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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 %. Ascidies, 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

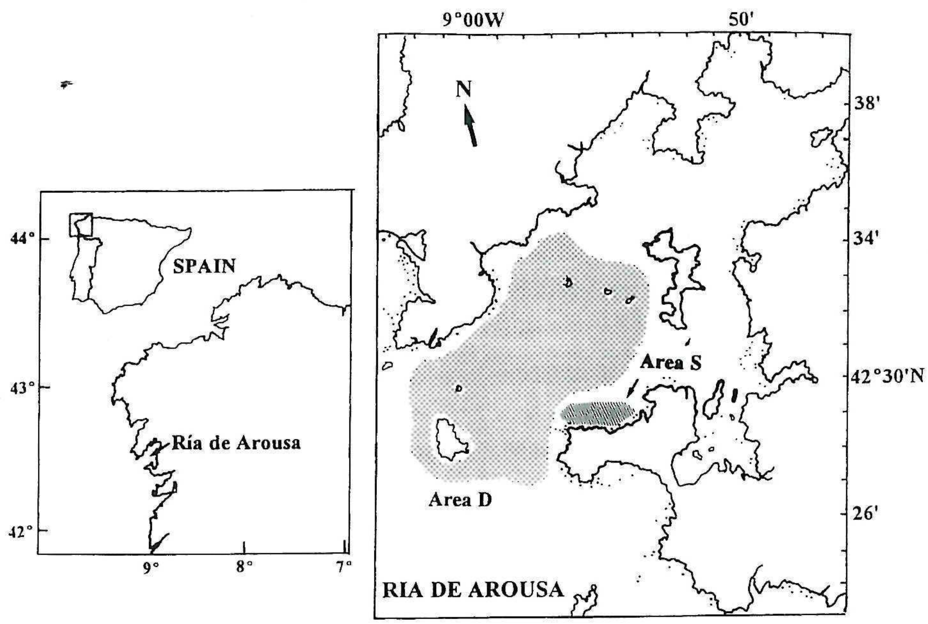

Figure 1. *Maja squinado.* Sampling areas in the Ría de Arousa (Galicia, NW Spain), Area S: shallow, rocky area (1-8 m depth), Area D: deep area (15-40 m depth).

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 crypsis, 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 tubiculous 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) Kützing, *Champia parvula* (C. Agardh) Harvey and *Chondracanthus teedii* (Roth) Kützing, 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
Apoglosum ruscifolium
Callophillis laciniata
Callymenia reniformis
Cryptopleura ramosa
Halarachnion ligulatum
Mesophyllum liquenoides
Pterothamnion crispum
Rhodophyllis divaricata

Phylum PORIFERA
Class Demospongia
Fam. Mycalidae
Mycale contarenii
Mycale rotalis
Fam. Esperiopsidae
Esperiopsis fucorum
Desmacidon fructicosum
Fam. Myxillidae
Myxilla rosacea
Myxillidae sp.
Iophonopsis nigricans
Fam. Hymedesmiidae
Hymedesmia dujardini
Fam. Anchinoidae
Pronax plumosum
Fam. Clathriidae
Microciona strepsitoxa
Fam. Haliclonidae
Haliclona oculata
Haliclona spp.
Fam. Halichondriidae
Halichondria bowerbanki
Fam. Hymeniacidonidae
Hymeniacidon sanguinea
Fam. Dysideidae
Dysidea fragilis
Class Calcarea
Fam. Sycettidae
Sycon ciliatum
Fam. Grantiidae
Grantia compressa
Leuconia nivea
Leuconia balearica

Phylum CNIDARIA
Class HYDROZOA
Fam. Aglaopheniidae
Aglaophenia octodonta
Aglaophenia pluma
Fam. Campanulariidae
Clytia hemisphaerica
Laomedea flexuosa
Obelia dichotoma
Obelia geniculata
Fam. Plumulariidae
Antennella secundaria
Fam. Sertulariidae
Amphisbetia operculata
Dynamena pumila
Sertularella mediterranea
Sertularia distans
Class ANTHOZOA
Order Zoanthidea
Parazoanthus arenaceus
Order Actiniaria
Actinothoe sphyrodeta
Actiniaria sp.
Calliactis parasitica

Phylum ANNELIDA
Class Polychaeta
Fam. Sabellidae
Potamilla torelli
Branchiomaldane vincentii
Dasychone bombyx
Jasmineira elegans
Sabella pavonina
Fam. Serpulidae
Serpula vermicularis
Hydroides norvegica
Pomatoceros triqueter
Pomatoceros lamarckii
Salmacina incrustans
Fam. Spirorbidae
Spirorbis spirorbis
Spirorbis militaris

Phylum MOLLUSCA
Class Bivalvia
Anomia ephippium
Hiatella arctica
Mytilus edulis

Phylum CRUSTACEA
Class CIRRIPEDIA
Balanus amphitrite
Balanus crenatus
Balanus perforatus
Elminius modestus
Verruca stroemia
Class MALACOSTRACA
Fam. Ampeliscidae
Ampelisca sp.
Fam. Ampithoidae
Ampithoe ramondi
Sunamphitoe pelagica
Fam. Aoridae
Aora typica
Microdeutopus chelifer
Microdeutopus damnoniensis
Fam. Corophiidae
Corophium sextonae
Fam. Ischryroceridae
Ericthonius brasiliensis
Jassa falcata
Fam. Isaeidae
Isaea montagui

Phylum BRYOZOA
Cellepora pumicosa
Celleporina hassali
Chartella papiracea
Electra pilosa
Scruparia chelata
Tubulipora plumosa

Phylum CHORDATA
Class Ascidiacea
Fam. Cionidae
Ciona intestinalis
Fam. Polyclinidae
Aplidium sp.
Polyclinidae spp.
Fam. Didemnidae
Didemnum coriaceum
Didemnum fulgens
Didemnum lahillei
Didemnum maculosum
Diplosoma spongiforme
Fam. Ascidiidae
Ascidia mentula
Ascidia virginea
Ascidiella aspersa
Ascidiella scabra
Fam. Styelidae
Botryllus schlosseri
Botrylloides leachi
Distomus variolosus
Polycarpa pomaria
Polycarpa tenera
Polycarpa violacea
Styela canopus
Fam. Pyuridae
Pyura sp.
Fam. Molgulidae
Molgula amesophleba
Molgula bleizii
Molgula socialis

MASKING SPECIES

Phylum PHYCOPHYTA
Div. Chlorophyta
Cladophora albida
Cladophora cf. hutchinsiae
Cladophora cf. rudolphiana
Cladophora laetevirens
Enteromorpha clathrata
Enteromorpha crinita
Enteromorpha prolifera
Ulva rigida

Div. Phaeophyta
Bifurcaria bifurcata
Cystoseira baccata
Cystoseira usneoides
Desmarestia aculeata
Dictyopteris sp.
Dictyota dichotoma
Ectocarpus fasciculatus
Halopteris filicina
Himanthalia elongata
Hincksia granulosa
Laminaria ochroleuca
Saccorhiza polyschides
Sargassum muticum
Sphacellaria sp.
Div. Rhodophyta
Acrosorium venulosum
Ahnfeltia plicata
Apoglosum ruscifolium
Asparragopsis armata
Boergensienella martensiana
Bonnemaisonia asparragoides
Bonnemaisonia sp.
Bornetia secundiflora
Calliblepharis jubata
Callithamnion tetricum
Callophillis laciniata
Callymenia reniformis
Ceramium echinotum
Ceramium rubrum
Ceramiun ciliatum
Champia intrincata
Chondria dasyphylla
Chondria scintillans
Chylocladia verticilata
Corallina officinalis
Dasya sp.
Delesseria sanguinea
"Falkenbergia rufolanosa"
Gastroclonium ovatum
Gelidium attenuatum
Gelidium latifolium
Gelidium sesquipedale
Gigartina acicularis
Gigartina falcata
Chondracanthus teedii
Gracilaria verrucosa
Griffithsia sp.
Halarachnion ligulatum
Heterosiphonia plumosa
Hypoglosum hypoglosoides
Jania cf. corniculata
Jania cf. rubens
Laurencia obtusa
Laurencia pinnatifida
Lomentaria articulata
Lomentaria clavellosa
Microcladia granulosa
Monosporum pedicellatus
Nitophyllum punctatum
Ophidocladus simpliciusculus
Pleonosporium borreri
Plocamium cartilagineum
Polyneura hilliae
Polysiphonia bodriaei
Polysiphonia elongata
Polysiphonia ferulacea
Pterocladia capillacea
Pterosiphonia complanata
Rhodymenia holmesi
Rhodymenia pseudopalmata
Sphaerococcus coronopifolius

Phylum PORIFERA
Class Demospongia
Fam. Callyspongiiae
Siphonochalina sp.

Phylum CNIDARIA
Class HYDROZOA
Fam. Aglaopheniidae
Aglaophenia acacia
Aglaophenia kirchenpaueri
Aglaophenia octodonta
Aglaophenia parvula
Aglaophenia pluma
Aglaophenia tubulifera
Gymnangium montagui
Lytocarpa myriophyllum
Fam. Haleciidae
Halecium beanii
Halecium halecinum
Halecium labrosum
Fam. Lafoeidae
Lafoea dumosa
Fam. Plumulariidae
Kirchenpaueria pinnata
Nemertesia antenina
Nemertesia ramosa
Plumularia setacea
Polyplumaria flabellata
Thuiaria thuja
Fam. Sertulariidae
Abietinaria abietina
Abietinaria filicula
Amphisbetia operculata
Diphasia attenuata
Diphasia nigra
Salacia desmoides
Sertularella ellisii
Sertularella fusiformis
Sertularella gayi
Sertularella mediterranea
Sertularella polyzonias
Sertularia argentea
Fam. Tubulariidae
Tubularia larynx
Class ANTHOZOA
Order Gorgonacea
Lophogorgia sp.
Order Pennatulacea
Virgularia mirabilis

Phylum BRYOZOA
Cellaria salicornioides
Crisia eburnea
Filicrisia geniculata
Scrupocellaria reptans

Table 1 (continued) - (suite tableau 1).

SPECIES RELATED TO EPIBIONTS AND MASKING MATERIAL

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

SPECIES NOT RELATED TO EPIBIONTS AND MASKING MATERIAL

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

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

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

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

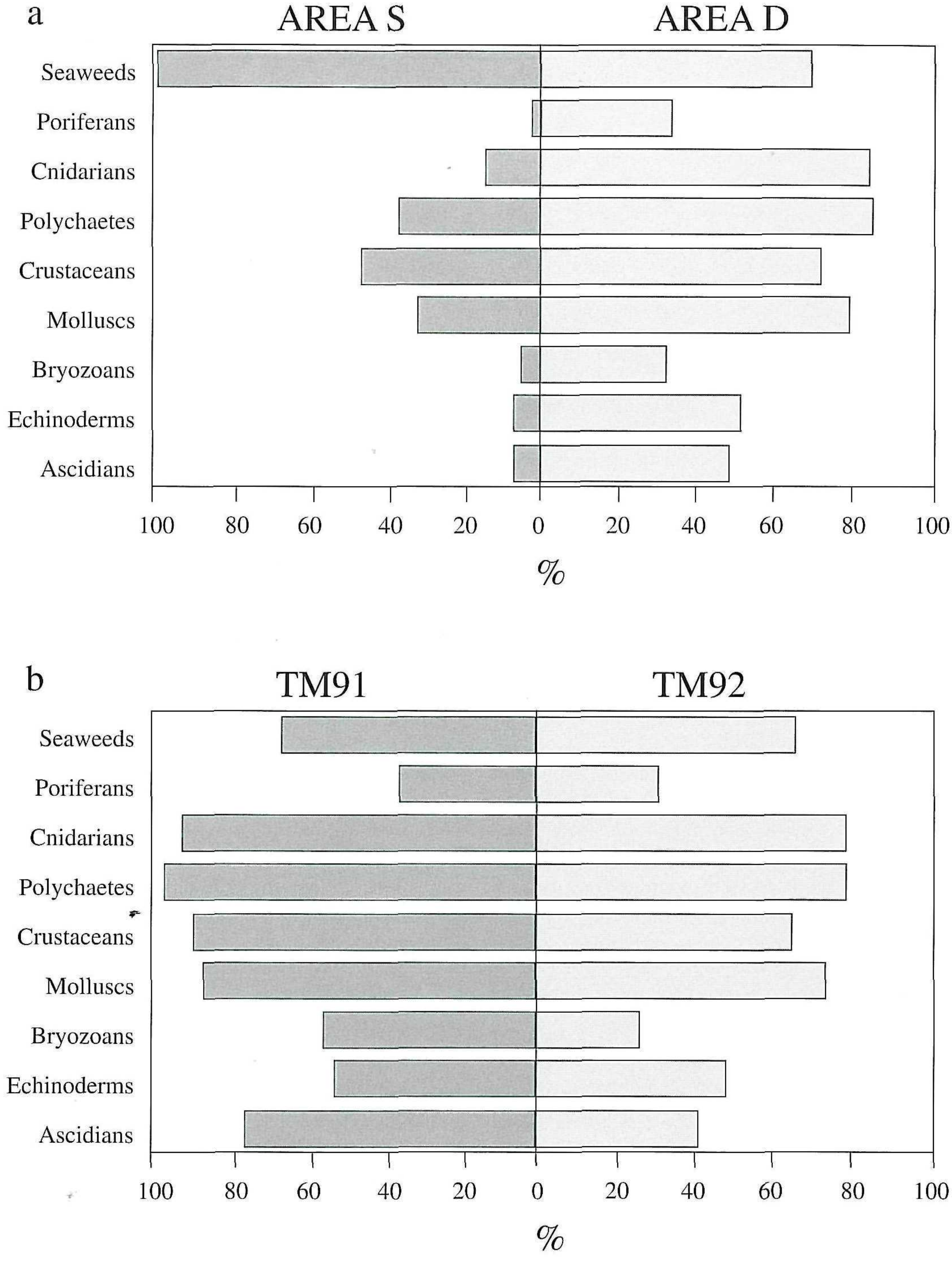

Figure 2. Frequency of appearance on *M. squinado* of each floral and faunal group. a) frequency of appearance by habitat (AREA S = shallow water individuals, AREA D = deeper water individuals), b) frequency of appearance within the area D, depending on the time elapsed since the terminal moult. TM91, 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 ornementales et les épibiontes encroûtantes les plus abondantes, exprimé en fonction de leur groupe faunistique ou floristique.

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

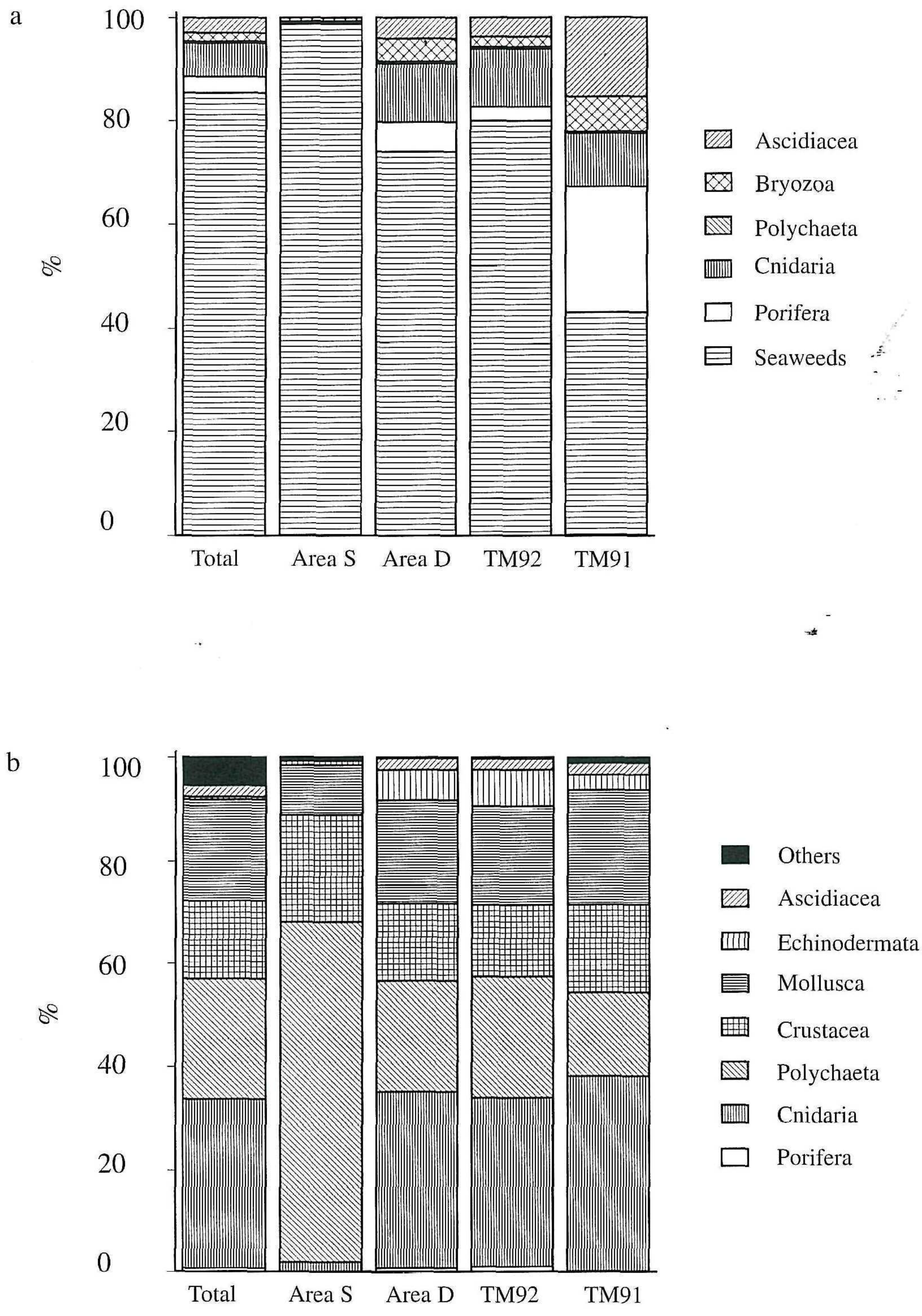

Figure 3. a) Percentage of *Maja squinado* covered surface, corresponding to each faunal and floral group (masking material and encrusting epibiosis), b) percentage of the number of individuals or colonies (non-encrusting epibiosis and associated fauna) from each faunal group with respect to all the 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					
Sycon ciliatum	100,0	0,0	100,0	100,0	100,0
Cnidaria					
Aglaophenia tubulifera	45,8	72,7	45,7	64,0	29,9
Sertularella spp.	33,8	0,3	33,8	26,2	35,7
Sertularia distans	11,0	0,0	11,1	2,2	22,2
Actiniaria undet.	0,5	27,3	0,4	1,3	0,1
Others	8,9	0,0	9,0	6,3	12,1
Polychaeta					
Pomatoceros triqueter	60,8	1,8	69,2	24,4	79,4
Spirorbis spirorbis	26,3	94,7	16,8	65,1	0,2
Hydroides norvegica	3,4	0,0	3,8	1,5	5,4
Platynereis dumerilii	2,2	3,3	2,0	2,1	2,0
Others	7,3	0,2	8,2	7,9	13,0
Crustacea					
Balanus perforatus	55,6	3,2	58,9	42,9	88,6
Isaea montagui	6,9	0,0	7,3	25,6	3,8
Gammaropsis maculata	6,8	1,6	7,1	0,9	1,5
Pisidia longicornis	5,1	0,0	5,4	23,5	3,9
Aora typica	1,7	11,3	1,1	0,3	0,0
Dexamine spinosa	1,6	25,8	0,1	0,0	0,0
Ampithoe ramondi	1,0	11,3	0,3	0,9	0,0
Dynamene magnitorata	1,0	13,7	0,0	0,0	0,0
Microdeutopus chelifer	0,7	12,1	0,0	0,0	0,0
Sunamphithoe pelagica	0,6	9,7	0,0	0,0	0,0
Others	6,9	11,3	7,0	5,9	2,2
Mollusca					
Anomia ephippium	66,7	3,4	68,1	93,0	24,2
Mytilus galloprovincialis	24,8	0,0	25,5	2,8	71,2
Bittium reticulatum	1,5	55,2	0,3	0,5	0,2
Rissoa parva	1,0	22,4	0,5	0,8	0,1
Gibbula cineraria	0,1	5,2	0,0	0,0	0,0
Jujubinus exasperatus	0,1	3,4	0,1	0,1	0,0
Rissoa membranacea	0,1	6,9	0,0	0,0	0,0
Others	5,7	3,5	5,5	2,8	4,3
Echinodermata					
Aslia lefevrei	7,1	0,0	70,5	78,5	86,3
Ophiothrix fragilis	13,1	0,0	13,8	7,5	5,5
Amphipholis squamata	10,0	100,0	9,9	4,2	7,3
Antedon bifida	5,4	0,0	5,4	9,6	0,9
Others	5,8	0,0	0,4	0,2	0,0
Ascidiacea					
Polycarpa pomaria	24,9	0,0	25,2	15,3	54,0
Ascidiella scabra	11,0	100,0	10,1	6,8	2,3
Didemnum maculosum	10,3	0,0	10,4	18,6	0,0
Molgula amesophleba	10,0	0,0	10,1	11,9	1,2
Polycarpa tenera	9,3	0,0	9,4	0,0	3,5
Ciona intestinalis	7,6	0,0	7,7	23,7	5,7
Molgula sp.	7,0	0,0	7,0	8,5	8,1
Polycarpa violacea	6,3	0,0	6,4	5,1	12,6
Ascidia sp.	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, permited 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 *Hyas 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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References

Abelló P. & Macpherson E. 1992. Epibiosis and rhizocephalan infestation patterns in relation to the reproductive biology of *Lithodes ferox* (Filhol, 1885) (Anomura: Lithodidae). *Journal of Crustacean Biology*, **12** (4): 561-570.

Abelló P., Villanueva R. & Gili R. M. 1990. Epibiosis in deep-sea crab populations as indicator of biological and behavioural characteristics of the host. *Journal of the Marine Biological Association of the United Kingdom*, **70**: 687-695.

Aldrich J. C. 1976. The spider crab *Libinia emarginata* Leach, 1815 (Decapoda Brachyura), and the starfish, an unsuitable predator but a cooperative prey. *Crustaceana*, **31**: 151-156.

Bürgi A. 1968. Contribution à l'étude du comportement vis-à-vis d'objets étrangers chez les Majidae. *Vie et Milieu*, **19**: 215-304.

Coen L. D. 1986. Tropical plant-animal associations: interactions between herbivorous crabs, macroalgae and a coral host. In: *Proceedings IV International Congress of Ecology*, pp. 1-116. Syracuse University: New York.

Connell J. H. & Keough M. J. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: *The Ecology of Natural Disturbance and Patch Dynamics* (S.T.A. Pickett & P.S. White eds), pp. 125-151. Academic Press: San Diego.

Dudgeon D. 1980. Some inter- and intraspecific differences in the decorating patterns of majid crabs (Crustacea: Decapoda) from the coastal waters of Hong Kong. In: *Proceedings of the First International Marine Biology Workshop: the Marine Flora and Fauna of Hong Kong and southern China, Hong Kong* (B.S. Morton & C.K. Tseng eds), pp. 825-835. Hong Kong University Press: Hong Kong.

Fauvel P. 1923. *Polychètes errantes. Faune de France, 5*. 488 pp.

Fauvel P. 1927. *Polychètes sédentaires. Faune de France, 16*. 494 pp.

González-Gurriarán E., Fernández L., Freire J., Muiño R. & Parapar J. 1993. Reproduction of the spider crab *Maja squinado* (Brachyura: Majidae) in the southern Galician coast (NW Spain). ICES *Shellfish Committee* ICES C.M. **1993/K:19**, 15pp.

González-Gurriarán E. & Freire J. 1994. Movement patterns and habitat utilization in the spider crab *Maja squinado* (Herbst) (Decapoda, Majidae) measured by ultrasonic telemetry. *Journal of Experimental Marine Biology and Ecology*, **184**: 269-291.

González-Gurriarán E., Freire J., Parapar J., Sampedro M. P. & Urcera M. 1995. Growth and moulting seasonality of the spider crab, *Maja squinado* (Herbst) (Decapoda: Majidae) in experimental conditions: implications for juvenile life history. *Journal of Experimental Marine Biology and Ecology*, **189**: 183-203.

Graham A. 1988. *Molluscs: Prosobranch and Pyramidellid Gastropods*. Synopses of the British Fauna (New Sereis) N° 2. 2nd. ed. The Linnean Society of London & The Estuarine Brackish-Water Sciences Association: London. 662 pp.

Hartnoll R. G. 1963. The biology of Manx spider crabs. *Proceedings of the Zoological Society of London*, **141**: 423-496.

Hayward P. J. & Ryland J. S. (Eds.). **1990.** *The marine fauna of the British Isles and the North West Europe.* Vol. 1 & 2. Oxford Science Publications. Clarendon Press: Oxford. 996 pp.

Kilar J. A. & Lou R. M. 1986. The subleties of camouflage and dietary preference of the decorator crab, *Microphrys bicornutus* Latreille (Decapoda, Brachyura). *Journal of Experimental Marine Biology and Ecology,* **101**: 143-160.

Knudsen J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and Anomura of Puget Sound, Washington. *Pacific Science,* **18**: 3-33.

Le Foll D. 1993. Biologie et exploitation de l'araignée de mer *Maja squinado* (Herbst) en Manche Ouest. IFREMER, RI.DRV - 93.030 - RH/Brest. 517 pp.

Lewis E. G. 1976. Epizoites associated with *Bathynectes superbus* (Decapoda: Portunidae). *Fishery Bulletin,* **74** (1): 225-227.

Lincoln R. J. 1979. *British marine Amphipoda: Gammaridea.* British Museum (Natural History): London. 658 pp.

Maldonado M. & Uriz M. J. 1992. Relationships between sponges and crabs: patterns of epibiosis on *Inachus aguiarii* (Decapoda: Majidae). *Marine Biology,* **113**: 281-286.

Mastro E. 1981. Algal preferences for decoration by the Californian kelp crab, *Pugettia producta* (Randall) (Decapoda, Majidae). *Crustaceana,* **41**: 64-70.

Millar R. H. 1970. *British Ascidians. Tunicata Ascidiacea.* Synopses of the British Fauna 1.. Academic Press: London.

Milne-Edwards A. 1872. Recherches sur la faune carcinologique de la Nouvelle-Calédonie. N. Arch. Mus. Hist. nat. Paris, **8**: 229-267, tab. 10-14.

Mori M. & Manconi R. 1990. Macroepizoites associated with *Paromola cuvieri* (Risso, 1816) (Decapoda, Homolidae) of the Ligurian Sea. *Crustaceana,* **58** (2): 124-129.

Pack Y. M. 1982. Masking behaviour and related biology of *Notomithrax ursus* (Oxyrhyncha: Majidae). Unpublished PhD Thesis, University of Canterbury: New Zealand.

Paul A. J., Feder H. M. & Jewett S. C. 1979. Food of the snow crab, *Chionoecetes bairdi* Rathbun, 1924, from Cook Inlet, Alaska (Decapoda, Majidae). *Crustaceana,* (Suppl.) **5**: 62-68.

Raibault A. 1968. *Paralaophonte ormieresi* n. sp, copépode harpacticoide trouvé sur les branchies de *Maia squinado* (Herbst) (Crustacea: Decapoda). *Bulletin de la Societé Zoologique de France,* **93**: 451-457.

Ross D. M. 1983. Symbiotic relations. In: *The Biology of Crustacea,* vol. 7. *Behaviour and Ecology* (F.J. Vernberg & W.B. Vernberg ed.), pp. 163-212. Academic Press: New York.

San Martín G. 1984. Estudio biogeográfico, faunístico y sistemático de los Poliquetos de la Familia de los Sílidos (Syllidae: Polychaeta) en Baleares. PhD Thesis, Universidad Complutense: Madrid. 529 pp.

Smaldon G. 1974. A note on the epizoites of porcelain crabs (Decapoda, Anomura). *Crustaceana,* **27** (3): 314-315.

Stêvcic Z. 1965. Contribution à la connaissance des organismes étrangers dans la cavité branchiale du crabe *Maja squinado* (Herbst). *Rapports et Procès Verbaux du Comité International pour l'Exploration de la Mer Méditerranée,* **18** (2): 179-180.

Stêvcic Z. 1968a. Parasiten und kommensalen des brutraumes der seespinne (*Maja squinado* Herbst). *Thalassa Jugoslavica,* **4**: 5-10.

Stêvcic Z. 1968b. Relations interspécifiques de l'Araignée de mer. *Rapports du Comité International pour l'Exploration de la Mer Mediterranée,* **129**: 147-149.

Stiller J. & Stêvcic Z. 1967. Epibionten der Meeresspinne (*Maja squinado* Herbst) nebst Beschreibung drei neuer entokommensaler Peritrichenarten. *Thalassa Jugoslavica,* **3** (1-6): 161-171.

Wicksten M. K. 1979. Decorating behavior in *Loxorhynchus crispatus* and *Loxorhynchus grandis* Stimpson (Brachyura, Majidae). *Crustaceana,* Suppl., **5**: 37-46.

Wicksten M. K. 1993. A review and a model of decorating behavior in spider crabs (Decapoda, Brachyura, Majidae). *Crustaceana,* **64** (3): 314-325.

Wilson, R. 1987. Substrate selection and decorating behaviour in *Acanthonyx petiveri* related to exoskeleton colour (Brachyura, Majidae). *Crustaceana,* **52**: 135-140.

Woods C. M. C. & McLay C. L. 1994a. Use of camouflage materials as a food store by the spider crab *Notomithrax ursus* (Brachyura: Majidae). *New Zealand Journal of Marine and Freshwater Research,* **28**: 97-104.

Woods C. M. C. & McLay C. L. 1994b. Masking and ingestion preferences of the spider crab *Notomithrax ursus* (Brachyura: Majidae). *New Zealand Journal of Marine and Freshwater Research,* **28**: 105-111.