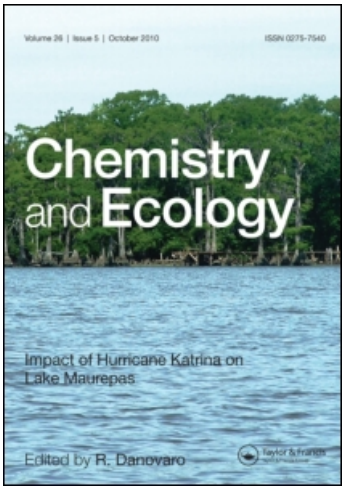

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Epizoites on Marine Invertebrates: With Particular Reference to Those Associated with the Pycnogonid Phoxichilidium Tubulariae Lebour, the Amphipod Caprella Linearis (L.) and the Decapod Corystes Cassivelaunus (Pennant)

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EPIZOITES ON MARINE INVERTEBRATES: WITH PARTICULAR REFERENCE TO THOSE ASSOCIATED WITH THE PYCNOGONID PHOXICHILIDIUM TUBULARIAE LEBOUR, THE AMPHIPOD CAPRELLA LINEARIS (L.) AND THE DECAPOD CORYSTES CASSIVELAUNUS (PENNANT)

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An account is given of a preliminary study of epizoites occurring on the pycnogonid Phoxichilidium tubulariae Lebour and the caprellid Caprella linearis (L.) from the southern North Sea; and on the burrowing crab Corystes cassivelaunus (Pennant) from the Solway Firth.

Each of these species appears to be associated with a distinctive and restricted epizoic fauna dominated respectively by ciliate and suctorian protozoans; hydroids (Campanularidae) and the anascan bryozoan Electra pilosa (L.); the hydroid Gonothyraea loveni (Allman) and the barnacle Balanus crenatus (Bruguière). These faunas are described in terms of their species-composition and distribution; and the three host species compared with reference to the habitats that they offer for exploitation. The ecological significance of invertebrates, particularly vagile forms, as habitats for sessile organisms is discussed in terms of their effects upon distribution and dispersal. The factors responsible for variations between the composition of epizoic faunas, and also the effects that these communities exert upon the host species are reviewed.

INTRODUCTION

The purpose of this paper is to give an indication of the composition, distribution and ecological significance of epozoic communities associated with aquatic, particularly marine, invertebrates, and to emphasize the possible importance of external metabolites (Lucas, 1947) and antibiotics

(Al-Ogily and Knight-Jones, 1977) as determining factors in the species-composition of these communities.

MATERIALS AND METHODS

The Project MASS study of offshore marine fouling has involved analysis of fouling communities from a wide range of structures and locations, particularly North Sea oil and gas production platforms (Pipe, 1979, 1980). Analysis of photographs, video-tape recordings and samples has revealed the presence of a complex assemblage of algae and invertebrates totalling over 200 species for the North Sea area, ranging from diatoms and protozoans to kelps and large tunicates. In addition to the sessile 'fouling' species, a diverse fauna of vagile invertebrates is also present, particularly in fouling dominated by 'turfs' of hydroids, e.g. Tubularia spp., Obelia spp., and Nemertesia spp., or arborescent bryozoans, e.g. Bugula spp. This fauna includes nemertines, polychaetes, nematodes, opisthobranchs, gastropods, pycnogonids, amphipods and decapods. The most commonly encountered species are the polychaetes Lepidonotus squamatus (L.), Phyllodoce spp., and Eulalia spp., the opisthobranch molluscs Tritonia spp. and Eubranchus spp.; the pycnogonid P. tubulariae-Lebour; the amphipods Jassa falcata (Montagu), Caprella linearis (L.) and stenothoids and the decapods Porcellana longicornis (L.), Hyas araneus (L.), H.coarctatus (Leach) and Cancer pagurus (L.).

Preliminary observations indicated the presence of an appreciable invertebrate fauna on P. tubulariae and C. linearis whereas the other, larger, arthropods e.g. P. longicornis, Hyas spp., and C. pagurus were almost entirely unfouled.

Individuals of P. tubulariae and C. linearis were extracted from a sample of the hydroids Tubularia indivisa L. and T. larynx Ellis & Solander taken from a depth of 19.5 m. (with reference to Lowest Astronomical Tide level) on a steel gas-production platform (53°05'N, 1°42'E) on 22-5-80.

Individuals of Corystes cassivelaunus were removed from beam trawl samples taken in Saltom Bay (26-9-79 and 29-1-80) and Parton Bay (26-9-79), Solway Firth.

In all cases, the material examined had been preserved in 4-10% formaldehyde solution. Identification and measurement of hosts and epizoites was carried out using standard equipment and techniques, an attempt being made to define the most important attachment sites and estimate the area of host surface colonized by each species.

RESULTS

Phoxichilidium tubulariae Lebour (Fig. 1)

53°05'N, 01°42'E (-19.5 m. L.A.T.)(22-5-80). Six adult individuals, two male and four female, were obtained from this location. Body length, taken as the distance from the proboscis/cephalon junction to the tip of the abdomen, ranged from 1.525 to 1.725 millimetres.

The overall incidence of fouling was 83.3%, one female of body length 1.700 mm. apparently bearing no epibiota. The remainder bore a generally sparse covering of unidentified filaments, possibly of the bacteria Leucothrix spp., stalked protozoans, probable peritrich ciliates and suctorians, and, in one case, of the hydroid Opercularella lacerata (Johnston). The distortion (presumably due to the use of formalin) of the protozoans was extensive, and consequently these organisms were regarded as one species for the purpose of this study. The total length of these forms ranged from 0.120 - 0.270 mm. The typical attachment sites for these organisms were the dorsal surfaces of the proximal regions of the limbs and lateral processes of the body. The chelae, claws and distal regions of the limbs and ventral surfaces in general were extremely lightly fouled. The ovigers, proboscis and central regions of the dorsal and ventral surfaces were almost entirely unfouled.

Total density of protozoans ranged from 1-59 per fouled host, 50-100% of these being confined to the dorsal surfaces. Surface coverage was in all cases less than 1%. The unidentified filamentous organisms (Leucothrix spp.?) occurred mainly on the dorsal surfaces of the trunk lateral processes and, much less commonly, on the chelifores. The filaments attained a maximum length of 0.050 mm. and a diameter of 0.005 mm. Surface coverage was approximately 1%.

The campanularid hydroid O. lacerata occurred as single zooids on one male individual of body length 1.525 mm. The colonies were confined to the dorsal surfaces of coxa 2, coxa 3, femur, tibia 1 and tibia 2 of the second and fourth limbs. Ten colonies, each attaining a height of 0.3 mm., were present. Surface coverage was approximately 1%. No gonophores were present. A diagrammatic summary of the distribution and abundance of these organisms is given in Figure 1.

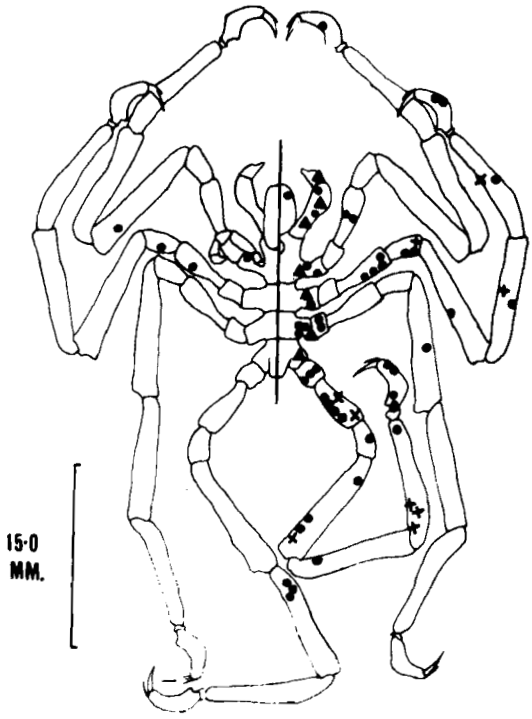

FIGURE 1 Phoxichilidium tubulariae: External morphology showing epizoite attachment sites.

▲ Bacterial filaments
● Sessile protozoans
✕ Opercularella lacerata

Caprella linearis (L.) (Fig. 2)

53°05'N, 01°42'E (-19.5 m. L.A.T.)(22-5-80). 259 individuals, 219 (84.5%) male and 40(15.44%) female, were examined from this location.

Body length, taken as the distance from the head to the telson, ranged from 3.475 to 16.00 mm.

The overall incidence of fouling was 3.48%, epizoites being confined to nine adult males (4.11% of total males) of body length 12.500 - 16.00 mm. 4.5% of males within

this size range were fouled. No epibionts were present on females or juveniles.

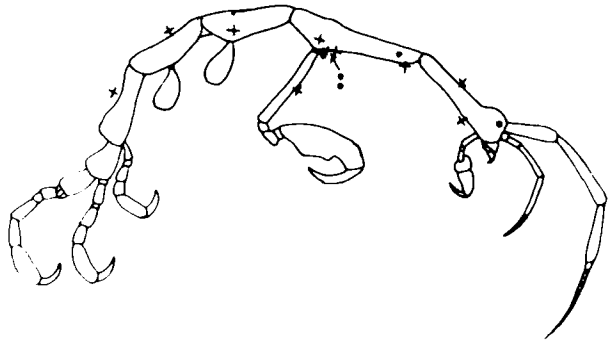

FIGURE 2 Caprella linearis: External morphology (of male) showing epizoite attachment sites.
● Campanularidea
x Electra pilosa

The epifauna consisted of an unidentified species of campanularid hydroid [possibly Obelia dichotoma (L.)] and of the encrusting anascan bryozoan Electra pilosa.

The hydroid occurred on five (55.56%) of the fouled hosts (1.93% of the total sample). Each colony consisted of an annulated stolon plus a single distal zooid. The total length of each colony was in the range 0.500 mm. - 1.000 mm. The total density of hydroids varied from 1 - 6 colonies/zooids per fouled host. The principal attachment sites were the mid-dorsal and mid-ventral areas of the body, particularly, with respect to the ventral sites, near the bases of the second gnathopods and of the branchial lobes. In one host a damaged stolon was also present on the antero-ventral surface of the ischium of the second gnathopod. Total surface coverage by this epizoite was in all cases less than 1%. No gonophores were present. Electra pilosa occurred on 8 (99.89%) of the fouled hosts, 3.09% of the total sample. Each host bore 1 - 3 separate colonies, each colony consisting of 1 - 6 zooids. The mean number of colonies per host was 1.88 with each colony

containing a mean of 1.73 zooids. Each zooid measured approximately 0.45 x 0.3 mm. The principal attachment sites were the ischia of the second gnathopods, the lateral and ventral surfaces of the first, second and third thoracic segments particularly near the bases of the gnathopods. Individual zooids also occurred on the mid-dorsal surface of the first, fifth and sixth thoracic segments.

Total surface coverage by this epizoite ranged from less than 1 to 1+%.

A diagrammatic summary of the distribution and abundance of these organisms is given in Figure 2.

Corystes cassivelaunus (Pennant)(Fig. 3)

(a) Parton Bay (Solway Firth)(26-9-79) Five adult individuals, four male and one female, were obtained from this location.

Body length, taken as the distance from the rostrum to the posterior edge of the carapace, ranged from 24.5 - 28.2 mm. The overall incidence of fouling was 20%, epizoites being confined to two adult males. Both these individuals bore a sparse covering of the campanularid hydroid Gonothyraea loveni. The colonies of this species were mainly 1.0 - 3.0 mm. in length, attaining a maximum of 7.0 mm. The principal

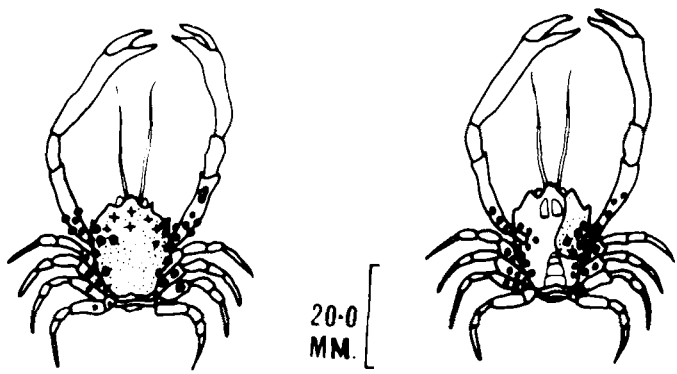

FIGURE 3 Corystes cassivelaunus: External morphology showing epizoite attachment sites.
■ Podocoryne sp. + Balanus crenatus
● Gonothyraea loveni ▨ Electra pilosa
▩ Conopeum reticulum

attachment sites were the lateral and antero-dorsal areas of the carapace including the rostrum, the maxillipeds, the proximal regions of the chelipids and also the general antero-ventral region including the areas near the limb-bases and mouth. Total surface coverage by this epizoite was estimated at 5% No gonophores were present.

One fouled individual (body length 25.0 mm.) bore 3 Balanus crenatus all of 3.0 - 4.0 mm. maximum diameter. Two of these occurred on the dorsal surface of the carapace immediately posterior to the post-ocular teeth, the third on the ventral side adjacent to the mouthparts.

(b) Saltom (Solway Firth)(26-7-79). Nine adult individuals, all male, were examined from this location. Body length, taken as the distance from the rostrum to the posterior edge of the carapace ranged from 23.5 - 33.3 mm. The overall incidence of fouling was 77.8%, epizoites being absent from two individuals of body length 24.3 and 33.3 mm. Each fouled host bore a covering of campanularid hydroids, probably G. loveni. The colonies of this species were mainly 2.0 - 5.0 mm. in length, attaining a maximum of 15.0 mm. The attachment sites were again the lateral, antero-ventral and antero-dorsal areas of the carapace, particularly around the limb bases, the proximal regions of the limbs and the chelipeds. Total surface coverage by G. loveni varied from less than 1% to 5%. No gonophores were present.

Balanus crenatus occurred on two individuals (an incidence of 22.2%) of body length 30.5 mm. and 29.3 mm. In both cases this species was confined to the antero-dorsal region of the carapace, mainly in the area immediately posterior to the post-ocular teeth.

The barnacles present on the larger host occurred in a group of 20 individuals, the group being composed of two distinct size classes of maximum diameter 0.5 mm. (12 individuals) and 3.0 - 4.0 mm. (8 individuals) respectively. Three barnacles, all of maximum diameter 1.0 - 1.5 mm., were present on the smaller host again in the area posterior to the post-ocular teeth. Total surface coverage by this epizoite was estimated to be 5% and 1% respectively.

An encrusting colony of the athecate hydroid Podocoryne sp. was present on a host of body length 30.9 mm. The hydroid was located on the dorsal surface of the ischium of the fourth pereiopod. The area of the colony was estimated at 30 $mm.^2$, surface coverage being 1 + %.

The encrusting anascan bryozoan Conopeum reticulum occurred on one host (body length 29.2 mm.). The colony

encrusted most of the dorsal and antero-lateral areas of the carapace. Surface coverage was 35%.

A diagrammatic summary of the distribution and abundance of these epizoites is given in Figure 3.

DISCUSSION

1. Discussion of results

Preliminary analysis of the three host species indicates the presence of distinctive epizoic communities. These communities are restricted in terms of species-composition, distribution on the available surfaces of the host and also, in the case of Caprella linearis, distribution with respect to the size-range exploited within the available host population.

Species composition. Although the epizoites identified during this study are drawn from a wide range of taxa i.e. bacteria, Protozoa, Coelenterata, Arthropoda (Crustacea) and Bryozoa, the total number of species present on each host is small i.e. P. tubulariae - four species, C. linearis - two species, C. cassivelaunus - five species. This situation contrasts markedly with the much richer assemblages found on other aquatic arthropods e.g. on the gastropod shells of hermit crabs (Conover, 1979; Cuadras and Pereira, 1977; Stachowitsch, 1977, 1980) and on the external surfaces of freshwater Cladocera (Green, 1974).

Distribution on host surfaces. For each host species, the distribution of epizoites was largely localized into distinct sites. Although between-host differences were, in some cases, marked, e.g. the relative absence of fouling from the mid-dorsal area of P. tubulariae in comparison with C. linearis and C. cassivelaunus, there were definite areas of common exploitation. Thus, the most commonly fouled areas for all three host species were the proximal regions of the limbs and the mid- and antero-ventral region particularly near the limb bases. In C. linearis and C. cassivelaunus the dorsal regions were often fouled. Areas generally bearing little or no fouling were antennae, eyes, claws and distal regions of limbs, except chelipeds/chelifores, and the posterior appendages.

Distribution within host population. Results for the host species indicate a general low density of epizoite infestation. Thus total surface coverages varied from 0 - 35%. The small numbers of P. tubulariae and C. cassi-

velaunus (from 2 sites) examined imply that the values for fouling incidence on these hosts (83.3% and 20% and 77.8% respectively) should be treated with caution. In C. linearis fouling was confined to 3.48% of the total sample, all fouled individuals being adult males of body length 12.5 - 16.0 mm. The large size of the sample and the presence of a wide size-range of individuals suggest the opearion of a definite active or passive process of selective colonization.

2. Occurrence and effects of epizoites

The colonization of aquatic, particularly marine, animals and plants by invertebrates is a widely reported and described phenomenon (e.g. Sieburth, 1975). Such associations have been studied from many aspects. The epifaunal communities of particular host species e.g. Dardanus arrosor (Cuadras and Pereira, 1977), Pelvetia canaliculata (Dunstone et al, 1979), Nemertesia antennina (Hughes, 1979), Mytilopsis sallei (Rao and Rao, 1975), Sertularia operculata (Round et al, 1961), Arca spp. (Scanland, 1979), and Flustra foliacea (Stebbing, 1971) have been investigated in terms of community structure and ecology. Wider taxa, e.g. freshwater Cladocera (Green, 1974) and pagurids (Stachowitsch, 1977), have also been dealt with in this manner. The significance of these relationships has, however, received comparatively little consideration. Major effects imposed upon the host range from the purely mechanical to much more complex ecological/behavioural influences.

Physical effects. The presence of epizoites on a host will exert two obvious effects i.e. an increase in body size and weight; and an obscuration of the body surface with a possible hindrance of limb, appendage and sense organ function. In plant hosts an effect may be exerted upon photosynthetic activity. An increase in body size/weight/volume is known to induce a decreased swimming rate in cladocerans (Green, 1974). In the same study it was shown that increased energy demand arising from maintenance of normal activity (e.g. swimming and ventilation) induced a reduction in egg production. Hindrance of oxygen uptake induced increased mortality under conditions of lower ambient oxygen concentration. Some organisms employ either 'cleaning' mechanisms, e.g. carideans (Bauer, 1979) and pycnogonids (King, 1973), or anti-biotics (e.g. Al-Ogily and Knight-Jones, 1977) to prevent surface fouling.

Ecological and behavioural effects. The increase in body size of hermit crab gastropod shells has been shown to confer an intra-specific competitional advantage upon the host (Wright, 1973). Relationships between hermit crabs and the symbiotic anemone Calliactis parasitica are known to involve complex behavioural patterns by host and epizoite (Ross, 1960, 1979a and 1979b). In this association a definite protection against predation e.g. by Octopus (Ross, 1971) is conferred. Epizoic communities are utilized as camouflage by molluscs e.g. clams (Vance, 1978) and decapod crustaceans e.g. Loxorhynchus crispatus (Wicksten, 1979).

3. Host-epizoite interactions

This aspect of the relationship is less well studied. The hard surfaces of a host may provide the only available area for colonization by sessile epifauna in an otherwise unsuitable environment. They may be as such provide a significant contribution to the distributional range of these species (Allen, 1953). Colonization of a vagile host may provide a means of dispersal for epizoites with larval stages of short duration and must be considered as a possible major influence on the distribution of fouling organisms.

The presence of sessile organisms on such a host may ensure that they are maintained free of sediment. The morphological and behavioural characteristics of the host may confer protection from predators on the symbionts either by provision of inaccessible settlement sites or by rapid movement. Food particles and metabolic products gleaned from the host may be significant factors in the nutrition of epizoites. The bryozoan Membranipora membranacea epizoic upon the kelp Nereocystis luetkeana is known to derive some direction nutritional input from the host (De Burgh and Fankboner, 1978). Similarly, the algal epiphytes of Zostera have been shown to take up carbon and nitrogen from the leaves of the host (McRoy and Goering, 1974). Although some of the factors involved in the settlement of epibionts (e.g. Hayward and Harvey, 1974a; Wallace, 1978) and their subsequent growth and colony development (e.g. Hayward and Harvey, 1974b; Buss, 1979; Stebbing, 1973) have been analysed, the linkages between the biology of host and epibiont(s) have been comparatively neglected. The existence of such linkages is convincingly demonstrated by the relationship between the ecdysial

cycle of the decapod Calacarius macandreae and reproduction in its ectoproct epibiont Tricella koveni (Eggleston, 1971). Similarly, the pre-emergence behaviour of the ephemeropteran Ephemera danica is vital for successful emergence of its phoretic epibiont, the larvae of the chironomid Epoicladius ephemerae (Svensson, 1979). A consideration of the complex factors involved in the establishment and maintenance of such highly synchronized relationships and restricted communities (Forester, 1979; Foster et al, 1978; Lindley, 1978) implies that much of the underlying basis of these associations is chemical. A consideration of non-predatory relationships in planktonic organisms (Lucas, 1947) suggests the possibility that external metabolites may be, at least in part, responsible for the establishment of these far from random associations. A further detailed analysis of specific host-symbiont associations from this viewpoint could reveal that the interdependence of such associates operates on a chemical level in addition to a purely physical utilization of available surface.

The identification of the substances involved and the elucidation of their modes of synthesis and action (e.g. Al-Ogilvy and Knight-Jones, 1977) would assist in a deeper comprehension of anti-fouling mechanisms. Such an understanding must be the key to a new approach to the design of anti-fouling strategies for artificial surfaces.

Further evidence for the existence of such chemical factors is provided by a comparison of the epifauna occurring on inert surfaces with that on invertebrate hosts from the same area. Preliminary analysis of fouling on plastic surfaces, polythene sheeting and sea-bed drifters, from the Solway Firth reveals the presence of a rather more complex epifaunal community than that occurring on C. cassivelaunus from the same area. Floating polythene is fouled by campanularid hydroids, Pomatoceros triqueter, B. crenatus, Anomiidae, Alcyonidium spp., E. pilosa, C. reticulum and tubuliporid bryozoans. Sea-bed drifters bear the ascidian Botryllus schlosseri (Pallas) in addition to these species. Clearly the differences between the communities on the inert and invertebrate substrata are an indication of the operation of the biological and chemical influences that have been suggested.

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