J. Mar. Biol. Ass. U.K. (2000), **80**, 719–724
Printed in the United Kingdom

An analysis of the nematocysts of the beadlet anemone *Actinia equina* and the green sea anemone *Actinia prasina*

Phillip C. Watts*, A. Louise Allcock†, Sean M. Lynch and John P. Thorpe

Port Erin Marine Laboratory, School of Biological Sciences, University of Liverpool, Port Erin, Isle of Man, IM9 6JA.
*Present address: Laboratory 1.03, Donnan Laboratories, School of Biological Sciences, University of Liverpool, Crown Street, Liverpool, L69 7ZD. E-mail: p.c. watts@liv.ac.uk
†Present address: National Museums of Scotland, Chambers Street, Edinburgh, EH1 1JF

Numerous studies of their population genetics have reported incipient reproductive isolation among sympatric populations of the common intertidal beadlet anemone *Actinia equina*. This has lead to certain morphs being raised to specific status. A study of the nematocysts of the green sea anemone *Actinia prasina* and three genetically isolated morphs of *A. equina* was undertaken to establish that mean nematocyst length could act as diagnostic phenotypic characters within a morphologically variable group. The results support genetic and ecological evidence for the specific status of the three red/brown coloured morphs of *A. equina*. The data are discussed with respect to the ecology of *Actinia* and concepts of species, but more work is required before the specific status of *A. prasina* can be confirmed.

INTRODUCTION

The intertidal beadlet anemone *Actinia equina* (L.) is common on rocky intertidal and shallow subtidal habitats throughout the British Isles. Its known geographic distribution ranges from the Kola Peninsula, along the west coast of Europe, throughout the Mediterranean and Black seas, to the west African coast (Stephensen, 1935; Manuel, 1988; Shick, 1991). The colour of *A. equina* is highly variable and numerous different colour varieties or 'morphs' have been described (Tugwell, 1856; Gosse, 1860; Stephensen, 1935), which has raised considerable debate as to whether certain morphs constitute different species. Some of the colour morphs were assigned specific status by several early workers (e.g. Dalyell, 1848; Tugwell, 1856), but Gosse (1860) considered all the forms as varieties of a single species.

Carter & Thorpe (1981) used isozyme electrophoresis and reproductive evidence to separate Stephensen's (1935) *Actinia equina mesembryanthemum* and *A. equina fragacea* into the different species *Actinia equina* (L.) and *Actinia fragacea* (Tugwell) respectively. Due to the apparent lack of diagnostic phenotypic characters, subsequent taxonomic work on *A. equina* has generally been based upon genetic analysis. Electrophoretic data and ecological differentiation have led to a morph of *A. equina* being given specific status as *Actinia prasina* (Gosse) (Haylor et al., 1984). *Actinia prasina* has a green column with a green pedal disc bordered by a blue line around the limbus and occupies a low shore distribution (Haylor et al., 1984; Solé-Cava & Thorpe, 1987, 1992).

Other research, however, focused upon pedal disc colour (e.g. Quicke et al., 1983; Quicke & Brace, 1984), which varies more discontinuously than column colour. Within *A. equina*, three genetically distinct morphs with different intertidal distributions were identified (Quicke et al., 1983; Quicke & Brace, 1984) which are referred to as the Up (upper-shore), Mid (mid-shore) and Low (lower-shore) morphs. All three morphs have red or brown columns, but the Low morph can be readily identified because it has a green/grey pedal disc bordered by a blue line. The Up and Mid morphs both have red/pink coloured pedal discs and could only be identified using a diagnostic allozyme locus until it was demonstrated that there are nematocysts differences between them (Watts & Thorpe, 1998). The Low morph has been separated from *A. prasina* (also found mainly on the low shore) on the grounds of column colour alone, but recent genetic evidence (Perrin, 1993; Lynch, 1996) suggests that they may be conspecific.

Cnidae (stinging cells) are characteristic of the Cnidaria and are essential to their mode of life. Within the Actiniaria two categories of cnidae can be readily discerned, the spirocysts and the nematocysts. Although spirocysts are thought to be of limited systematic value (Cutress, 1955; Manuel, 1988), nematocysts may offer useful characters for distinguishing between both higher taxa and difficult taxonomic groups (Fautin, 1988; Manuel, 1988). Several distinct size-classes of the same nematocyst type are often present within a tissue, although the functional significance of this is not known (Mariscal, 1974). A preliminary comparison of nematocyst distribution and abundance between a mixture of red/pink pedal disc morphs and *A. prasina* found no significant differences (Solé-Cava & Thorpe, 1987, 1992). A later study, however, revealed significant differences in nematocyst size between the red/pink and green/grey pedal disc morphs of *A. equina* (Allcock et al., 1998). Subsequently, it was found that the size of the nematocysts from the acrorhagi allows phenotypic identification of the Up and Mid morphs of *A. equina* (Watts & Thorpe, 1998). No nematocyst studies, however, have described the size distribution of nematocysts throughout the different tissues of the Up, Mid and Low morphs or have

Table 1. *Mean nematocyst length (μm) for three genetic morphs of the beadlet anemone* Actinia equina *and the green sea anemone* A. prasina.

	Actinia equina									*Actinia prasina*		
Tissue	Upper-shore morph			Mid-shore morph			Low-shore morph					
Nematocyst Type	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Acrorhagi												
Holotrich	240	41.85	3.37	240	52.49	5.26	240	51.48	4.11	240	50.38	3.72
Pharynx												
Microbasic *b*-mastigophore I	240	13.67	0.61	240	15.54	0.90	240	13.38	0.58	240	12.86	0.51
Microbasic *b*-mastigophore II	240	23.95	1.08	240	25.84	1.21	240	24.46	0.62	240	20.74	0.62
Mesenteric filaments												
Microbasic *b*-mastigophore I	240	13.00	0.83	240	14.65	0.97	240	12.74	0.40	240	12.88	0.72
Microbasic *b*-mastigophore II	68	19.77	1.82	138	19.46	0.59	162	17.56	0.62	193	17.80	0.46
Microbasic *b*-mastigophore III	—	—	—	85	32.86	1.34	87	32.75	2.17	131	32.22	1.31
Microbasic *p*-mastigophore	240	19.36	1.31	240	23.55	2.08	240	21.26	0.69	240	21.25	0.83
Tentacles												
Microbasic *b*-mastigophore I	116	12.37	0.64	152	14.57	0.97	219	13.41	0.45	213	12.86	0.44
Microbasic *b*-mastigophore II	240	20.13	0.65	240	22.59	0.96	240	19.97	0.75	240	20.74	1.06
Column												
Microbasic *b*-mastigophore	240	14.67	0.51	240	17.08	1.22	240	14.17	1.24	240	14.99	0.76
Pedal disc												
Microbasic *b*-mastigophore	240	14.12	0.35	240	15.80	0.17	240	12.55	0.42	240	13.04	1.05

N, number; SD, standard deviation.

specifically investigated *A. prasina*. Given the extensive taxonomic confusion within '*A. equina*' and the putative usefulness of nematocysts for taxonomy, further research seems warranted. The aims of this study, therefore, are to provide a description of the nematocysts in *A. prasina* and the three morphs of *A. equina* and to relate these data to previous genetic work.

MATERIALS AND METHODS

Actinia prasina and the three morphs of *Actinia equina* were sampled from Fleshwick Bay (OS grid reference SC 202715), a sheltered bay on the west coast of the Isle of Man which contains both the sheltered boulder habitats (typical of *A. prasina* and the Low morph) and more exposed vertical rock faces (preferred by the Up and Mid morphs). To standardize for size, the maximum and minimum diameter of the pedal disc of each anemone was measured using dial callipers. The length of certain nematocysts may vary with body size of the sea anemones (Chintiroglou, 1996) or their weight (Chintiroglou & Simsiridou, 1997). Thus specimens were taken whose average pedal disc diameter was 18–20 mm since this appeared to be the most frequent size-class on the shore, facilitating collection of rarer animals (*A. prasina* and the Up morph). Different morphs were collected as close together as their ecological separation allowed whilst anemones of the same morph were collected from a minimum of 2 m apart to minimize the chance of collecting clonemates. Since the Up and Mid morphs are indistinguishable on the shore 55 red pedal disc animals were collected between mean tide level and mean high water neap to ensure that enough of the Up morph, which is relatively uncommon around the Isle of Man (Perrin, 1993), had been collected. Eight individuals of each of the Low morph and *A. prasina* were collected. Horizontal starch gel electrophoresis was employed to identify the Up and Mid morphs (for details of methods see Solé-Cava & Thorpe, 1987 or Lynch, 1996). Gels were stained for malate dehydrogenase since this enzyme is diagnostic for these morphs (Quicke & Brace 1984; Lynch, 1996). Eleven Up morph anemones were obtained out of the mixed (Up and Mid morph) sample.

Because feeding and aggressive behaviour may reduce nematocyst numbers all anemones were kept in individual pots, with the seawater replaced every 23 d, for at least a week before tissue samples were collected. Simple tissue squashes were made from small ($<1\,mm^3$) pieces of tissue and stained using 0.1% methylene blue solution (see Manuel, 1988). Nematocysts were viewed using a Zeiss phase-contrast binocular microscope at ×1000 and measured using an eyepiece graticule calibrated against a stage graticule. As nematocyst length may vary with tissue location (Cutress, 1955) all major types of nematocysts were measured in tissue from specific areas. Only undischarged nematocysts were measured since large changes in volume may occur after discharge (Godknecht & Tardent, 1988).

Six different tissue regions were studied: acrorhagi, tips of tentacles, central pharynx, mesenteric filaments, mid-column and the centre of the pedal disc. Nematocyst types were identified following Cutress (1955). Within randomly selected fields of view 15 nematocysts of each type were measured. Two replicate samples were measured from each tissue for eight anemones of each morph. Where two or more discrete nematocysts sizes were present within a tissue they were counted separately and suffixed I, II, etc., according to size. Rarer types of nematocysts (i.e. where 15

https://doi.org/10.1017/S002531540000254X Published online by Cambridge University Press

Table 2. *Hierarchical analysis of variance of nematocyst length for three genetic morphs of* Actinia equina *and* Actinia prasina.

Tissue	Source of variation					
	Within tissue		Within morphs		Between morphs	
Nematocyst Type	*F*	*P*	*F*	*P*	*F*	*P*
Acrorhagi						
Holotrich	0.55	ns	69.16	<0.001*	754.23	≪0.001*
Pharynx						
Microbasic *b*-mastigophore I	1.07	ns	7.31	<0.001*	144.30	≪0.001*
Microbasic *b*-mastigophore II	1.53	<0.05	11.11	<0.001*	63.86	≪0.001*
Mesenteric filaments						
Microbasic *b*-mastigophore I	1.36	ns	9.00	<0.001*	99.61	≪0.001*
Microbasic *b*-mastigophore II	—	—	3.94	<0.001*	42.71	≪0.001*
Microbasic *b*-mastigophore III	—	—	—	—	0.13	ns
Microbasic *p*-mastigophore	1.00	ns	29.44	<0.001*	383.91	≪0.001*
Tentacles						
Microbasic *b*-mastigophore I	—	—	3.91	<0.001*	55.87	≪0.001*
Microbasic *b*-mastigophore II	0.93	ns	8.67	<0.001*	132.74	≪0.001*
Column						
Microbasic *b*-mastigophore	0.98	ns	19.75	<0.001*	267.80	≪0.001*
Pedal disc						
Microbasic *b*-mastigophore	0.53	ns	11.93	<0.001*	285.90	≪0.001*

F, *F*-value; *P*, probability; ns, not significant; *, indicates a significant ($P<0.05$) result after a sequential Bonferroni correction for multiple testing.

Table 3. *Probability values for Tukey pairwise comparisons of mean nematocyst length between the upper- (U), mid- (M), and lower-shore (L) morphs of* Actinia equina *and* Actinia prasina *(P).*

Tissue	Pairwise Comparison					
Nematocyst Type	U–M	U–L	U–P	M–L	M–P	L–P
Acrorhagi						
Holotrich	≪0.001	≪0.001	≪0.001	ns	<0.05	ns
Pharynx						
Microbasic *b*-mastigophore I	≪0.001	ns	ns	≪0.001	≪0.001	ns
Microbasic *b*-mastigophore II	≪0.001	ns	<0.05	≪0.001	≪0.001	ns
Mesenteric filaments						
Microbasic *b*-mastigophore I	≪0.001	ns	ns	≪0.001	≪0.001	ns
Microbasic *b*-mastigophore II	ns	≪0.001	≪0.001	≪0.001	≪0.001	ns
Microbasic *p*-mastigophore	≪0.001	≪0.001	≪0.001	≪0.001	≪0.001	ns
Tentacles						
Microbasic *b*-mastigophore I	≪0.001	<0.01	ns	≪0.001	≪0.001	ns
Microbasic *b*-mastigophore II	≪0.001	ns	ns	≪0.001	≪0.001	<0.01
Column						
Microbasic *b*-mastigophore	≪0.001	≪0.001	ns	≪0.001	≪0.001	≪0.001
Pedal disc						
Microbasic *b*-mastigophore	≪0.001	≪0.001	≪0.001	≪0.001	≪0.001	<0.01

ns, not significant.

could not be encountered readily) were specifically searched for and all encountered were measured.

All data were analysed using MINITAB (1991) statistical software. The size–frequency of each nematocyst population was tested for normality using the NSCORES procedure (Minitab, 1991); no significant ($P>0.01$) departures from normality were detected. Nematocyst length data were analysed using a three level nested (hierarchical) ANOVA (Zar, 1984), with the within-tissue variation nested within the between-anemone variation, and both sources of variability being nested within that occurring among the different morphs. Unbalanced data (i.e. data with unequal sample sizes) were analysed with a general linear model of ANOVA; because these data included the

https://doi.org/10.1017/S002531540000254X Published online by Cambridge University Press

rarer nematocysts the within-tissue and within-morph variance could not always be calculated. A table-wide type-I error rate of $\alpha=0.05$ was maintained using a sequential Bonferroni correction (Rice, 1989). Following a rejection of the null hypothesis a Tukey multiple comparison test (Zar, 1984) was calculated to locate which morphs had different nematocyst parameters.

RESULTS

Three categories of nematocyst were identified: the holotrich, microbasic *b*-mastigophore (=*b*-rhabdoid) and microbasic *p*-mastigophore (=*p*-rhabdoid). A few of the smaller microbasic *b*-mastigophores often showed a gradation towards the structure of a basitrich. Since the armature of the shaft could not be resolved and the majority of the nematocysts possessed a full central shaft when undischarged they were all considered to be microbasic *b*-mastigophores; Manual (1988) regards basitrichs and microbasic *b*-mastigophores to be synonymous.

The qualitative distribution of nematocyst types throughout the tissues revealed no differences between the green *Actinia prasina* and the morphs of *Actinia equina* except that the microbasic *b*-mastigophore III population is absent from the mesenteric filaments of the Up morph (Table 1). No significant ($P>0.05$) variation in nematocyst size was found within tissues after correction for multiple testing (Table 2). All nematocyst populations tested showed significant differences in size between anemones of the same morph after a Bonferroni correction ($P<0.05$), although the within-morph variation for the microbasic *b*-mastigophore III nematocysts was not tested because of small sample size (Table 2). Similarly, all nematocyst populations, except the microbasic *b*-mastigophore III from the mesenteric filaments, demonstrated highly significant variation in size ($P<0.001$) among morphs (Table 2) with all comparisons remaining significant ($P<0.05$) after correction for multiple testing.

The Mid morph has larger nematocysts than the Up and Low morphs and *Actinia prasina* for all but one nematocyst population (Table 1); these differences are significant for almost all of the pairwise comparisons (Table 3). *Actinia prasina* and the Low morph showed consistent similarities in nematocyst lengths except for three nematocyst populations (Tables 1 & 2). The Up morph differed from *A. prasina* and the Low morph in approximately half of the nematocyst populations (Table 3), but revealed no pattern to the size differentiation.

DISCUSSION

The distribution of nematocyst types given here include those presented for *Actinia equina* by Solé-Cava & Thorpe (1987, 1992), except that in this study microbasic *b*-mastigophores were not considered to be present in the acrorhagi (Table 1). The presence of microbasic *b*-mastigophores was noted to increase in smaller acrorhagi where it was difficult to make a clean dissection, and since the microbasic *b*-mastigophores found in this study were of the same size as those from the neighbouring column tissue they were considered to be contaminants. The exact part dissected from the mesenteric filaments cannot be given due to their convoluted nature, although it is probable that the distal parts were examined. Indeed, the difficulty in exact dissection as well as their low abundance may explain why the microbasic *b*-mastigophore III nematocyst population was not found by Allcock et al. (1998). The lack of within-tissue variation in nematocyst length, however, suggests that a tissue sample from one area should be representative and supports previous data (see Allcock et al., 1998).

Differences in nematocyst type and distribution are only to be expected in distantly related taxa or among individuals at different stages of maturity (Cutress, 1955). The absence of the microbasic *b*-mastigophore III population from the mesenteric filaments of the Up morph (Table 1) implies that it may be the most distantly related taxon, but it is more probable that this nematocyst population was overlooked since it was relatively rare. This perhaps demonstrates the difficulty in only being able to study fresh tissue as it would obviously be desirable to search further for this nematocyst population.

Previous work has found no significant differences between *Actinia prasina* and a mixture of red/pink pedal disc morphs of *A. equina* (Solé-Cava & Thorpe, 1987, 1992). These analyses, however, may have been confounded by not distinguishing among the Up and Mid morphs and, furthermore, the sizes of the animals used were not standardized. Assuming that interbreeding will effect a similar size distribution of nematocyst lengths, the highly significant differences in nematocyst lengths among morphs provide support for previous genetic work suggesting that there are a number of species within '*Actinia equina*' (see Quicke & Brace, 1983, 1984; Quicke et al., 1985; Solé-Cava & Thorpe, 1987; Perrin, 1993; Lynch, 1996). It may be concluded that the Up, Mid and Low morphs of *A. equina* are all reproductively isolated and should therefore be considered separate species.

From genetic studies, Perrin (1993) suggested that the Low morph was conspecific with *A. prasina*. In addition, these taxa have similarly coloured pedal discs bordered by a blue line, have a low strength of attachment to substrate (Quicke & Brace, 1983; Perrin, 1993), prefer low shore cryptic habitats (Quicke & Brace, 1984; Haylor et al., 1984; Perrin, 1993) and display reduced levels of aggression (Brace & Reynolds, 1989). Furthermore, the analysis of nematocyst lengths between *A. prasina* and the Low morph resulted in the most similarities from the pairwise comparisons of anemone taxa (Table 3). Despite this and, contrary to the genetic data of Perrin (1993), the significant differences present in some type of cnidae between the Low morph and *A. prasina* are indicative of them being distinct species. Although Perrin (1993) did not find any MDH heterozygotes within *A. prasina*, more recent genetic data (S.M. Lynch, unpublished data) have identified some '*A. prasina*' from Fleshwick Bay as being heterozygous at the MDH-1 locus. It is therefore possible that the '*A. prasina*' sample taken for this study also contained green-columned Mid morphs. Atypical genotypes have also been noted in the red/brown column morphs (Quicke & Brace, 1983). This result is important as it demonstrates that neither column nor pedal disc colour can be used reliably to discriminate among the morphs of British '*A. equina*'. Since anemones cannot synthesize pigments, rather they

assimilate them from their diet (Lubbock & Allbut, 1981; Shick, 1991) their colour is likely to be environmentally determined and cannot be used as a diagnostic character. Confirmation of the specific status of *A. prasina*, therefore, cannot be given and should await a full genetic analysis with a concurrent description of the nematocysts. It must be remembered that similarities in nematocyst length do not necessarily imply that the subjects are conspecific (e.g. Schmidt, 1972 found no significant differences in nematocyst lengths between *A. equina* and *A. fragacea*) but rather may simply reflect a recent common origin.

Since *A. equina* morphs have failed to breed under laboratory conditions, a biological species concept (Mayr, 1963) is hard to enforce and is also incompatible with hybrids or asexual species. The recognition species concept (Lambert & Paterson, 1983) may seem more appropriate for actiniid species; differential aggressive behaviour among morphs (Brace & Reynolds, 1989) will have direct consequences for the breeding structure and hence speciation within *A. equina*. Yet since aggressive behaviour will almost certainly be coupled with the nematocysts, as will virtually all aspects of anemone ecology, the importance of nematocysts to coelenterate speciation and taxonomy is clearly paramount. Other species concepts require a measure of phenotypic cohesion, which is clearly more problematic in *Actinia* since cnidarians are characterized by possession of a tissue-grade construction (Shick, 1991). Although recently the usefulness of nematocysts has perhaps been questioned (Fautin, 1988; Williams, 1996; Chintiroglou & Simsiridou, 1997), this study and others (Solé-Cava et. al., 1985; Allcock et al., 1998) have demonstrated that the phenotypic resolution needed for recognizing cnidarian species can be acquired through use of the cnidom.

The authors would like to thank Chris Bridge for histological and microscopical advice and Dr John Bishop for help with statistics. Dr C. Östman and an anonymous referee provided helpful comments on the manuscript.

REFERENCES

Allcock, A.L., Watts, P.C. & Thorpe, J.P., 1998. Divergence of nematocysts in two colour morphs of the intertidal beadlet anemone *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom*, **78**, 821–828.

Brace, R.C. & Reynolds, H.A., 1989. Relative intraspecific aggression and pedal disc colour phenotypes of the beadlet anemone *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom*, **69**, 273–278.

Carter, M.A. & Thorpe, J.P., 1981. Reproductive, genetic and ecological evidence that *Actinia equina* var *mesembryanthemum* and var *fragacea* are not conspecific. *Journal of the Marine Biological Association of the United Kingdom*, **61**, 71–93.

Chintiroglou, C.C., 1996. Biometric study of *Edwardsia claparedii* (Panceri) cnidome (Actiniaria: Anthozoa). *Belgian Journal of Zoology*, **126**, 177–180.

Chintiroglou, C.C. & Simsiridou, M., 1997. Biometric investigations on the cnidae of the sea anemone *Actinia equina mediterranea* form I *sensu* Schmidt, 1972. *Israel Journal of Zoology*, **43**, 5–11.

Cutress, C.E., 1955. An interpretation of the structure and distribution of cnidae in the Anthozoa. *Systematic Zoology*, **4**, 120–137.

Dalyell, J.G., 1848. *Rare and remarkable animals of Scotland represented from living subjects with practical observations on their nature*. London: Van Voorst.

Fautin, D.G., 1988. Importance of nematocysts to Actinian taxonomy. In *The biology of nematocysts* (ed. D.A. Hessinger and H.M. Lenhoff), pp. 487–500. California: Academic Press.

Godknecht, A. & Tardent, P., 1988. Discharge and mode of action of the tentacular nematocysts of *Anemonia sulcata* (Anthozoa: Cnidaria). *Marine Biology*, **100**, 83–92.

Gosse, P.H., 1860. *Actinologia Britannica. A history of the British sea anemones and corals*. London: Van Voorst.

Haylor, G.S., Thorpe, J.P. & Carter, M.A., 1984. Genetic and ecological differentiation between sympatric colour morphs of the common intertidal sea anemone *Actinia equina*. *Marine Ecology Progress Series*, **16**, 281–289.

Lambert, D.M. & Paterson, H.E.H., 1983. On 'bridging the gap between race and species': the isolation species concept and an alternative. *Proceedings of the Linnean Society, New South Wales*, **107**, 501–514.

Lubbock, R. & Allbutt, C., 1981. The sea anemone *Actinia equina* tolerates allogenic juveniles but alters their phenotype. *Nature, London*, **293**, 474–475.

Lynch, S.M., 1996. *Empirical studies of allozyme based ecological genetics of the Genus* Actinia *(Anthozoa: Actiniaria) and other marine invertebrates*. PhD thesis, University of Liverpool.

Manuel, R.L., 1988. *British Anthozoa*. London: Academic Press.

Mariscal, R.N., 1974. Nematocysts. In *Coelenterate biology: reviews and new perspectives* (ed. L. Muscatine and H.M. Lenhoff), pp. 129–178. New York: Academic Press.

Mayr, E., 1963. *Animal species and evolution*. Cambridge, MA: Harvard University Press.

Minitab Inc., 1991. *MINITAB reference manual*, Release 8. Rosemont, PA: Quickset Inc.

Perrin, M.C., 1993. *Aspects of the ecology and genetics of* Actinia *colour morphs*. PhD thesis, University of Liverpool.

Quicke, D.L.J. & Brace, R.C., 1983. Phenotypic and genotypic spacing within an aggregation of the anemone *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom*, **63**, 493–515.

Quicke, D.L.J. & Brace, R.C., 1984. Evidence for the existence of a third ecologically distinct morph of the anemone *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 531–534.

Quicke, D.L.J., Donoghue, A.M. & Brace, R.C., 1983. Biochemical genetic and ecological evidence that red/brown individuals of the anemone *Actinia equina* comprise two morphs in Britain. *Marine Biology*, **77**, 29–37.

Quicke, D.L.J., Donoghue, A.M., Keeling, T.F. & Brace, R.C., 1985. Littoral distributions and evidence for differential post-settlement selection on the morphs of *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 1–20.

Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 531–534.

Schmidt, H., 1972. Prodromus zu einer Monographie der Mediterranen Aktinien. *Zoologica*, **121**, 1–146.

Shick, J.M., 1991. *A functional biology of sea anemones*. London: Chapman & Hall.

Solé-Cava, A.M. & Thorpe, J.P., 1987. Further genetic evidence for the reproductive isolation of the green sea anemone *Actinia prasina* Gosse from the common intertidal beadlet anemone *Actinia equina* [L]. *Marine Ecology Progress Series*, **38**, 225–229.

Solé-Cava, A.M. & Thorpe, J.P., 1992. Genetic divergence between colour morphs in populations of the common intertidal sea anemones *Actinia equina* and *Actinia prasina* (Anthozoa: Actiniaria) in the Isle of Man. *Marine Biology*, **112**, 243–252.

Solé-Cava, A.M., Thorpe, J.P. & Kaye, J.G., 1985. Reproductive isolation with little genetic divergence between *Urticina* (=*Tealia*) *felina* and *U. eques* (Anthozoa: Actiniaria). *Marine Biology*, **85**, 279–284.

Stephensen, T.A., 1935. *The British sea anemones*. London: The Ray Society.

Tugwell, G., 1856. *A manual of sea anemones commonly found on the English coast*. London: Van Voorst.

Watts, P.C. & Thorpe, J.P., 1998. Phenotypic identification of three genetically differentiated morphs of the intertidal beadlet anemone *Actinia equina* (Anthozoa: Cnidaria). *Journal of the Marine Biological Association of the United Kingdom*, **78**, 1365–1368.

Williams, R.B., 1996. Measurements of cnidae from sea anemones (Cnidaria: Actiniaria): statistical parameters and taxonomic relevance. *Scientia Marina*, **60**, 339–351.

Zar, J.H., 1984. *Biostatistical analysis*, 2nd ed. New Jersey: Prentice-Hall Inc.

Submitted 27 January 2000. Accepted 13 April 2000.