matters arising

Niche breadth in Bryozoans

O'CONNOR *et al.*[1] consider a resource gradient with an optimum point for a particular species. Other factors being equal, individuals migrating to a new environment will tend to select the optimum, or near optimum. As population density increases, the advantages of being near the optimum may be offset by intraspecific competition[2]. Migrants may therefore choose a sub-optimal point on the resource gradient. As population density increases so will the range of resource gradient used.

O'Connor *et al.*[1] use the phenomenon of an increase in range with population density as a test for intraspecific competition. This is not a suitable test because range will increase with population density even in the absence of intraspecific competition. If intraspecific competition was not occurring and individuals chose the resource optimum with an associated variance from a normal distribution (say, mean of zero and variance of unity), then the expected range would increase with population density (going from five to fifty individuals the expected range would increase from 2.32 to 4.50 (ref. 3)). It is not necessary to postulate a normal distribution or even a resource optimum for an expected increase of range with population density.

Using the epiphytic bryozoan *Alcyonidium hirsutum* settling on the serrated wrack *Fucus serratus*, it is probably permissible to replace the percentage cover used by O'Connor *et al.*[1] by the numbers of individuals over a wide range of settlement density, provided that settled individuals are of the same age[4]. The optimum on the particular resource gradient used has been investigated previously[5].

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O'CONNOR ET AL. REPLY—We accept the point raised by Harvey *et al.*[1] but it does not alter our earlier conclusion that *Alcyonidium hirsutum* shows increased niche breadth in the presence of intraspecific competition and decreased niche breadth in the presence of interspecific competition. Range on the resource gradient is indeed correlated statistically with the number of bryozoan settlements on each *Fucus serratus* frond, but because these fronds vary in age along their length, it is less reasonable to assume that the resulting colonies should be of equal age. In practice the partial correlation coefficient between *Alcyonidium* abundance (percentage cover) and its range, controlling for the number of faces colonised on each plant (and thus for the effect suggested by Harvey *et al.*) was 0.506 ($P<0.05$). That is, *Alcyonidium* shows increased range in resource utilisation as its own population levels rise, and does so independently of the statistical artefact suggested.

For the other three bryozoan species whose distribution we analysed, we reported small positive correlations between range and abundance, in small samples containing some unmeasured interspecific competition. Correcting for the possible statistical effect by partial correlation left us with positive correlations in the case of *Flustrellidra hispida* ($r_p=0.419$, $P<0.2$) and *Electra pilosa* ($r_p=0.215$, $P<0.3$), but with a negative value in the case of *Membranipora membranacea* ($r_p=-0.463$, $P<0.2$). Thus only for this species might our first results have originated in a sample-size effect, though as we pointed out previously, we have available to us only samples which are subject to some degree of interspecific competition which tends to reduce niche breadth anyway. In summary, therefore our results still indicate that intraspecific and interspecific competition lead respectively to increase and decrease in niche breadth in *A. hirsutum* and possibly in other bryozoan species as well.

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THE claim of O'Connor *et al.*[1] that distributional and density data for the bryozoan *Alcyonidium hirsutum* growing on *Fucus* fronds demonstrate the effects of both intra- and interspecific competition on niche width is unsound for both methodological and theoretical reasons. A positive correlation would be expected between the number of bryozoan colonies and the 'population level' as measured by percentage cover, and therefore the positive relationship found between the range of segments utilised and the population level is explicable without recourse to competition theory. On fronds which are more suitable overall, some of the less favoured segments would become acceptable, so that the frond is colonised more heavily and over a wider range of segments Other models will also produce this result. If darts are thrown at a linear target the range between darts should increase with the dart 'population size'.

Regarding interspecific competition we note that in the no-, one-, and two-competitor cases, decreasing sample sizes are used. A narrower niche width would thus be expected in the cases with competitors irrespective of interspecific effects. The utilisation curves for the first two cases, however, do not differ significantly (Kolmogorov–Smirnov two-sample test[2]), negating conclusions based on supposed differences between them. The two-competitor curve is based on too few colonised segments (18) for much confidence to be placed in supposed trends; furthermore, when allowance is made for the modal shift there is no significant difference between this and the non-competitor curve. Finally, B.

$$(\ln B = -\Sigma p_i \ln p_i)$$

is an accepted measure of niche width[3,4]. The value for the one-competitor case is higher than for the no-competitor curve, contrary to the prediction of O'Connor *et al.*[1].

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