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Infection of intertidal barnacles by the parasitic isopod *Hemioniscus balani* in north-east England

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Prevalence of the parasite *Hemioniscus balani* (Isopoda: Cryptoniscidae) was determined in intertidal barnacles *Semibalanus balanoides* collected from north-east England during winter 1989–1990 and March 2000. Infection by female and male stages of the parasite were low (0.0–13.6% and 0.0–9.9%, respectively). Female stages were usually more prevalent lower down the shore, and were more common among larger barnacles. The observed rates of parasitism are similar to those recorded in the region 40–50 years ago.

This study reports intertidal infection rates of the protandrous hermaphrodite *Hemioniscus balani* Buchholz in the barnacle host *Semibalanus balanoides* in north-east England. *Hemioniscus balani* has an ectoparasitic stage on calanoid copepods, which produces male cryptonisci stages that settle on rocky substrata. The male enters the mantle cavity of a barnacle (at least 14 intertidal and subtidal species are susceptible to infection—Crisp, 1968) and attaches itself to an ovary. There, it transforms into a sessile female stage and develops an enlarged brood sac, thus impairing barnacle egg production. Once fully developed, the parasite ruptures to liberate its larvae into the surrounding water.

Hemioniscus balani has been reported from Atlantic (east and west) and Pacific (east) coasts of the Northern Hemisphere, and from South African coasts (Sandison, 1954; but see Vader, 1983). Around Europe, it occurs from the River Gironde in France (46°N) to northern Norway (>70°N) (Vader, 1983). Within the British Isles, the highest intertidal infection rates occur in south-west England (>90%), where *Semibalanus balanoides* (=*Balanus balanoides* in the earlier literature) is an important host species lower down the shore.

Infection rates of *H. balani* in the host *S. balanoides* were studied at nine intertidal locations between the Tyne and Blyth estuaries (Figure 1). The spring tidal range in the region is ~4.1 m, and *S. balanoides* is the dominant barnacle species throughout the intertidal barnacle range. All nine sites were surveyed during the winter of 1989–1990, and three were re-surveyed during March 2000.

Infection rates (per cent *H. balani* found/*S. balanoides* examined) were determined by carefully dislodging barnacles with a scalpel blade into a container of formaldehyde solution to rapidly immobilize the motile male stages. The vertical extent of the barnacle zone in the region is approximately 3 m. Collections were made from the top 1 m (upper level), middle 1 m (middle level) and bottom 1 m (lower level) at each site, except where a suitable barnacle substratum was unavailable at a given level. Barnacles were examined under a binocular microscope in the laboratory. Those that were not fully intact (i.e. from which the parasite may have been lost) were excluded from the analysis.

General pattern of infection levels

Between October 1989 and March 1990 a total of 10,097 barnacles were examined, yielding 207 female (2.7%) and 131 male (1.3%) *H. balani* parasites. Infection rates per sample ranged from 0–13.6% for female stages (median=1.2%) and 0–9.9% for male stages (median=0.8%) (Figure 2).

Parasites of both sexes were found throughout the barnacle zone. Female parasite stages were generally more common lower down the shore (Kruskal–Wallis test, H=6.94, df=2, P=0.03), although this was not always true (e.g. Blyth South Beach, more in middle level: χ^2=29.8, df=2, P<0.0001; also see Cullercoats-D). In Norway, Vader (1983) found that female stages were also more prevalent lower down the shore. Previous records in the British Isles do not quantify zonation *per se*, although in south-west England, *S. balanoides* is itself mainly restricted to the lower parts of the shore.

No overall effect of tidal level was found with male parasites (Kruskal–Wallis test, H=3.23, df=2, P=0.199), although localized exceptions were again evident. For example, male parasites were usually more abundant in the lowest level at Cullercoats-C (χ^2=22.0, df=2, P<0.0001) and Cullercoats-E (χ^2=16.0, df=2, P<0.0001).

Crisp (1964, 1968) and Vader (1983) found that *H. balani* tended to be more common at exposed sites. No such relationship was apparent in this study. Indeed, some of the highest levels of infection occurred in the more sheltered sites (e.g. North Shields, Blyth Quayside and Ferry). Furthermore, Cullercoats-D was one of the most sheltered sites of those surveyed at Cullercoats Bay, yet the highest levels of infection were consistently found there.

Multiple infections

Only one instance was found of two female stages inhabiting the same barnacle (~0.5% of those barnacles infected); otherwise, barnacles were single-infected. This appears to be the general rule along British (Southward & Crisp, 1954; Crisp & Southward, 1958) and Californian coastlines (Blower & Roughgarden, 1987), although multiple infections may be more common elsewhere (e.g. Sandison, 1954; Vader, 1983).

Males were found inside the same barnacle as an early stage female on several occasions. The highest number of *H. balani* recorded together was five, comprising one female and four males (October 1989, Cullercoats-G), suggesting that the motile cryptonisci have a finely honed ability to locate conspecifics.

Host size and infection

The relationship between host size (mean of basal width and length) and infection by female stages was examined in 132

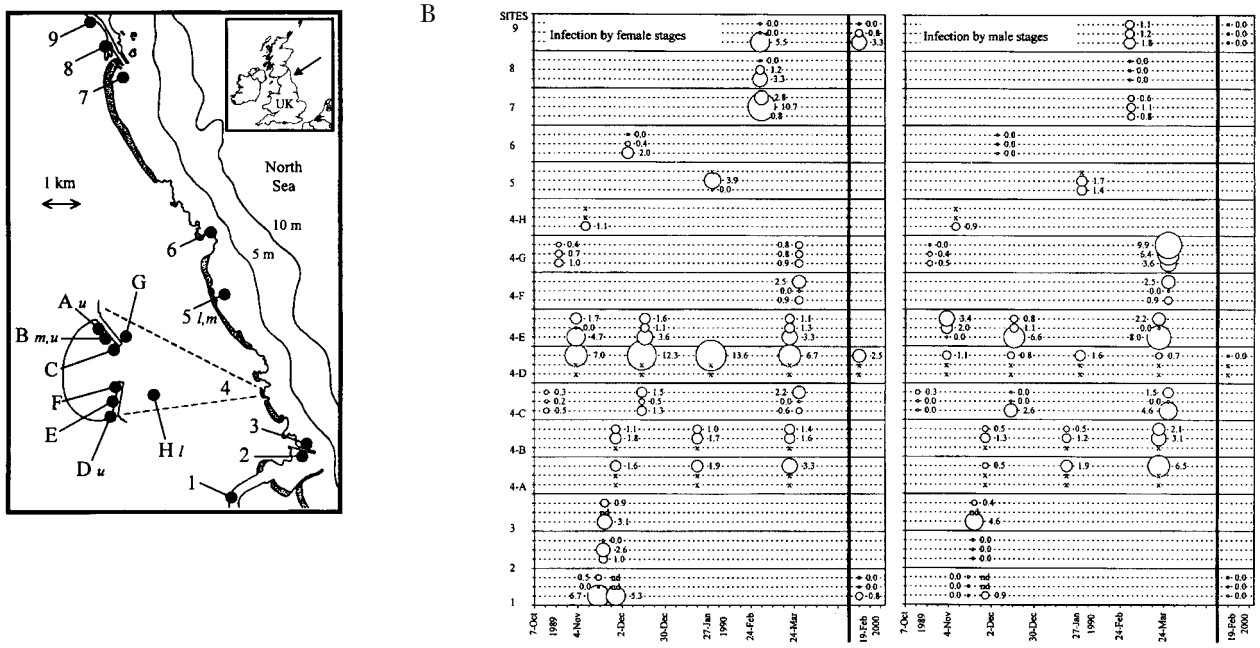

Figure 1. (A) Barnacle collection sites along north-east English coastline (55°01′N to 55°08′N). 1, North Shields (concrete wall); 2, Inside wall, north Tyne pier; 3, Outside wall, north Tyne pier; 4, Cullercoats Bay [A–C: Inner wall, north pier; D–F: Inner wall, south pier; G: Outer wall, north pier; H: rocky reef]; 5, Whitley Bay (rocks protruding sand); 6, St Mary's Lighthouse (rocky shore); 7, Blyth South Beach (wooden post); 8, Blyth quayside (wooden posts); 9, Blyth ferry terminal (concrete posts). Barnacles occurred at all three tidal levels, except: *u*, upper only; *m*,*u*, middle and upper only; *l*, lower only; *l*,*m*, lower and middle only. (B) Infection rates of *Hemioniscus balani*. Circle diameters are proportional to infection rates (adjacent number=percentage) at the lower, middle and upper levels of each site. x, barnacles absent from that level; nd, not determined. See Figure 1 for site details.

barnacles from Cullercoats-E lower in November 1990 (male numbers were insufficient to justify investigation). The probability of infection increased significantly with barnacle size (logistic regression, z=2.51, P=0.012). A similar relationship was reported for *H. balani* in the intertidal host *Chthamalus fissus* in California, but apparently not in the co-existing host *C. dalli* (Blower & Roughgarden, 1988).

Temporal trends

Analysis of short-term (October 1989 to March 1990) variability in female stage infection was possible with data from Cullercoats A-upper, C-upper, D-upper and E-lower, but no significant temporal changes were evident (site with lowest P value: D-upper level, χ^2=5.12, df=3, P=0.16). With male stage infections, data from Cullercoats C-lower, E-lower, G-middle and G-upper were analysed. Of these, three sites showed significant increases in male numbers between October and March (most conservative site: C-lower, χ^2=9.13, df=2, $P<0.01$), whilst the fourth did not (E-lower, χ^2=4.85, df=2, P=0.09).

Three sites with relatively high infection rates in 1989–1990 were re-surveyed in March 2000: a total of 930 barnacles were examined from North Shields, Cullercoats-D and Blyth Ferry, producing 12 (1.3%) female and 0 male parasites (Figure 2). At North Shields and Blyth, where barnacles were collected from all three tidal levels, female infections were again concentrated lower down the shore, indicating that this is a stable feature of these sites. Infection rates did not differ from 1989/90 data (paired *t*-tests on arcsine-transformed data; females: t_5=1.71, P=0.14; males: t_5=1.65, P=0.15). These results are comparable to those of Vader (1983), who noted stability in the vertical distribution of female *H. balani* infecting *S. balanoides* in Norway, with only slight year-to-year changes in infection rates.

Southward & Crisp reported in 1954 that *H. balani* infection rates along the North Sea coastline of the British Isles were usually low (<10%) in *S. balanoides*. Thus, the infection rates of *H. balani* recorded in this study are comparable with those recorded 40–50 years previously.

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