*Hydrobiologia* **426:** 193–201, 2000.
*G. Liebezeit, S. Dittmann & I. Kröncke (eds), Life at Interfaces and Under Extreme Conditions.*



# Relevance of crustacean carapace wettability for fouling

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*Key words:* crustaceans, carapace, biofouling, surface wettability

**Abstract**

Carapace wettability and density of fouling organisms (bacteria, diatoms, protozoa, fungi, macro-organisms) were investigated for 45 crustacean species (Hoplocarida, Decapoda) from 15 families in the Gulf of Thailand. The results show that crustaceans can create and maintain characteristic carapace wettabilities. About 21 species (47%) possess highly wettable carapaces with contact angles below 20°. Contact angles between 20° and 40° were recorded for four species (2%), angles between 40° and 60° for eight species (4%) and from 60° to 70° for 11 (24%) species. One species, *Alpheus euphrosyne* (Alpheidae, Decapoda), exhibited an extremely low surface wettability (contact angle: 91°). Densities of colonisers and contact angles did not correlate. Very low wettability by water ($\theta > 90°$) may only contribute little to fouling reduction in *A. euphrosyne* which showed the most hydrophobic carapace surface and was colonised by the lowest numbers of bacteria among all species and no other colonisers at all. We conclude that surface wettability is of little relevance for antifouling defence in crustaceans.

## Introduction

Many artificial and natural surfaces become rapidly colonised upon exposure to the sea. Sessile marine organisms secrete a variety of adhesive materials to attach to surfaces (Hascall, 1973: Chamberlain, 1976; Corpe, 1980; Sutherland, 1980; Lindner, 1984; Webster et al., 1985; Cooksey & Cooksey, 1986; Waite, 1987, 1990; Jensen & Morse, 1988; Young et al., 1988; Decho, 1990; Abu et al., 1991; Fletcher et al., 1991; Neu & Marshall, 1991; Read et al., 1991; Hoagland et al., 1993). Typically, adhesives produced by bacteria and diatoms consist of polysaccharides, but proteins and lipids may also be present. Glycoproteins and sulfur containing protein-polysaccharide-complexes have been described in protozoan attachment. Fungi secrete similar types of adhesives. Glues of macro-organisms frequently consist of mucopolysaccharides, glycoproteins, silk and/or quinone-tanned proteins. These substances have to provide strong attachment to a variety of surfaces to avoid detachment by water currents or predators.

As a prerequisite for the establishment of adhesive bonds, a glue must be able to wet a surface (Wistuba, 1980). Adhesion is mediated by intermolecular forces which are acting across the glue/substratum interface. When a droplet of a liquid is placed on a surface, a characteristic equilibrium contact angle ($\theta$) can be observed between the liquid and the surface. This contact angle reflects the energetic state of the glue/surface/medium system. An angle of $\theta = 0°$ indicates complete wetting. Larger contact angles ($0° < \theta < 180°$) indicate progressively poorer (incomplete) surface wetting. The smaller $\theta$, the more energy is required to separate the glue from the surface. Furthermore, a non wetting adhesive leads to the formation of small bubbles at the interface during the hardening of the glue. The resulting smaller contact area and higher stress within the molecular structure of the glue increase the risk of fracture (Wistuba, 1980).

Several studies reported that surface wettability influences substratum preferences and/or attachment strength of fouling organisms on artificial substrata. However, there is considerable uncertainty concern-

ing the efficiency of substratum wettability as a broad spectrum antifouling mechanism because some organisms are more likely to settle on hydrophobic while others prefer hydrophilic materials (Fletcher & Loeb, 1979; Absolom et al., 1983; Brewer, 1984; Fletcher & Baier, 1984; Crisp et al., 1985; Rittschof & Costlow, 1989; Roberts et al., 1991). One approach to assess the significance of wettability in the marine environment is to study the role of surface wettability of long-lived marine organisms as a defence mechanism against colonisation. Crustaceans were selected as study organisms because many species appear remarkably clean despite a strong colonisation pressure and a carapace longevity of several months (Shields, 1992; Becker, 1996; Carman & Dobbs, 1997). Wolff (1959) reported that crustaceans living under a strong current regime are less infested by other organisms than usual. There are several small crustacean species with highly hydrophobic surfaces, e.g. copepods of the genera Halectinosoma and Ectinosoma (Ectisomatidea, Harpactoidea), (G. Sach, pers. comm.).

The hypothesis was that if a given wettability could efficiently deter most potential foulers, then it could be expected to have evolved as an antifouling adaptation in some species. A body surface which provides weak attachment to colonisers could produce this effect. Antifouling mechanisms should be beneficial if they reduce otherwise adverse effects by fouling organisms, e.g. increased energy expense for locomotion, damage of the body surface with increasing risk of infections, lower egg production, disruption of the moulting cycle (Glynn, 1970; Turner et al., 1979; Nagasawa, 1987; Xu & Burns, 1991; Weissmann et al., 1993).

The following questions were addressed in the present study:

1. Are crustaceans able to create characteristic surface wettabilities despite adsorption and colonisation processes (Baier, 1970) which should lead to convergent carapace wettabilities in different species?

2. Do crustaceans possess surface wettabilities which reduce or impede colonisation (e.g. by interfering with the adhesion of colonisers glues)?

3. What relevance does surface wettability have as a defence mechanism compared to other mechanisms?

## Materials and methods

Crustaceans were collected between March 1991 and April 1993 along the eastern coast of the Gulf of Thailand (Becker, 1996). They were collected from fishing ports, gill nets, by SCUBA-diving and by hand along the shoreline. All crabs were in intermoult stage with hard carapaces. The specimens designated for enumeration of colonisers other than fungi were preserved in 4% formalin. Crustaceans which were used for wettability measurements were also taken alive to the laboratory and killed by deep freezing ($-15$ °C) to avoid alterations of the molecular surface structure as far as possible. Carapace pieces were cut off, treated ultrasonically (Iuchi 20, 40 W, 30 min), rinsed with distilled water and dried in a dry oven at 30 °C, which was slightly above the temperature of the sea water (25 °C–28 °C). Carapace wettability was estimated by contact angles measurements with bidistilled water as reference liquid through a stereomicroscope equipped with a goniometer eyepiece. Droplets (1 $\mu$l) of doubly distilled water were placed on the carapaces and the left and right angle of one droplet were measured. Measurements were considered for data evaluation if the difference between the right and left angle did not exceed 5°. At least 10 measurements were made from each of 3–5 different specimens per species.

The number of fouling organisms on the carapaces were estimated as described earlier (Becker, 1996). Bacteria, diatoms and protozoa were collected quantitatively by embedding in Parlodion (Sechler & Gundersen, 1971), stained with acridine orange (bacteria) or Alcian blue and Ziehl Neelsen (diatoms, protozoa) and counted by epifluorescence and light microscopy. Counts were made on 3–5 randomly selected specimens of each species. In order to estimate fungal densities, live specimens were transported to the laboratory. Fungal densities were estimated by isolating them on a selective medium (DIFCO 2216 marine agar with 0.5 $gl^{-1}$ Gentamicin) according to Marszalek et al. (1979). Unfilmed carapace pieces (1–3 $cm^2$) were rinsed with sterile seawater (filtered through 0.2 millepore filters and sterilized in a Yamato SD-41 autoclave) to remove unattached spores. The pieces were scraped over the medium and finally placed on the agar. Agar plates were incubated at 37 °C and the number of fungal colonies was recorded daily with a digital colony counter (EUDS DE-3, Kayaguchi) until the colony number levelled out.

Macro-organisms were counted directly on the carapaces using a stereomicroscope (VMZ Japan).

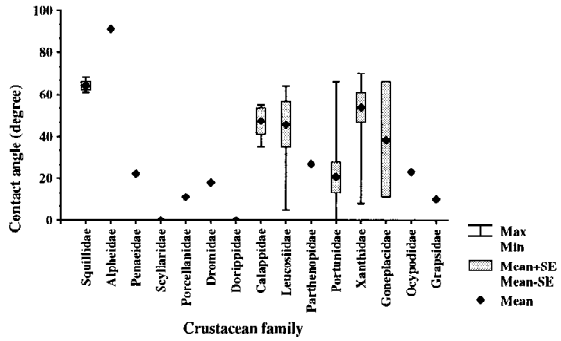


*Figure 1.* Carapace wettability of investigated crustacean families.

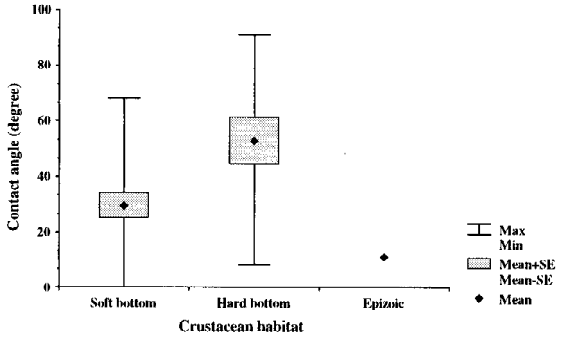


*Figure 2.* Comparison of carapace wettability between soft and hard bottom inhabiting species.

Coverage (%) of the carapaces by macro-organisms was determined by the dot method adopted from random sampling systems (Nair et al., 1984). Statistical analyses (Spearman rank test, Mann–Whitney-*U*-test, linear regression analyses) were carried out using Statistica software package. An index called 'colonisation degree' was used to get an estimate of the colonisation by all categories of colonisers (bacteria, diatoms, protozoa, fungi, macro-organisms). The 'colonisation degree' was calculated as follows: the highest mean density of each fouling group found on any species was set as 100%. Densities of the same fouling group on other crab species were calculated proportionally. The mean %-coverage by the five fouling groups yielded the 'colonisation degree' on a given host species.

## Results

### *Contact angle measurements*

A total of 45 crustacean species from 15 families was investigated. Mean contact angles ranged from 0° to 91° (Table 1). Although a few species showed a wide range of contact angles (e.g. *Harpiosquilla harpax*, *Leucosia craniolaris*, *Acrania novemspinosa*, *Ixa cylindrus*) most species exhibited narrowly defined, specific carapace wettability. Some variability was presumably caused by surface structures, roughness, adsorbed molecules and colonisers. A narrow species-specific carapace wettability range permits the assumption that those conspecifics that had served for fouling assessment fall within the same range of carapace wettability.

Twenty-one species possess highly wettable surfaces ($\theta$ <20°). Less wettable surfaces with mean contact angles between 20° and 60° were found on 12 species. Contact angles between 60° and 70° were recorded on 11 of the species. Very low wettability was found only on *Alpheus euphrosyne* ($\theta$ = 91°). Consistent differences of contact angles between different families were not detected (Spearman rank: $p$ = 0.785, Figure 1). Hard bottom species tended to exhibit slightly higher contact angles than soft bottom species (Figure 2), but this was not significant (Spearman rank: $p$ = 0.137, *U*-test: $p$ = 0.551).

### *Fouling assessment*

Colonisation data have been already published elsewhere (Becker, 1996) and will only be summarized here. One hundred percent of the species investigated were colonised by bacteria. Bacterial densities ranged from $7 * 10^2$ to $2.87 * 10^5$ mm$^{-2}$. More than $10^4$ cells mm$^{-2}$ were recorded on nine species. Lowest densities were found on *Alpheus euphrosyne*. Diatoms were found on 18 species (40%) ranging from 20 per cm$^2$ to $7.4 * 10^3$ cm$^{-2}$. High diatom densities ($4.1–7.4 * 10^3$ cm$^{-2}$) occurred on *Etisus* c.f. *laevimanus*, *Thalamita crenata*, and *Metapograpsus quadridentatus*. Sessile protozoa were detected on eight species (18%). The number of protozoa ranged from 10 to 500 per cm$^{-2}$ on fouled crustaceans. Hyphens of fungi were not detected. Attached spores of fungi were discovered on 17 species (38%). The densities remained below 1 per cm$^2$ carapace surface on all species but Conchoecetes artificiosus (2.2 cm$^{-2}$). Macroorganisms were found on eight species. *Hexapus anfractatus* was regularly (23% of all individuals) colonised by pedunculate barnacles. An unidentified actinian species occurred on 18% of the *Dorippe facchino* specimens. Xanthid crabs were regularly colonised by bryozoa (*Akatopora* c.f. *tincta*, Hastings; Key, pers. com.), covering 2–11% of the carapaces. Very few individuals of *Ater-*

*Table 1.* Overview about investigated crustacean species, number of collected specimens (*N*), carapace size, carapace contact angle measurements (mean, standard error (S.E.), range) and natural substratum of the crustaceans

| Crustacean species | *N* | Min.–Max. carapace width [cm] | Mean Contact angle [degree] S.E. | | Range | Substratum |
|---|---|---|---|---|---|---|
| **Squillidae (Hoplocarida)** | | | | | | |
| *Oratosquilla interrupta* (Kemp) | 58 | 1.0–1.4 | 61 | 7 | 29–81 | Sand; in burrows |
| *Oratosquilla nepa* (Latreille) | 75 | 2.0–2.5 | 68 | 3 | 46–77 | Sand; in burrows |
| *Harpiosquilla harpax* (de Haan) | 50 | 1.4–1.7 | 63 | 12 | 20–93 | Sand; in burrows |
| **Alpheidae (Decapoda)** | | | | | | |
| *Alpheus euphrosyne*, de Man | 48 | 2.1–2.4 | 91 | 3 | 81–96 | underneath rocks |
| **Penaeidae (Decapoda)** | | | | | | |
| *Trachypenaeus fulvus*, Dall | 23 | 1.8–2.3 | 22 | 7 | 3–59 | nectobenthic, sand |
| **Scyllaridae (Decapoda)** | | | | | | |
| *Scyllarus* c.f. *sordidus* (Stimpson) | 75 | 1.2–1.5 | 0 | 0 | 0–36 | unspecific |
| *Thenus orientalis* (Lund) | 29 | 3.0–4.0 | 0 | 0 | 0 | muddy sand; partly burying |
| **Porcellanidae (Decapoda)** | | | | | | |
| *Porcellanella picta* (Stimpson) | 26 | 0.5–0.7 | 11 | 3 | 5–17 | exposed, on Anthozoa |
| **Dromidae (Decapoda)** | | | | | | |
| *Conchoecetes artificiosus* (Fabricius) | 13 | 2.2–3.3 | 18 | 6 | 0–58 | sand, mud; partly burying |
| **Dorippidae (Decapoda)** | | | | | | |
| *Dorippe facchino* (Herbst) | 63 | 1.0–1.5 | 0 | 0 | 0–8 | sand, mud; partly burying |
| *Dorippe frascone* (Herbst) | 19 | 2.5–3.0 | 0 | 0 | 0 | sand, mud; partly burying |
| **Calappidae (Decapoda)** | | | | | | |
| *Calappa philargius*, L. | 27 | 6.5–8.2 | 35 | 3 | 18–43 | sand, broken shells; partly burying |
| *Matuta lunaris* (Forskål) | 22 | 3.0–4.1 | 52 | 9 | 5–76 | sand; partly burying |
| *Matuta banksii*, Leach | 17 | 3.2–3.8 | 55 | 3 | 39–68 | sand; partly burying |
| **Leucosiidae (Decapoda)** | | | | | | |
| *Leucosia craniolaris* (L.) | 41 | 1.2–2.0 | 59 | 6 | 7–91 | sand; partly burying |
| *Acrania novemspinosa*, Adams & White | 75 | 2.6–2.9 | 64 | 15 | 5–109 | sandy mud; partly burying |
| *Acrania erinaceus* (Fabricius) | 18 | 1.6–2.1 | 60 | 3 | 49–66 | sand; partly burying |
| *Ixa cylindrus* (Fabricius) | 200 | 5.0–6.1 | 40 | 6 | 5–71 | mud; partly burying |
| *Iphiuculus spongiosus*, Adams & White | 19 | 2.9–3.7 | 5 | 1 | 0–8 | sand, mud, algae; partly burying |
| **Parthenopidae (Decapoda)** | | | | | | |
| *Cryptopodia fornicata* (Fabricius) | 39 | 5.3–6.5 | 27 | 6 | 7–58 | sand, broken shells; partly burying |
| **Portunidae (Decapoda)** | | | | | | |
| *Scylla serrata* (Forskål) | 154 | 6.5–12.3 | 63 | 3 | 50–78 | mud; partly burying |
| *Portunus pelagicus* (L.) | 207 | 7.5–15.6 | 0 | 0 | 0–5 | sand, mud; partly burying |
| *Portunus pulchicristatus*, Gordon | 123 | 2.8–1.6 | 0 | 0 | 0 | sandy mud; partly burying |
| *Portunus tweediei* (Shen) | 213 | 2.0–1.4 | 3 | 1 | 0–8 | sand, mud; partly burying |
| *Portunus gracilmanus* (Stimpson) | 31 | 3.2–2.2 | 5 | 2 | 0–8 | sand, mud; partly burying |
| *Portunus hastatoides* (Fabricius) | 52 | 3.5–1.9 | 3 | 1 | 0–7 | sand, mud; partly burying |
| *Charybdis feriatus* (L.) | 14 | 4.2–8.7 | 44 | 7 | 0–78 | hard bottom |
| *Charybdis truncata*, Fabricius | 19 | 3.4–4.0 | 3 | 1 | 0–8 | sandy mud; partly burying |
| *Charybdis* c.f. *affinis*, Dana | 23 | 2.9–4.0 | 4 | 1 | 0–7 | sandy mud; partly burying |
| *Charybdis anisodon* (de Haan) | 204 | 2.8–4.5 | 66 | 5 | 47–80 | sandy mud; partly burying |
| *Thalamita crenata* (Latreille) | 23 | 2.6–3.5 | 58 | 11 | 7–83 | between rocks |

*Continued on p. 197*

*Table 1. Continued*

| Crustacean species | *N* | Min.–Max. carapace width [cm] | Mean S.E. | Contact angle [degree] | Range | Substratum |
|---|---|---|---|---|---|---|
| *Thalamita sima*, Milne–Edwards | 18 | 2.9–4.2 | 6 | 2 | 0–9 | between rocks |
| *Podophthalmus vigil* (Fabricius) | 53 | 4.2–8.3 | 14 | 8 | 5–25 | sand, sandy mud; partly burying |
| **Xanthidae (Decapoda)** | | | | | | |
| *Atergatis intergerrimus* (Lamarck) | 6 | 8.0–12.5 | 64 | 5 | 53–74 | hard bottom, coral reefs, gravel |
| *Atergatis floridus* (L.) | 3 | 5.1–7.3 | 66 | 3 | 49–79 | coral gravel |
| *Lophozymus pictor* (Fabricius) | 17 | 5.2–8.3 | 68 | 3 | 60–80 | hard bottom, coral reefs |
| *Halimede ochtodes* (Herbst) | 7 | 4.1–5.7 | 47 | 2 | 42–62 | sand, mud; partly burying |
| *Galene bispinosa* (Herbst) | 18 | 3.8–5.6 | 59 | 7 | 36–61 | sand, mud; partly burying |
| *Etisus* c.f. *laevimanus*, Randall | 108 | 3.7–5.8 | 49 | 5 | 36–61 | intertidal; between rocks |
| *Sphaerozius nitidus*, Stimpson | 32 | 1.0–1.5 | 8 | 3 | 3–9 | between rocks |
| *Sphaerozius* sp. | 9 | 5.6–7.4 | 70 | 3 | 61–83 | between rocks |
| **Goneplacidae (Decapoda)** | | | | | | |
| *Hexapus anfractatus*, Rathbun | 229 | 1.1–2.5 | 11 | 7 | 3–38 | mud; in holothurian burrows |
| *Eucrate alocki*, Serène | 37 | 2.0–4.1 | 66 | 5 | 51–81 | sand, broken shells, partly burying |
| **Ocypodidae (Decapoda)** | | | | | | |
| *Dotilla wichmani*, de Haan | 33 | 0.4–0.6 | 23 | 10 | 0–60 | intertidal, muddy sand; in burrows |
| **Grapsidae (Decapoda)** | | | | | | |
| *Metapograpsus quadridentatus*, Stimpson | 113 | 1.9–3.2 | 10 | 4 | 3–27 | intertidal; between rocks |

*gatis intergerrimus*, *A. floridus*, *Lophozymus pictor* and *Sphaerozius* sp. were without bryozoa. One individual of *L. pictor* (Xanthidae) was also colonised by *Spirorbis* sp. (Serpulidae, Polychaeta). *M. quadridentatus* was frequently colonised by barnacles (*Balanus variegatus*) accounting for 4% average cover of carapace and macroalgae (5% cover). *B. variegatus* was also detected on one specimen of *Ixa cylindrus*.

*Wettability and carapace colonisation*

Statistical analyses (linear regression models, Spearman-rank-test) failed to show any correlation ($p > 0.05$) between contact angles and any of the coloniser taxa category (bacteria through macrofauna) or the colonisation degree (Table 2, Figures 3 and 4). Transformation of data (log, ln, square root) also failed to yield a significant correlation between contact angles and density of foulers ($p > 0.05$). These analyses strongly suggest that wettability has very little influence on the colonisation by fouling organisms. This conclusion will be graphically supported by the following distance weighted least square line fits (Figures 3 and 4): bacterial densities remained almost constant between $\theta = 0°$ and 68° but decreased towards higher contact angles. However, a contact angle of $\theta > 70°$ was only detected on a single species. On carapaces with contact angles between 40° and 60°, more diatoms and protozoa settled than on other carapaces. A maximum of fungi was recorded within 10–30°. Highest cover by macro-organisms was found on carapaces with contact angles from 66° to 68°. However, these maxima for diatoms, protozoa, fungi and macro-organisms remained small. The overall colonisation degree (Figure 4b) resembles the plot which was obtained for bacteria, partly due to the lack of other colonisers on many species.

A comparison of the colonisation on crustaceans with that on artificial substrata exposed in the same area suggest that wettability contributes little (if at all) to antifouling defence (Figure 5). Two crustacean species (*Alpheus euphrosyne*, *Cryptopodia fornicata*) showed wettabilities similar to those of two artificial

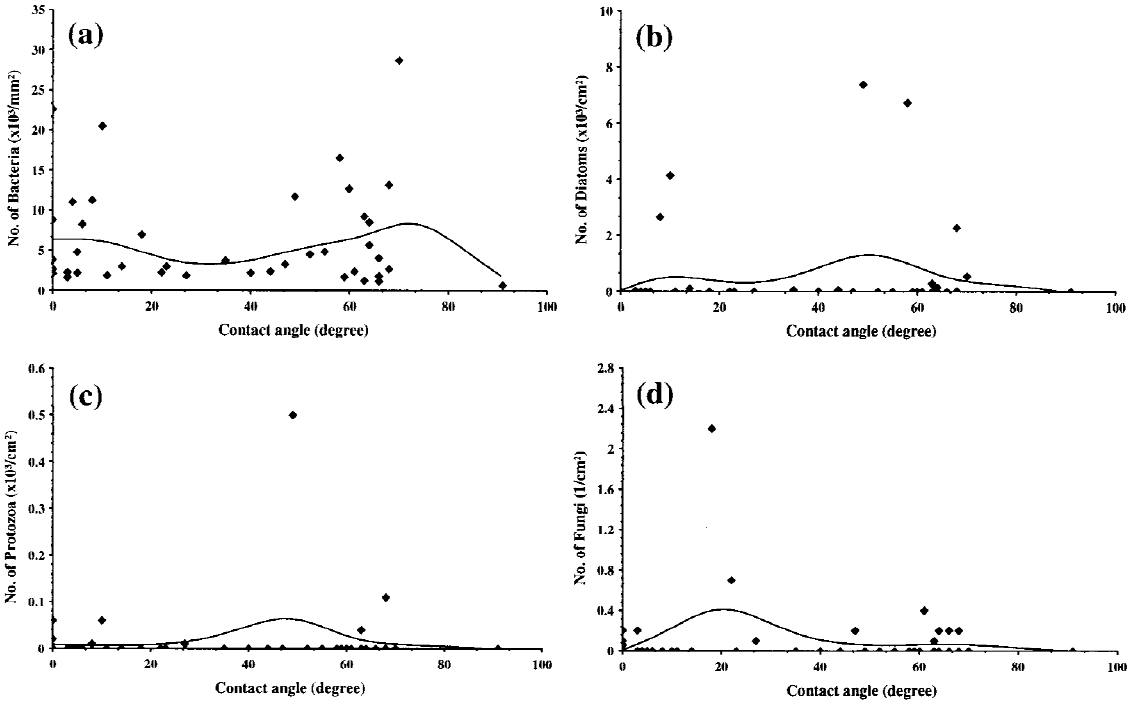


*Figure 3.* Distance weighted least square line fit of carapace wettability and densities of bacteria (3a), diatoms (3b), protozoa (3c) and fungi (3d).

*Table 2.* Results of Spearman Rank test and regression analysis for correlation between carapace wettability and density of epibionts

| Group of epibionts | Spearman correlation | *p*-level | Linear regression (r) | *p*-level |
|---|---|---|---|---|
| Bacteria | −0.0859 | 0.5747 | −0.0618 | 0.6903 |
| Diatoms | 0.1949 | 0.1995 | 0.0992 | 0.5224 |
| Protozoa | −0.0616 | 0.6876 | 0.0846 | 0.5850 |
| Fungi | −0.0235 | 0.8784 | −0.0830 | 0.5921 |
| Macro-organisms | 0.1445 | 0.3438 | 0.1223 | 0.4292 |
| Colonisation degree | −0.0936 | 0.5410 | 0.0158 | 0.9191 |

materials (glass; ETFE, a fluorpolymer) exposed in parallel experiments (see Becker et al., 1997). Both artificial materials became (*U*-test: $p < 0.05$) much more densely colonised by all groups of foulers within 5–8 days of exposure than carapaces of corresponding wettability.

## Discussion

Surprisingly, some crustaceans can maintain a characteristic carapace surface wettability despite adsorption (molecular fouling) and colonisation processes. In general, upon exposure to natural waters, wettability quickly decreases on wettable surfaces and increases on non-wettable surfaces. Thus, the contact angles on various surfaces should converge towards approximately 75°–85° (see Baier, 1970). This implies that crustaceans possess mechanisms to restrict alterations of surface characteristics by adsorption and colonisation processes. It still has to be determined which processes are involved in maintaining the observed species specific wettability. Mechanisms similar to those involved in repair mechanisms or release of 'coating-substances' through pore channels within the cuticle (Green & Neff, 1972; Stevenson, 1985) may be involved. The composition of the epicuticle which is the top layer of the integument will determine the wettability of crustaceans. Epicuticles contain both hydrophobic and hydrophilic compounds. They consist of quinone-tanned proteins, lipids, glycoproteins and calcium salts (Denell, 1960; Stevenson, 1985). Recently, Compere & Goffinet (1995) detected that

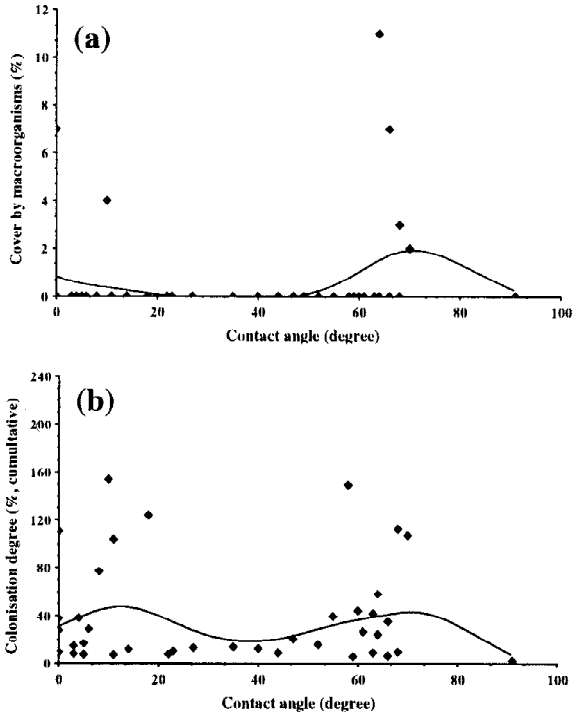


*Figure 4.* Distance weighted least square line fit of carapace wettability and densities of macroorganisms (4a) and the colonisation degree (4b).

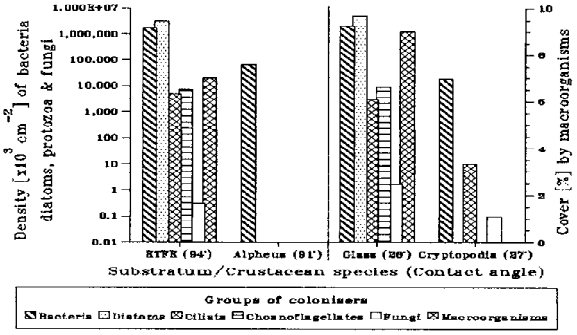


*Figure 5.* Colonisation of crustacean carapaces and artificial substrata with similar wettability after 8 days of exposure (ETFE: Ethylenefluorethylene).

the surface coat in *Carcinus maenas* contains polyanionic sites and acid mucopolysaccharides. The latter substances and calcium are likely to increase wettability while lipids and some hydrophobic proteins will decrease wettability. Surface wettability in recently moulted crustaceans may differ from surface wettability of intermoult specimens. The present study considered only crustaceans with fully calcified carapaces. If carapace wettability would be a major defense mechanism, one may expect that it is established at an early stage of the intermoult period to provide protection.

The present study strongly suggests that surface wettability is not an efficient antifouling adaptation in crustaceans. While the absence of colonisers may be caused by defence mechanisms other than carapace wettability, the presence of fouling organisms on a given surface proves that its wettability is not by itself a sufficiently strong antifouling mechanisms. Thus, according to the present results, wettabilities with water contact angles of $\theta < 70°$ may be rejected as possible broad-spectrum defense mechanism. Very low wettability by water ($\theta > 90°$) may contribute to fouling reduction to some extent (see *Alpheus euphrosyne*). The wettability of *Alpheus euphrosyne* is close to a range (approx.: $95° < \theta < 104°$) reported to be less densely fouled by bacteria than surfaces with other wettabilities (Dexter, 1979). Indeed, *A. euphrosyne* was the least fouled species with the lowest number of bacteria, while other fouling groups were lacking. However, some other crustacean species (e.g. *Harpiosquilla harpax, Leucosia craniolaris, Eucrate alocki*) showed more wettable carapaces than *A. euphrosyne* but were similarly little fouled.

So far, only Vrolijk et al. (1990) suggested that two gorgonian corals possess minimal adhesive surfaces which prevent fouling in conjunction with other mechanisms. Despite some promising results in antifouling research (Dexter, 1979; Bultmann et al., 1984; Fletcher & Baier, 1984; Rittschof & Costlow, 1989; Roberts et al., 1991; Lindner, 1992), there is some doubt about the efficiency of surface wettability as an antifouling mechanism under natural conditions (Becker, 1993; Becker et al., 1997). Wettability effects may be easily dwarfed by other abiotic factors and biological interactions under natural conditions. A substrate will eventually become colonised even if it initially offers unfavorable conditions in terms of adhesion. Many colonisers can adapt their attachment mechanisms to the surface properties (Lindner, 1984; Paul & Jeffrey, 1985; Webster et al., 1985; Van Loosdrecht et al., 1987).

If wettability is inefficient or its effects inconsistent in colonisation processes under natural conditions, it is unlikely that it has evolved as an antifouling mechanism in the first place. Low densities of colonisers suggest that the investigated crustaceans possess other antifouling mechanisms to restrict colonisation. Several studies indicated mechanisms by which crustaceans may fend off fouling species. These may

be: moulting, grooming, behaviour (hiding, burying), immune response, chemical defence by bioactive compounds and cleaning by other organisms (Barnes & Bagenal, 1951; Glynn, 1970; Stevenson, 1985; White et al., 1985; Weng, 1987; Bauer, 1989; Gil-Turnes et al., 1989; Shields, 1992; Gili et al., 1993; Svavarsson & Davidsdottir, 1994; Becker & Wahl, 1996; Wahl et al., 1998). It remains to be studied how some crustaceans are able to maintain a distinct carapace wettability and its ecological significance.

## References


Absolom, D. R., F. V. Lamberti, Z. Policova, W. Zingg, C. J. Van Oss & A. W. Neumann, 1983. Surface thermodynamics of bacterial adhesion. Apl. envir. Microbiol. 10: 90–97.

Abu, G. O., R. M. Weiner, J. Rice & R. R. ColwellL, 1991. Properties of an extracellular adhesive polymer from the marine bacterium *Schewanella colwelliana*. Biofouling 3: 69–84.

Baier, R. E., 1970. Surface properties influencing biological adhesion. In Manly, R. S. (ed.), Adhesion in Biological Systems. Academic Press, New York, London: 15–48.

Barnes, H. & T. B. Bagenal, 1951. Observations on *Nephrops norvegica* (L.) and on an epizooic population of *Balanus crenatus* Brug. J. mar. biol. Ass. U.K. 30: 369–380.

Bauer, R. T., 1989. Decapod crustacean grooming: functional morphology, adaptive value and phylogenetic significance. In Felgenhauer, B. E., L. Walting & A. B. Thistle (eds), Functional Morphology of Feeding and Grooming in Crustacea, Crustacean Issues 6, F. R. Schram (ed.), A. A. Balkema, Rotterdam, Brookfield: 49–74.

Becker, K., 1993. Attachment strength and colonisation pattern of two macrofouling species on substrata with different surface tension (in situ studies). Mar. Biol. 117: 301–309.

Becker, K., 1996. Epibionts on carapaces of some malacostracan crustaceans from the Gulf of Thailand. J. crust. Biol. 16: 92–104.

Becker, K. & M. Wahl, 1996. Behavioural patterns as natural antifouling mechanisms of tropical marine crabs. J. exp. mar. Biol. Ecol. 203: 245–258.

Becker, K., S. Siriratanachai & T. Hormchong, 1997. Influence of initial substratum surface tension on marine micro- and macrofouling in the Gulf of Thailand. Helgoländer. wiss. Meeresunters. 51: 445–461.

Brewer, R. H., 1984. The influence of the orientation, roughness and wettability of solid surfaces on the behaviour and attachment of planulae of *Cyanea* (Cnidaria: Scyphozoa). Biol. Bull. 166: 11–21.

Bultman, J. D., J. R. Griffith & D. E. Field, 1984. Fluoropolymer coatings for the marine environment. In Costlow, J. D. & R. C. Tipper (eds), Marine Corrosion and Biodeterioration – An Interdisciplinary Study. E. & F. N. Spon. Ltd., London: 237–243.

Carman, K. R. & F. C. Dobbs, 1997. Epibiotic microorganisms on copepods and other marine crustaceans. Microscopy Res. Techn. 37: 116–135.

Chamberlain, A. H. L., 1976. Algal settlement and secretion of adhesive materials. In Sharpley, J. M. & A. M. Kaplan (eds), Proc. 3rd Intern. Biodegrad. Symp., Appl. Sci., London: 417–432.

Compere, P. & G. Goffinet, 1995. Cytochemical demonstration of acid mucopolysaccharides in the epicuticular surface coat of the crab *Carcinus maenas* (L.) (Crustacea, Decapoda). Belg. J. Zool. 125: 95–100.

Cooksey, K. E. & B. Cooksey, 1986. Adhesion of fouling diatoms to surfaces: some biochemistry. In Evans, L. V. & K. D. Hoagland (eds), Algal Biofouling. Elsevier, Amsterdam: 41–53.

Corpe, W. A., 1980. Microbial surface components involved in adsorption onto surfaces. In Bitton, G. & K. C. Marshall (eds), Adsorption of Micro-organisms to Surfaces. Wiley Interscience Publ., New York: 105–143.

Crisp, D. J., G. Walker, G. A. Young & A. B. Yule, 1985. Adhesion and substrate choice in mussels and barnacles. J. Coll. Interf. Sci. 104: 40–50.

Decho, A. W., 1990. Microbial exopolymer secretions in ocean environments: their role(s) in the food webs and marine processes. Oceanogr. mar. Biol. Ann. Rev. 28: 73–153.

Denell, R., 1960. Integument and exoskeleton. In Waterman, T. H. (ed.), The Physiology of Crustacea, Vol. I. Academic Press, New York-London: 449–473.

Dexter, S. C., 1979. Influence of substratum critical surface tension on bacterial adhesion – In situ studies. J. Coll. Interf. Sci. 70: 346–354.

Fletcher, M. & G. I. Loeb, 1979. Influence of substratum characteristics on the attachment of a marine *Pseudomonad* to solid surfaces. Apl. envir. Microbiol. 37: 67–72.

Fletcher, M., J. M. Lessmann & G. I. Loeb, 1991. Bacterial surface adhesives and biofilm matrix polymers of marine and freshwater bacteria. Biofouling 4: 120–140.

Fletcher, R. L. & R. E. Baier, 1984. Influence of surface energy on the development of the green alga *Enteromorpha*. Mar. Biol. Lett. 5: 251–254.

Gil-Turnes, M. S., M. E. Hay & W. Fenical, 1989. Symbiotic marine bacteria defend crustacean embryos from a pathogenic fungus. Science 240: 116–118.

Gili, J. M., P. Abello & R. Villanueva, 1993. Epibionts and intermoult duration in the crab *Bathynectes piperitus*. Mar. Ecol. Progr. Ser. 98: 107–113.

Glynn, P. W., 1970. Growth of algal epiphytes on a tropical marine isopod. J. exp. mar. Biol. Ecol. 5: 88–93.

Green, P. J. & M. R. Neff, 1972. A survey of the fine structure of the integument of the fiddler crab. Tissue Cell 4: 137–171.

Hascall, G. K., 1973. The stalk of the suctorian *Tokophyra infusionum*: histochemistry, biochemistry and physiology. J. Protozool. 20: 701–704.

Hoagland, K. D., J. D. Rosowski, M. R. Gretz & S. C. Roemer, 1993. Diatom extracellular polymeric substances: function, fine structure, chemistry and physiology. J. Phycol. 29: 537–566.

Jensen, A. R. & D. E. Morse, 1988. The bioadhesive of *Phragmotopoma californica* tubes: a silk cement containing L-Dopa. J. comp. Physiol. B. 158: 317–324.

Lindner, E., 1984. The attachment of macrofouling invertebrates. In Costlow, J. D. & R. C. Tipper (eds), Marine Corrosion and Biodeterioration – An Interdisciplinary Study. E. & F. N. Spon. Ltd., London: 184–201.

Lindner, E., 1992. A low surface energy approach in the control of marine biofouling. Biofouling 6: 193–205.

Marszalek, D. S., S. M. Gerchakov & L. R. Udey, 1979. Influence of substrate composition on marine microfouling. Apl. envir. Microbiol. 38: 987–995.

Nagasawa, S., 1987. Exosceletal scars by bacterial attachment to copepods (Short communication). J. Plankton. Res. 9: 749–753.

Nair, N. B., K. Dharmaraj, P. K. Abdul Azis, M. Arunchalam & K. Krishna Kumar, 1984. Ecology of biofouling on *Crassostrea madrasensis* (Preston) (Mollusca: Bivalvia) in a tropical backwater. Proc. Indian Acad. Sci. (Anim. Sci.) 93: 419–430.

Neu, T. R. & K. C. Marshall, 1991. Microbial 'footprint': a new approach to adhesive polymer. Biofouling 3: 101–112.

Paul, J. H. & W. H. Jeffrey, 1985. Evidence for seperate adhesion mechanisms for hydrophilic and hydrophobic surfaces in *Vibrio proteolytica*. Apl. envir. Microbiol. 50: 431–437.

Read, S., S. T. Moss & E. B. G. Jones, 1991. Attachment studies of aquatic hyphomycetes. Phil. Trans. r. Soc., Lond. B 344: 449–457.

Rittschof, D. & J. D. Costlow, 1989. Bryozoan and barnacle settlement in relation to initial surface wettability: a comparision of laboratory and field studies. In Ros, E. D. (ed.), Topics in Marine Biology. Scient. Mar. 53: 411–416.

Roberts, D., D. Rittschof, E. Holm & A. R. Schmidt, 1991. Factors influencing initial larval settlement: temporal, spatial and surface molecular components. J. exp. mar. Biol. Ecol. 150: 203–211.

Sechler, G. E. & K. Gundersen, 1971. New technique for microscopic examination of the fouling community of submerged opaque surfaces. Appl. Microbiol. 20: 140–143.

Shields, J. D., 1992. Parasites and symbionts of the crab *Portunus pelagicus* from Moreton Bay, Eastern Australia. J. crust. Biol. 12: 94–100.

Stevenson, J. R., 1985. Dynamics of the integument. In Bliss, D. E. & L. H. Mantel (eds), The Biology of Crustacea. Academic Press, London: 2–42.

Sutherland, I. W., 1980. Polysaccharides in the adhesion of marine and freshwater bacteria. In Berkeley, R. C. W., J. M. Lynch, J. Melling, P. R. Rutter & B. Vincent (eds), Microbial Adhesion to Surfaces. Ellis Horwood, Chichester: 330–338.

Svarvarson, J. & B. Davidsdottir, 1994. Foraminiferan (Protozoa) epizoites on arctic isopods (Crustacea) as indicators of isopod behaviour. Mar. Biol. 118: 239–246.

Turner, J. T., M. T. Poster & S. B. Collard, 1979: Infestation of the estuarine copepod *Acartia tonsa* with the ciliate *Epistylis*. Trans. am. microsc. Soc. 98: 136–138.

Van Loosdrecht, M. C. M., J. Lyklema, W. Norde, G. Schraa & A. Zehnder, 1987. Electrophoretic mobility and hydrophobicity as a measure to predict the initial steps of bacterial adhesion. Apl. envir. Microbiol. 53: 1898–1901.

Vrolijk, N. H., N. M. Targett, R. E. Baier & A. E. Meyer, 1990. Surface characteristics of two gorgonian coral species: Implications for a natural antifouling defence. Biofouling 2: 39–54.

Wahl, M., K. Kroeger & M. Lenz, 1998. Non-toxic protection against epibiosis. Biofouling 12: 205–226.

Waite, J. H., 1987. Nature's underwater adhesive specialist. Int. J. Adhesion Adhesives 7: 9–15.

Waite, J. H., 1990. The phylogeny and chemical diversity of quinone-tanned glues and varnishes. Comp. Biochem. Physiol. 97B: 19–29.

Webster, D. R., K. E. Cooksey & R. W. Rubin, 1985. An investigation of the involvement of cytoskeletal structures and secretion in gliding motility of the marine diatom, *Amphora coffaeformis*. Cell Motility 5: 103–122.

Weissmann, P., D. J. Lonsdale & J. Yen, 1993. The effect of peritrich ciliates on the production of *Acartia hudsonica* in Long Island Sound. Limnol. Oceanogr. 38: 613–622.

Weng, T. H., 1987. The parasitic barnacle, *Sacculina granifera* Boschma, affecting the commercial sand crab, *Portunus pelagicus* (L.), in populations from two different environments in Queensland. J. Fish Diseases 10: 221–227.

White, K. N., N. A. Ratcliffe & M. Rossa, 1985. The antibacterial activity of haematocyte clumps in the gills of the shore crab, *Carcinus maenas*. J. mar. biol. Ass. U. K. 65: 857–870.

Wistuba E., 1980. Kleben und Klebstoffe. Chemie in unserer Zeit 14: 124–133.

Wolff, T., 1959. Epifauna on certain decapod crustacea. Proc. XVth Congr. Zool. London: 1060–1061.

Young, G. A., A. B. Yule & G. Walker, 1988. Adhesion in the anemones *Actinia equina* L. and *Metridium senile* (L.). Biofouling 1: 137–146.

Xu, Z. & C. W. Burns, 1991. Effect of the epizoic ciliate, *Epistylis daphniae*, on growth, reproduction and mortality of *Boeckella triarticulata* (Thomson) (Copepoda: Calanoidea). Hydrobiologia 209: 183–189.