common trawl net with large (up to 20 m wide) but flat (0.7-1.5 m high) mouth, heavily rigged, made of panels with decreasing meshes, and fitted to a cod end of 38-40 mm stretched mesh size.

In addition to this gear, important catches of mantis shrimp come from a modified beam trawl that is specifically employed in several Mediterranean areas to catch sole (*Solea* spp.), scallops (*Aequipecten opercularis* (L., 1758) and *Pecten jacobaeus* (L., 1758)). This gear, as employed in the northern and middle Adriatic (called “rapido”, Giovanardi & Piccinetti-Manfrin, 1984; Fabi & Sartor, 2002), resembles a toothed beam-trawl, has a mouth of a wide iron frame, and is fitted with skis. A similar fishing gear (without skis) is used in other areas, such as the delta of the river Ebro, where it is locally known as “rastell”. The “rastell” fishery targets specifically purple dye murex (*Bolinus brandaris* (L., 1758)), but has important spot-tail mantis by-catch.

The mantis shrimp is usually caught as towed-net by-catch, but also by set nets: along the Italian coasts, the gears most suited to the catch of this species are the standard trammel net, especially in the eastern Ligurian and Tyrrhenian seas, and the gill net, mostly along the Adriatic Sea (Fabi & De Ranieri, 1998).

It is difficult to estimate the size of the fleet that exploits *S. mantis* due to the fact that this species does not represent the main target of a specific “métier”; thus, potentially, all the trawlers, if working on suitable bottoms, may catch this species.

Maximum sizes landed are 37-40 mm CL, but commonly the catches are composed of individuals of 25-31 mm CL. *S. mantis* is landed and commercialized fresh. Although its catches are important only in Italy and Spain, the species is present on all Mediterranean markets. Its commercial interest lies more on the high densities reached by the mantis shrimp than on its relatively low market value.

Regarding the size structure of the catch, Abelló & Martín (1993) found that on the Catalan coast the smallest size fully recruited is 13-14 cm TL (26 mm CL), similar to the mean size of the catch 14-15 cm TL (29-30 mm CL), calculated from the smallest size fully recruited. This is indicative of a fishery based on the exploitation of recruits. In the north-central Adriatic, the size of the smallest individuals landed ranged from 18 to 22 mm CL, while in the western Italian seas they measured about 15 mm CL (Frogia, 1996; Fabi & Sartor, 2002).

Although *S. mantis* is abundant down to 120 m depth at a few locations, the highest CPUEs (Catch-Per-Unit-Effort) are reported for depths shallower than 50 m in Tuscany (Righini & Baino, 1996) and 60 m in the Ebro delta area (Abelló & Martín, 1993). In the northern and central Adriatic, the fishery is located on muddy bottoms at depths ranging from 5 to 60 m.

Catchability and abundance estimations

Information on burrowing behaviour of the species and its daily variation is found in Manfrin & Piccinetti (1970) and Atkinson et al. (1997). The burrowing behaviour of *Squilla mantis* makes it vulnerable to the bottom trawl only when individuals are out of their burrows. Catches obtained during a 24-h sampling period by Frogia & Giannini (1989) show that the activity of the mantis shrimp peaks at night, between sunset and sunrise. This behaviour makes the species less vulnerable to the fishery in areas where trawling is forbidden at night, e.g., in Spanish waters.

Seasonal variations in catchability result from reduced out-of-burrow activity, because females rarely exit their burrow when they are incubating their egg mass (decreasing their catchability) in spring and early summer (Giovanardi & Piccinetti-Manfrin, 1984; Frogia, 1996). Additionally, catches also diminish in spring and summer because the adults disappear from the population after spawning (Abelló & Martín, 1993).

Conversely, catches are much increased in winter, when mating takes place (Piccinetti & Piccinetti-Manfrin, 1971). Catches are further increased in late autumn (November-December) with the incorporation of new recruits (Abelló & Martín, 1993). In the Adriatic, the catch increases in autumn (November-December) also, as a by-catch of the sole fishery (Piccinetti & Piccinetti-Manfrin, 1995).

The reproductive behaviour the species also influences the relative proportion of males and females in the catches by season: females outnumber males only in winter (mating season), while the sex-ratio is biased towards males in spring and summer (Piccinetti & Piccinetti-Manfrin, 1971). Do Chi (1975a) reported a seasonally varying sex-ratio for landings at the port of Sète (Gulf of Lion) where

males predominate in the catches from April to August, coinciding with the lowest catches and the egg-laying and incubation period of females.

Catches may vary 10-fold in the course of the year: e.g., in a survey off the Catalan coast (port of L'Ametlla de Mar), Abelló & Sardà (1989) reported monthly catches of c. 10 000 kg mo⁻¹ from November to March and c. 1 000 kg mo⁻¹ from May to July.

Additionally, weather and sea conditions represent an important influence on the catchability of this species. For example, catches are reported to increase after prolonged bad weather conditions in the Adriatic (e.g., after a strong sea storm), probably because of disturbance of the burrow systems as a result of the high turbidities (Giovanardi & Piccinetti-Manfrin, 1984; Righini & Baino, 1996).

Trawl surveys (MEDITS, Mediterranean International Trawl Surveys) allowed to estimate the density of *S. mantis* populations at 1.95 and 1.70 kg km⁻², for 1994 and 1995, respectively, in the northern and central Adriatic Sea (Piccinetti-Manfrin, 1999). In the Spanish Mediterranean, values of up to 5.89 kg km⁻² have been estimated from MEDITS data in the 10-50 m depth interval in the Alicante sector, 1.16 kg km⁻² in the Ebro delta in the 50-100 m depth stratum, or of 1.70 kg km⁻² in the Valencia sector in the 10-50 m depth range. These values must be taken as minimum estimates, as they were taken by trawling during day-time, and it is known that this species has a nocturnal maximum of activity (Righini & Baino, 1996).

The CPUE of commercial otter trawlers was found to vary from <0.1 kg h⁻¹ in summer to 1-2 kg h⁻¹ in autumn (November-December) in the northern and central Adriatic from 1982 to 1991 (Petruzzi et al., 1988; Piccinetti & Piccinetti-Manfrin, 1995). Values of up to 4 kg h⁻¹ in autumn were reported by Manfrin et al. (1998) from the same area in the period 1985-1997, coinciding with the increasing trend in the catches reported in fig. 4.

Observations carried out from 2000 to 2002 on the "rapido" fisheries, reported maximum monthly catches of about 1.6 kg h⁻¹ in the Ligurian and Tyrrhenian Seas, and of about 15 kg h⁻¹ in the central Adriatic (Fabi & Sartor, 2002). This difference is due to the higher abundance of the species in the Adriatic Sea, as well as to the greater size of the fishing gear and fishing vessels used in this area.

The catch rates of the trawling fleet of the port of Sant Carles de la Ràpita (representing 50-60% of the total production of Catalonia or c. 25% of the Spanish production) are shown in fig. 5, to illustrate the high temporal variability of the CPUE of *S. mantis*. The figure shows that *S. mantis* is a highly seasonal resource, with highest catches from August to March. Daily catches vary from 30 to 40 kg/boat. In spring and summer, daily catches diminish to c. 5 kg/boat. As fishing effort is fairly constant throughout the year in this area (Abelló & Martín, 1993), the fluctuations observed can be clearly attributed to the life cycle of the species.

The development of the average monthly CPUE (kg/boat/day) obtained with traditional bottom trawl nets in the northern Tyrrhenian Sea showed a similar trend: the highest values were observed from September to April. A comparable pattern was also reported by Baino et al. (1988) for the monthly landings recorded for the fleet of Livorno (southern Ligurian Sea). In the north-central Adriatic, maxima in landings are reported for late autumn (Frogliia, 1996).

MONITORING THE FISHERY

Landings

Catches of *Squilla mantis* are well documented from FAO statistics (FAO, 2000), but only for Italy (fig. 4). It is the most important crustacean species for the northern and central Adriatic fishery by weight (Frogliia, 1996), with average annual landings of 3000 tons and a slightly rising trend since 1990 (fig. 4). In the Ionian and Sardinia GFCM divisions (Italy), landings are currently c. 500 tons annually, down from c. 1 000 tons in the 1970s and 1980s. Along the Italian coasts, in addition to the northern and central Adriatic, important landings of *S. mantis*

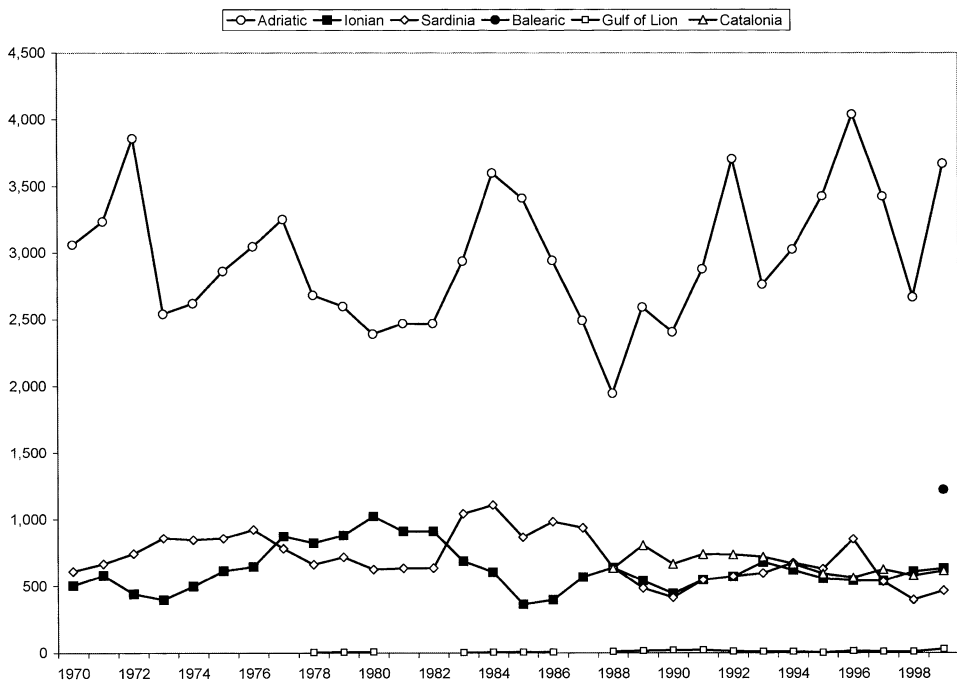


Fig. 4. Official landings (t) of *Squilla mantis* (L., 1758) by GFCM (Genereal Fisheries Council for the Mediterranean) management units. (Source: FAO-GFCM (FAO, 2000); for Catalonia: own unpubl. data.)

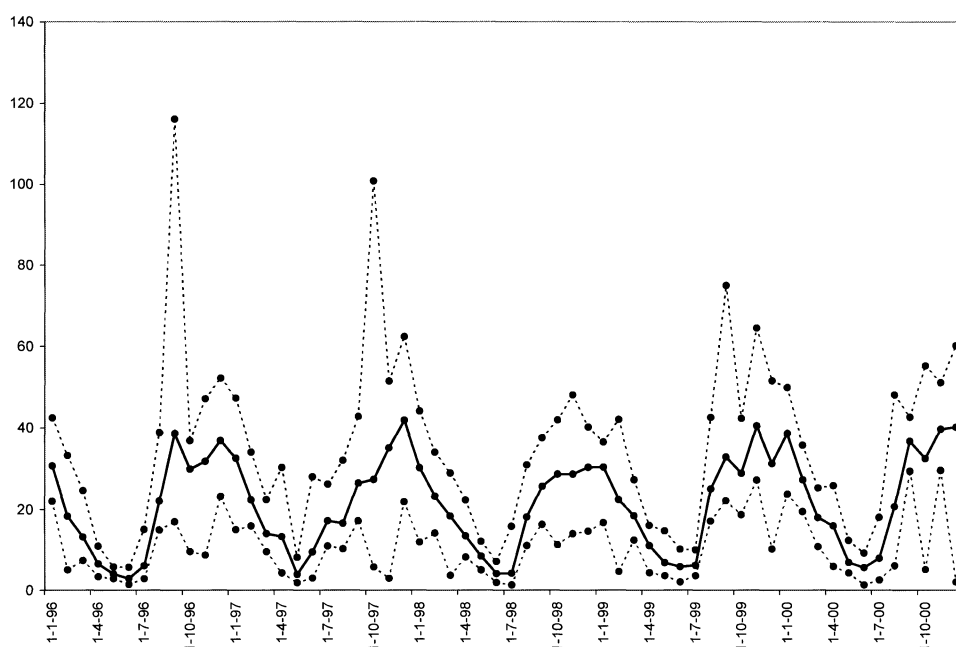


Fig. 5. Minimum, average, and maximum CPUE (kg/day/boat) of *Squilla mantis* (L., 1758) in the port of Sant Carles de la Ràpita (south Catalonia, own unpubl. data).

come from a specific area of the eastern Ligurian Sea, in front of the harbour of Viareggio (Baino et al., 1988).

The catches in Spain are also important (1 222 tons in 1999 in the Mediterranean), but were not reported in the FAO statistics until 1999. Sparse data available to us on the mantis shrimp fishery in Spain indicate that the landings were around 300–400 tons in the Gulf of Cadiz between 1984 and 1992, mainly from the mouth of the rivers Guadalquivir and Guadiana (Sobrino et al., 1994). Catches in this area decreased to c. 50 tons between 1995 and 1999, but they are recovering to those former values in recent years (300 tons in 2001, I. Sobrino, pers. comm.). On the Spanish Mediterranean coasts, the species is not found in commercial abundance in the Alboran Sea (Gil de Sola, 1993). It becomes abundant again in the Gulf of Valencia and on the Ebro continental shelf, both in Catalonia and in Valencia. The landings in Catalonia ranged between 600 and 800 tons between 1989 and 1996 (Abelló & Martín, 1993; and own unpubl. data; fig. 4), contributing to half of the Spanish Mediterranean production. In the Gulf of Lion (France) the catches of *S. mantis* are very low (fig. 5; Campillo, 1992).

In general, all catch of this species is commercialized fresh (live whenever possible), and there does not exist an implemented minimum legal size at the moment. Discard is limited to specimens damaged during the catch (especially

in the case of set nets) or to very small specimens (less than 20 mm CL), very scarce in the catches, due to their low market value.

ASSESSMENT OF THE IMPACT OF FISHING ON THE POPULATION

No formal assessments are made for this fishery, only data from trawl surveys (MEDITS) and landings (official statistics), where they exist, are amenable to analysis.

Fishing and natural mortality estimates

The only mortality estimates of this species (table Ic) come from the work of Abelló & Martín (1993).

MANAGEMENT OF THE FISHERY

Management structure

The fishery for *Squilla mantis* is not specifically regulated. It belongs to the general multi-species trawl fishery practised on continental shelves in the Mediterranean (see Caddy, 1993; Farrugio et al., 1993; for a general description), with seasonal changes of target species. The most important co-occurring species are the shrimp *Melicertus kerathurus* (Forskål, 1775), the sole *Solea solea* (L., 1758), the cuttlefish *Sepia officinalis* L., 1758, and the red mullets *Mullus* spp. (cf. Abelló & Martín, 1993).

A common fishing regulation is in force for the countries belonging to the European Union. Regulation 1626/1994 requires a minimum stretched mesh size of 40 mm and prohibits to fish inside the 3-mile zone from the coast or on bottoms shallower than 50 m depth.

At the level of local management, there are some restrictions on fishing time, e.g., existence of seasonal closures in Italy or limitation to 12 working hours a day in many ports of Catalonia; this last measure does not allow to fish at night, the period with the highest catchability of *S. mantis*. Periods of two-month closed seasons, mainly in spring, have been implemented in recent years in the Spanish Mediterranean trawl fishery.

Economic value

In the port of Sant Carles de la Ràpita (where half of the production of Catalonia is landed), the unit price ranged from 1.5-3 Euro/kg when catches are high (>25 kg/day/boat) to 6-7 Euro/kg when catches are low (<10 kg/day/boat) in

2001. There is a very clear inverse relationship between offer and demand, because markets are local. Additionally, ripe mantis shrimp reach higher prices than males or unripe females (Abelló & Martín, 1993).

Statistics of the ISTAT (Italian Institute of Statistics) reported an average price (at first sale) of mantis shrimp of about 3.3 Euro/kg for Italy in 1996.

DISCUSSION

Fisheries of *Squilla mantis* are found in the Mediterranean mostly in the vicinity of major river mouths: Po, Ebro, Rhone, and Nile. The life cycle of this species is quite well defined: the spawning period is concentrated from winter to spring and planktonic larvae are mostly found in summer, with the settlement of post-larvae occurring from the end of summer to mid-autumn. Recruitment to the fishery starts in late autumn, with full recruitment being reached between January and May. The population at sea generally consists of 3 year-classes and the life span is estimated at about 3 years.

The mantis shrimp is a benthic species, strongly related to bottom sediments as demonstrated by its burrowing behaviour and by the composition of its diet. The species also shows a territorial pattern of behaviour.

A marked seasonality in the catches can be recognized, whereby catches are obtained mainly in the winter-spring months. This pattern is explained by the dynamics of the exploited population, not by a seasonal reallocation of effort. The population structure varies seasonally due to the incorporation of recruits (winter-spring) and the disappearance of adults (summer-autumn). The fishery is mainly based on the exploitation of a single cohort constituted by the recruits of the previous year, and is highly recruitment-dependent. The levels of the catches have remained fairly constant in the 1990's (fig. 4), due to the high resource turnover of the species (Abelló & Martín, 1993).

The fact that egg-bearing females do not exit their burrow during incubation may protect this species from fishing. The catchability is lower in some periods of the day and it is influenced by weather conditions; these could also represent important factors to protect the species from fishing pressure.

Additionally, the upper 50 m (or inner 3 miles from shore) of the continental shelf are closed to trawl fishing in the Mediterranean, thus protecting a significant part of the depth range of this species. In the Mediterranean, trawling is locally forbidden at night (e.g., Spain), when out-of-burrow activity is higher, enhancing the protection of this resource. Conversely, the use of heavy trawling gear, which damages the muddy bottoms where *Squilla mantis* lives, can be a negative factor in the conservation of this species.

For a better management of *S. mantis* fisheries it is important to improve the information data base on this species (catches and landings, effort, prices), to study the impact caused by the trawl fishery, and to monitor abundance and population parameters.

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