



Epibiosis and masking material in the spider crab *Maja squinado* (Decapoda: Majidae) in the Ría de Arousa (Galicia, NW Spain)

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Abstract: Majid crabs present a marked masking behaviour, which, in addition to the phenomenon of epibiosis on their exoskeleton, constitutes a complex camouflage system to ward off predators. This paper presents a study on the floral and faunal composition of the epibiont and masking material of the decapod *Maja squinado* in the Ría de Arousa (Galicia, NW Spain). A total of 309 taxa were identified. Seaweeds (87 species), cnidarians (48), polychaetes (46), crustaceans (36) and molluscs (30) were the groups with a higher number of species. The frequency of occurrence of these groups was about 70%. Ascidians, poriferans, bryozoans and echinoderms were less important in number of species and frequency of occurrence. The quantitative impact of each of these groups and their species composition varies considerably, and depends on the area of the ría where *M. squinado* was found and the time that had elapsed since the terminal moult. The pre-pubertal spider crabs found in shallow water areas showed strong masking behaviour, while epibiosis was very scarce. Once individuals have undergone the pubertal moult, epibiosis begins, while the masking behaviour decreases and finally disappears.

Résumé : Les crabes majidés ont un comportement de camouflage bien marqué, auquel s'ajoute l'installation d'épibioses sur leur exosquelette, l'ensemble les protégeant des prédateurs. Cette étude porte sur la composition floristique et faunistique des épibiontes et du matériel prélevé dans le milieu par le décapode *Maja squinado* de la Ría de Arousa (Galice, NW de l'Espagne). En tout, 309 taxons ont été identifiés. Les algues (87 espèces), cnidaires (48), crustacés (36) et mollusques (30) sont les groupes qui présentent le plus grand nombre d'espèces. La fréquence d'apparition de tous ces groupes se situe autour de 70 %. Ascidiens, éponges, bryozoaires et échinodermes sont aussi présents, mais en moins grand nombre en ce qui concerne aussi bien le nombre d'espèces que leur fréquence d'apparition. L'importance quantitative et le nombre d'espèces de chacun de ces groupes faunistiques montrent une grande variabilité selon la zone où les spécimens de *M. squinado* sont récoltés et selon le temps écoulé après la mue terminale. Les araignées de mer trouvées dans les zones de faible profondeur montrent un comportement de camouflage remarquable, alors que l'épibiose est très rare. Lorsque les individus ont atteint la mue de puberté, le phénomène d'épibiose commence à se développer tandis que le comportement de camouflage diminue progressivement et finit par disparaître.

Keywords: epibiosis, camouflage, decapoda, *Maja squinado*.

Introduction

The camouflage phenomenon is widespread among the decapods of the family Majidae (Bürgi, 1968; Dudgeon, 1980; Wicksten, 1993; Woods & McLay, 1994a, b). This

phenomenon, which occurs both actively by masking behaviour, and passively by epibiosis, is highly extended among the populations of *Maja squinado* (Herbst) on the coast of Galicia.

Epibiosis basically involves mutualistic and commensal relationships with the most critical factor for colonization being the availability of a suitable substratum (Ross, 1983;

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Maldonado & Uriz, 1992). The decapod body may be a semi-permanent substratum for the settlement of marine organisms such as epibiotic species on the exoskeleton as well as in the branchial cavities; this has been studied in anomurans (Smaldon, 1974) as well as in brachyurans (Lewis, 1976) and particularly in *M. squinado* (Stiller & Stêvcic, 1967; Stêvcic, 1965; 1968a; Raibault, 1968).

In addition to the epibiosis on the crustacean body, a remarkable masking behaviour takes place, specially in members of the Family Majidae, which corresponds to the active acquisition by the crab of material from the surrounding environment, which protects itself against predators. As early as 1872, Milne-Edwards had already discovered the existence of masking in crustaceans and the role of carapace hooks in Oxyrhyncha as mechanisms for the attachment of sponges, bryozoans and other marine animals. Later, characterization and classification of the material used, led progressively to ethological studies, centered mainly on the animal's ability to adapt its flora and fauna composition to the environment in which it lives (see Bürgi, 1968).

A great deal of the current literature refers to camouflage of the majid crabs (Bürgi, 1968; Wicksten, 1979, 1993; Dudgeon, 1980; Woods & McLay, 1994a, b). The present study deals with both phenomena, camouflage and epibiosis, as part of a more broad-ranging project on the biology of the spider crab *Maja squinado* on the coast of Galicia (NW Spain).

Materials and Methods

The spider crabs analysed were collected from different zones of the Ría de Arousa (Galicia, NW Spain). In a first area, a rocky shallow zone (1-8 m) consisting of rocky kelp belts, a total of 40 immature individuals were caught in July, August, and December, 1992 (area S) (Fig. 1). The rest of the animals analysed, comprising 244 mature females taken from a deeper zone (15-40 m) with bottoms composed of rock and soft sediment, were caught monthly from December 1991 to May 1993 (area D). These females came from two cohorts: multiparous females (TM91, 36 individuals) that underwent the terminal moult during the summer 1991 or earlier, and have initiated their second reproductive cycle (>12 months since their terminal moult), and primiparous females (TM92, 208 individuals) that moulted during the summer 1992 and are in their first reproductive cycle (0-12 months since the terminal moult). Both cohorts were differentiated based on observation of abrasion of the carapace, signs of recent ecdysis (hardness of the carapace, etc.), type of epibionts and their life history, and life history of *Maja squinado* (González-Gurriarán *et al.*, 1993, 1995).

The identification of the epibiont species was made together with specialists in marine benthos (see Acknowledgements) and using specific literature on different groups, e. g. Fauvel, 1923; 1927; Millar, 1970; Lincoln, 1979; San Martín, 1984; Graham, 1988, and Hayward & Ryland, 1990 for the identification and

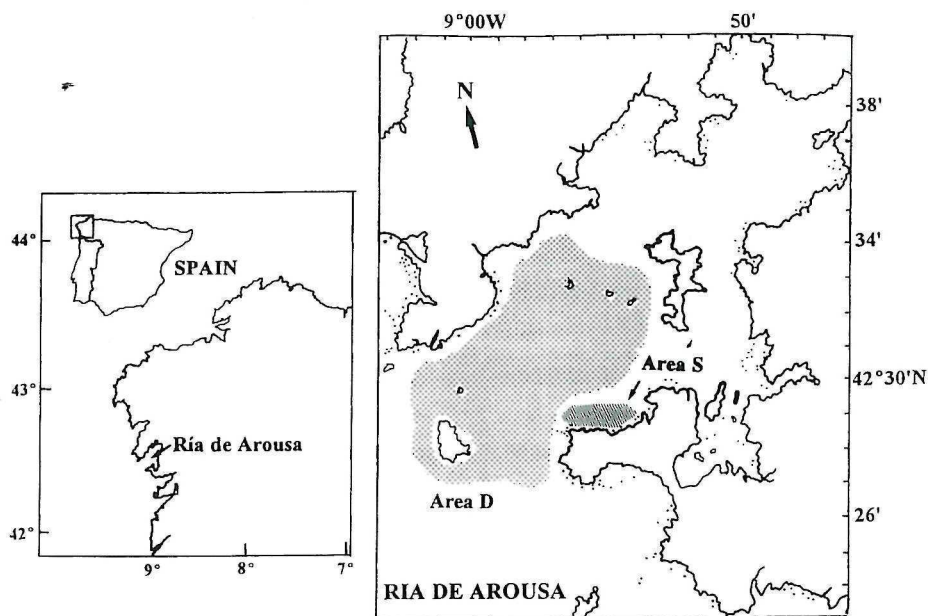


Figure 1. *Maja squinado*. Sampling areas in the Ría de Arousa (Galicia, NW Spain), Area S: shallow, rocky area (1-8 m depth), Area D: deep area (15-40 m depth).

Figure 1. *Maja squinado*. Zones d'échantillonnage dans la Ría de Arousa (Galice, NW de l'Espagne), Area S : zone rocheuse peu profonde (1-8 m), Area D : zone profonde (15-40 m).

taxonomic ordination of the species. The criteria used in the definition of the abundance of epibiosis and masking material, depend on the type of growth that the particular organism undergoes. In the case of masking material (e.g. seaweeds) and the encrusting sessile epibiont fauna (e.g. colonial ascidians, bryozoans and poriferans) the percentage of covering was estimated using a grid. For the non-encrusting sessile epibionts (e.g. colonial hydrozoans, serpulid and spirorbid polychaetes and solitary ascidians) or non-sessile fauna (e.g. gastropods, errant polychaetes), the number of individuals or colonies was quantified.

Results

A wide variety of organisms, both epibiont and masking species, were found on the carapace of the spider crab. A total of 309 taxa, most of which identified at the species level, have been characterized as components of the epibiont or masking flora and fauna on *Maja squinado* in the Ría de Arousa. The seaweeds made up the greatest number of taxa (83), followed by annelids (46), cnidarians (44), crustaceans (36), molluscs (30), ascidians (23), poriferans (20), bryozoans (10), echinoderms (6) and pycnogonids (3).

Table 1 presents the catalogue of the identified species, which have been grouped into four categories based on their relationship to the host :

Group 1.- Epibiont organisms:

Settled in situ on the exoskeleton of *Maja squinado*, they have a mutualistic relationship with it. In addition to protecting the host against predation by crabs, these species may benefit, in turn, of sediment resuspended by the host, of protection from slow-moving predators and of a better dispersion for sessile species. They include small-sized rhodophytes, most of the poriferans, small and medium-sized colonies of hydrozoans, tubicolous polychaetes, bivalve molluscs, crustaceans (cirripedes and tubicolous amphipods), encrusting bryozoans and colonial ascidians. For the most part they share suspensivore habits.

The amphipod *Isaea montagui* Milne Edwards is a special case, having a commensal relationship with *Maja squinado*, whereby this species benefits from the host by obtaining food from the debris of its diet or faeces. This is the only epibiont found having this type of relationship.

Group 2.- Masking species, actively collected in the milieu by the host:

These are pieces of perennial seaweeds, like *Cystoseira* and *Sargassum*, and large-sized (about 1-2 cm) colonial hydrozoan species.

Group 3.- Fauna related to the epibionts:

It mainly consists of polychaetes, isopods, amphipods and molluscs (Polyplacophorans, Prosobranchs and Opisthobranchs) with carnivorous and herbivorous trophic habits.

Group 4.- Fauna having no specific relation to the host:

They are species typical of the milieu where *Maja squinado* is found and they likely invade its carapace as adults. They mostly include epifaunal species with detritivore habits, made up chiefly of polychaetes and echinoderms.

If we consider the total number of spider crabs studied, the taxa that stand out in terms of frequency of occurrence are polychaetes (78.7%), cnidarians (75.1%), seaweeds (73.4%), molluscs (72.8%) and crustaceans (68.4%). The most common species, in order of importance were the polychaete *Pomatoceros triqueter* (Linnaeus) (61.8%) and the mollusc *Anomia ephippium* Linnaeus (59.5%), followed by hydrozoans of the genera *Aglaophenia* (both in terms of its role as a masking species and as epibiont) and *Sertularella* (in this case as epibiont), the barnacle *Balanus perforatus* Bruguière and the holothurian *Aslia lefevrei* (Barrois), all of which with frequencies of over 30% (Table 2).

Spider crabs caught in area S (Fig. 2a) showed a high frequency of seaweeds which were always covering the crabs. The most common species were *Cystoseira* spp. (75.0%), *Enteromorpha* spp. (50.0%) and *Sargassum muticum* (Yendo) Fensholt (45.0%) (Table 2); *Calliblepharis jubata* (Goodenough & Woodward) Kützting, *Champia parvula* (C. Agardh) Harvey and *Chondracanthus teedii* (Roth) Kützting, appeared only on these individuals. Other taxa, seen to a lesser extent were crustaceans (47.5%), polychaetes (37.5%) and molluscs (32.5%). Among the most common of these groups were the isopod *Dynamene magnitorata* Holdich (30.0%), the amphipods *Dexamine spinosa* (Montagu) (22.5%), *Ampithoe ramondi* (20.0%) and *Sunamphitoe pelagica* (Milne Edwards) (15.0%), the polychaete *Spirorbis spirorbis* (Linnaeus) (30.0%) and the molluscs *Bittium reticulatum* da Costa (32.5%) and *Rissoa parva* da Costa (15.0%). All the above-mentioned species may be considered typically associated with the shallow water spider crabs (Table 2).

In individuals from deep water areas (area D), the frequency of occurrence of seaweeds decreased in comparison with individuals from area S, especially the most typical shallow water species such as *Sargassum*, *Cystoseira* and *Enteromorpha*. Only the calcareous seaweeds *Mesophyllum lichenoides* (Ellis) Lemoine and *Corallina officinalis* L. were more numerous on deep water spider crabs than on shallow waters crabs, with the former appearing only on these individuals. The most common animal epibionts on crabs from deep area were cnidarians, specially hydrozoans (84% vs 15% on crabs from area S), polychaetes (85.1%), molluscs (78.9%) and crustaceans (71.6%) (Fig. 2a). The species or genera having the highest frequencies of appearance were the seaweed *Plocamium cartilagineum* (L.) Dixon, the hydrozoans *Aglaophenia*

Table 1. Taxa identified on the carapace of *Maja squinado* in the Ría de Arousa, differentiated in terms of their relationship to the host.
Tableau 1. Taxons identifiés sur la carapace de *Maja squinado* de la Ría de Arousa, classés en fonction de leurs relations avec l'hôte.

EPIBIONT SPECIES

Phylum PHYCOPHYTA Div. Rhodophyta <i>Apoglossum ruscifolium</i> <i>Callophillis laciniata</i> <i>Callymenia reniformis</i> <i>Cryptopleura ramosa</i> <i>Halarachnion ligulatum</i> <i>Mesophyllum liquenoides</i> <i>Pterothamnion crispum</i> <i>Rhodophyllis divaricata</i>	Fam. Halichondriidae <i>Halichondria bowerbanki</i> Fam. Hymeniacionidae <i>Hymeniacidon sanguinea</i> Fam. Dysideidae <i>Dysidea fragilis</i> Class Calcarea Fam. Syctetidae <i>Sycon ciliatum</i> Fam. Grantiidae <i>Grantia compressa</i> <i>Leuconia nivea</i> <i>Leuconia balearica</i>	Class ANTHOZOA Order Zoanthidea <i>Parazoanthus arenaceus</i> Order Actiniaria <i>Actinothoe sphyrodeta</i> <i>Actiniaria</i> sp. <i>Calliactis parasitica</i>	Phylum CRUSTACEA Class CIRRIPIEDIA <i>Balanus amphitrite</i> <i>Balanus crenatus</i> <i>Balanus perforatus</i> <i>Elmintus modestus</i> <i>Verruca stroemia</i> Class MALACOSTRACA Fam. Ampeliscidae <i>Ampelisca</i> sp. Fam. Ampithoidae <i>Ampithoe ramondi</i> <i>Sunamphitoe pelagica</i> Fam. Aoridae <i>Aora typica</i> <i>Microdeutopus chelifer</i> <i>Microdeutopus damnoniensis</i> Fam. Corophiidae <i>Corophium sextonae</i> Fam. Ischyroceridae <i>Erichthonius brasiliensis</i> <i>Jassa falcata</i> Fam. Isaeidae <i>Isaea montagui</i>	Phylum CHORDATA Class Ascidiacea Fam. Cionidae <i>Ciona intestinalis</i> Fam. Polyclinidae <i>Aplidium</i> sp. <i>Polyclinidae</i> spp. Fam. Didemnidae <i>Didemnum coriaceum</i> <i>Didemnum fulgens</i> <i>Didemnum lahillei</i> <i>Didemnum maculosum</i> <i>Diplosoma spongiforme</i> Fam. Ascidiidae <i>Ascidia mentula</i> <i>Ascidia virginea</i> <i>Ascidiaella aspersa</i> <i>Ascidiaella scabra</i> Fam. Styelidae <i>Botryllus schlosseri</i> <i>Botrylloides leachi</i> <i>Distomus variolosus</i> <i>Polycarpa pomaria</i> <i>Polycarpa tenera</i> <i>Polycarpa violacea</i> <i>Styela canopus</i> Fam. Pyuridae <i>Pyura</i> sp. Fam. Molgulidae <i>Molgula amesophleba</i> <i>Molgula bleizii</i> <i>Molgula socialis</i>
Phylum PORIFERA Class Demospongia Fam. Mycalidae <i>Mycale contarenii</i> <i>Mycale rotalis</i> Fam. Esperiopsidae <i>Esperiopsis fucorum</i> <i>Desmacion fruticosum</i> Fam. Myxillidae <i>Myxilla rosacea</i> <i>Myxillidae</i> sp. <i>Iophonopsis nigricans</i> Fam. Hymedesmiidae <i>Hymedesmia dujardini</i> Fam. Anchinoidae <i>Pronax plumosum</i> Fam. Clathriidae <i>Microciona strepsitoxa</i> Fam. Haliclonidae <i>Haliclona oculata</i> <i>Haliclona</i> spp.	Phylum CNIDARIA Class HYDROZOA Fam. Aglaopheniidae <i>Aglaophenia octodonta</i> <i>Aglaophenia pluma</i> Fam. Campanulariidae <i>Clytia hemisphaerica</i> <i>Laomedea flexuosa</i> <i>Obelia dichotoma</i> <i>Obelia geniculata</i> Fam. Plumulariidae <i>Antennella secundaria</i> Fam. Sertulariidae <i>Amphisbetia operculata</i> <i>Dynamena pumila</i> <i>Sertularella mediterranea</i> <i>Sertularia distans</i>	Phylum ANNELIDA Class Polychaeta Fam. Sabellidae <i>Potamilla torelli</i> <i>Branchiomaldane vincentii</i> <i>Dasychone bombyx</i> <i>Jasmineira elegans</i> <i>Sabella pavonina</i> Fam. Serpulidae <i>Serpula vermicularis</i> <i>Hydroides norvegica</i> <i>Pomatoceros triquetus</i> <i>Pomatoceros lamarckii</i> <i>Salmacina incrustans</i> Fam. Spirorbidae <i>Spirorbis spirorbis</i> <i>Spirorbis militaris</i>	Phylum BRYOZOA <i>Cellepora pumicosa</i> <i>Celleporina hassali</i> <i>Chartella papiracea</i> <i>Electra pilosa</i> <i>Scruparia chelata</i> <i>Tubulipora plumosa</i>	

MASKING SPECIES

Phylum PHYCOPHYTA Div. Chlorophyta <i>Cladophora albida</i> <i>Cladophora cf. hutchinsiae</i> <i>Cladophora cf. rudolphiana</i> <i>Cladophora laetevirens</i> <i>Enteromorpha clathrata</i> <i>Enteromorpha crinita</i> <i>Enteromorpha prolifera</i> <i>Ulva rigida</i>	<i>Aunfeltia plicata</i> <i>Apoglossum ruscifolium</i> <i>Asparagopsis armata</i> <i>Boergensienella mariensiana</i> <i>Bonnemaisonia asparagoides</i> <i>Bonnemaisonia</i> sp. <i>Bornetia secundiflora</i> <i>Calliblepharis jubata</i> <i>Callithamnion tetricum</i> <i>Callophillis laciniata</i> <i>Callymenia reniformis</i> <i>Ceramium echinotum</i> <i>Ceramium rubrum</i> <i>Ceramium ciliatum</i> <i>Champia intricata</i> <i>Chondria dasyphylla</i> <i>Chondria scintillans</i> <i>Chylocladia laciniata</i> <i>Corallina officinalis</i> <i>Dasya</i> sp. <i>Delesseria sanguinea</i> <i>"Falkenbergia rufolanosa"</i> <i>Gastroclonium ovatum</i> <i>Gelidium attenuatum</i> <i>Gelidium latifolium</i> <i>Gelidium sesquipedale</i> <i>Gigartina acicularis</i> <i>Gigartina falcata</i>	<i>Chondracanthus teedii</i> <i>Gracilaria verrucosa</i> <i>Griffithsia</i> sp. <i>Halarachnion ligulatum</i> <i>Heterosiphonia plumosa</i> <i>Hypoglossum hypoglossoides</i> <i>Jania cf. corniculata</i> <i>Jania cf. rubens</i> <i>Laurencia obtusa</i> <i>Laurencia pinnatifida</i> <i>Lomentaria articulata</i> <i>Lomentaria clavellata</i> <i>Microcladia granulosa</i> <i>Monosporum pedicellatus</i> <i>Nitophyllum punctatum</i> <i>Ophidocladus simpliciusculus</i> <i>Pleonosporium borrii</i> <i>Plocamium cartilagineum</i> <i>Polyneura hilliae</i> <i>Polysiphonia bodriai</i> <i>Polysiphonia elongata</i> <i>Polysiphonia ferulacea</i> <i>Pterocladia capillacea</i> <i>Pterosiphonia complanata</i> <i>Rhodomenia holmesi</i> <i>Rhodomenia pseudopalmata</i> <i>Sphaerococcus coronopifolius</i>	Phylum PORIFERA Class Demospongia Fam. Callyspongiidae <i>Siphonochalina</i> sp. Phylum CNIDARIA Class HYDROZOA Fam. Aglaopheniidae <i>Aglaophenia acacia</i> <i>Aglaophenia kirchenpaueri</i> <i>Aglaophenia octodonta</i> <i>Aglaophenia parvula</i> <i>Aglaophenia pluma</i> <i>Aglaophenia tubulifera</i> <i>Gymnangium montagui</i> <i>Lytocarpa myriophyllum</i> Fam. Haleciidae <i>Halecium beanii</i> <i>Halecium halecinum</i> <i>Halecium labrosium</i> Fam. Lafoeidae <i>Lafoea dumosa</i> Fam. Plumulariidae <i>Kirchenpaueria pinnata</i> <i>Nemertesia antenina</i> <i>Nemertesia ramosa</i> <i>Plumularia setacea</i> <i>Polyplumaria flabellata</i>	<i>Thuiaria thuja</i> Fam. Sertulariidae <i>Abietinaria abietina</i> <i>Abietinaria filicula</i> <i>Amphisbetia operculata</i> <i>Diphasia attenuata</i> <i>Diphasia nigra</i> <i>Salacia desmoides</i> <i>Sertularella ellisii</i> <i>Sertularella fusiformis</i> <i>Sertularella gayi</i> <i>Sertularella mediterranea</i> <i>Sertularella polyzonias</i> <i>Sertularia argentea</i> Fam. Tubulariidae <i>Tubularia larynx</i> Class ANTHOZOA Order Gorgonacea <i>Lophogorgia</i> sp. Order Pennatulacea <i>Virgularia mirabilis</i> Phylum BRYOZOA <i>Cellaria salicornioides</i> <i>Crisia eburnea</i> <i>Filicrisia geniculata</i> <i>Scrupocellaria reptans</i>
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Table 1 (continued) - (suite tableau 1).

SPECIES RELATED TO EPIBIONTS AND MASKING MATERIAL

Phylum ANNELIDA	Fam. Spintheridae	<i>Synisoma acuminatum</i>	<i>Pseudoprotella phasma</i>	<i>Hinia incrassata</i>
Class Polychaeta	<i>Spinther oniscoides</i>	Order Amphipoda	<i>Pthisica marina</i>	<i>Jujubinus exasperatus</i>
Fam. Aphroditidae	Fam. Syllidae	Fam. Calliopidae		<i>Melanella alba</i>
<i>Harmothoe impar</i>	<i>Autolytus benazzii</i>	<i>Apherusa cf. jurinei</i>	Phylum PYGNOGONIDA	<i>Onoba semicostata</i>
<i>Lepidonotus clava</i>	<i>Brania pusilla</i>	Fam. Dexaminidae	Fam. Nymphonidae	<i>Rhaphitoma linearis</i>
<i>Subadyte pellucida</i>	<i>Exogone naidina</i>	<i>Dexamine spinosa</i>	<i>Nymphon gracile</i>	<i>Rissoa membranacea</i>
<i>Lagisca extenuata</i>	<i>Exogone verugera</i>	<i>Triaeta gibbosa</i>	Fam. Achellidae	<i>Rissoa parva</i>
<i>Halosydna gelatinosa</i>	<i>Myrianida pinnigera</i>	Fam. Gammaridae	<i>Achelia sp.</i>	<i>Tricolia pullus</i>
<i>Pholoe inornata</i>	<i>Plakosyllis brevipes</i>	<i>Gammarus locusta</i>	Fam. Callipallenidae	Subclass Opisthobranchia
Fam. Eunicidae	<i>Sphaerosyllis prolifera</i>	Fam. Isaeidae	<i>Callipallene sp.</i>	<i>Aplysia punctata</i>
<i>Eunice vittata</i>	<i>Syllis columbretenensis</i>	<i>Gammaropsis maculata</i>		<i>Archidoris pseudoargus</i>
Fam. Euprosinidae	<i>Syllis gerlachi</i>	<i>Isaea montagui</i>	Phylum MOLLUSCA	<i>Doris ocelligera</i>
<i>Euprosine foliosa</i>	<i>Syllis gracilis</i>	Fam. Leucothoidae	Class Polyplacophora	<i>Doris sp.</i>
Fam. Nereidae	<i>Syllis krohni</i>	<i>Leucothoe spinicarpa</i>	<i>Acanthochitona crinita</i>	<i>Goniodoris nodosa</i>
<i>Nereis pelagica</i>	<i>Syllis prolifera</i>	Fam. Lysianassidae	<i>Callochiton septemvalvis</i>	<i>Lamellaria perspicua</i>
<i>Leptonereis glauca</i>	<i>Trypanosyllis zebra</i>	<i>Lysianassidae sp.</i>	<i>Lepidochitona corrugata</i>	<i>Polycera quadrilineata</i>
<i>Platynereis dumerilii</i>		Fam. Melitidae	Class Gastropoda	Class Bivalvia
Fam. Phyllodocidae	Phylum CRUSTACEA	<i>Elasmopus rapax</i>	Subclass Prosobranchia	<i>Musculus marmoratus</i>
<i>Phyllodoce sp.</i>	Class MALACOSTRACA	<i>Maera inaequipes</i>	<i>Acmaea virginea</i>	<i>Musculus sulpectus</i>
<i>Mysta picta</i>	Order Isopoda	Fam. Podoceridae	<i>Bittium reticulatum</i>	
<i>Eulalia aurea</i>	<i>Dynamene bidentata</i>	<i>Podocerus variegatus</i>	<i>Brachistomia rissoides</i>	
<i>Phyllodoce mucosa</i>	<i>Dynamene magnitorata</i>	Fam. Caprellidae	<i>Cerithiopsis tubercularis</i>	
	<i>Janira sp.</i>	<i>Caprella sp.</i>	<i>Gibbula cineraria</i>	

SPECIES NOT RELATED TO EPIBIONTS AND MASKING MATERIAL

Phylum ANNELIDA	Fam. Terebellidae	Fam. Veneridae	Fam. Porcellanidae	Class Ophiuroidea
Class Polychaeta	<i>Amphitritides gracilis</i>	<i>Venerupis pullastra</i>	<i>Pisidia longicornis</i>	<i>Amphipholis squamata</i>
Fam. Arenicolidae	<i>Polycirrus sp.</i>		Fam. Xanthidae	<i>Ophiocoma nigra</i>
<i>Arenicolidae sp.</i>		Phylum CRUSTACEA	<i>Pilumnus hirtellus</i>	<i>Ophiothrix fragilis</i>
Fam. Cirratulidae	Phylum MOLLUSCA	Class Malacostraca		Class Echiuroidea
<i>Cirriformia tentaculata</i>	Class Bivalvia	Order Decapoda	Phylum ECHINODERMATA	<i>Paracentrotus lividus</i>
Fam. Spionidae	Fam. Cardiidae	Fam. Palaemonidae	Class Crinoidea	Class Holothuroidea
<i>Polydora caeca</i>	<i>Parvicardium papillosum</i>	<i>Palaemon sp.</i>	<i>Antedon bifida</i>	<i>Aslia lefevrei</i>

spp., *Sertularella* spp. and *Nemertesia* spp., the polychaete *Pomatoceros triqueter*, the barnacle *Balanus perforatus* and the mollusc *Anomia ephippium* (Table 2). These species and genera, together with the calcareous seaweeds already cited, the bryozoans *Scrupocellaria reptans* (Linnaeus) and *Cellepora pumicosa* (Pallas), the holothurian *Aslia lefevrei* and the ascidian *Didemnum maculosum* (Milne Edwards) (practically absent on immature individuals), may be considered species typical of deep water individuals (area D).

Ascidians and bryozoans were the groups that denote the most important differences in terms of frequency of appearance among the mature spider crabs of the area D (Fig. 2b). Both taxa, practically absent in immature animals, were extremely common on sexually mature spider crabs and exhibit a sharp increase in frequency of appearance with time, once the animal has undergone the terminal moult (ascidians: 43.0% in TM92, 78.9% in TM91; bryozoans: 27.8% in TM92, 57.9% in TM91). A year or more after the terminal moult, *Didemnum maculosum* continued to be the most common ascidian (31.6% in TM91), although the great

increase experienced by *Polycarpa pomaria* (Savigny) is noteworthy (Table 2). The most common bryozoans were *Cellepora pumicosa* and *Scrupocellaria reptans* (39.5% and 44.7%, respectively, in TM91).

Crustaceans also increased in frequency between TM92 and TM91, although to a lesser extent. This increase may be primarily attributed to the barnacle *Balanus perforatus* (76.3% in TM91). Hydrozoans generally maintained or increased their frequencies in TM91 as compared to TM92, as evidenced by *Aglaophenia* and *Sertularella*. This increase in frequency of appearance of the associated fauna as *Maja squinado* ages, also occurred in polychaetes. *Pomatoceros triqueter* was even more visible on the TM91 spider crabs (84.2%), and therefore continues to be the most characteristic species. *Spirorbis spirorbis* was the only polychaete that decreased in frequency and after a typical presence on juveniles of the area S, almost disappeared on TM91 (2.6%). As far as the molluscs are concerned, *Anomia ephippium* was still the most frequent species, and the most noteworthy variation was the sharp increase in the presence of *Mytilus galloprovincialis* (Lamarck) in TM91 (50%).

Table 2. Frequency of appearance (% presence) of the most common species on *M. squinado*. It includes the data relative to all the individuals studied (TOTAL), in relation to their habitat (AREA S = shallow water individuals, AREA D = deeper waters) and to the time elapsed since the terminal moult. TM91, terminal moult in 1991 or before 1991: time elapsed is >12 months. TM92, terminal moult in 1992: time elapsed is 0-12 months.

Tableau 2. Fréquence d'apparition (présence en %) des espèces les plus communes sur *M. squinado*. Les données sont relatives à tous les individus étudiés (TOTAL) en rapport avec leur habitat (AREA S = individus des eaux peu profondes, AREA D = individus des eaux profondes) et avec le temps passé depuis la mue terminale. TM91, mue terminale en 1991 ou avant 1991 : le temps écoulé est >12 mois. TM92, mue terminale en 1992 : le temps écoulé est de 0 à 12 mois).

	TOTAL	AREA S	AREA D	TM92	TM91
Seaweeds					
<i>Boergensienella martensiana</i>	2,3	15,0	0,4	0,4	0,0
<i>Calliblepharis jubata</i>	2,7	20,0	0,0	0,0	0,0
<i>Callophillis laciniata</i>	5,6	5,0	5,7	3,6	18,4
<i>Ceramium rubrum</i>	5,6	12,5	4,6	5,4	0,0
<i>Champia intricata</i>	1,7	12,5	0,0	0,0	0,0
<i>Chondria scintillans</i>	4,0	10,0	3,1	3,1	2,6
<i>Corallina officinalis</i>	10,3	5,0	11,1	11,2	10,5
<i>Cryptopleura ramosa</i>	6,3	15,0	5,0	5,8	0,0
<i>Cystoseira</i> spp.	22,6	75,0	13,8	15,7	2,6
<i>Dictyota dichotoma</i>	9,3	32,5	5,7	6,7	0,0
<i>Enteromorpha</i> spp.	17,6	5,0	11,9	14,3	0,0
<i>Chondracanthus teedii</i>	1,3	10,0	0,0	0,0	0,0
<i>Mesophyllum lichenoides</i>	12,0	0,0	13,8	9,0	42,1
<i>Plocamium cartilagineum</i>	19,9	30,0	18,4	20,2	7,9
<i>Pterocladia capillacea</i>	4,7	15,0	3,1	2,7	5,3
<i>Pterosiphonia complanata</i>	8,0	7,5	8,0	7,6	10,5
<i>Sargassum muticum</i>	14,3	45,0	9,6	10,8	2,6
Porifera					
<i>Hymeniacidon sanguinea</i>	7,0	0,0	7,7	6,7	13,2
<i>Sycon ciliatum</i>	12,0	0,0	13,8	14,8	7,9
<i>Syphonochalina</i> sp.	8,3	2,5	8,8	8,1	13,2
Cnidaria					
<i>Actinothoe sphyrodeta</i>	4,7	0,0	5,4	4,5	10,5
<i>Aglaophenia</i> spp.	33,9	7,5	37,5	38,1	34,2
<i>Aglaophenia</i> spp. (epibiosis)	41,2	2,5	46,4	43,0	65,8
<i>Gymnangium montagui</i>	3,0	0,0	3,4	2,2	10,5
<i>Nemertesia</i> spp.	25,2	5,0	28,4	28,7	26,3
<i>Sertularella gayi</i>	7,6	2,5	8,4	8,1	10,5
<i>Sertularella</i> spp.	4,0	0,0	4,6	3,6	10,5
<i>Sertularella</i> spp. (epibiosis)	37,5	0,0	42,5	36,8	76,3
<i>Sertularia distans</i>	6,6	0,0	7,7	5,8	18,4
Polychaeta					
<i>Dasychone bombyx</i>	10,3	0,0	11,1	7,6	31,6
<i>Harmothoe impar</i>	9,6	0,0	11,1	10,3	15,8
<i>Hydroides norvegica</i>	7,3	0,0	8,4	6,7	18,4
<i>Nereis pelagica</i>	5,0	2,5	5,4	3,6	15,8
<i>Platynereis dumerilii</i>	20,3	15,0	20,7	19,3	28,9
<i>Pomatoceros triquetus</i>	61,8	12,5	69,0	66,4	84,2
<i>Spirorbis spirorbis</i>	11,3	30,0	8,4	9,4	2,6
<i>Syllis gracilis</i>	2,0	0,0	2,3	0,9	10,5
Crustacea					
<i>Ampithoe ramondi</i>	5,0	20,0	2,7	3,1	0,0
<i>Aora typica</i>	6,0	10,0	5,0	5,8	0,0
<i>Balanus perforatus</i>	37,5	5,0	42,5	36,8	76,3
<i>Dexamine spinosa</i>	3,3	22,5	0,4	0,4	0,0
<i>Dynamene magnitorata</i>	4,7	30,0	0,8	0,9	0,0
<i>Gammaropsis maculata</i>	16,9	5,0	18,8	20,6	7,9

Table 2 (continued) - (suite tableau 2).

	TOTAL	AREA S	AREA D	TM92	TM91
<i>Isaea montagui</i>	18,9	0,0	21,5	21,5	21,1
<i>Pisidia longicornis</i>	11,3	0,0	13,0	11,7	21,1
<i>Sunamphithoe pelagica</i>	2,0	15,0	0,0	0,0	0,0
Mollusca					
<i>Anomia ephippium</i>	59,5	5,0	67,0	67,3	65,8
<i>Bittium reticulatum</i>	8,6	32,5	5,0	4,0	10,5
<i>Hiatella arctica</i>	16,3	2,5	17,6	15,7	28,9
<i>Musculus marmoratus</i>	11,6	0,0	13,0	13,9	7,9
<i>Mytilus galloprovincialis</i>	19,6	0,0	22,2	17,5	50,0
<i>Rissoa parva</i>	5,0	15,0	3,4	3,6	2,6
Bryozoa					
<i>Cellepora pumicosa</i>	14,6	0,0	16,9	13,0	39,5
<i>Scrupocellaria reptans</i>	18,3	5,0	19,5	15,2	44,7
Echinodermata					
<i>Amphipholis squamata</i>	19,3	17,5	19,5	19,7	18,4
<i>Aslia lefevrei</i>	30,6	0,0	34,5	33,6	39,5
<i>Ophiothrix fragilis</i>	19,9	0,0	23,0	22,9	23,7
Asciidiacea					
<i>Ciona intestinalis</i>	6,3	0,0	7,3	6,7	10,5
<i>Didemnum maculosum</i>	19,9	0,0	23,0	24,5	31,6
<i>Distomus variolosus</i>	6,0	0,0	6,9	5,8	13,2
<i>Polycarpa pomaria</i>	4,3	0,0	5,0	2,7	18,4

The fact that the frequency of occurrence of seaweeds remains constant one year after the pubertal moult, is due to the marked increase of *Mesophyllum lichenoides* (TM92 = 9,0%; TM91 = 42.1%) and *Callophyllis laciniata* (Hudson) Kützinger (TM92 = 3.6%; TM91 = 18.4%) which compensate for the strong decrease or in some cases the disappearance of the green and brown seaweeds, such as *Enteromorpha*, *Cystoseira* and *Sargassum*.

Masking species and encrusting epibiosis (Table 3)

Seaweeds were the dominant group in terms of percentage of covering of the total surface occupied by the masking and encrusting epibiont material, reaching a value of 85.5% in the total number of spider crabs analysed (Fig. 3a) and a mean covering per spider crab ($\bar{x}_c$) of 23.4% (sd = 25.9).

In individuals found in the shallow area, seaweeds were practically the only organisms used in masking, comprising 98.8% of the surfaced covered ($\bar{x}_c$ = 67.6%, sd = 13.1). The seaweed covering was made up primarily of brown (*Sargassum*, *Cystoseira*) and green (*Enteromorpha*) seaweeds. Among the typical epibiont organisms, poriferans, ascidians, and bryozoans were represented each by a single species which constitutes 100% of the covering of each group (*Syphonochalina* sp., *Scrupocellaria reptans*, and *Aplydium* sp., respectively) (Table 3).

In samples from the deep zones (area D), the abundance of seaweeds decreased in contrast to shallow water animals (Fig. 3a) accounting for 74.8% of the covered surface ($\bar{x}_c$ = 13.9%, sd = 16.4). A decrease was in proportion to the time elapsed since the terminal moult: 43.3% of the surface covered in TM91 ($\bar{x}_c$ = 4.0%, sd = 4.8), as compared to 80% observed in TM92 ($\bar{x}_c$ = 15.6%, sd = 17.1). Nevertheless, the most abundant epibiont species, the rhodophyte *Mesophyllum lichenoides*, only reached high values in TM91, accounting for 38.8% of the surface covered by seaweeds (Table 3).

Cnidarians constituted the second most abundant group, although they covered a much smaller surface area than seaweeds (6.4%). This group, which was scarce on spider crabs in the shallow area, showed a high presence in the deep area and were found to be the foremost material used in masking (Fig. 3a). They showed a similar relative abundance in TM91 and TM92, but with some variations in terms of specific composition (Table 3). In the TM92 spider crabs, the organisms chosen for camouflage were mainly *Aglaophenia* (TM92 = 30.6%, TM91 = 32.6%) and *Nemertesia* (TM92 = 35.9%, TM91 = 17.1%), whereas in TM91, there were others, equally large species and abundant in the environment, such as *Sertularella gayi* (Lamouroux) (TM91 = 16.3%, TM92 = 9.0%) and *Lytocarpa myriophyllum* (Linnaeus) (TM91 = 11.5%, TM92 = 0.0%).

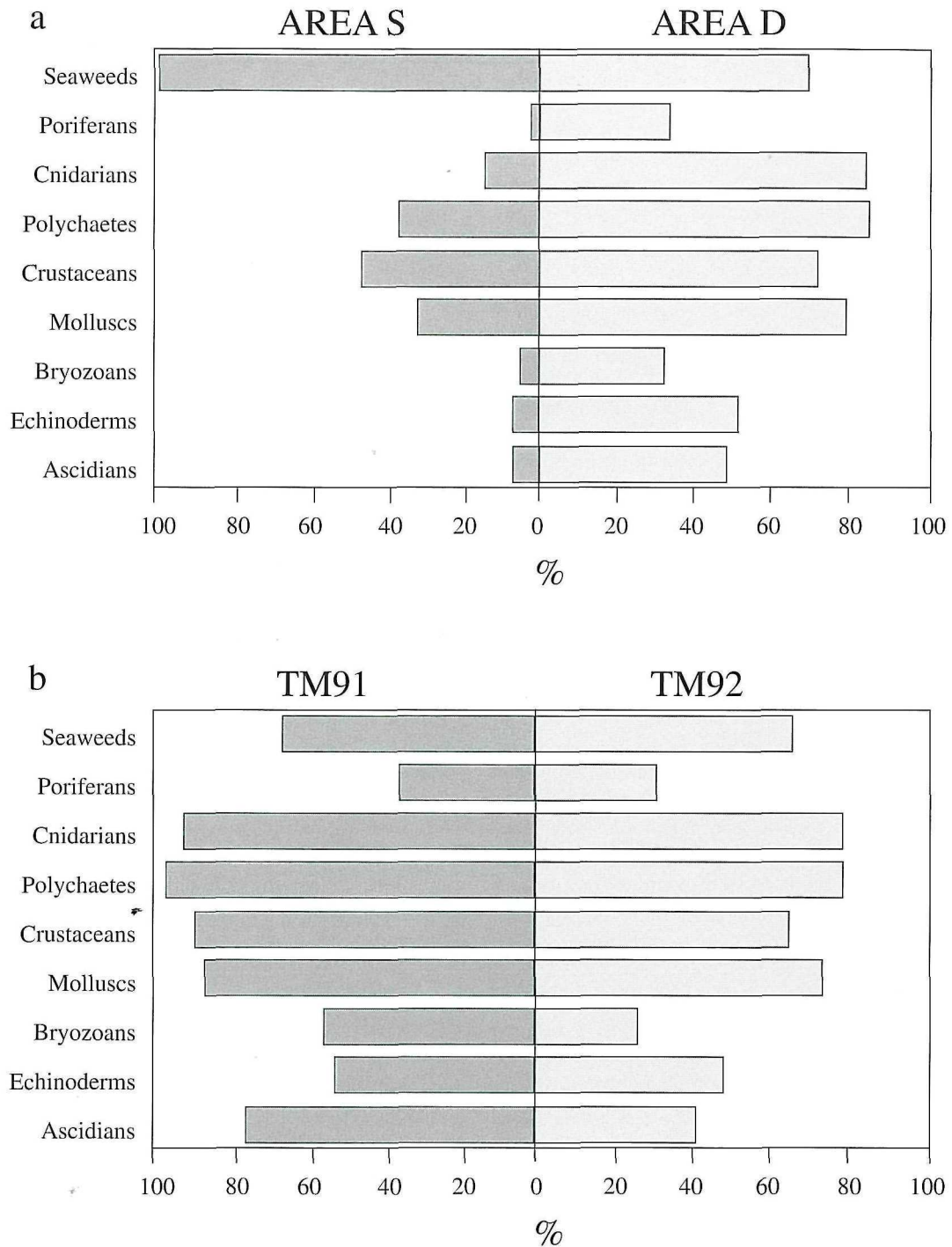


Figure 2. Frequency of appearance on *M. squinado* of each floral and faunal group. a) frequency of appearance by habitat (AREA S = shallow water individuals, AREA D = deeper water individuals), b) frequency of appearance within the area D, depending on the time elapsed since the terminal moult. TM91, terminal moult in 1991 or before 1991: time elapsed is >12 months. TM92, terminal moult in 1992: time elapsed is 0-12 months.

Figure 2. Fréquence d'apparition de chaque groupe floristique et faunistique sur *M. squinado*. a) fréquence d'apparition par habitat (AREA S = individus des eaux peu profondes, AREA D = individus des eaux profondes), b) fréquence d'apparition dans la zone D, selon le temps passé depuis la mue terminale. TM91, mue terminale en 1991 ou avant 1991 : le temps écoulé est >12 mois. TM92, mue terminale en 1992 : le temps écoulé est de 0 à 12 mois).

Table 3. Percentage of the surface covered by the more abundant masking species and encrusting epibionts on the carapace of *M. squinado*, expressed in terms of its faunal or floral group.**Tableau 3.** Pourcentage de la surface de carapace de *M. squinado* recouverte par les espèces ornamentales et les épibiontes encroûtantes les plus abondantes, exprimé en fonction de leur groupe faunistique ou floristique.

	TOTAL	AREA S	AREA D	TM92	TM91
Seaweeds					
<i>Mesophyllum lichenoides</i>	2,7	0,0	5,3	0,0	38,8
Others	97,3	100,0	94,7	100,0	61,2
Porifera					
<i>Hymeniacidon sanguinea</i>	23,0	0,0	21,4	39,7	32,6
<i>Syphonochalina</i> sp.	17,0	100,0	12,3	3,9	10,9
<i>Desmacidon fruticosum</i>	12,3	0,0	11,6	29,1	12,7
<i>Halichondria bowerbanki</i>	10,7	0,0	23,2	7,8	16,3
<i>Hymedesmia dujardini</i>	9,3	0,0	8,8	0,0	12,3
<i>Haliclona</i> sp.	7,0	0,0	3,2	0,0	2,6
<i>Mycale contarenii</i>	3,7	0,0	3,5	4,9	7,4
<i>Pronax plumosum</i>	1,6	0,0	1,5	14,6	0,0
Others	15,4	0,0	16,0	0,0	5,2
Cnidaria					
<i>Aglaophenia</i> spp.	36,6	44,5	34,5	30,6	32,6
<i>Nemertesia</i> spp.	32,0	15,3	31,2	35,9	17,1
<i>Sertularella gayi</i>	7,4	6,9	7,1	9,0	16,3
<i>Amphisbetia operculata</i>	5,7	0,0	5,6	5,9	0,8
<i>Lophogorgia</i> sp.	4,2	33,3	3,7	6,0	0,2
<i>Gymnangium montagui</i>	2,9	0,0	6,9	2,5	9,7
<i>Halecium beanii</i>	2,4	0,0	2,3	4,2	0,0
<i>Lytocarpia myriophyllum</i>	1,5	0,0	1,4	0,0	11,5
<i>Sertularella</i> spp.	1,5	0,0	1,5	0,1	8,2
Others	5,8	0,0	5,8	5,8	3,6
Polychaeta					
<i>Salmacina incrustans</i>	100,0	0,0	100,0	100,0	100,0
Bryozoa					
<i>Scrupocellaria reptans</i>	58,1	100,0	48,7	27,6	55,5
<i>Cellepora pumicosa</i>	28,7	0,0	35,2	12,6	39,5
<i>Scruparia chelata</i>	6,7	0,0	8,3	17,2	0,6
<i>Crisia eburnea</i>	3,5	0,0	4,3	11,5	3,0
<i>Cellaria salicornioides</i>	2,2	0,0	2,8	28,7	0,0
Others	0,8	0,0	0,7	2,4	1,4
Ascidacea					
<i>Didemnum maculosum</i>	51,8	0,0	53,2	68,5	63,4
<i>Distomus variolosus</i>	16,6	0,0	18,7	0,0	5,3
<i>Didemnum lahillei</i>	12,2	0,0	11,6	0,0	22,9
<i>Didemnum</i> sp.	6,1	0,0	6,3	14,3	0,7
<i>Aplydium</i> sp.	3,4	100,0	3,0	2,9	0,0
<i>Didemnum coriaceum</i>	1,7	0,0	1,8	0,0	5,4
Polyclinidae spp.	1,6	0,0	1,6	14,3	0,0
Others	6,6	0,0	3,8	0,0	2,3

Ascidians, bryozoans and especially sponges increased their relative abundance in the TM91 spider crabs.

Non-encrusting epibiosis and associated fauna (Table 4)

Considering the total number of spider crabs analysed, cnidarians (33.0%), polychaetes (23.2%), molluscs (19.5%)

and crustaceans (15.4%) were the most abundant groups of epibionts in terms of percentage of the number of individuals or colonies (Fig. 3b). *Aglaophenia tubulifera* (Hincks) and *Sertularella* spp. were the cnidarians with the highest percentage of colonies in their group (45.8% and 33.8%, respectively) (Table 4). Among polychaete species,

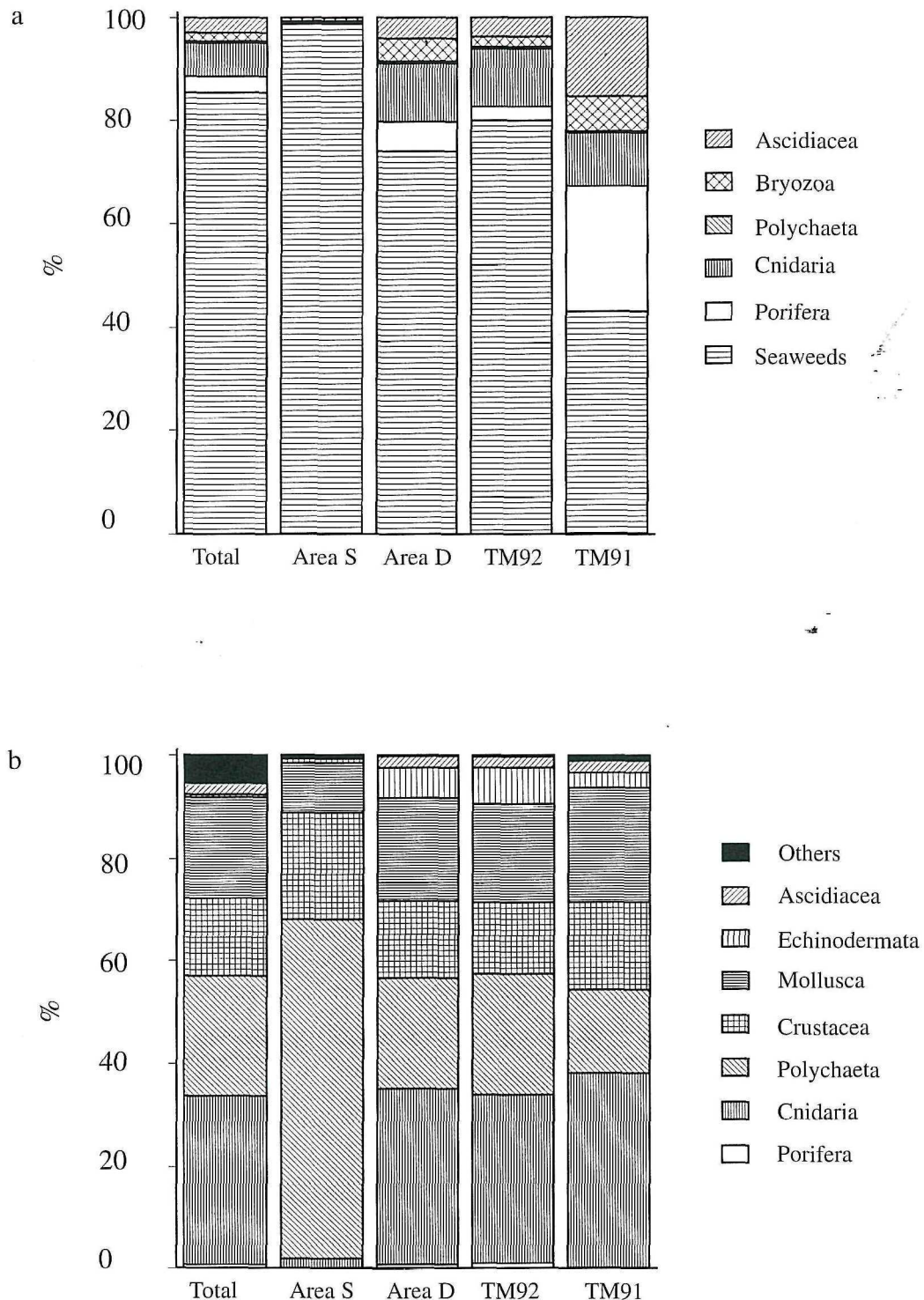


Figure 3. a) Percentage of *Maja squinado* covered surface, corresponding to each faunal and floral group (masking material and encrusting epibiosis), b) percentage of the number of individuals or colonies (non-encrusting epibiosis and associated fauna) from each faunal group with respect to all the individuals studied (TOTAL), to their habitat and to the time elapsed since the terminal moult (TM91 and TM92, see figure 2).

Figure 3. a) Pourcentage de surface de *Maja squinado* recouverte, correspondant à chaque groupe faunistique et floristique (matériel de camouflage et épibiose encroûtante), b) pourcentage du nombre total d'individus ou de colonies (épibiose non encroûtante et faune associée) de chaque groupe en rapport avec le nombre total d'individus étudiés (TOTAL), leur habitat et le temps écoulé depuis la mue terminale (TM91 et TM92, voir figure 2).

Table 4. Percentage of the number of individuals of the most abundant non-encrusting epibiont species and associated fauna on the carapace of *M. squinado*, expressed in terms of its faunal group.**Tableau 4.** Pourcentage du nombre d'individus des espèces épibiontes non encroûtantes et de la faune associée les plus abondantes, sur la carapace de *M. squinado*, exprimé en fonction de leur groupe faunistique.

	TOTAL	AREA S	AREA D	TM92	TM91
Porifera					
<i>Sycon ciliatum</i>	100,0	0,0	100,0	100,0	100,0
Cnidaria					
<i>Aglaophenia tubulifera</i>	45,8	72,7	45,7	64,0	29,9
<i>Sertularella spp.</i>	33,8	0,3	33,8	26,2	35,7
<i>Sertularia distans</i>	11,0	0,0	11,1	2,2	22,2
<i>Actiniaria undet.</i>	0,5	27,3	0,4	1,3	0,1
Others	8,9	0,0	9,0	6,3	12,1
Polychaeta					
<i>Pomatoceros triqueter</i>	60,8	1,8	69,2	24,4	79,4
<i>Spirorbis spirorbis</i>	26,3	94,7	16,8	65,1	0,2
<i>Hydroides norvegica</i>	3,4	0,0	3,8	1,5	5,4
<i>Platynereis dumerilii</i>	2,2	3,3	2,0	2,1	2,0
Others	7,3	0,2	8,2	7,9	13,0
Crustacea					
<i>Balanus perforatus</i>	55,6	3,2	58,9	42,9	88,6
<i>Isaea montagui</i>	6,9	0,0	7,3	25,6	3,8
<i>Gammaropsis maculata</i>	6,8	1,6	7,1	0,9	1,5
<i>Pisidia longicornis</i>	5,1	0,0	5,4	23,5	3,9
<i>Aora typica</i>	1,7	11,3	1,1	0,3	0,0
<i>Dexamine spinosa</i>	1,6	25,8	0,1	0,0	0,0
<i>Ampithoe ramondi</i>	1,0	11,3	0,3	0,9	0,0
<i>Dynamene magnitorata</i>	1,0	13,7	0,0	0,0	0,0
<i>Microdeutopus chelifer</i>	0,7	12,1	0,0	0,0	0,0
<i>Sunamphithoe pelagica</i>	0,6	9,7	0,0	0,0	0,0
Others	6,9	11,3	7,0	5,9	2,2
Mollusca					
<i>Anomia ephippium</i>	66,7	3,4	68,1	93,0	24,2
<i>Mytilus galloprovincialis</i>	24,8	0,0	25,5	2,8	71,2
<i>Bittium reticulatum</i>	1,5	55,2	0,3	0,5	0,2
<i>Rissoa parva</i>	1,0	22,4	0,5	0,8	0,1
<i>Gibbula cineraria</i>	0,1	5,2	0,0	0,0	0,0
<i>Jujubinus exasperatus</i>	0,1	3,4	0,1	0,1	0,0
<i>Rissoa membranacea</i>	0,1	6,9	0,0	0,0	0,0
Others	5,7	3,5	5,5	2,8	4,3
Echinodermata					
<i>Aslia lefevrei</i>	7,1	0,0	70,5	78,5	86,3
<i>Ophiothrix fragilis</i>	13,1	0,0	13,8	7,5	5,5
<i>Amphipholis squamata</i>	10,0	100,0	9,9	4,2	7,3
<i>Antedon bifida</i>	5,4	0,0	5,4	9,6	0,9
Others	5,8	0,0	0,4	0,2	0,0
Ascidacea					
<i>Polycarpa pomaria</i>	24,9	0,0	25,2	15,3	54,0
<i>Ascidella scabra</i>	11,0	100,0	10,1	6,8	2,3
<i>Didemnum maculosum</i>	10,3	0,0	10,4	18,6	0,0
<i>Molgula amesophleba</i>	10,0	0,0	10,1	11,9	1,2
<i>Polycarpa tenera</i>	9,3	0,0	9,4	0,0	3,5
<i>Ciona intestinalis</i>	7,6	0,0	7,7	23,7	5,7
<i>Molgula sp.</i>	7,0	0,0	7,0	8,5	8,1
<i>Polycarpa violacea</i>	6,3	0,0	6,4	5,1	12,6
<i>Ascidia sp.</i>	3,3	0,0	3,4	8,5	1,2
Others	10,3	0,0	10,3	1,6	11,4

the most abundant were primarily *Pomatoceros triqueter* (60.8%), and *Spirorbis spirorbis* (26.3%). *Anomia ephippium* (66.7%) and *Mytilus galloprovincialis* (24.8%) were important in terms of number of individuals within molluscs, and *Balanus perforatus* was the most important crustacean, accounting for 55.6% of the total number of this group.

The relative abundance of large groups of epibionts varied considerably between individuals found in deep and shallow waters (Fig. 3b). Polychaetes (66.3%), and to a lesser extent, crustaceans (20.7%) and molluscs (9.7%), were the most abundant groups on spider crabs in area S. Epibiont polychaetes of these individuals were represented almost totally by *Spirorbis spirorbis* (94.7%). The amphipod *Dexamine spinosa* (25.8%) and the molluscs *Bittium reticulatum* (55.2%) and *Rissoa parva* (22.4%), were highly abundant in shallow water individuals, given their trophic relationship with ornamental seaweeds used by *Maja squinado*. *Aglaophenia tubulifera* was the only epibiont hydrozoan found on shallow water spider crabs.

In deep water spider crabs (area D), the most abundant animals were cnidarians (34.4% of the total number of epibionts), followed by polychaetes (21.4%), molluscs (19.9%) and crustaceans (15.3%). The most important cnidarian species were *Aglaophenia tubulifera* (area D = 45.7%), which dominated in the TM92 spider crabs, and *Sertularella* spp., chiefly *S. mediterranea* Hartlaub (area D = 33.8%), which was the most abundant species in the TM91 spider crabs. The tubicolous polychaete *Pomatoceros triqueter* was characteristic of individuals from area D (69.2%), especially in older individuals (TM91: 79.4%). The most abundant amphipods on shallow water spider crabs disappeared almost totally, along with the camouflage, in the area D spider crabs. In this latter zone, the authentic epibiont species *Balanus perforatus* dominated, specially in the TM91 spider crabs (88.6%). Likewise, among molluscs, the species characteristic of area S were replaced by epibiont species on mature individuals, particularly *Anomia ephippium* (TM92: 93.0%) and *Mytilus galloprovincialis* (TM91: 71.2%).

Discussion

As reported earlier (Wicksten, 1979, 1993; Dudgeon, 1980), habitat is a determining factor in the epibiosis and masking of the majids. An important aspect in the biology of *Maja squinado* in the Ría de Arousa is the migration and the resulting change in habitat that the species undergoes, once the terminal moult has been carried out (González-Gurriarán & Freire, 1994). During the pre-pubertal stage and immediately after the pubertal moult, spider crabs are found in rocky areas having clear, shallow waters, and kelp belts with an abundance of small seaweeds which they use

for camouflage. In the post-pubertal stage these animals are found in deeper waters on bottoms having a mixture of rock and soft sediment. The composition of camouflage and epibiont material reflects the changes in habitat that the animal undergoes as it migrates from shallow water areas to deeper waters. The differences observed in the composition of carapace covering are due to the fact that the most common and abundant organisms on the carapace are also those that are the most plentiful in the milieu where the animal is located, as happens in other majids (Wicksten, 1993).

The substantial quantitative importance of the seaweeds on spider crabs in shallow waters may be attributed to their abundance in the environment, as well as the pronounced masking behaviour exhibited by these animals. Thus, species from the genus *Cystoseira*, which are available all the year round, are the most common and most abundant on the carapace of juveniles. Like other majids (Wicksten, 1993), the spider crab uses flexible material from its habitat, easy to handle with its chelae, and easily hooked on the setae of the exoskeleton such as large sized seaweeds and hydrozoans. The other taxa which cover spider crabs in the shallow area, are pioneer species in colonization of hard infralittoral marine substrates, such as the polychaete *Spirorbis spirorbis*, and also members of a fauna related to the seaweeds either because of their herbivorous nature, namely the molluscs *Bittium reticulatum* and *Rissoa parva*, or because they use seaweeds as a substratum for their tubes, e.g. the amphipods *Dexamine spinosa*, *Ampithoe ramondi* and *Sunamphitoe pelagica*.

Like other majids such as *Maiopsis panamensis* Faxon, *Macrocheira kaempferi* de Haan, *Mithrax spinosissimus* (Lamarck), *Loxorhynchus crispatus* Stimpson and *L. grandis* Stimpson (Wicksten, 1979; Dudgeon, 1980), *Maja squinado* starts losing its masking habit once it is fully grown (González-Gurriarán *et al.*, 1995) and less vulnerable to predators. The masking behaviour disappears completely, approximately one year after the terminal moult. This change in behaviour, which takes place at the same time as migration to deeper areas, brings about a gradual increase in the relative importance of epibiont component, in contrast to self-camouflage. Like other spider crabs which totally drop their masking habit in the adult stage, such as *L. crispatus* and *L. grandis* (Wicksten, 1979), carapaces of individuals that underwent the terminal moult at an earlier point in time, TM91, are primarily covered with epibiont organisms and invasive species, which in turn serve as masking material. It is unlikely that epibiosis originates from the material initially used by *M. squinado* in ornamentation, since there is no clear correlation between the preference of masking material used by individuals that have recently carried out the terminal moult, TM92, and the epibiont species later identified on TM91 animals.

The individuals from the deep area bear organisms which do not appear in those from shallow waters, such as ascidians (except *Aplidium* sp.), bryozoans (except *Scrupocellaria reptans*), or the encrusting seaweed *Mesophyllum lichenoides*. The quantitative importance of these epibionts gradually increases with time starting from the terminal moult. This pattern has also been observed in other typical epibiont species, namely the barnacle *Balanus perforatus*, the tubicolous polychaete *Pomatoceros triqueter*, and the hydrozoans of the genera *Aglaophenia* and *Sertularella*. The increase in abundance of the epibiont species with increasing time after the terminal moult, permitted to differentiate the deep water individuals, TM92 and TM91. This epibiont increase is due to the stability of the substratum, i.e. the carapace of *Maja squinado*, after the terminal moult (Hartnoll, 1963; Le Foll, 1993; González-Gurriarán, *et al.*, 1995).

The masking behaviour of *M. squinado*, which is quite pronounced in juveniles and gradually decreases in adults once they have achieved the terminal moult, supports the general belief that this behaviour corresponds to a protection mechanism to ward off predators (Pack, 1982; Wicksten, 1993; Woods & McLay, 1994a, b), and not a mean of camouflage to make it easier to catch prey. Only two species of spider crabs have been seen to catch active prey, namely *Hias lyratus* Dana and *Macropodia rostrata* (Linnaeus) (Wicksten, 1993). Moreover, judging from observation of stomach contents of animals from the Ría de Arousa (unpublished data), *M. squinado* mainly consumes seaweeds and epibenthic organisms, primarily sessile or slow-moving animals, as do other majids (Hartnoll, 1963; Knudsen, 1964; Stêvcic, 1968b; Aldrich, 1976; Paul *et al.*, 1979; Mastro, 1981; Kilar & Lou, 1986; Coen, 1986; Wilson, 1987). Our data indicate that *M. squinado* in the Ría de Arousa feeds chiefly on laminarians, the holothurian *Aslia lefevrei*, ascidians and the echinoid *Paracentrotus lividus* (Lamarck), and this would not appear to imply a direct relationship between masking material and diet, as reported by Woods & McLay (1994a, b) for *Notomithrax ursus* (Herbst).

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