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Use of camouflaging materials in some brachyuran crabs of the Mediterranean infralittoral zone

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Abstract: In their natural environment, some Brachyura from the shallow water infralittoral zone use several camouflage techniques, and many kinds of objects, to conceal their presence on the substratum. In this study we offered to different species of Mediterranean Brachyura a wide choice of materials to be used for their camouflaging, in order to verify weather, in any of the species considered, there is the tendency to make a precise choice among the objects left at their disposal. We observed individuals of Brachyura in an aquarium. The crabs had several types of objects at their disposal, either of a biological (animals, animal remains, plants) or non-biological origin (grains of sand and plastic materials), that we had previously obtained during open sea dives or removed from specimens caught in traps. We noticed that the tested animals exhibited a clear tendency in their choice of objects. Their choice was related to substantial differences in the morphology and bio-mechanics of the limbs used for catching and holding objects. Differences in superficial structures on other parts of the exoskeleton, such as hooks, bristles and bumps, also influenced the choice. Finally, the choice of some particular camouflaging materials can also be related to the characteristics of the habitat of the species, both for biotic or abiotic factors.

Résumé : *Utilisation de matériels pour le camouflage par certains Brachyoures de la zone infralittorale méditerranéenne.* Dans leur environnement naturel, certains Brachyoures de la zone infralittorale peu profonde utilisent différentes techniques de camouflage et différents types d'objets pour se dissimuler. Nous avons offert à différentes espèces de Brachyoures méditerranéens un large choix de matériels utilisables pour leur camouflage afin de vérifier si certaines espèces observées tendent à faire un choix précis parmi les objets proposés. Les individus ont été observés en aquarium. Les crabes ont eu différents matériels à leur disposition, aussi bien d'origine biologique (animaux, restes d'animaux, plantes) que non-biologique (grains de sable, matières plastiques), préalablement récoltés lors de plongées en mer ou retirés de la surface d'individus capturés dans la nature à l'aide de pièges. Les animaux testés montrent une tendance nette dans le choix des objets. Ce choix est lié à leur préférence pour un type de substrat et aux différences de morphologie et d'aptitude bio-mécanique des appendices utilisés pour saisir et retenir les objets. Le choix est également influencé par l'existence de structures superficielles particulières sur d'autres parties de l'exosquelette, tels que crochets, soies ou excroissances. Le choix du matériel utilisé dans le camouflage est également lié aux particularités (biotiques ou abiotiques) de l'habitat caractéristique de chaque espèce.

Keywords: Brachyura, choice, camouflage, cryptic behaviour.

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Introduction

Crustaceans, both crabs and shrimps, are among the most highly sought-after prey in the submarine world.

Consequently, these animals have had to develop behavioural strategies adapted to avoid their predators. For this reason, many decapod crustaceans in Mediterranean coastal waters exhibit camouflage. Some crabs are hidden by covering their carapace with various objects such as pieces of seaweed, sponges, grains of sand, tunicates, echinoderms, shells etc., as already described in crabs from various parts of the world by several authors (e.g. Wicksten, 1980; Mastro, 1981; Wilson, 1987; Woods & McLay, 1994 a, b). Very often, a various numbers of epibionts are found on the exoskeleton of adults of species whose young live in more superficial waters. These include mostly encrusting algae, bryozoans, tunicates, serpulidae, hydrozoans, sponges and barnacles (Smaldon, 1974; Lewis, 1976; Mori & Manconi, 1990; Parapar et al., 1997; Fernandez et al., 1998). True mutualistic symbiosis is established between the epibionts and the crabs (Ross, 1983; Maldonado & Uriz, 1992), at least until moulting occurs. Shallow water crabs, like juveniles of the Family Majidae, mostly use erect seaweed as camouflage, since they inhabit zones characterized by a conspicuous thick carpet of seaweed where it is easy to hide. Juvenile forms and small species use the seaweeds as camouflage, to avoid their small size to make their capture too easy by predators (Fernandez et al., 1998). Many algae, among those used by the crabs, also contain toxic substances which discourage predators (Hay, 1992; Stachowicz & Hay, 1999; Pereira et al., 2000; Pereira et al., 2002; Sotka & Hay, 2002; Jormalainen et al., 2003). The case of the Family Dromiidae is particularly interesting, as these crabs of rocky substrates only use sponges for their camouflage.

We have investigated the camouflage of some Brachyura in our marine laboratory aquaria for two years, in order to point out any preferences in the choice of the camouflaging materials, and have submitted our results to statistical analyses. The species selected in this study are among the most typical living in the Mediterranean infralittoral zone.

Materials and methods

The behaviour of some species of Brachyura coming from three areas of the coastal zone of the channel of Piombino (Areas A, B, C, Fig.1) has been studied over a two-year observation period (1999-2000)

The following Brachyura families are known to cover their carapaces with various objects and six species from these families were studied :

Dromiidae:
Dromia personata (Linnaeus, 1759)
Dorippidae:
Ethusa mascarone (Herbst, 1785)
Medorippe lanata (Linnaeus, 1767)
Majidae:

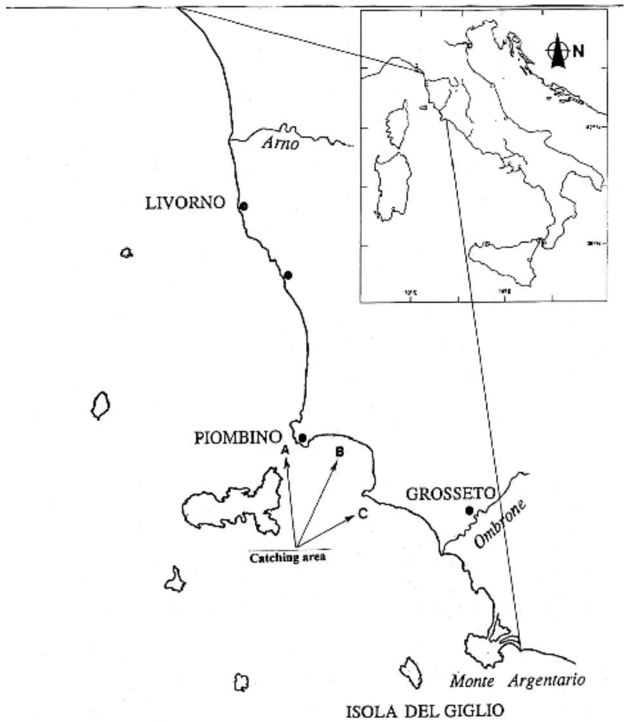

Figure 1. Areas in the Piombino Channel where the Brachyura in the study were caught
Figure 1. Zones du Canal de Piombino où les Brachyoures on été capturés.

Pisa corallina (Risso, 1816)
Macropodia longirostris (Fabricius, 1775)
Maja crispata Risso, 1827

Aquaria with a capacity of 500 L (one aquarium for each species) were provided with sand or stone substrate and running seawater. They were fitted with automatic filters and cooled by thermostat-controlled devices to maintain the temperature at 16 °C. The aquaria were set on a 12:12 hours light-dark cycle; in the case of *Medorippe lanata* the cycle was realized by a 20 W fluorescent bulb to simulate light conditions at 60-90 m depth. We tested the crabs as soon as possible after capture, so that their reactions were not influenced by a long captivity period.

For every species, each animal was tested during one day, and then transferred in another aquarium for one week and regularly fed. After seven days the animal was tested again. In the meantime seven other individuals of the same species, one a day, were tested in the same way; this practice was repeated during ten weeks, so that each animal was tested for ten times, by offering it the same material for camouflage every time.

In order to observe a possible tendency to choose among different objects at their disposal, we supplied the animals with objects they can generally find and use in their natural environment, chosen from material attached on individuals

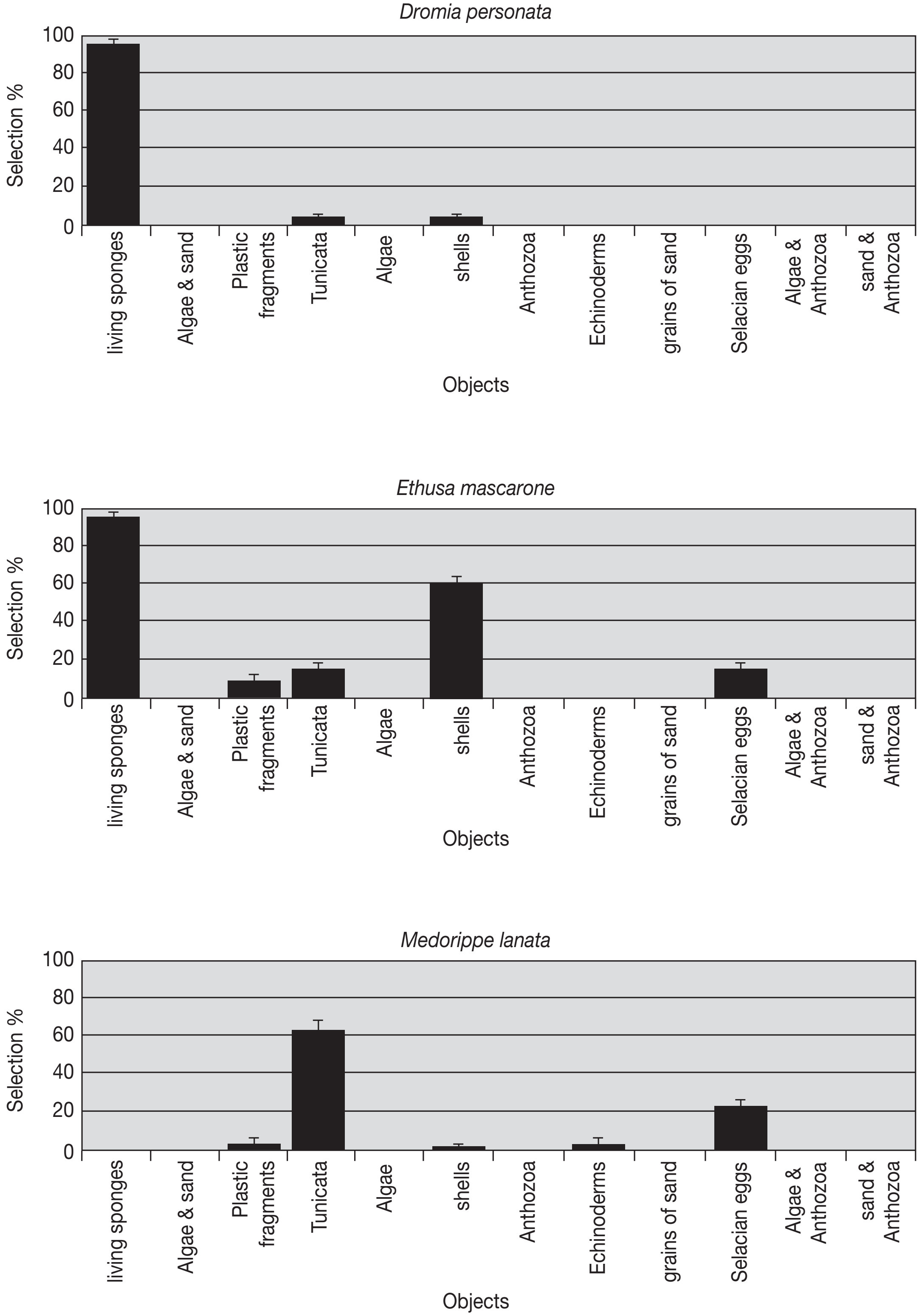

Figure 2. Mean choice percentage and SE (Standard Error) (n = 8) for the species *Dromia personata*, *Ethusa mascarone* and *Medorippe lanata*.

Figure 2. Pourcentage de choix moyen et SE (erreur standard) (n = 8) pour les espèces *Dromia personata*, *Ethusa mascarone* et *Medorippe lanata*.

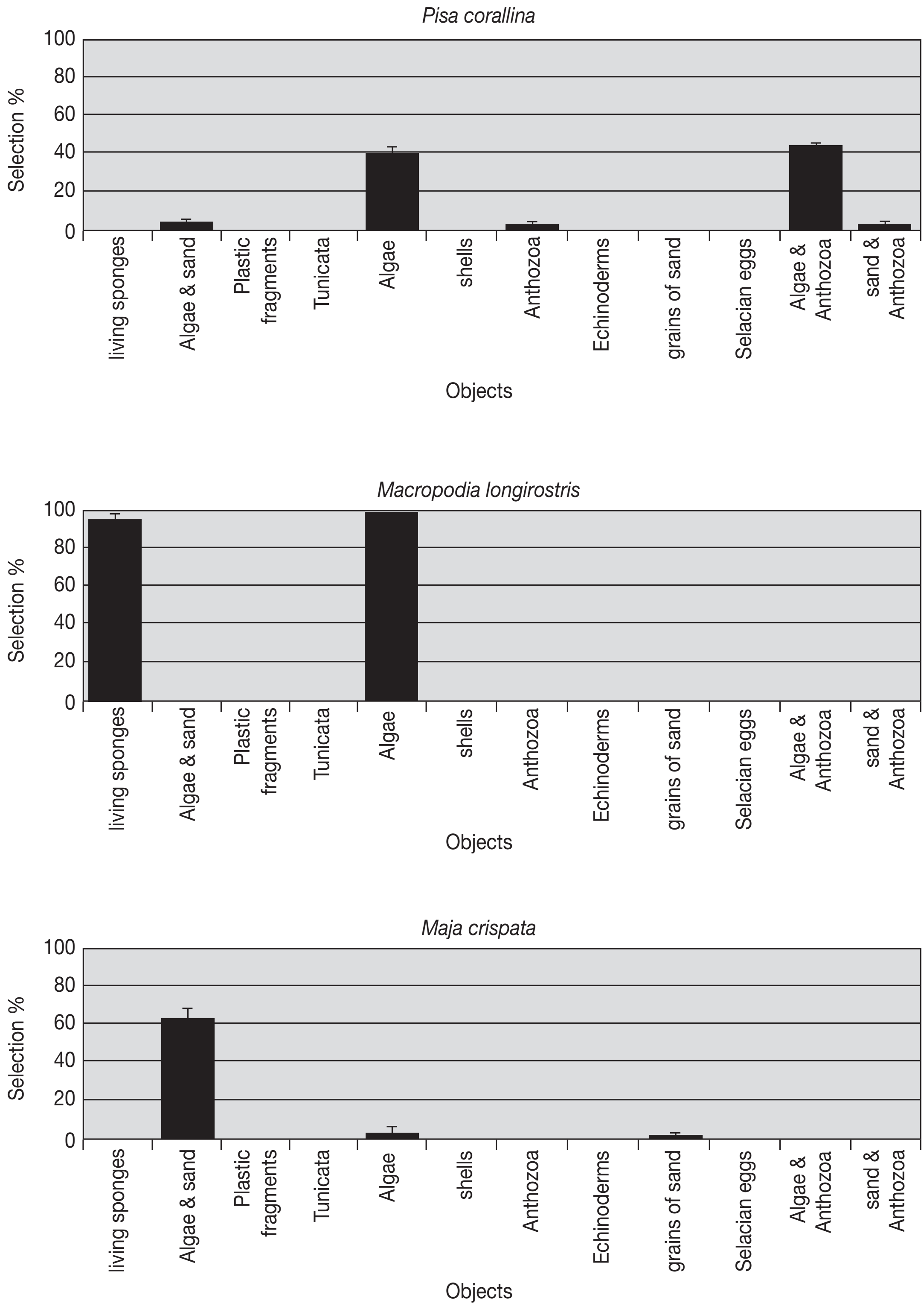

Figure 3. Mean choice percentage and SE (Standard Error) (n = 8) for the species *Pisa corallina*, *Macropodia longirostris* and *Maja crispata*.

Figure 3. Pourcentage de choix moyen et SE (erreur standard) (n = 8) pour les espèces *Pisa corallina*, *Macropodia longirostris* et *Maja crispata*.

caught in our nets and from direct observations during open sea SCUBA diving. Such material included:

• Seaweeds of various shapes and colours *Codium bursa* (L.) C. Ag., *Caulerpa taxifolia* (Vahl) Ag., *Flabellia petiolata* (Turra) Borges., *Halopteris scoparia* (L.) Sauvag., *Padina pavonica* (Thivy), *Corallina mediterranea* Aresch., *Peysonnellia squamaria* (Gmel.) Dec.

• Porifera *Spongia officinalis* L., *Hippospongia communis* (Lam.), *Axinella polypoides* (Schmidt)

• Anthozoa colonies *Alcyonium palmatum* Pall., *Eunicella cavolinii* (Koch)

Shells *Mytilus galloprovincialis* Lam., *Venus verrucosa* L., *Tapes decussatus* (L.)

• Echinoderms *Psammechinus microtuberculatus* (Blainville), *Paracentrotus lividus* Lam., *Thyone fusus* (Mull.), *Trachythyone elongata* (Dub.-Kor.);

• Tunicates *Phallusia mammilata* (Cuvier), *Ciona intestinalis* (L.), *Microcosmus sulcatus* Coquebert

• Selachian egg capsules

• Synthetic sponges, coloured pieces of plastic and pebbles of different sizes were also offered

In order to complete our data, photographs of the observed crabs were taken.

The hypothesis that the different study species could choose between different objects was statistically tested by subjecting the results for each species (n = 80) to the χ^2 test (degree of freedom = 1). The null hypothesis to be tested was: there is no significant difference between the results of choices of camouflaging materials expected by chance and what was observed in the experiments. The probability of success for a given object is 1/12 because the choice among the 12 different objects is purely casual, and the probability of failure (i.e. the choice of any other object among the eleven others) is 11/12. A probability level of $p < 0.05$ ($\chi^2 = 3.84$) was taken as significant.

Results

The results are given as percent frequencies in Figures 2 and 3 and described below for each species.

Dromia personata. Out of the 8 individuals observed, four constantly showed the tendency to use their 4th and the 5th pair of subchelate pereopods to hold live sponges of a similar colour to their own exoskeletons. The exoskeleton is entirely covered in adults with dark brown setae (Fig. 4) and in younger individuals with light brown setae. One of these four individuals only measured 0.8 cm across its exoskeleton (Fig. 5), and covered itself with fragments of live sponges, refusing all other objects however small. The other four individuals all chose living sponges in 9 trials out of 10; in the remaining cases they chose tunicates twice and shells twice.

Taking the choice of a live sponge as a favourable event (success), the probability of obtaining 76 successes out of 80 possibilities purely by chance (null hypothesis) is remarkably low: p (76, 80) < 0.001 ($\chi^2 = 786.2$). Thus the statistical test is highly significant, allowing rejection of the null hypothesis and confirming the hypothesis that *Dromia personata* is capable of choosing living sponges among different objects.

Ethusa mascarone. Out of a total of 80 tests on this species, we observed that the specimens preferred to cover their cephalothorax, with bivalve shells (Fig. 6) holding the shell with pereopods 4 and 5 in 48 (60%) cases. On 13 occasions (16.25%) they chose a *Raja* egg capsule, in 12 (15%) the animals hid under tunicates, and in 7 cases (8.75%) they used pieces of coloured plastic.

Taking the choice of a shell as a favourable event (success), the probability of obtaining 48 successes out of 80 possibilities purely by chance (the null hypothesis) is lower than the accepted level of significance: p (48, 80) < 0.001 ($\chi^2 = 279.4$). Thus the statistical test is significant, confirming the hypothesis that the species *Ethusa mascarone* prefers bivalve shells among different objects.

Medorippe lanata. This crab showed a marked preference for large tunicates (Fig. 7) 52 out of 80 cases (65%). It often also chose *Raja* egg capsules, i.e. in 21 cases (26.25%), and on 3 occasions it used pieces of plastic and tiny echinoderms. It chose to cover itself with bivalve shells only once.

Taking the choice of tunicates as a favourable event (success), the probability of obtaining 52 successes out of 80 possibilities (null hypothesis) is lower than the accepted level of significance: p (52, 80) < 0.001 ($\chi^2 = 336.1$). The statistical test is thus significant allowing rejection of the null hypothesis and confirming the hypothesis that the species *Medorippe lanata* prefers large tunicates among different objects.

Pisa corallina. This species mostly covered itself with seaweed and anthozoans (in 38 cases: 47.5%), in 32 cases (40%) it used seaweed alone and on only 4 occasions (5%) it employed seaweed plus sand (5%). In the remaining trials, we observed that the species used *Eunicella* fragments plus sand in 3 cases (3.75%) and *Eunicella* fragments alone in 3 other cases (3.75%).

Taking the choice of seaweed as a favourable event (success), the probability of obtaining 74 successes out of 80 possibilities purely by chance (the null hypothesis) is remarkably low: p (74, 80) < 0.001 ($\chi^2 = 741.5$). Thus the statistical test is significant, allowing rejection of the null hypothesis and confirming the hypothesis that the species *Pisa corallina* prefers seaweeds among different objects.

Macropodia longirostris. It showed an overwhelming tendency to cover itself with seaweeds (80 out of 80 trials), but showed no particular preference in any of the tests for one particular species.

Figure 4. Adult individual of *Dromia personata* with a fragment of yellow sponge as camouflage.
Figure 4. Individu adulte de *Dromia personata* camouflé avec un fragment d'éponge jaune.

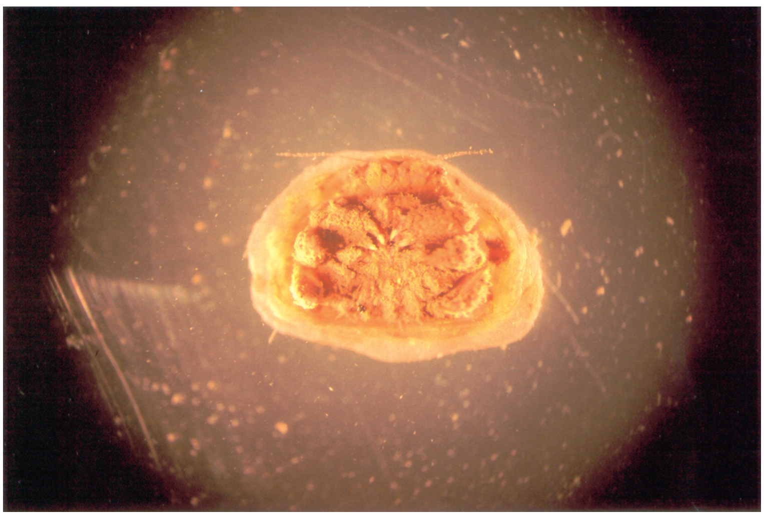

Figure 5. Juvenile individual of *Dromia personata* with a fragment of sponge as camouflage.
Figure 5. Jeune individu de *Dromia personata* camouflé avec un fragment d'éponge.

Maja crispata. This species also showed a dominant tendency to cover itself with seaweeds and sand (76 times out of 80). Only once an individual (1.25%) covered itself solely with sand grains, taken by the chelae and deposited between setae and hooks, whilst 3 individuals, only once, used only algae (3.75%).

Taking the choice of seaweed plus sand as a favourable event (success) the probability of obtaining 76 successes out of 80 purely by chance is definitely low: p (76, 80) < 0.001 ($\chi^2 = 787.5$). The statistical test is thus significant allowing rejection of the null hypothesis and confirming the hypothesis that the species *Maja crispata* exhibits a clear preference for seaweeds plus sand among different objects.

Discussion

These laboratory experiments confirm the mimetic habits of these Brachyura of using material from their natural environment, as already reported in the literature (Wicksten, 1980; Mastro, 1981; Wicksten, 1986; Holthuis, 1987; Wilson, 1987; Riedl, 1991; Falciai & Minervini, 1992; Wicksten, 1993; Woods & Mc Lay, 1994 a, b; Stachowicz & Hay, 1999). All these species use cryptic mimicry which is closely related to their environment where they can find suitable objects for camouflage. In our experiments, we found that the slowest moving crabs were *Dromia*, *Maja*, *Pisa* and *Macropodia*, all of which usually carry or attach seaweed or sponges on their carapaces.

A dark brown colour and a thick downy carapace should be sufficient to render *Dromia personata* difficult to discern in its rocky environment, but the crab gains even more security in covering itself with sponges (most of the time) which it tears from rocks with its strong chelae. It is interesting to note that, in the aquarium, *Dromia personata* hides sometimes with brightly coloured sponges, that certainly do not render it less visible on the substrate. This demonstrates how strongly it "needs" to carry a sponge on its carapace. Its evident preference for live sponges, demonstrated in our laboratory tests, supports the hypothesis that live sponges, of any colour, provide a higher level of protection due to the emission of repulsive substances (Cariello & Zanetti, 1979; Cariello et al., 1980 a, b; Ghiretti & Cariello, 1984). Young individuals were also found to use exclusively fragments of live sponges to cover their carapace (Fig. 5).

In the majority of cases, *Ethusa mascarone* picked thin objects with which it covered itself: they are caught with the 5th pereopods supplied with pseudopincers (Fig. 6) while the 4th pereopod is equipped with a claw well adapted for keeping flat objects on carapace. As *Ethusa* prefers flat, lightweight structures, it can easily carry objects larger than the cephalothorax itself. Moreover, in nature, it lives on sand and gravel, even in quite deep waters (-75 m). Consequently, it is obliged to make use of pieces of dead animals (shells) or other objects deposited on the sea bottom, as there is no seaweed at this depth. *Ethusa* can also bury itself to hide from predators.

Figure 6. Individual of *Ethusa mascarone* covered with a *Mytilus galloprovincialis* valve.
Figure 6. Individu de *Ethusa mascarone* recouvert d'une valve de *Mytilus galloprovincialis*.

Figure 7. *Medorippe lanata* hiding under a large tunicate.
Figure 7. *Medorippe lanata* camouflé sous un grand tunicier.

Medorippe lanata (Fig. 7), which lives on similar substrates as *Ethusa* does, exhibited a similar behaviour but preferred to use large tunicates as a cover. This crab moves quite rapidly and leaps by pushing with its long 3rd pereopods. The 2nd pereopods on the other hand are useful for balancing the weight it carries with respect to its body.

Pisa corallina, which lives in shallow waters, prefers to cover its carapace, rostrum, chelae and walking legs with seaweeds of different shapes and colours and impales them, as *Maja* and *Macropodia* do, on the small clusters of barbed, hooked setae characteristic of the species.

Maja crispata, of the Majidae family, lives at deeper levels, usually between 20 and 30 m depth, but it can also be found at just a few metres depth. Even in laboratory, this crab showed the most marked tendency to cover itself completely with seaweeds and other objects, leaving no free space at all, even on pereopods and chelipeds, so that it resembled a real tuft of seaweed.

Macropodia longirostris behaved similarly to *Maja crispata* and in fact both live in the same marine environment. Because of their form, it is difficult for these crabs to move within the thick carpet of seaweed, which can grow up to 7-10 cm high on the rocks. By covering themselves with seaweeds, the crabs not only hide from predators, but also avail themselves of the substances discharged by the cut thalus which usually contain metabolites distasteful, if not toxic, to predators (McKey, 1979; Hay et al., 1987, 1988; Hay & Fenical, 1988; Paul & van Alstyne, 1988; Guerriero et al., 1992; Dini et al., 1994; Galgani et al., 1996; Amade et al., 1998). These substances mingle with the crabs' odour, disguising olfactory cues.

Over the two-year experimental period, we observed interesting morphological and behavioural analogies and homologies in the study species. The long 2nd and 3rd pereopods in *Ethusa* and *Medorippe*, far longer than in the other species, and the identical actions these appendages perform in these crabs can be considered morphological homologies (Remane, 1952) extended to behaviour. The same applies to the modification of 4th and 5th pereopods into subchelae or pseudopincers in *Medorippe*, *Ethusa*, and *Dromia* and their migration to a dorsal position (Wickler, 1961, 1967). The instinct to cover the carapace with seaweed in *Pisa*, *Maja*, *Macropodia* is still another example. Even young individuals transferred to the experimental aquarium displayed this trait; a fact that leads to the conclusion that the observed behaviour is hereditary and innate (Lorenz, 1961, 1965a, b). Crabs of the same genus living in different geographic areas act in the same way. *Ethusa vossi*, a new species from the Ivory Coast and Nigeria, is almost identical in morphology to *Ethusa mascarone* from the Mediterranean Sea and behaves in a similar way (Manning & Holthuis, 1981). Majidae, from New Zealand waters (Woods & Mc Lay, 1994a, b), from the Atlantic (Fernandez et al., 1998) or Pacific oceans (Wicksten, 1980, 1993), all display similar ornamental cover patterns, although each species is influenced by the ecological characteristics of the environment. In our aquaria, *Macropodia longirostris* and

Maja crispata covered themselves with *Caulerpa taxifolia*, a tropical seaweed that cannot generally be found in areas where the crabs were caught, but which they nevertheless used, together with typically Mediterranean seaweeds. When the crabs do not have a wide variety of objects at their disposal, their first and main impulse is to cover themselves with anything, even if it is totally unfit for concealing the animals. If given the choice, however, the crabs will use the most suitable materials to hide in their natural habitat.

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