INTERGRADATION IN NORFOLK WATERS BETWEEN SOME SPECIES OF *AUTOLYTUS* (POLYCHAETA, SYLLIDAE).

by

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Résumé

Sur les côtes Nord du Norfolk, dans la zone intercotidale et en dragages, on constate que, chez les couches de Syllidiens de la sous-famille des Autolytinae :

1. - Les espèces *Autolytus prolifer* et *A. edwardsi* qui, dans les eaux côtières françaises et suédoises (selon Gidholm) sont uniquement mais très nettement séparées par leur couleur, sont réunies ici par quelques individus présentant toute une gamme de couleurs intermédiaires ;

2. - Les espèces *A. prolifer* et *A. brachycephalus*, d'autre part, semblent présenter les termes les plus éloignés d'une évolution dont les lacunes sont comblées par de nombreux intermédiaires en ce qui concerne l'allure générale de la souche, les crêtes dorsales des sétigères, la raideur ou la souplesse des cirrophores, les longueurs relatives des cirres et des cirrophores, la répartition des glandes sur la face dorsale des sétigères et la denture du trépan.

Les stolons s'élèvent facilement à partir des souches de type *brachycephalus*, moins facilement à partir de celles de type *prolifer* et plus du tout à partir de celles de type *edwardsi*, d'ailleurs bien rares ; ils se croisent librement entre eux et avec certains stolons planctoniques, quelle que soit leur origine, ce qui nous permet d'admettre provisoirement que tous ces phénotypes constituent une population panmictique. Il ne nous paraît pas souhaitable, néanmoins, de faire tomber en synonymie *A. brachycephalus* et *A. edwardsi* avec *A. prolifer* (nom prioritaire), leurs caractères spécifiques distincts étant nettement établis dans les autres régions européennes (2).

Introduction

Although the stocks of most of the species of autolytoid (Hamond, 1966, pp. 397-400) found in Norfolk waters (Hamond, 1963) agree closely with the descriptions and figures of Gidholm (1966), it appears that three species which are clearly separable in Swedish and French waters, namely *Autolytus prolifer* (O.F. Müller), *A. brachycephalus* (von Marenzeller), and *A. edwardsi* de Saint-Joseph, are connected in Norfolk waters by intermediates. In this paper an attempt is made to assess the nature of this intermediacy by morphological observations on the stocks and by the mating reactions of the stolons.

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Material and methods

Autolytoids were collected along the North Norfolk coast intertidally or in dredgings, and their stolons reared whenever possible in culture (Hamond, in press). Separate cultures were maintained of the same taxon from different localities, and their stolons were put together in small dishes of filtered seawater under the binocular microscope, to see if they would mate. In spite of the precautions already described (Hamond, in press), mortality was extremely heavy.

Intergradation between stocks of *A. prolifer* and *A. edwardsi*

Gidholm's findings (1966), that *A. prolifer* and *A. edwardsi* are valid species separable solely but unequivocally by their respective colour schemes, certainly hold good for the populations at Kristineberg (examined by both of us), Roscoff (only by him), and Plymouth (only by me), but the only four Norfolk specimens which at all resembled *edwardsi* were all intermediate between it and *prolifer* (Table 1) as regards colour. Morphologically, the Norfolk members

TABLE 1

CHARACTER	A	B	C	D
General colour of body	pale greyish or greenish	pinkish	pinkish	uniform pink or orange pink (1)
Pre-proventricular red stripe on wall of body cavity	very strong and clear	rather faint	very faint, and hardly discernible	absent
Cream-coloured granules on dorsal surface of gut.	closely packed into a longitudinal stripe; no stray granules.	loosely packed into a longitudinal stripe; few stray granules.	as B, but fainter and more diffuse; many stray granules.	no stripe; only scattered granules, few or many.

A. True *A. edwardsi*, as at Plymouth and Kristineberg.

B. Two specimens at ELWST among *Laomedea dichotoma* var. *plana*, cast up at West Runton on May 13th, 1964.

C. A specimen on *Alcyonium digitatum*, and another on *Eudendrium ramosum*; both coelenterates were growing just below ELWST on the Scaup at Hunstanton, Norfolk, on November 1st, 1963.

D. True *A. prolifer*, as at Kristineberg and widespread in Norfolk waters.

of the *prolifer-edwardsi* complex all resemble the specimen of *prolifer* shown in Fig. 1; the trepan of this *prolifer* is shown in Fig. 2, 1 (which is also exactly like the trepans of the four Norfolk *edwardsi*) and those of four other specimens of *prolifer* from an offshore locality (W. 38; Hamond, 1963) in Figs. 2,2 to 2,5 to illustrate the relatively constant form of the teeth and the wide variation found in the infradental spines (which, however, are rarely so developed as in Fig. 2, 3 and 2,5).

(1) Never "uniform leaden grey" as in Fauvel (1923).

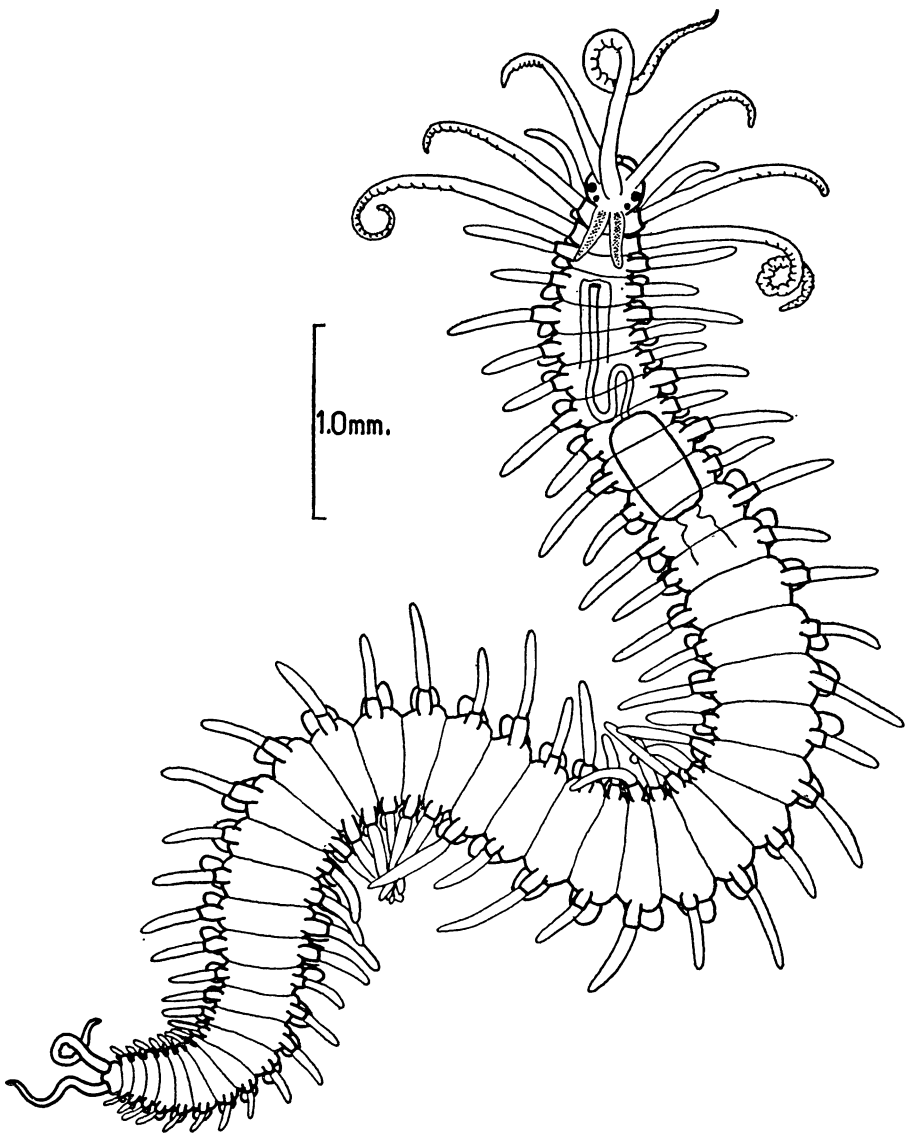

FIG. 1
Prolifer-type stock without stolons, creeping slowly.

Redescription of *A. brachycephalus*

This redescription is felt to be necessary owing to the wide range of variation to be described subsequently.

Body long and slim, with numerous setigers (ca. 60 for 1 cm when complete, Fig. 3), the front part being relatively slender, translucent and tapering evenly towards the head from the region of the proventricle, behind which the body becomes linear in its middle third and tapers away once more towards the tail; in stolonising

individuals the linearity continues as far as the budding zone. The head is thus about three-fifths as wide as the setigers in the middle of the body. Viewed from above, the bulging sides of the setigers are slightly angular, the angle being halfway back along the side in the setigers of the front half and tending gradually to about two-thirds of the way back in the rearmost setigers of the rear half; the greatest width of any setiger is about 130 per cent of its least width. The dorsal side of each setiger, especially of those behind the proventricle, is steeply angulate, the crest of the angle lying about two-thirds or three-quarters of the way back being surmounted by a sharply marked troch (a ciliated transverse band) between two transverse hoops of gland-cells; these gland-cells are very conspicuous,

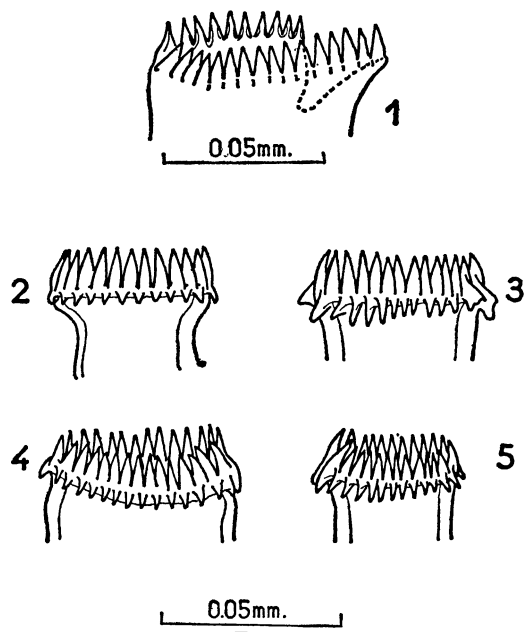

FIG. 2

1: trepan of specimen shown in Fig. 1. - 2 to 5: trepans of four *prolifer*-type stocks from W. 38, to show variation.

especially on the setigers in front of the proventricle, where they appear as widely spaced double hoops of glassy granules.

The tongue-shaped, parallel-sided nuchal organs extend to the middle of the second setiger. The head and its appendages present no unusual features; the dorsal cirri are much shorter than their respective cirrophores, which themselves are about as long as the width of their respective setigers. In an individual worm, the cirrophores and cirri (Gidholm's cirrostyli) tend to alternate slightly in length between successive setigers, except that there are two adjacent shorter cirrophores on setigers 7 and 8.

Parapodia broadly based, rounded and bluntly pointed, projecting from the body by an amount roughly proportional to the length of the cirrophore on that setiger. Pharynx with one complete S-bend;

proventricle long, barrel-shaped and very conspicuous, with a smooth pearly texture, its corners only slightly rounded, filling the body cavity over three setigers. Trepan with from 20 to 30 teeth of which about 10 or 15 are markedly larger than the others, between which they are irregularly spaced around the trepan; basal ring moderately

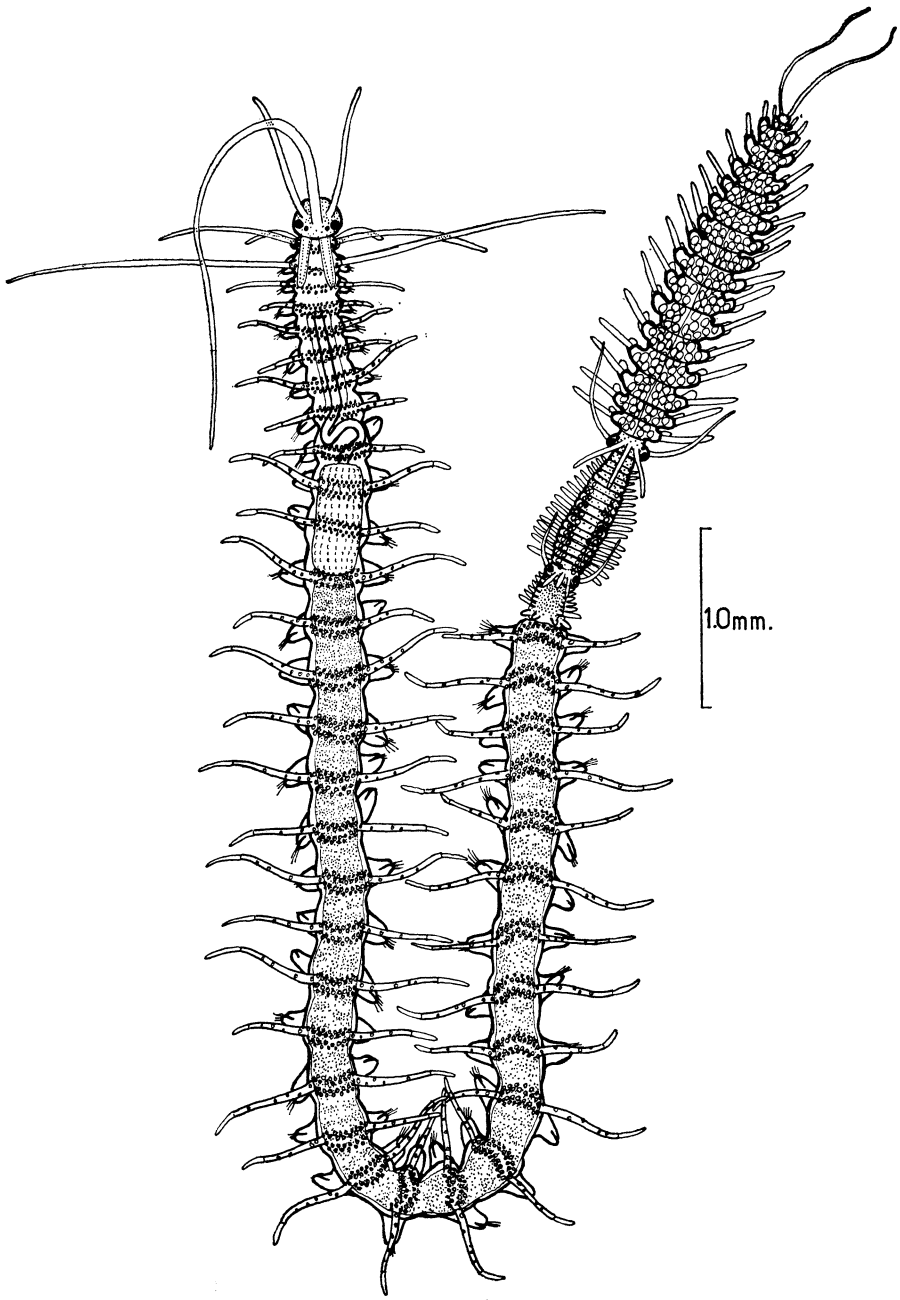

FIG. 3

Extreme *brachycephalus*-type stock with a chain of female stolons, crawling rapidly.

distinct, infradental spines small and faint or sometimes entirely absent.

General colour of head and bodywall translucent or faintly cloudy pink (among *Laomedea*) or cloudy reddish-pink (among *Eudendrium*). Trepan and pharynx silvery white, sometimes with the adjacent inner side of the bodywall tinted red as in *A. edwardsi* (but very much less conspicuous although not necessarily paler). Proventricle pearly grey flushed with pink (pink very noticeable in specimens from among *Eudendrium*, but hardly so in those from *Laomedea*); the intestine is strongly coloured in brown and yellow in the adults, or in deep yellow and off-white in smaller examples, sometimes with the yellow (or off-white) granules tending to be gathered into a mid-dorsal streak in a very faint imitation of *A. edwardsi*. However, this feature and the above-mentioned red tint do not always go together, and the granules are always liberally scattered over the rest of the gut as well. Parapodia greyish white. One specimen in about twenty or fifty has the whole of the bodywall, head, and appendages of a faint cloudy translucent green, the gut being normally coloured; such specimens have sofar been found only intertidally, among algae or *Laomedea*.

Intergradation between stocks of *A. brachycephalus* and *A. prolifer*

In Figs. 4 to 6 are shown parts of six specimens, representing the entire range of variation in a group of thirty-six *Autolytus* which crept out of a sample (volume about 0.8 litre) consisting of 34 small *Ciona intestinalis* and several colonies each of the hydroids *Eudendrium rameum, Halecium halecinum, Laomedea bicuspidata,* and small *Bougainvillia ramosa.* The tunicates and hydroids were all picked by hand from where they grew naturally just below ELWST on the shells and stones of Hunstanton Scaup, on September 9th, 1964. Of the *Autolytus,* six superficially resembled *A. prolifer* (though none had the *edwardsi* coloration) and the rest *A. brachycephalus,* but on closer examination a complete spectrum of variation was found from the most "extreme" *brachycephalus,* though "moderate" *brachycephalus,* to *prolifer.*

The "extreme" form of *brachycephalus* (Figs. 3 and 6, 2) is characterised by having (1) setigers which are noticeably "slim-waisted" in front of the parapodia, and whose dorsal hump is sharply angulate and markedly backward-leaning, (2) the head and body in front of the proventricle held straight and seemingly rigid when crawling on a level surface, although readily bent or deformed on meeting an obstacle or squeezing through a gap, (3) cirrophores about as long as the width of the setiger bearing them, much longer than their respective cirri, and held rigidly at right angles to the body, and (4) a trepan whose teeth, although all of the same shape, include a few distinctly larger teeth unevenly distributed among the smaller and more numerous teeth. According to Gidholm (1966) such a specimen would belong unquestionably to *brachycephalus;* indeed, his photograph (1966, fig. 19A) shows a specimen, otherwise typical of "extreme" *brachycephalus,* which is "moderate" in one important

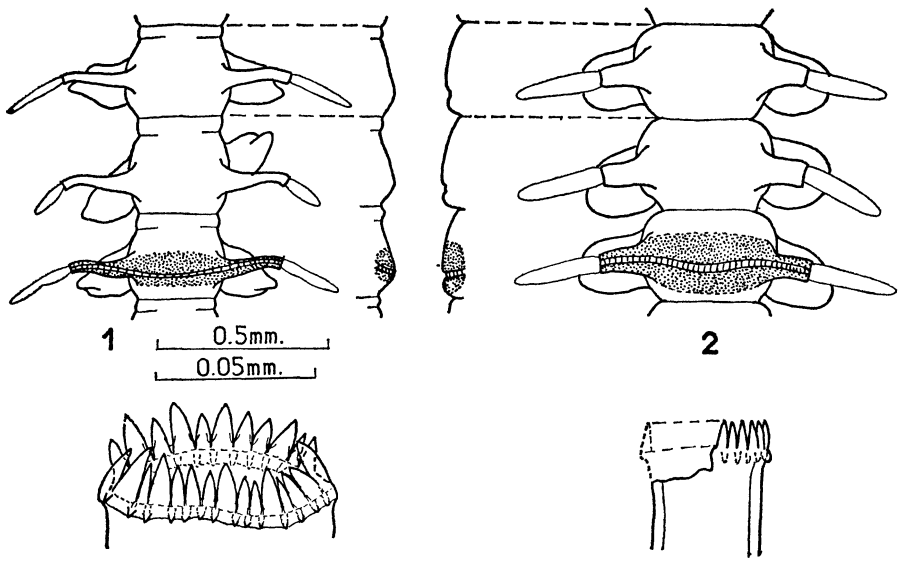

FIG. 4

1: moderate *brachycephalus*-type stock; otherwise as in Fig. 4,2 - 2: *prolifer*-type stock. Three setigers (0.5 mm scale) from middle of body in dorsal view with (projected to one side) the dorsal surfaces of these setigers in lateral view. Dotted area (shown completely on only one setiger) shows distribution of gland cells; the troch is the transverse double line with ladder-like connections. Below, the trepan (0.05 mm scale) after dissection (damaged in the figure).

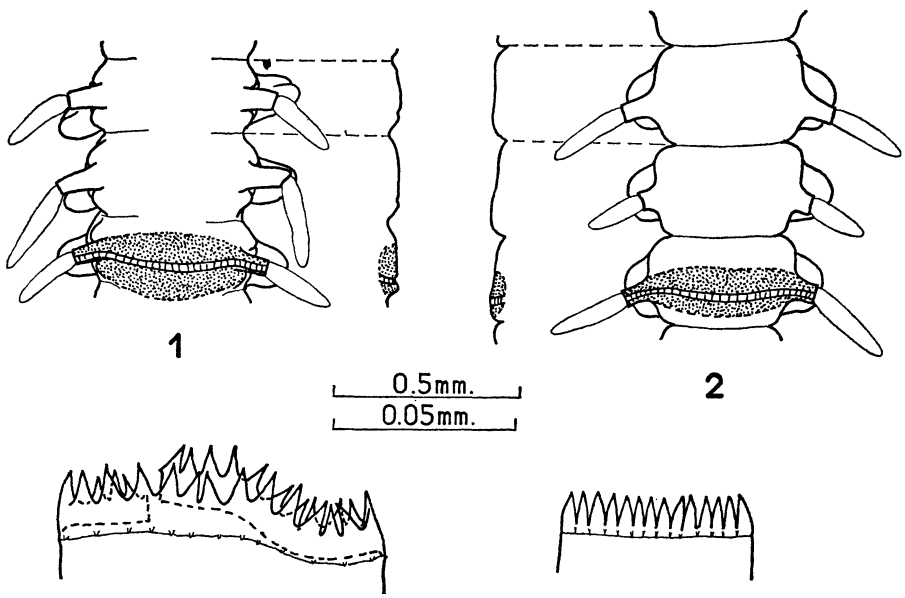

FIG. 5

1: borderline *prolifer-brachycephalus*-type; otherwise as in Fig. 4,2 - 2: *prolifer*-type; otherwise as in Fig. 4,2.

respect (the cirrophores are mostly shorter than the cirri borne by them). At the other end of the spectrum of variation, Norfolk "*prolifer*" has (1) setigers which bulge out in front of the parapodia as much as, or even more than, they do behind them, (2) an extremely sinuous body which curls or twists readily even when not confronted by any obstacle, (3) very short cirrophores, and (4) a trepan with equal teeth (Figs. 1; 2, 1; 4, 2; 5, 2). The respective degrees of development of each of these characters are strongly correlated in any given individual from Norfolk waters, irrespective of its habitat or of its place in the spectrum of variation; however, Gidholm's photograph (see above) suggests that these correlations may not hold good for populations elsewhere.

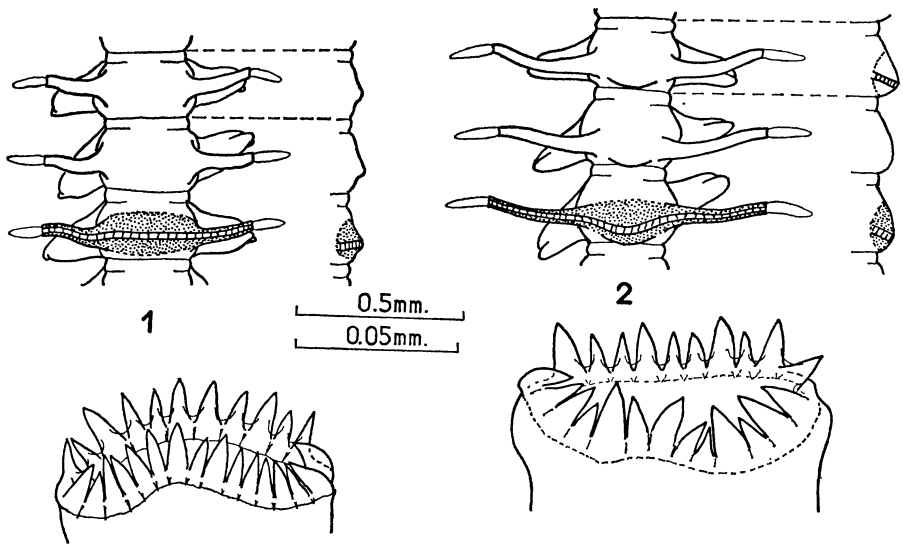

FIG. 6

1: moderate *brachycephalus*-type; otherwise as in Fig. 4,2 - 2: extreme *brachycephalus*-type; otherwise as in Fig. 4,2.

The specimens shown in Figs. 4, 1 and 6, 1 are equally clearly *brachycephalus,* but are less extreme in all their characters than that shown in Figs. 6, 2. The remaining specimen (Fig. 5, 1) is almost exactly intermediate; it is referred to *brachycephalus* by a very small margin since the teeth, although all very much alike, are not quite so even as in the two presumed specimens of *prolifer* (Figs. 4, 2 and 5, 2), and also because the sides of the setigers do not bulge out ahead of the parapodia to the same extent as in *prolifer.*

The *prolifer* in this sample could also be distinguished at sight by their colour (a relatively uniform and opaque pink with a strong orange tinge), by the small oval proventricle, and by the fact that nlither the proventricle nor the dorsal transverse rows of gland-cells could be seen without careful inspection, whereas the *brachycephalus* were of a transparent pale brownish red or very faint magenta colour, with conspicuous transverse rows of gland-cells on each setiger, and a large and clearly visible proventricle of a pale pink with a silvery sheen like satin, giving the pearly effect previously mentioned. Later

samples have included specimens which were only moderately opaque, whose colour embraced every shade of pink between those mentioned, and in which the form of the proventricle was apparently identical in those with bulging setigers and in those without them (making due allowance for the worm crawling actively or staying still). Of these intermediates (which were few, and all in dredgings) at least one had setigers of the most moderate *brachycephalus* type together with an apparently *prolifer*-type trepan; such intermediates always occurred among much more numerous specimens of typical *brachycephalus,* which ranged from "extreme" to "moderate" as described above for the Hunstanton sample.

The position of an individual in the spectrum of variation bears some relation to its habitat (Fig. 7); thus, in Blakeney Harbour, the very numerous specimens among *Laomedea* spp. are almost of the extreme type, whereas the few found among *Kirchenpaueria pinnata* are roughly 60 per cent extreme and 40 per cent moderate with an occasional *prolifer* (less than 10 per cent). Most of the rather few West Runton specimens are of the moderate type. In dredgings, all these types are found, but no *edwardsi* (which appears to be restricted to near low-tide mark); the most moderate types form a much larger percentage of the total population offshore than they do anywhere else except for among *Kirchenpaueria* (Blakeney Harbour) or at West Runton (among *Corallina* and sessile organisms near low-tide mark). In this connection, it must be emphasised that the Scaup at Hunstanton is not so much low intertidal as uppermost sublittoral, so that the collection at low water of typical offshore organisms (*Alcyonium digitatum*, as well as those in the above sample) and the relative abundance of moderate and *prolifer*-like forms, are each less exceptional than they might appear (Hamond, 1963).

Cross-matings within the range of variation.

Mating in *Autolytus* takes place only between stolons (Gidholm, 1965); if the stocks are fed on hydroids in beakers of seawater with continuous aeration in a controlled-temperature enclosure, the stolons are budded off in quantity and will mate either with each other or with stolons of the same species taken in the plankton ("wild stolons").

Attempts were made to rear the stolons from as many phenotypes within the above spectrum of variation as possible, in order to determine whether there were any mating barriers. No *edwardsi* stocks were ever found with stolons, nor would they live for more than a few days in culture; *prolifer* fed fairly well and liberated a few misshapen sickly stolons which were quite incapable of mating, although two of the healthiest females elicited sexual responses from several males of *brachycephalus.* Under favourable circumstances, the extreme and fairly extreme types of *brachycephalus* (forming the bulk of the population feeding intertidally on *Laomedea* spp.) liberated large numbers of stolons, which if healthy mated freely among themselves. At best, however, these stolons are very delicate, having at 17 °C a maximum lifetime of about five days after liberation and being capable of satisfactory matings only for the first three days; if

slightly unwell, or as a warning of imminent premature death, the males would often fail to mate even when apparently in perfect condition.

Wild stolons were also brought in to be mated with cultured stolons. The cross (wild female X cultured male) was hardly ever attempted, since the very efficient mechanisms governing the meeting of the sexes in the open sea (to be described in a future paper) ensured that every wild female had been mated with before capture; however, numerous wild males were crossed with cultured virgin females, with whom they mated just as readily as did cultured males, neither set of crossings giving any indication of a mating barrier. This is important, since the offshore populations giving rise to the wild stolons consist far more of *prolifer* and moderate *brachycephalus* and correspondingly less of extreme *brachycephalus*, than do the intertidal populations; moreover, these two populations feed on the polyps of different species of hydroid and therefore their stocks tend to be differently coloured, although the cultured and wild stolons look almost exactly the same.

It seems probable, therefore (although direct proof is lacking, due to heavy mortality), that some at least of the wild males were budded off from *prolifer*-like stocks and yet mated freely with females derived from extreme *brachycephalus*. Genetic results in the classical sense could not be obtained, since no way has yet been found of rearing the larvae after hatching.

Discussion

In the absence of a sterility barrier or of any other evidence to the contrary, it seems probable that in North Norfolk waters both the intertidal and the offshore *Autolytus* of the *brachycephalus-prolifer-edwardsi* complex form a single, very variable but reproductively homogeneous, population; this amonts to a repression of speciation, which may be linked to the local environment and which has been demonstrated in some other North Norfolk animals (polychaetes, Hamond, 1966; copepods, Hamond, 1968). Alternatively, it is possible that the Norfolk *"edwardsi"* are stray examples of the genuine *edwardsi* (*sensu* Gidholm, 1966) which have found their way into Norfolk waters and are able to exist there without stolonising; however, the way in which their colours intergrade with those of *prolifer* (Table 1) makes this unlikely.

At the moment, the sinking of *A. brachycephalus* and *A. edwardsi* in the synonymy of *A. prolifer* does not seem to be justified since, even if the absence of any sterility barrier in the Norfolk material were far more firmly established than at present, these three taxa appear to be clearly distinct at the species level in French and Swedish waters. Comparative studies on the biometry and reproductive biology of all these populations would be of interest.

Since different phenotypes are numerically dominant in different habitats, it appears that the genetic system underlying this range of variation interacts with the effects, either of the food or of the physicochemical parameters of the environment (for instance the diurnal range of temperature, salinity or light intensity), to determine

which phenotypes are favoured at the expense of the others in any given habitat; the exact way in which any phenotypic feature confers selective advantage is quite unknown.

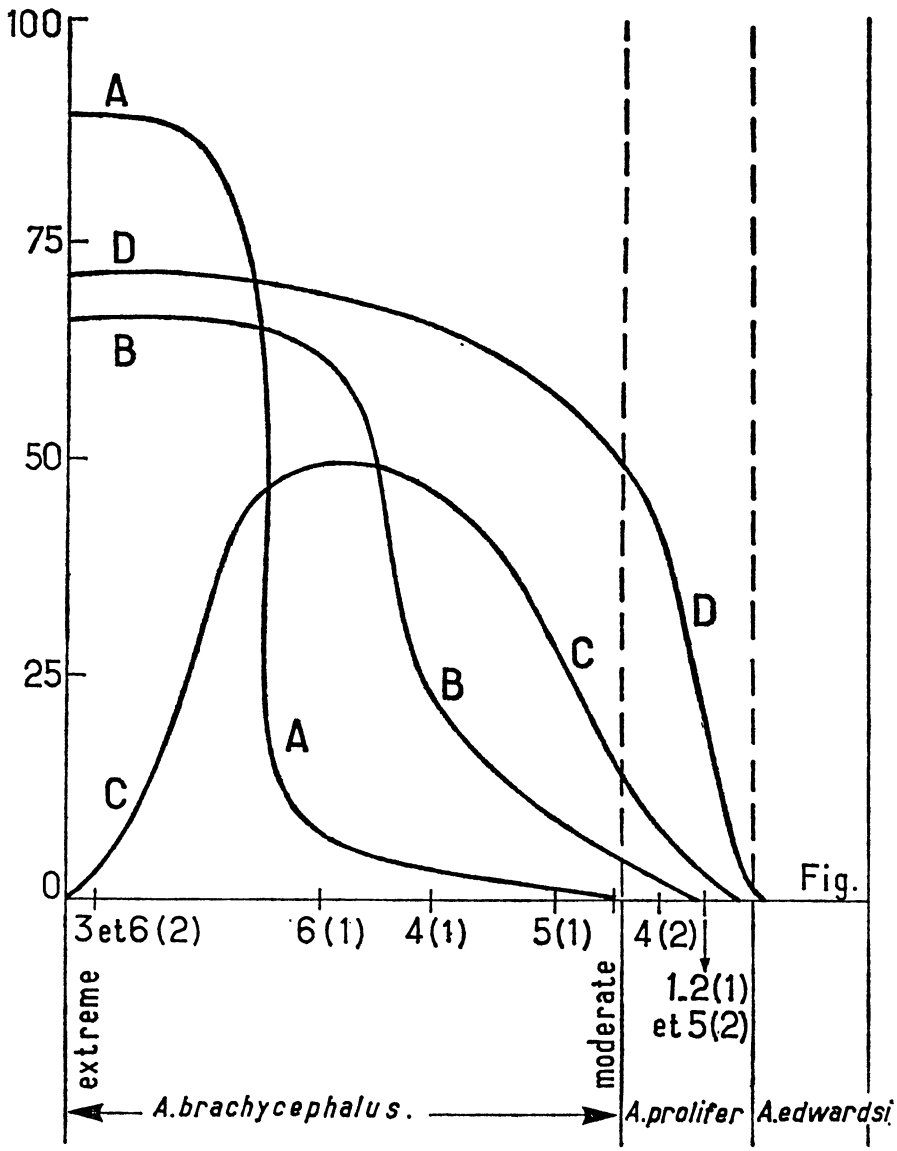

FIG. 7

Relative abundances of types in various North Norfolk habitats.

X-axis: percentage likelihood that a given type will include most of the *Autolytus* in a given sample from one of the localities named below.

Y-axis: the spectrum of variation (arbitrary scale) from extreme *brachycephalus* at left to *edwardsi* at right, the positions of the various figured phenotypes being shown at their positions in the spectrum.

Curves: A-among *Laomedea* spp. in Blakeney Harbour; B-among *Kirchenpaueria* in Blakeney Harbour; C-near low-tide mark at West Runton, among *Corallina* and sessile colonial animals; D-subtidally on Hunstanton Scaup and offshore in dredgings.

Summary

Representatives of a sample of *Autolytus* stocks from Hunstanton, Norfolk, are described to show the range of variation in colour connecting *A. edwardsi* with *A. prolifer*, and the range of morphological variation connecting the latter with *A. brachycephalus*; subsequent samples showed similar ranges of variation. Attempts were made to culture these taxa, and to cross-mate the stolons so obtained. The ease with which a given phenotype fed or bred in the laboratory corresponded approximately to its position in the spectrum of variation; the "extreme" type of *brachycephalus* furnished the most numerous stolons, whereas *prolifer* produced hardly any stolons and *edwardsi* none at all. However, male stolons were obtained from two populations of stocks in which the numerical proportions of the various phenotypes were markedly different; either group of males mated equally readily with females derived from only one of these populations, and no evidence could be found of any sterility barrier. It is provisionally concluded that all *Autolytus* of the *brachycephalus-prolifer-edwardsi* complex in North Norfolk waters, whether dwelling intertidally or offshore, are members of a single highly variable but reproductively homogeneous population.

Zusammenfassung

An die Küste Norfolks, sowohl im Gezeitenzone wie bei benthonischen Sammlungen in die Nähe des Küstes, findet Man Ammengenerationen der Gattung *Autolytus*, der zeigten alle Uebergangsstadien (1) in Farbe zwischen *A. prolifer* und *A. edwardsi*, und (2) in verschiedene morphologische Weisen zwischen *A. prolifer* und *A. brachycephalus*.

Ammen im Laboratorium gezüchteten von *A. brachycephalus* gaben viele Stolonen, Ammen von *A. prolifer* aber sehr wenig ; Ammen von *A. edwardsi* (an diese Küste sehr selten) könnte nicht zu Knospenbildung gebracht werden. Es scheint möglich zu sein, dass die Stolonen alle diesen Phänotypen durchaus miteinander fertil waren, und im Ganzen bilden sie in diesem Sinne eine homogene Gruppe. Trotzdem scheint es aber noch zwecklos, *A. brachycephalus* und *A. edwardsi* als Synonymen mit *A. prolifer* zu betrachten ; im schwedischen und französichen Gewässern sind alle drei Arten im spezinsch Sinne sehr wohl getrennt.

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