

## Relationships between sponges and crabs: patterns of epibiosis on *Inachus aguiarii* (Decapoda: Majidae)

M. Maldonado and M. J. Uriz

Centre d'Estudis Avançats de Blanes (CSIC), Camí de Santa Bàrbara s/n, E-17300 Blanes (Gerona), Spain

Date of final manuscript acceptance: January 15, 1992. Communicated by O. Kinne, Oldendorf/Luhe

**Abstract.** The association between sponges and the crab *Inachus aguiarii* Brito Capello, 1876 was studied by analysing the relationships between sponge distributional patterns on the crab carapaces and several morphological and biological crab parameters. Juveniles, mature females and mature males were differentiated on the basis of sex dimorphism and terminal puberty moult. All three groups were fouled to different degrees by sponges. Percent sponge cover was related to carapace size only in mature males whereas mature females, all but one of which were ovigerous, were extensively covered regardless of their size. It is proposed that some behavioural patterns unique to females, such as long resting periods in sponge-rich microhabitats, are responsible for these high sponge covers in females. Sponges showed two trends in the colonization of the carapace, leading to either a monopolizing or a sharing of the available carapace surface. The sponge species found on the carapaces studied are not obligatory epibionts of crabs, but are believed to reflect the sponge population characterizing the crab home range.

### Introduction

Epibiosis is a widespread phenomenon among benthic sessile organisms, involving relationships ranging from commensalism (e.g. Williams and Moyse 1988, Abelló et al. 1990) to mutualism (e.g. Bloom 1975, Vance 1978, Feifarek 1987, Pitcher and Butler 1987).

The availability of a suitable substratum is one of the critical factors for sponge colonization (Rützler 1970). Some decapod crustaceans, particularly those of the families Majidae and Dromiidae, offer a supplementary surface appropriate for the settlement of diverse sessile organisms (Polimanti 1911, McLay 1983). These relationships have been well documented for the family Dromiidae (e.g. Dembowska 1926, Fenizia 1935, Carlisle 1953) and the genus *Maja* Lamarck of the family Majidae (Bürgi 1968) which actively catch and even select epi-

bionts using their chelipeds and paraeopods. In contrast, little is known on the epibiosis of crabs of the genus *Inachus* Weber, probably due to the lack of biological and behavioural studies on these species. However, the only available report of epibiosis on *Inachus*, largely based on information on the epibiotic sponge population (Arroyo et al. 1976), presumes a passive role of crabs in the acquisition of the epibionts.

The aim of the present study was to describe the patterns of association between sponges and the crab *Inachus aguiarii*. We achieved our goal by examining the relationships between abundance, diversity and strategies of spatial occupation by sponges, and some morphological and biological parameters characterizing the host crabs.

### Materials and methods

#### Sampling

A total of 35 specimens of *Inachus aguiarii* (Crustacea: Decapoda: Majidae) from six sampling stations located in the Alboran Sea and the Ibero-Moroccan Gulf (Fig. 1, Table 1) were examined. The samples were collected on the Fauna-I Cruise conducted from the R.V. "García del Cid" (Spanish Research Council) using a bottom trawl with a mouth size of 60 × 350 cm and a codend mesh size of 35 mm.

#### Study methods

Identification of sponge specimens removed from the crabs under a binocular stereomicroscope followed standard methodology (Rützler 1978). Estimates of the carapace area covered by sponges were derived from point-counting on a stereological grid (Gundersen 1984); paraeopods were not considered because of partial loss, due to either predation or damage during collection.

#### Numerical methods

Crabs were grouped into three categories (juveniles, mature females, mature males) based on their biological features (sex dimorphism

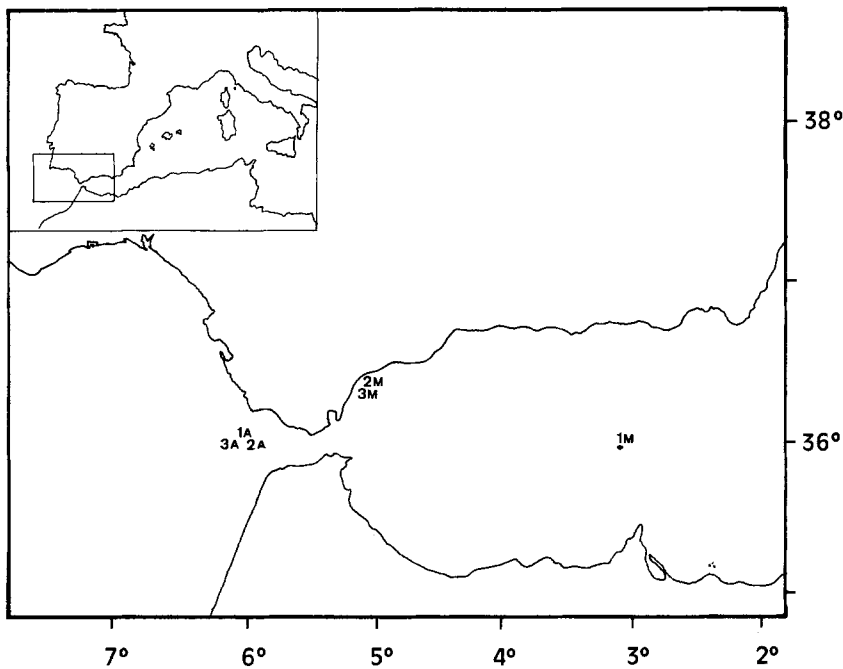


Fig. 1. Location of sampling stations

Table 1. Sampling stations where *Inachus aguiarii* specimens were collected

Stn	Location	Depth (m)	Bottom
1M	35°57'N, 3°01'W to 35°57'N, 3°02'W	45–52	Rock and boulders
2M	36°25'N, 5°00'W to 36°26'N, 4°59'W	30–30	Rock with <i>Lithothamium</i> sp.
3M	36°24'N, 5°00'W to 36°25'N, 5°01'W	30–32	Rock with <i>Lithothamium</i> sp.
1A	36°05'N, 6°08'W to 36°05'N, 6°09'W	38–42	Boulders and organogenous gravel
2A	36°04'N, 6°01'W to 36°04'N, 6°02'W	80–76	Organogenous gravel
3A	36°08'N, 6°01'W to 36°08'N, 6°02'W	34–33	Boulders and organogenous gravel

and terminal pubertary moult). Data were either log-transformed or arcsin-transformed when necessary to comply with the requirements of the different analyses. The effects of mean carapace size and mean percent cover of sponges for the three crab categories were tested for using one-way ANOVA. Multiple comparisons of means followed the Tukey-Kramer's test (Tukey 1953, Kramer 1956).

The relationships between carapace size, sponge cover and number of sponge species were described using regression analysis. Representative variables affecting sponge spatial distribution on the crabs (cover of the single largest sponge species and that of the remaining species, and the number of species) were combined to elaborate and index (*I*) reflecting patterns of spatial occupation:

$$I = \frac{(S_d - S_r)}{S_c \ln(N+1)} \cdot 100 = \frac{C_d - C_r}{\ln(N+1)}$$

where  $S_d$  = area covered by the single largest sponge species,  $S_r$  = total area covered by the remaining sponge species,  $S_c$  = carapace area,  $C_d$  = percent cover of the carapace occupied by the single largest sponge species,  $C_r$  = percent cover of the carapace occupied by the remaining sponge species,  $N$  = no. of sponge species. This index was plotted against the total cover (%) in order to highlight possible strategies of space partitioning by sponges in mature crabs.

Hierarchical cluster analysis was performed on a sponge-species-per-crab-specimen matrix to examine similarities in the epibiotic sponges of the different crabs. The sponge species only present on one crab were excluded from the analysis, as well as those present on two crabs if such sponges were the only species on both crabs. Two metric dissimilarity measures excluding double zeros, the Marczewski-Steinhaus distance and the percentage of remoteness, were applied to presence/absence and cover data, for the qualitative and quantitative clusterings, respectively (Pielou 1984). The clusters were built using the aggregation algorithm UPGMA (Legendre and Legendre 1983). Correspondence analysis was also applied to the sponge-species-per-crab matrix containing % cover data.

## Results

### Relationships between sponge cover and carapace size

Significant differences ( $p < 0.001$ ) in mean area of carapaces were found among all three crab categories (Tables 2 and 3). Post-hoc multiple comparisons test showed the males as the only group responsible for the size effects detected in the ANOVA (Tukey-Kramer test,  $p < 0.001$ ). Thus, female and immature crabs did not show mean size differences, being notably smaller than males.

Significant differences in mean percent cover ( $p < 0.006$ ) were observed (Tables 2 and 3). The subsequent pairwise comparisons indicated that the female group was responsible for the differences detected (Tukey-Kramer test,  $p < 0.017$ ). The high percent cover implied that the carapace was better hidden in mature females than in the remaining groups considered.

**Table 2.** *Inachus aguiarii*. Data for carapace area (log-transformed) and percent sponge cover (untransformed). Both data sets display homoscedasticity according to the Bartlett test

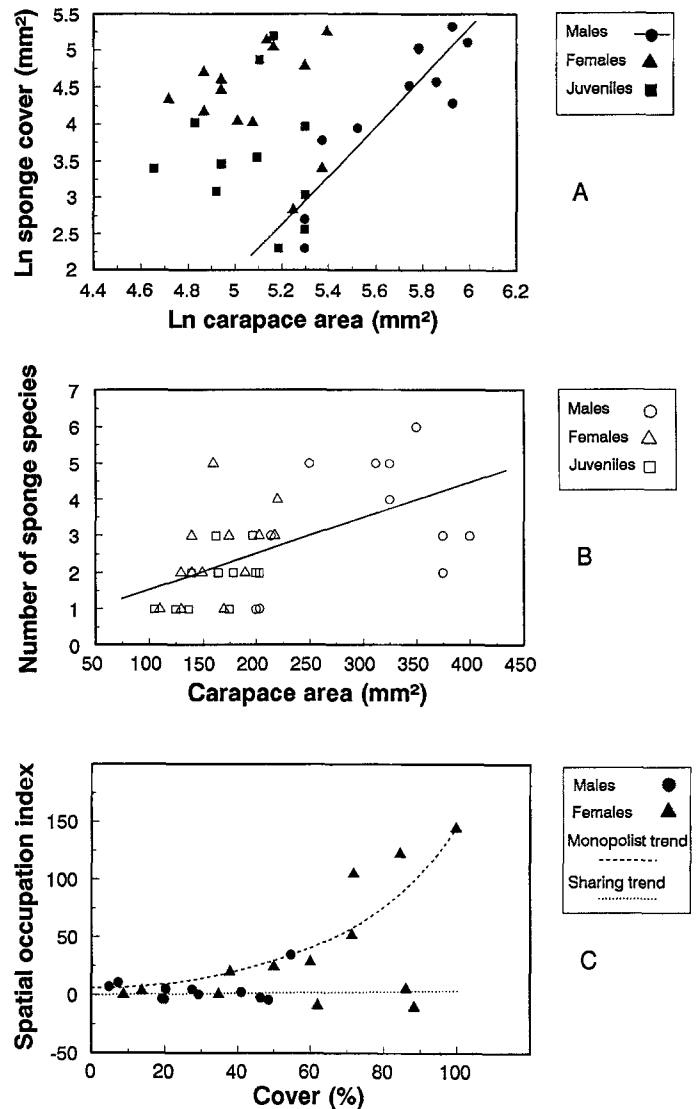
	ln Carapace area (mm <sup>2</sup> )			Sponge cover (%)		
	Males	Fe- males	Juve- niles	Males	Fe- males	Juve- niles
N	11	13	11	11	13	11
Mean	5.682	5.078	5.072	29.012	59.362	30.012
SD	0.262	0.213	0.212	16.503	28.788	25.400

**Table 3.** *Inachus aguiarii*. Summary of one-way analysis of variance for means of carapace size and percent cover. Data for carapace area are log-transformed

Source	df	SS	MS	F	p
Carapace area	2	2.778	1.389	26.364	<0.001
Error	32	1.686	0.053		
% Cover	2	7 286.666	3 643.333	6.098	<0.006
Error	32	19 120.170	597.505		

**Table 4.** Alphabetic list of the 33 sponge species found on *Inachus aguiarii*. Species marked with an asterisk were not included in cluster and correspondence analyses

- 1 *Anchinoe coriaceous* (Friedstedt, 1885)
- 2 *Anchinoe tenacior* Topsent, 1925 \*
- 3 *Anchinoe* sp. \*
- 4 *Batzella inops* (Tosent, 1891) \*
- 5 *Chalinula limbata* (Montague, 1818)
- 6 *Callyspongia septimaniensis* Griessinger, 1971 \*
- 7 *Dysidea fragilis* (Montague, 1818)
- 8 *Esperiopsis fucorum* (Esper, 1794) \*
- 9 *Gelliodes fibulatum* (Schmidt, 1862) \*
- 10 *Halichondria panicea* (Pallas, 1766)
- 11 *Halichondria bowerbanki* Burton, 1930
- 12 *Halichondria* sp.
- 13 *Haliclona cinerea* (Grant, 1826) \*
- 14 *Haliclona stirpescens* (Topsent, 1925)
- 15 *Haliclona* sp. A
- 16 *Haliclona* sp. B
- 17 *Hemimycale columella* (Bowerbank, 1874)
- 18 *Hymeniacion sanguinea* (Grant, 1826)
- 19 *Iophon hyndmani* (Bowerbank, 1866)
- 20 *Iophonopsis nigricans* (Bowerbank, 1866)
- 21 *Microcionia spinarcus* Carter and Hope, 1889 \*
- 22 *Microcionia toxitenus* (Topsent, 1925) \*
- 23 *Mycale contarenii* (Martens, 1824) \*
- 24 *Mycale macilenta* (Bowerbank, 1866) \*
- 25 *Mycale retifera* (Topsent, 1924) \*
- 26 *Mycale rotalis* (Bowerbank, 1874) \*
- 27 *Myxilla rosacea* (Lieberkühn, 1859)
- 29 *Pronax dives* (Topsent, 1891)
- 30 *Reniera mamillata* Griessinger, 1871
- 30 *Reniera* sp.
- 31 *Sigmatocella annexa* (Schmidt, 1870) \*
- 32 *Tedania anhelans* (Lieberhühn, 1859) \*
- 33 *Ulosa stuposa* (Esper, 1794) \*

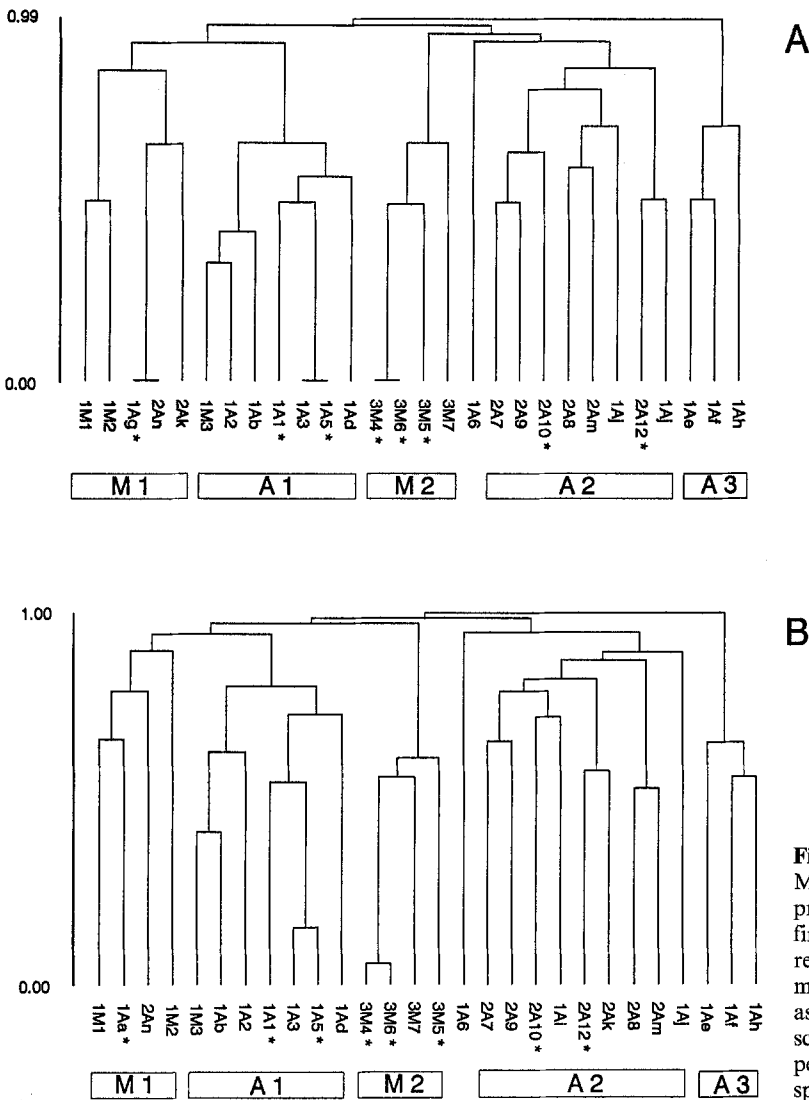


**Fig. 2.** *Inachus aguiarii*. (A) Relationships between carapace area and sponge cover. Only that of males fitted a lineal regression [ln sponge cover (%) = -14.75 + 3.34 ln carapace area (mm<sup>2</sup>); r<sup>2</sup> = 0.79; p < 0.01]. (B) Relationships between sponge species number and carapace area (r = 0.57; p < 0.01). (C) Plot of the spatial occupation index vs total sponge cover showing two trends in the spatial strategies of epibiotic sponges. Crabs fitting the trend with a positive slope showed values of H' between 0 and 0.75, whereas crabs fitting the trend with a slope close to zero showed values of H' between 0.79 and 2.11

The regression analysis between sponge cover and carapace area (Fig. 2A) demonstrated that the sponge cover increased linearly with increasing carapace area for the mature males only (r<sup>2</sup> = 0.79, p < 0.01). Both variables were unrelated in the cases of juveniles and mature females.

**Trends in carapace occupation**

A total of 168 epibiotic sponge specimens representing 33 species were found on the 35 crab carapaces studied (Table 4).



**Fig. 3.** *Inachus aguiarii*. (A) Dissimilarity (according to Marcewski-Steinhaus distance) among crabs based on presence/absence data on the epibiotic sponges. The two first digits of the labels refer to the sampling station; the remaining digits indicate either males (numbers) or females (letters). Immature specimens are marked with an asterisk. See “Results – Camouflage variability” for description of groupings. (B) Dissimilarity (according to percentage remoteness) among crabs based on percent sponge cover data

The number of sponge species per crab was correlated ( $r=0.57, p < 0.01$ ) with carapace size (Fig. 2B), but other additional factors (i.e. specific strategies of spatial occupation) might affect this relationship as well. Two main trends were shown in the partitioning of carapace space by sponges when the spatial occupation index,  $I$ , was plotted vs the total cover (Fig. 2C): (1) when  $I$  increased with increasing overall cover, the specific diversity ( $H'$ ) was  $0 \leq H' < 0.79$  and the space could be considered monopolized by a single species; (2) when  $I$  was maintained near zero in spite of the increasing cover, the diversity was higher ( $0.75 \leq H' \leq 2.11$ ) and the space might be regarded as shared. In this case several species were usually present and none occupied more than 50% of the overall cover. Instead, they displayed percentages notably lower than 50%.

The presence of the sponges *Halichondria panicea*, *Iophon hyndmani* (Bowerbank, 1866), *Iophonopsis nigricans* (Bowerbank, 1866), *Myxilla rosacea* (Lieberkühn, 1859) and *Pronax dives* (Topsent, 1891) was limited to those crabs whose carapaces were not monopolized. In the crabs whose carapaces were monopolized, the dominant

species was different in every case, as well as the secondary ones, if present. Cover rarely reached 100% of the carapace area and, consequently, the substratum was not a limited factor. In addition, no overgrowth was observed among the studied sponges as corresponding to a non-limited space (Sarà 1970).

Camouflage variability

The qualitative and quantitative clusters performed using the epibiotic sponges as descriptors (Table 4) differentiated five groups of crabs, mainly revealing affinity between specimens belonging to the same sampling station (Fig. 3A, B). Agreement between groups resulting from the qualitative and quantitative clusterings was particularly high, since the location of Crab 2Ak was the only one modified. Crabs from Stn 3M were included in Group M2. Crabs from Stn 2A were mainly clustered into a relatively homogeneous group (A2). All of the crabs from Stn 1A were distributed into two major groups (A1 and A3), but some of these specimens were

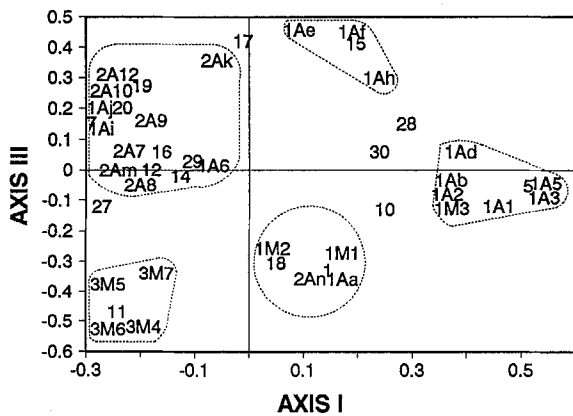


Fig. 4. *Inachus aguiarii*. Plot of sponge species and crab specimens in the space defined by the first and third ordination axes. Groups are outlined according to the quantitative clustering (Fig 3 B). Numbers (without letters) refer to the sponge species listed in Table 4. Numbers with letters represent crab specimens as in Fig. 3 A

scattered in Groups A2 and M1. Finally, Group M1 contained crabs from station 1M (Alboran Island) together with specimens from the two Atlantic stations.

Clustering indicated affinities between the sponge cover on crabs from Alboran Island and that on Atlantic crabs. In contrast, crabs from the other Mediterranean station constituted a well discriminated group, free of Atlantic individuals.

When correspondence analysis was performed, the first and third axes of the ordination space also separated the major groups of crabs obtained from the cluster analyses (Fig. 4), whereas the second axis was only a quadratic function of the first. The variance explained by the first three axes was 12.80%, 11.74% and 11.34%, respectively. These low values complicate the biological interpretation of the axis, but an Atlanto-Mediterranean gradient can be indentified along the third axis.

## Discussion and conclusions

The comparisons carried out among females, males and juveniles indicated that the three groups were differently fouled by sponges. Mature crabs offered a stable substratum whose epibiotic cover was expected to increase with increasing size. However, only males fitted the hypothesis, since females were extensively fouled regardless of their size. This suggests that the females studied, usually ovigerous, were better hidden than males and juveniles and consequently better protected (Polimanti 1911, McLay 1983). That is, the epibiosis on crabs, besides protecting the whole population by crypsis, might indirectly deflect the predation pressure from ovigerous females towards other, less hidden populational targets (males and juveniles). Some behavioural patterns specific to females such as long resting periods in sponge-rich microhabitats (e.g. crevices), similar to those observed in other Majidae (Hazlett and Rittschof 1975), could be responsible for the epibiosis enhancement found in fe-

males of *Inachus aguiarii*. The periodic moulting occurring in juveniles is believed to be the major factor responsible for the absence of correlation between sponge cover and carapace area in the immature crabs.

The multiple comparisons of mean percent cover suggested that covering was very rapidly restored in juveniles after moulting, since no significant differences in percent cover were found between juveniles and mature males in spite of the instability inherent in the carapaces of juveniles.

Unlike that which occurs in the genus *Maja* (Bürgi, 1968), sponge occupation is believed to develop without any choice by *Inachus aguiarii*, as in other species of this genus (Arroyo et al. 1976). The usual presence of very small sponge specimens attached to the carapaces indicates colonization by larvae and supports the passive behaviour of the crab in this association. Thus, in a given microhabitat, arrival of sponges at the carapace would occur randomly, and depending on the spatial strategy displayed by the colonizing species, the substratum will be either monopolized or shared. The species especially inclined towards sharing substrata were *Iophon hyndmani* and *Iophon nigricans* at Stn 2A, *Halichondria panicea* at Stn 1M and *Myxilla rosacea* at several stations. In contrast, when the substratum was monopolized no characteristic species pool was noticed, since both the dominant and the remaining species were different in every case. The size of the sample studied was presumed to be insufficient for detecting characteristic species in this case.

The similarity detected among crabs on the basis of their epibiotic sponges was usually low. Taking into account that the site (represented by the sampling station) notably influences the resulting groups of crabs in cluster analyses, the specific composition of the carapace fouling is believed to reflect the sponge population from every crab habitat. This implies a more effective crypsis by matching the background (McLay 1983). Likewise, no sponge species seems to absolutely require the epibiosis on crabs in order to live, since the sponges found in the present study can occur on several other substrata (authors' current research).

This association shows a certain unbalanced mutualistic nature: sponges use crabs opportunistically as suitable substrata facilitating their dispersion, whereas the epibiosis influences crab survival, if a reliable role in protecting both individuals as well as their eggs against predation is assumed. Nevertheless it is difficult to demonstrate costs and gross benefits unequivocally, and even more so to quantify them (Addicot 1984).

*Acknowledgements.* This research was carried out under a Generalitat de Catalunya grant and the funds of the Fauna Iberica II Program (CICYT PB89-0081). We are very grateful to Drs. J. Romero and C. Duarte for comments on the manuscript. We also thank the anonymous reviewers for constructive criticisms.

## Literature cited

- Abelló, P., Villanueva, R., Gili, J. M. (1990). Epibiosis in deep-sea crab populations as indicator of biological and behavioural characteristics of the host. *J. mar. biol. Ass. U.K.* 70: 687-695

- Addicot, J. F. (1984). Mutualistic interactions in population and community processes. In: Price, P. W., Slobodchikoff, C. N., Gaud, W. S. (eds.) Novel approaches to interactive systems. John Wiley & Sons, New York, p. 437–455
- Arroyo, M. C., Uriz, M. J., Rubió, M. (1976). *Inachus thoracicus* (Crustacea Decapoda), substrato pasivo de Demospongia. Investigación pesq. 40(1): 15–57
- Bloom, S. A. (1975). The motile escape response of a sessile prey: a sponge-scallop mutualism. J. exp. mar. Biol. Ecol. 17: 311–321
- Bürgi, A. (1968). Contribution à l'étude du comportement vis-à-vis d'objets étrangers chez les Majidae. Vie Milieu 2: 215–304
- Charlisle, A. I. (1953). Observation on the behaviour of *Dromia vulgaris* Milne Edwards, with simple ascidians. Pubbl. Staz. zool. Napoli 24: 142–151
- Dembowska, W. S. (1926). Study on the habits of the crab *Dromia vulgaris* M.E. Biol. Bull. mar. biol. Lab., Woods Hole 50: 163–178
- Feifarek, B. P. (1987). Spines and epibionts as antipredator defenses in the thorny oyster *Spondylus americanus* Hermann. J. exp. mar. Biol. Ecol. 105: 39–56
- Fenzia, G. (1935). La *Dromia vulgaris* (M. Edw.) e le sue abitudini. Archo. zool. ital. 21: 509
- Gundersen, H. J. G. (1984). Stereology and sampling of biological surfaces. In: Echelin, P. (ed.) Analysis of organic and biological surfaces. John Wiley & Sons, New York, p. 477–507
- Hazlett, B., Rittschof, D. (1975). Daily movements and home range in *Mithrax spinosissimus* (Majidae, Decapoda). Mar. Behav. Physiol. 3: 101–118
- Kramer, C. Y. (1956). Extension of multiples range tests to group means with unequal numbers of replication. Biometrics 12: 307–310
- Legendre, L., Legendre, P. (1983). Numerical ecology. Elsevier, New York
- McLay, C. L. (1983). Dispersal and use of sponges and ascidians as camouflage by *Cryptodromia hilgendorfi* (Brachyura: Dromiacea). Mar. Biol. 76: 17–32
- Pielou, E. C. (1984). The interpretation of ecological data. John Wiley & Sons, New York
- Pitcher, C. R., Butler, A. J. (1987). Predation by asteroids, escape response, and morphometrics of scallops with epizoic sponge. J. exp. mar. Biol. Ecol. 112: 233–249
- Polimanti, O. (1911). Studi di fisiologia ecologica e sulla simbiosi di *Suberites domuncula* (Olivi) con la *Dromia vulgaris* (M. Edw.). Zool. Jb. (Abt. allg. Zool. Physiol. Tiere) 30: 359
- Rützler, K. (1970). Spatial competition among Porifera: solution by epizoism. Oecologia 5: 85–95
- Rützler, K. (1978). Sponges in coral reefs. In: Stoddart, D. R., Johannes, R. E. (eds.) Coral reefs: research methods. Monogr. oceanogr. Methodol. (UNESCO) 5: 299–313
- Sará, M. (1970). Competition and cooperation in sponge populations. Symp. zool. Soc. Lond. 25: 273–284
- Tukey, J. W. (1953). The problem of multiple comparisons. Department of Statistics, Princeton University
- Vance, R. R. (1978). A mutualistic interaction between a sessile marine clam and its epibionts. Ecology 59(4): 679–685
- Williams, R., Moyse, J. (1988). Occurrence, distribution, and orientation of *Poecilasma kaempferi* Darwin (Cirripedia: Pedunculata) epizoic on *Neolithodes grimaldi* Milne-Edwards and Bouvier (Decapoda: Anomura) in the Northeast Atlantic. J. Crustacean Biol. 8(2): 177–189