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Phil. Trans. R. Soc. Lond. B 1998 **353**, 453-464

doi: 10.1098/rstb.1998.0222

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Natural and anthropogenic dispersal mechanisms in the marine environment: a study using cheilostome Bryozoa

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The global geographic ranges occupied by 197 species of cheilostomate Bryozoa found in British waters were obtained by a literature survey. Morphological grade, larval mode, environmental tolerance, species abundance and the ability to raft and to foul shipping were all investigated as traits potentially able to affect the geographic ranges of these bryozoan species. When considered independently all variables except larval mode had a significant correlation with the geographic range occupied by a species. However, when controlling for the potentially confounding effects of the other covariates, only the ability to foul or raft and species abundance had a significant effect on median geographic range and only fouling and abundance had a significant effect over global ranges. The strength of the association between fouling ability and range suggests that transport upon the hulls of ships is a very important dispersal mechanism for bryozoans, as it is thought to be also for various other marine taxa. Potential long-term (evolutionary) consequences of increased ranges brought about by anthropogenic mechanisms are discussed.

Keywords: dispersal; geographic range; fouling; rafting; Bryozoa

1. INTRODUCTION

Although every species has a finite duration, it is evident that human influences have accelerated the rate of extinction of many taxa (see review by Hanski *et al.* 1995). With many more anthropogenic extinctions predicted to occur, the processes controlling the generation and maintenance of species diversity have become an important issue for biologists (e.g. Heywood 1995). One important buffer against extinction is the geographic range occupied by a species. Evidence from the fossil record indicates that species that are geographically widespread are generally longer-lived than those with restricted geographic ranges (Jackson 1974; Shuto 1974; Scheltema 1978; Hansen 1978, 1980; Jablonski 1991, 1995; Jablonski & Raup 1995). Furthermore, the amount and frequency of genetic exchange between distant populations is thought to be an important determinant of both the tempo and mode of speciation (Shuto 1974; Scheltema 1978; Jablonski 1986; reviewed by Jablonski & Lutz 1983). The geographic range of a species, therefore, is likely to be a major factor in both the maintenance and generation of species diversity. Hence an understanding of the mechanisms that control the geographic extents of species is an important part of evolutionary theory and conservation biology.

Much work has focused on identifying species-level traits that control geographic range; such traits as larval mode (Shuto 1974; Hansen 1978, 1980; Scheltema 1978, 1986, 1989; Jablonski 1986; but cf. Ó Foighil 1989; Bhaud 1993; Emler 1995), environmental tolerance (Jackson 1974; Hansen 1978, 1980; Bhaud, 1993), and the ability to float or

raft (Highsmith 1985; Jackson 1986; Johannesson 1988; Jokiel 1989; Ingólfsson 1995), have all been identified or suggested as being major determinants of geographic ranges of species. Other, more general, life history traits may also affect geographic range. For example, rarity and geographic range are considered to be interdependent (Brown 1984; Gaston 1990), and among rock-dwelling tropical Pacific molluscs, those resistant to predation were inferred to be more proficient in crossing oceanic barriers than more vulnerable species (Vermeij 1987).

It is now evident that many marine species have been introduced into new habitats by man, for example through transport in ballast water (Carlton 1985; Carlton & Geller 1993), by fouling the hulls of ships (Carlton & Scanlon 1985; Carlton & Hodder 1995), and through incidental transportation with commercial species (see Carlton (1987) for a brief history of these mechanisms). Any investigation of natural dispersal mechanisms should make allowance for appropriate anthropogenic factors such as these. Species particularly liable to transport by such mechanisms are expected to show increased geographic ranges. Currently, over very large distances, human-mediated transport may be far more important for dispersal than natural methods (Carlton 1987). However, quantitative comparisons of the relative significance of various methods of dispersal are lacking. Clearly, as many factors may influence the geographic range of a species, investigations into ranges should consider all possible traits relevant to the lifestyle of the taxon in question. Determining which of these traits actually has an effect on range, however, may be difficult because of

possible interactions between such a large number of traits, each allowing dispersal over various spatial scales and frequencies.

Bryozoans are a speciose and abundant aquatic phylum capable of using a variety of potential dispersal mechanisms, as they demonstrate great catholicity in their exploitation of substrates. With over 5000 extant species (Horowitz & Pachut 1994), all colonial, filter feeders and almost exclusively sessile, they are often major constituents of marine benthic communities. Most Recent species are marine and belong to the order Cheilostomatida. The cheilostomes are further split into two organizational grades (formerly suborders), the Anasca and the Ascophora. Anascans typically have lightly calcified zooids, and the ascophorans heavily calcified zooids with frontal shields (Gordon 1993). Although most cheilostomes have a brooded lecithotrophic (coronate) larva that usually settles within a few hours of release (e.g. Nielsen 1981; Ryland 1981; Keough 1989), a few species possess a non-brooded, planktotrophic (cyphonautes) larva that may have a potential planktonic life of up to eight weeks (e.g. Yoshioka 1982). In some modern classifications species with cyphonautes larvae are sometimes placed in the suborder Malacostegina, although this is almost certainly paraphyletic (Taylor 1987).

Some bryozoan species are epiphytic upon macroalgae and therefore may be dispersed by rafting and also many bryozoans are commercially important fouling species (Ryland 1965, 1967). Carlton (1985) considered transport by ballast water to be possible, but there is very little detailed evidence for this, although Carlton & Geller (1993) found larvae of the anaskan *Membranipora membranacea* in ballast water. However, this species, which is very common and has a cyphonautes larva, is almost exclusively an epiphyte of subtidal kelp and does not normally foul non-algal substrata. Bryozoans, presumably, foul the insides of ballast tanks and it is assumed that these species will be included with the known fouling species.

Overall, however, the diverse ecologies of bryozoans provide an excellent opportunity to compare the effects on geographic range of natural and anthropogenic dispersal mechanisms and general life history traits. This study uses known global geographic ranges of British cheilostome species to assess the influence of a variety of traits upon geographic range. Specifically, the following questions are asked: (i) what is the relative importance of each mode of dispersal in determining geographic range?; (ii) how do univariate analyses, which ignore the influences of other traits, affect the interpretation of the data when compared with an approach which controls for the affects of the other variables?

2. METHODS

The British fauna of cheilostome bryozoans was chosen because this is probably the best described bryozoan fauna in the world, and for most species the life history and other parameters are well-known. All species used for this analysis are completely sessile after larval metamorphosis. Data on geographic ranges were obtained from Ryland & Hayward (1977) and Hayward & Ryland (1979). Species ranges were further checked and supplemented using the following literature: Uttley & Bullivant (1972); Hayward

& Cook (1979, 1983); Hayward (1980, 1988, 1995); Gordon (1984, 1985, 1986, 1989); Vine (1986); Winston & Heimberg (1986); Zabala & Maluquer (1988); Gordon & Mawatari (1992); Hayward & Thorpe (1995); Soule *et al.* (1995); Seo (1996); and Stevens *et al.* (1996). Additional data on the Waters Collection (Manchester Museum) was obtained from Pettitt (1995).

Many different methods of measuring geographic range exist (see Gaston (1996) for summary of range measures). Because this study uses global ranges, estimation of the actual areal coverage of species, which is the ideal measure of geographic extent, is clearly a very difficult task. Diagonal range was used as this estimator of geographic extent showed the greatest correlation ($r > 0.82$, for all comparisons) with other range measures, such as maximum linear range, maximum marine range, maximum latitudinal range, maximum longitudinal range and number of geographical provinces. Therefore, diagonal range is assumed to be a reasonable indicator of the geographic extent a species. For each species the diagonal range was calculated using $(NS^2 + EW^2)^{1/2}$, where NS and EW represent the maximum linear North–South and East–West distances (across water and land) of the species' known geographic endpoints respectively (Gaston 1996). This distance was then rounded to the nearest 1000 km. Distances were measured using the *Times Atlas of the World* (1994) and the *Times Map of the World* (1994); for each species the largest available map that covered the complete range was used. By necessity, the range measurements will contain some error because the surface of a sphere has been extrapolated on to a flat page. However, both of the map projections used a pseudo-cylindrical projection designed to reduce distortions in area and shape; this, and rounding the estimates of range, should reduce any biases incurred through using flat rather than spherical map projections. Using data from published literature, every species was assigned a code for each of the six dispersal traits considered potentially influential in determining geographic range (table 1). Estimates of species abundance were somewhat subjective and were taken from Ryland & Hayward (1977), Hayward & Ryland (1979), and Ward (1988).

Overall the data may be thought of as a series of 'partial' tables showing the distribution of geographic ranges within a trait while maintaining one of the other covariates at a constant value (Agresti 1984); by ignoring all other dispersal traits a collapsed (or 'marginal') table is effectively produced. Analysis of the partial tables enables the effects of other variates to be controlled (Agresti 1984). An investigation into three-way (or greater) interactions would be compromised due to small sample sizes and was, therefore, not attempted.

Kruskal–Wallis tests (Sokal & Rohlf 1995) were used to analyse differences in range for each trait while ignoring the potential effects of other variates (marginal tables) and controlling for potential effects of each of the other variables (partial tables). The analyses were performed using the NPARIWAY procedure of SAS (1989). Each trait was also separately regressed against range using the LOGISTIC procedure of SAS Institute Inc. (1989). Finally, a stepwise logistic regression analysis was undertaken; this procedure controls for the other variables present in the model. All variables were initially forced

Table 1. Six species traits potentially important in determining the geographic ranges of British cheilostome species and a brief rationale for inferring differential dispersal abilities within these traits

(Categories within each of the traits hypothesized *a priori* to increase geographic range are ranked higher than those thought to give a more restricted range. No *a priori* assumptions were made concerning the relative dispersal capabilities among each of the species traits.)

life history trait	explanation of species trait
morphological grade	
anascan (2)	anascans possess fewer taxonomic characters, which may possibly lead to taxonomic undersplitting and artificially increasing species' ranges
ascophoran (1)	
larval mode	
cyphonautes (2)	cyphonautes larvae have a longer lifespan than coronate larvae and should therefore be dispersed further than coronate larvae
coronate (1)	
environmental tolerance	
intertidal (3)	codes are for the shallowest recorded depth. Shallower habitats are assumed to experience greater environmental fluctuations. Species found at greater depths are assumed to be more stenotopic
0–50 m (2)	
> 50 m (1)	
ability to raft	
yes (2)	species which grow on algae have the potential for dispersal by rafting and should possess wider geographical ranges than non-rafting species
no (1)	
ability to foul	
yes (2)	known fouling species will have greater ranges than non-fouling species through transport upon shipping traffic
no (1)	
species abundance	
common (3)	species that are more abundant will be encountered more frequently in surveys and collections. They will therefore have greater apparent ranges than rarer species
frequent (2)	
occasional (1)	

into the analysis and traits that did not improve the fit of the model (at $P > 0.05$) were removed. Variables that improved the fit of the model (at $P < 0.30$) were allowed to re-enter the model. The stepwise procedure continued until the same variate had been entered and removed in consecutive steps.

Logistic regression allows regression of binary or categorical data. This technique relates the proportions (p) of a dependent variable to an independent variable (X). As the relationship between such data is bounded between zero and one and is typically sigmoidal, a cumulative distribution function is used to model the data. The expected value, p_i , of the dependent variable, given a value of the independent variable, X_i , is estimated using the model:

$$p_i = [e^{\beta_0 + \beta X_i}] / [1 + e^{\beta_0 + \beta X_i}].$$

The logit transformation, $g(x) = \ln [p/1-p]$, is used to make the logistic function linear, i.e. $g(x) = \beta_0 + \beta X$, and unbounded. A maximum likelihood function is used to estimate the regression line as the dependent variable is binomially distributed. The 'score test for the proportional odds assumption' tests the modelling assumption used by SAS when regressing ordinal data (environmental tolerance, abundance and geographic range in this analysis); a significant result would invalidate the assumption of the model. The null hypothesis that there is no relationship between the logit and geographic range was tested using G . The G -value is the difference of log-likelihood of the model without and with the independent variate(s) multiplied by minus two. Under the assumption that the regression slope is equal to zero, the G -value will approximately follow a χ^2 distribution with 1 d.f. (Hosmer & Lemeshow 1989, p. 15; Sokal & Rohlf 1995, p. 770). The use of logistic regression facilitates interpretation of the data, as exponentiating the slope (the difference between two logits) estimates the odds ratio for a difference of one unit of the independent variable (e.g. the difference between being anascan or ascophoran). The odds ratio approximates how much more likely (or unlikely) it is for the outcome to be present (increased range in this example and throughout this study) among those with the variate (ranked higher, see table 1) than those without (Hosmer & Lemeshow 1989, p. 41). For example, if 15 and 5 non-rafting species have narrow and wide ranges, respectively, then the odds that non-rafting species are found over longer ranges are $5/15 = 0.33$. If the odds for a large range in rafting species are 2, then analysis by odds ratios suggests that rafters are $2/0.33 = 6$ times more likely to be geographically widespread than non-rafters. Table 1 summarizes trait ranks and assumptions made *a priori* about dispersal capabilities. More detailed information on logistic regression technique and odds ratios may be found in Agresti (1984), Hosmer & Lemeshow (1989) and Sokal & Rohlf (1995).

Because of the nature of logistic regression, a categorical measure of range had to be used. Three categories were chosen to preclude very low cell frequencies but still offer a meaningful biological interpretation. The range categories corresponded to an approximate maximum (diagonal) distribution of (i) North Atlantic (0–10 000 km), (ii) half global (10 001–30 000 km) and (iii) global (> 30 000 km). It must be remembered that categories (i)–(iii) above represent 'one unit' of geographic range for the logistic regression; it was assumed that logistic regression would pick out globally important trends and also be less susceptible to minor errors in range estimation. By contrast, the Kruskal–Wallis analyses investigate differences in location over a scale of 1000 km.

As multiple tests were undertaken the results were corrected using a sequential Bonferroni method (Rice 1989). A type I error of $\alpha = 0.05$ was maintained for each single-trait test. For the Kruskal–Wallis analyses of partial tables, a table-wide correction was considered too conservative. Therefore each species trait was interpreted as significant after correction (at $\alpha = 0.05$) for the multiple tests within that trait, i.e. the actual traits themselves were considered to be the important units of analysis (see Rice 1989).

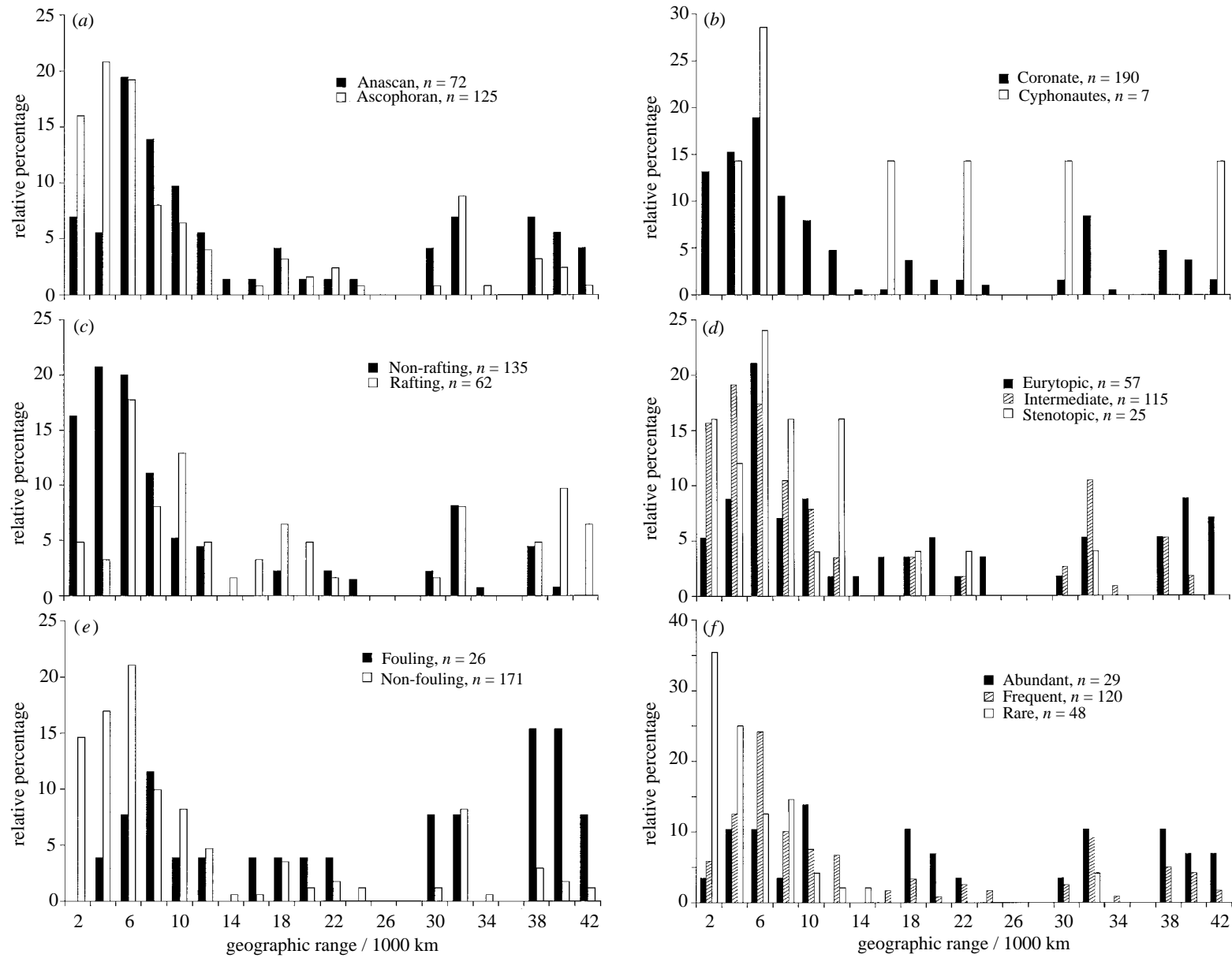


Figure 1. Relative percentage distributions of six species traits as a function of geographic range for British cheilostome bryozoan species. (a) Morphological grade; (b) larval mode; (c) ability to raft; (d) environmental tolerance; (e) ability to foul; (f) species abundance.

3. RESULTS

A total of 197 British cheilostome species are known in sufficient detail to obtain reliable geographic ranges (Ryland & Hayward 1977; Hayward & Ryland 1979; Hayward & Thorpe 1995); of these, 72 are anascans and 125 are ascophorans. Only six of these species (all anascans) are known to have cyphonautes larvae, and one species (*Pyripora catenularia*, also anascan) is inferred to have a cyphonautes larva (Ryland & Hayward 1977, p. 72). Fifty-seven species are intertidal and 140 subtidal (25 subtidal species are known only from depths greater than 50 m). Sixty-two species are epiphytes of macroalgae and 26 species are known to be fouling organisms. Twenty-nine species were classed as common, 120 species as frequent and the remaining 48 species as occasional. More detailed data concerning the distribution of the partial tables and specific ranges are too numerous to include in this paper, but are available from the first author on request.

A qualitative inspection of relative frequency distributions and median geographic ranges suggests that all traits have an effect upon geographic range (figure 1a–f; table 2). This is quantified by the Kruskal–Wallis tests where, before and after correction for multiple testing, all traits except larval mode significantly affect the geographic range occupied by a species (table 3). The same results are obtained through logistic regression, although morphological grade is non-significant after correction for multiple testing (table 3). The importance of fouling is particularly noticeable; fouling species are almost eight times more likely to be distributed in the next greater geographic range category than non-fouling species. Anascans and more environmentally tolerant species are approximately twice as likely to have an increased range. The odds of increased geographic range are just greater than three for species able to raft compared to non-rafters, and more abundant species are over four times more likely to be present in the next greater geographic range category (table 3).

When controlling for covarying traits, however, only the effects of fouling, abundance and rafting commonly show (after correction) a significant effect upon geographic range (70%, 45% and 42% of tests showing significant associations, respectively); morphological grade shows two (11%) significant results. Neither larval mode nor environmental tolerance demonstrate any significant effect on geographic range after corrections (table 4); the non-significance of larval mode is particularly notable.

The results from the Kruskal–Wallis tests are generally corroborated by the stepwise logistic regression, although the relative statistical importance of some traits in determining ranges varies. The effects of rafting, environmental tolerance, larval mode and morphological grade never contributed significantly to the regression model (table 5) and, therefore, all were excluded as explanatory covariables for determining geographic range (table 6). The proportional odds assumption was never violated throughout the modelling procedure ($P > 0.14$, for all steps) and the final model agreed well with the modelling assumptions ($P > 0.7$) (table 5).

The final model, which included only fouling and abundance as explanatory covariables, provided a highly significant ($P < 0.0001$) model fit with a very small, non-

Table 2. Number of species and diagonal geographic range median, maximum and minimum (to the nearest 1000 km) of 197 cheilostome bryozoan species occurring in the British fauna

(Ranges are given separately for each of the six species traits investigated.)

life history trait	sample size	diagonal geographic range/ 1000 km		
		median	maximum	minimum
morphological grade				
anascan	72	9	41	1
ascophoran	125	5	41	1
larval mode				
cyphonautes	7	14	41	1
coronate	190	6	41	4
environmental tolerance				
eurypotic	57	9	41	1
intermediate	115	6	39	1
stenotopic	25	5	30	1
ability to raft				
yes	62	11	41	1
no	135	5	39	1
ability to foul				
yes	26	30	41	4
no	171	6	41	1
species abundance				
common	29	18	41	2
frequent	120	7	41	1
occasional	48	4	30	1

significant residual χ^2 (table 6). The effect of fouling in increasing range is greater than that of species abundance. Fouling species are over five times more likely to have a greater geographic range than non-fouling species, and more abundant species are just less than four times more likely to have increased ranges than rarer species (table 6). Abundant, fouling species are obviously very likely ($P > 0.9$) to have cosmopolitan geographic ranges (figure 2). The change in the values of the regression slopes from those obtained by univariate analyses (tables 3 and 6) is due to the interaction between covariables. Because of the lack of effect of larval mode, environmental tolerance, morphological grade and rafting after controlling for fouling and species abundance, a subsequent investigation into the association between these traits was undertaken. Using the NPARIWAY procedure of SAS Institute Inc. (1989), Fisher's exact tests (Sokal & Rohlf 1995) were employed to test the null hypothesis that morphological grade, larval mode, environmental tolerance and rafting are independent of fouling and species abundance. The Fisher's exact tests show mostly significant associations (table 7). The only exceptions are morphological grade and larval mode, both of which demonstrate no significant association with species abundance (table 7).

4. DISCUSSION

Larvae have been traditionally assigned the role of principal dispersal agents for sessile, benthic marine

Table 3. *The ability of various life history traits to explain geographic range in cheilostome bryozoan species occurring in the British fauna*

(Probabilities of the null hypothesis for Kruskal–Wallis test and logistic regression are given before correction; tests significant after a sequential Bonferroni correction ($\alpha=0.05$ for each test) are displayed in bold type. (χ^2 , Kruskal–Wallis statistic; P_k , probability that the groups do not differ in location; β , logistic regression slope; s.e., standard error of β ; ψ , odds ratio; G , estimate of model fit; P_1 , probability that the logistic regression slope is equal to zero).)

life history trait	statistical test						
	Kruskal–Wallis		logistic regression				
	χ^2	P_k	β	s.e.	ψ	G	P_1
morphological grade	11.364	0.0007	0.6661	0.3060	1.9466	4.657	0.0309
larval mode	1.010	0.3184	0.8026	0.7921	2.2313	1.293	0.2554
environmental tolerance	11.885	0.0026	0.8896	0.2602	2.4342	12.784	0.0003
ability to raft	21.285	0.0001	1.1533	0.3150	3.1686	13.455	0.0002
ability to foul	22.492	0.0001	2.0454	0.4151	7.7323	24.695	0.0001
species abundance	30.930	0.0001	1.4457	0.2873	4.2448	29.493	0.0001

Table 4. *The ability of various life history traits to affect the geographic ranges occupied by cheilostome bryozoan species occurring in the British fauna while maintaining the other life history traits at a constant value*

(Probabilities for Kruskal–Wallis tests are given before correction; tests which are significant after a sequential Bonferroni correction ($\alpha=0.05$ for each potential dispersal trait) are displayed in bold type. (NA, only one category exists for this comparison, and, therefore, a test is not possible).)

traits maintained constant	potential dispersal trait					
	morphological grade	larval mode	environmental tolerance	ability to raft	ability to foul	species abundance
morphological grade						
anaskan	—	0.8638	0.1623	0.0011	0.0023	0.0494
ascorphan	—	NA	0.0848	0.0017	0.0099	0.0001
larval mode						
cyphonautes	NA	—	0.6139	0.0323	0.6959	0.0507
coronate	0.0013	—	0.0048	0.0001	0.0001	0.0001
environmental tolerance						
eurytopic	0.1989	0.7844	—	0.0188	0.0112	0.8866
intermediate	0.0270	0.9518	—	0.0231	0.0059	0.0001
stenotopic	0.3327	NA	—	0.1898	NA	0.2094
ability to raft						
yes	0.0472	0.1109	0.3344	—	0.0008	0.0608
no	0.0244	0.6103	0.6396	—	0.1601	0.0001
ability to foul						
yes	0.7754	0.2398	0.7060	0.0991	—	0.2584
no	0.0409	0.3637	0.1335	0.0054	—	0.0001
species abundance						
common	0.2685	0.1311	0.5402	0.5196	0.0377	—
frequent	0.0290	0.5937	0.1488	0.0020	0.0018	—
occasional	0.0037	NA	0.2350	0.3914	NA	—

invertebrates (e.g. Crisp 1978; Cameron 1986). Although this view was challenged a considerable time ago for ascidians (Kott 1974) and clonal invertebrates in general (Jackson 1986), few detailed empirical studies have since been undertaken. No analyses have compared the relative importance of more than one trait within a single taxon (although other mechanisms are frequently invoked as potential confounding variates). This study has demonstrated the potential of single-trait analyses to bias results,

and has also identified mechanisms important over both 'finer-scale' ranges and 'global' geographic ranges.

Including morphological grade in the analyses has allowed a crude investigation into taxonomic effects on general life history traits. That this effect proved to be weak suggests that either the taxonomic grades are heterogeneous with respect to life history traits, or such traits are relatively unimportant for dispersal. A possibly important consequence of the anascans being morphologically

Table 5. Summary of the steps taken to fit a stepwise logistic regression model; species traits were regressed against geographic range

(See table 6 for final model fit. d.f., degrees of freedom for model; S , score test for proportional odds assumption; P_s , probability that proportional odds assumption is violated; G_m , G -statistic model; P_m , probability of that regression slope is equal to zero; G_r , contribution of the removed variate to the G -statistic for the model containing that variate. Morphological grade was re-entered and subsequently removed. Model building terminated.)

procedure step	statistical estimates of model fit					
	d.f.	S	P_s	G_m	P_m	G_r
all variates entered	6	9.3444	0.1551	49.741	0.0001	—
ability to raft removed	5	7.2163	0.2050	49.602	0.0001	0.139
environmental tolerance removed	4	6.7694	0.1486	48.866	0.0001	0.736
larval mode removed	3	3.3992	0.3081	47.674	0.0001	1.192
morphological grade removed	2	0.6599	0.7189	46.566	0.0001	1.108

Table 6. The final model fitted after a stepwise logistic regression of six species-traits against geographic range

(β , intercept or slope parameter; SE, standard error of β ; ψ , odds ratio; G , G -statistic for model; P , probability of that regression slope is equal to zero. Residual χ^2 3.1889; 4 d.f.; $P=0.5267$.)

variate	model parameters				
	β	s.e.	ψ	G	P
intercept 1	-5.1206	0.9583	—	—	—
intercept 2	-3.7264	0.9158	—	—	—
ability to foul species	1.7423	0.4215	5.7105	—	—
abundance	1.3179	0.2981	3.7356	46.566	0.0001

simpler than the ascophorans is a potential bias in correctly identifying separate species: taxonomic under-splitting could artificially increase species' apparent ranges in anascans. However, if this is reflected in the results at all the effect is only weak, perhaps because misidentification in both taxa is equally prejudiced. Recent, detailed studies using scanning electron microscopy have found previously unrecognized species within some genera of ascophorans (Hayward & Thorpe 1995). In other groups (e.g. sponges) many morphologically simple species apparently possess cosmopolitan ranges (Solé-Cava *et al.* 1991; Knowlton 1993). The possible existence of cryptic morphological species cannot be ignored, yet by definition it is almost impossible to determine their prevalence. This factor was minimized by choosing cheilostome bryozoans, as many species show a high degree of zooidal

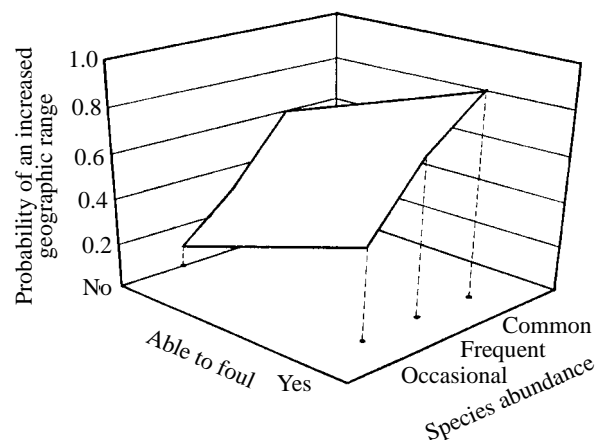


Figure 2. The effect of species abundance and the ability to foul on the probability of increased geographic range for cheilostome bryozoan species.

Table 7. Association between fouling and abundance and the four species traits non-significant in the stepwise logistic regression

(Probabilities are given for Fisher's exact test; those results which are significant after a sequential Bonferroni correction ($\alpha=0.05$) are presented in bold type.)

life history trait	associated trait	Fisher's exact probability
ability to foul	morphological grade	9.33×10^{-8}
	larval mode	4.86×10^{-4}
	environmental tolerance	1.29×10^{-6}
	ability to raft	3.80×10^{-7}
species abundance	species abundance	8.72×10^{-4}
	morphological grade	3.90×10^{-2}
	larval mode	2.19×10^{-1}
	environmental tolerance	2.53×10^{-5}
	ability to raft	2.37×10^{-6}

polymorphism, thereby providing a good range of morphological characters for species descriptions. Preliminary breeding and genetic data for eight Panamanian cheilostome species (Jackson & Cheetham 1990) suggest that morphospecies are 'good' biological species. Any study of geographic range in ctenostome bryozoans, by contrast, would be suspect because of the lack of phenotypic characters and the prevalence of morphologically cryptic species in this group (Thorpe *et al.* 1978a,b; Thorpe & Ryland 1979).

Ecological (Keough & Chernoff 1987; Keough 1989) and population genetical (Schopf 1973, 1974a,b, 1977) evidence supports the predicted poor dispersal ability of the brooded coronate larvae of cheilostomes. However, even the 2–8 week lifespan of a cyphonautes larva (actaeplanic *sensu* Scheltema 1971) will provide only a limited dispersal of a few hundred kilometres at most; cyphonautes larvae, unlike the teleplanic larvae of many molluscan species (Scheltema 1978, 1986, 1989), are unlikely to cross oceanic basins directly. The lack of effect demonstrated in this study between larval mode and

geographic range may, therefore, be expected; similar results have been obtained in previous analyses of bryozoan ranges (Jackson 1986; McKinney & Jackson 1989). Other clonal, sessile taxa (ascidians, scleractinian corals and hydroids) also demonstrate no significant association between larval mode and geographic range (Jackson 1986). However, as only a very few bryozoan species (about 5–10% of cheilostomes; Taylor 1988; see table 2) possess cyphonautes larvae, statistical power in detecting any effect of larval mode is low. The increased contribution to the logistic regression (compared to the Kruskal–Wallis tests) of larval mode may be an artefact of small sample size or may reflect the low association between larval mode and fouling and abundance (table 7).

Rafting has frequently been suggested to be an important dispersal mechanism for many taxa (Highsmith 1985; Jackson 1986; Johannesson 1988; Ó Foighil 1989; Worcester 1994; Ingólfsson 1995), including bryozoans (Jackson 1986; Keough & Chernoff 1987; Taylor 1988; McKinney & Jackson 1989). Early Tertiary cheilostome migrants crossing the Atlantic were more common in probable rafting genera than genera unlikely to raft (Cheetham 1960). Certainly epiphytic species have generally larger ranges (tables 2 and 4), but the ability to raft does not afford cosmopolitan geographic ranges (table 5). Although the time (and hence distance) over which macroalgae can remain unattached and healthy is largely unknown, transport between ocean basins is unlikely. Such consideration does not apply for species able to raft on waste plastic, driftwood or pumice. The latter substrate enables some coral species to maintain extremely large ranges (Jokiel 1989). Many bryozoans live only in algal holdfasts and never on the blades or stipes. As the holdfast is the part least likely to be torn off, the effect of rafting may have been compromised in this analysis by including species that are not particularly likely to raft. Identification of definite rafting species is clearly needed to quantify more exactly the importance of rafting.

To account for the low rate of speciation within malacostegans and the huge increase in the number of bryozoan species after the evolution of brooding, Taylor (1988) produced a conceptual model whereby infrequent rafting afforded both increased range and increased probability of speciation for species with coronate larvae. In contrast, the low rate of speciation within malacostegans was inferred to result from the increased gene-flow afforded by their cyphonautes larvae. The current study certainly lends credence to previous hypotheses suggesting that the ability to raft increases geographic range. As such, bryozoan evolution appears to be quite different from that of many molluscan species where larval mode is central not only to speciation rates, but also to geographic range and species longevities (Hansen 1978, 1980; Scheltema 1978; Jablonski 1986).

Eurytopy has been suggested to allow increased ranges in bivalves (Jackson 1974) and neogastropods (Hansen 1978, 1980), with other dispersal mechanisms (e.g. larval type) also interacting to determine geographic extent. That 'eurytopy' has no significant effect upon range (after controlling for other traits) in cheilostomes may reflect the naivety of the assumption that minimum depth is a valid measure of environmental tolerance for bryozoans. Many species of this phylum can be found on a much wider variety of substrata than species belonging to most other

groups of marine invertebrates (McKinney & Jackson 1989). Most bryozoan species may be regarded as generally eurytopic; this would account for their often wide geographic ranges (Jackson *et al.* 1985). The univariate significance of 'environmental tolerance' (table 2) probably reflects the greater incidence of fouling, rafting and greater abundance of species in shallower habitats. It is unclear how a truly representative estimate of eurytopy can be easily obtained for so many species.

Oceanographic phenomena (e.g. fronts, prevailing currents) may impede dispersal. The Aleutian–Commander Arc apparently poses an oceanographic barrier to dispersal in molluscs (Vermeij *et al.* 1990) and in the bull kelp, *Nereocystis luetkeana* (Miller & Estes 1989). Several barriers to dispersal exist in the tropical Pacific (Vermeij 1987). Fouling the hulls of ships, however, will enable natural oceanographic barriers to be crossed and provide a method of reaching a suitable (shallow water) environment, although dispersal will be very dependent on shipping routes and traffic frequency. Many bryozoan species are regarded as poor spatial competitors in benthic environments and have apparently evolved adaptations for an opportunistic, 'weedy' existence (McKinney & Jackson 1989). A striking consequence of the evolution of such a lifestyle and the general associated eurytopy is that it may have 'pre-adapted' bryozoans into being well suited to fouling. The effect of fouling, made evident by occurrences of introduced species in and around ports, has been previously recognized as giving potential for increasing the geographic range of bryozoans (Ryland 1967; Banta 1969) and many other taxa (Carlton & Scanlon 1985; Carlton 1987; Carlton & Hodder 1995), but actual ranges have not been quantified. The importance of fouling in increasing the geographic ranges of cheilostome bryozoan species is evident from the analyses here (tables 3 and 5). Therefore, the consequences of fouling must be considered in any biogeographic work before natural mechanisms are invoked to explain present-day patterns in geographic distribution. Presumably an analysis of fossil species ranges will be able to determine the importance of natural dispersal mechanisms.

The likely evolutionary consequences of species-level dispersal traits (for larvae, but are also applicable to any method of frequent dispersal) conferring large geographic ranges have been well documented; buffering against local environmental disturbances afforded to species with greater dispersal capabilities (and larger geographic ranges) results in such species having longer geological durations than species with restricted dispersal (Scheltema 1978; Hansen 1978, 1980; Jablonski 1986; reviewed by Jablonski & Lutz 1983). Because of the very short (geological) time that fouling has been (and will remain?) a dispersal mechanism, predictions about the geological lifespans of fouling species can only be very tentative: will fouling species be able to maintain large geographic ranges in the future?

Although the ecological importance of introducing invasive alien species is less well documented in marine than in terrestrial ecosystems, it is generally thought that diversity may be reduced through the extinction of native taxa (see review by McNeely *et al.* 1995). Phenotypic diversity will certainly be enhanced in fouling taxa because a wider variety of environments will be experienced. Geographic range may also control the rate and manner

of speciation (Shuto 1974; Scheltema 1978; Jablonski 1986; Vermeij 1987). A corollary of a differential ability to maintain gene-flow between allopatric populations is that species with greater dispersal capabilities speciate slowly in a few peripheral allopatric populations, and philopatric species are assumed to speciate more rapidly throughout their entire range by a variety of speciation methods. Allopatric populations may be founded from one or a few individuals, allowing divergence by selection or drift in peripheral isolates (peripatric speciation; Mayr 1954, 1982*a*). The models of Carson (founder-flush speciation; 1975) and Templeton (genetic transience; 1980) are both based around a period of rapid population expansion after a founder event and have been generalized by Slatkin (1996); if newly founded populations undergo rapid population expansion (e.g. due to relaxed competition/predation in the new habitat) then effects of drift may be relaxed and the probability of advantageous alleles being fixed is greater than for populations of constant size. Speciation by the traditional (or 'dumbbell') allopatric method (Mayr 1963; White 1978) requires a larger founding population (presumably by greater dispersal) and then establishment of a reproductive barrier to allow population divergence. For example, after an initially high dispersal and colonization rate via fouling (e.g. during historic times, Carlton 1987; Carlton & Hodder 1995), a subsequent barrier to gene-flow may result from the closure of shipping lanes or from the increased difficulty in fouling modern shipping. For species with seasonal reproduction, isolating barriers may result from a change in breeding season (allochronic speciation; White 1978; Mayr 1982*b*) if latitudinal ranges are greatly extended. An inadvertent consequence of fouling, therefore, may be to increase speciation rate and decouple speciation events from natural phenomena (e.g. transgressive–regressive cycles; Hansen 1978, 1980). Anthropogenic effects are important and should not be omitted from models predicting the future fates of species. As a moderate level of gene-flow between allopatric populations will presumably retard divergence (in the absence of strong selection) and estimates of gene-flow between populations of fouling (and rafting) species are unknown, such hypotheses are speculative at present.

Successful population establishment is more probable for clonal or hermaphroditic taxa (or gravid females of asexual species) with non-planktotrophic larvae, which are able to found populations from a single animal or very few individuals (Jackson 1986; Ó Foighil 1989). Consequently, these taxa may be subject to increased rates of divergence. It is also worthwhile noting that one ecological aspect aiding the establishment of invading species is low competition among resident species (Crawley 1986), an effect linked to trophic resources with filter-feeders (herbivores) being more likely to be successful invaders than detritivores or carnivores. All bryozoan species filter-feed and are hermaphrodites (Ryland & Bishop 1993). Although outcrossing appears to be routine (Schopf 1973; Ryland & Bishop 1993), tolerance of inbreeding (Jackson *et al.* 1993), the ability to self-fertilize (Maturio 1991; Hunter & Hughes 1993), and the ability to store sperm and undergo precocious insemination (Ryland & Bishop 1993) have been demonstrated in several species. Bryozoans are, therefore, unusually well

adapted to found new populations. Indeed, the life histories of many clonal taxa appear to be particularly amenable to successful invasion and founder-flush speciation. Further investigation into gene-flow, population divergence and the species ranges of other major groups of fouling organisms is needed to assess the importance of fouling in increasing species ranges and the probability of increased rates of speciation.

In addition to dispersal mechanisms previously discussed, bryozoans are also found living on plastics (Winston 1982; Harms 1990; Stevens *et al.* 1996) and motile hosts (sea snakes, Zann *et al.* 1975; Key *et al.* 1996; *Nautilus*, Landmann *et al.* 1987; turtles, Frazier *et al.* 1992; horse-shoe crabs, Key *et al.* 1996; *Janthina*, Taylor & Monks 1997), and a pelagic species has been recorded from the Antarctic (Peck *et al.* 1995); any attempt to explain dispersal through a single trait would be inappropriate. However, fouling can be interpreted as a dominant dispersal mechanism at present; at least, the effect of fouling is now so strong that the importance of other methods of dispersal is masked. Other, non-anthropogenic methods of dispersal must have been more important in the past (e.g. Cheetham 1960) and are undoubtedly still operating over a variety of spatial and temporal scales and frequencies. Estimates of the relative importance of various dispersal methods over different scales have been proposed (Jackson 1986; Johannesson 1988), but these authors excluded anthropogenic effects. Scale of dispersal for fouling depends on frequency of shipping traffic and the environmental tolerance of the fouling organism; for example, in many countries small boats are not permitted to use tributyltin antifouling paints, and larger shipping undertakes more effective fouling measures, traverses greater distances and presumably a wider variety of conditions. It is evident that fouling could provide a very rapid, reliable dispersal mechanism and is likely to be effective over scales from kilometres to globally. Although, such dispersal will mainly be restricted to ports (and suitable habitats encountered on shipping routes), other methods of dispersal may subsequently increase species ranges beyond these points of entry, given suitable conditions (note, however, that some fouling species (e.g. *Bugula neritina*, Ryland & Hayward 1977, p. 162) are in parts of their range outside their native habitat limited in distribution to ports and harbours).

This study, like others of its kind, is subject to biases present in the collection of the data and relies heavily on correct taxonomy and species descriptions from biological surveys. One such bias may be demonstrated by the strong effect of species abundance (tables 4 and 6), although determining whether rare species possess restricted ranges through inadequate surveying or by some real biological phenomenon is beyond the scope of this study (but see Gaston (1990) for a discussion of the causes and effects of rarity). Most authors have recognized the problem of species abundance in influencing apparent geographic ranges and have tried to minimize or control this bias (Vermeij 1987; Russell & Lindberg 1988; Scheltema 1989). Vermeij (1987) did not find rarity to be a strong determinant of range, but this result probably reflects the knowledge of molluscan distributions, which is probably better because of their large size and attractiveness to collectors. Furthermore, it must be recognized that as

ports and harbours are easily accessible to scientists they often have well described communities which may possibly bias the effect of fouling. Error in overestimating the importance of fouling in the current study was minimized by using different literature sources to estimate ranges and whether species were fouling or non-fouling.

It is evident from the univariate analyses that, with the exception of larval mode, any single species-trait could have been chosen and argued to be the most important control over dispersal in Bryozoa (or clonal animals in general). This result is apparently due to a very high association between these traits and the ability to foul, and species abundance (table 7). To understand the relative importance of various dispersal mechanisms, a hierarchical approach is needed. As an alternative to global surveys, Vermeij (1987; Vermeij *et al.* 1990) investigated the ability of species to cross specific oceanographic barriers. This approach may be used over various scales and is less susceptible to errors in estimating absolute species ranges whereas literature surveys may be particularly sensitive to outliers from inadequate taxonomy. Bhaud (1982, p. 465) has emphasized that 'numerous secondary dispersal mechanisms finally disrupt all correlation between the characteristics of the life cycle and the specific distributional area'. Thus it is imperative that studies thoroughly consider the biology of the taxa involved and control for all potentially confounding effects. A univariate analysis investigating a single trait is clearly too simplistic unless no alternative methods of dispersal are available to that taxon.

This work benefited greatly from comments made by Professor D. Jablonski on an early draft of this manuscript. Dr D. P. Gordon, Mr K. J. Tilbrook and Dr M. P. Johnson also provided valuable discussion and two anonymous reviewers further improved this work. This study was carried out while P.C.W. was supported by a Natural Environment Research Council studentship.

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