

Ecological segregation of systematically related stream insects

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Insects from a stream at Mont St. Hilaire, Quebec, were sampled monthly for 1 year. The degree of ecological difference between congeneric species in three orders was assessed by using a "coefficient of separation", similar to a modified Jaccard coefficient. It was found that species differed most in their season of occurrence, least in the substrates they occupied. The significance of this result in terms of the avoidance of competition is considered.

Introduction

Systematically related species, when examined carefully, are often found to be distinctly different ecologically. The usual interpretation of this is that such species are liable to compete for resources by virtue of commonly inherited adaptive systems, and that natural selection, by operating in such a way that it minimizes inter-specific interaction, has enabled the species to exist in the same area. The resources most likely to be the object of competition are space and food. It is the purpose of this article to examine the means by which a group of insects are ecologically separated during the aquatic stage of development.

Spatial separation may occur on different scales. On a large scale it would take the form of species occupying different stretches of the stream. On a medium scale species might occur on different substrates (referred to here as habitats). On a fine scale species might occupy different parts of the same habitat.

Food separation could involve size or type of food, or both. Assuming that growth rates of similar species are similar, and that food size separation is achieved by the possession of differently sized feeding structures, which are dependent upon body size differences, it would seem likely that food size separation is most easily produced through a staggering of the life histories of the species. Separation by food type could occur in the same way.

Our data allow us to examine the degree of ecological separation by large scale space (station), medium scale space (habitat), and food (inferred from temporal differences).

Methods

A stream 1.7 km (1 mi) long at Mont St. Hilaire, Quebec, was sampled monthly from March 1966 to February 1967. Four stations, spanning the length of the stream, and five discrete habitats (sand, gravel, stones, leaves, and leaf detritus) were sampled each month in the manner described by Mackay (1969). Usually only one sample was taken each month from each habitat in each station. Animals were counted, identified where possible, and some linear measurements (usually head width) taken. Further details of environments, organisms, and sampling procedures can be found in Mackay (1969).

The present analysis deals with congeneric species in three orders of insects, but considers only those identified to species level at all stages of development. The extremely rare species were excluded.

An estimate of the ecological segregation of two species is developed here and applied to the data grouped by station, by habitat, and by time, first to each category considered separately and then to the categories combined. The reasoning was as follows. If two species occur in separate habitats, such that individuals of the one never encounter those of the other, they are considered to be ecologically separated. The degree of separation is 100%. When a few individuals of each species encounter individuals of the other, the degree of separation is considered to be less than 100%. What then is 0%? In this paper we consider 0% separation to occur when the two species are equally represented in a habitat, station, or time category (this refers to numbers; an alternative which could be used, but is not here, is consuming biomass). Using this scale of 0% to 100% we shall assess the degree of separation between members of pairs of species in any one category (station, habitat, or time).

The method involves a numerical matching procedure. It first yields a measure of numerical equivalence from which its opposite, a measure of numerical difference or separation, is derived. Consider one station, for example, station *a*. Let *X* and *Y* denote the numbers of individuals of the more common and more rare species respectively at this station. Then the number of animals common to both species is *Y*. The additional numbers of the commoner species amount to *X* - *Y*. The number of animals

common to both species is now expressed in relation to the total, as a percentage, in the following way:

$$[1] E_{sa} = (100 \times Y) / \{(Y + (X - Y))\} = (100 \times Y) / X.$$

E_{sa} is the coefficient of numerical equivalence for station a . The coefficient of numerical equivalence for the station category as a whole is as follows:

$$[2] E_s = 100 \sum_n (Y/X),$$

where n is the number of subdivisions in the category. To obtain a measure of the ecological incompatibility of the two species within the category we calculate a coefficient of separation, G_s , by subtracting the coefficient of equivalence from 100:

$$[3] G_s = 100 - E_s = 100 - 100 \sum_n (Y/X).$$

In the same way G_h (habitat) and G_t (time) are calculated. The coefficient of numerical equivalence is similar to the Jaccard coefficient (Jaccard 1902) used for assessing floral and faunal resemblances. The coefficient of separation resembles the modified Jaccard coefficient used by Savage (1960). Williams (1951a) found a tendency for the Jaccard coefficient to increase with sample size, but no such dependence upon sample size was apparent in our coefficients.

Results

Table I gives the results of the four analyses. The combined data analysis gives large coefficients of separation for almost all pairs of species. With the three categories treated separately, it is found that time yields the greatest amount of separation, generally, and habitat the least. Thus $G_t > G_s > G_h$. This is revealed in two ways. A two-sided Student's t

test applied to pairs of mean coefficients gives a significant difference between two categories, time and habitat, $P < 0.005$; (station and time, $P 0.1 > 0.05$; station and habitat, $P 0.1 > 0.05$).

In 12 instances out of the 13, the analysis by time gives a larger coefficient than do the other two analyses (station and habitat). In the remaining instance $G_s > G_t > G_h$ (*Neophylax* spp.). The frequency of 12:1:0 thus appears to be different from a 1:1:1 ratio expected on the hypothesis that the number of occurrences of time giving the largest, intermediate, and smallest coefficients should be equal. This is tested for significance by χ^2 , and the results are shown in Table II; the same is done for the station and habitat coefficients.

As an alternative to absolute numbers we may use proportions in the various subdivisions of each category by multiplying values for the rarer species by an appropriate correction factor. The analysis of these adjusted data yields the same results as before, with the levels of significance slightly altered. For example, a χ^2 test of the adjusted time coefficients gives $P < 0.005$.

Similarly, to avoid possible bias in comparing the coefficients in categories which have different numbers of subdivisions (e.g. stations, 4; time, 12), we may group the time data into four blocks of 3 months (January, February, March, etc.) and proceed as above. Again this merely

TABLE I
Coefficients of ecological separation

Species	Category			
	Station (G_s)	Habitat (G_h)	Time (G_t)	Combined (G_c)
<i>Neophylax aniqua</i> and <i>N. nacatus</i>	100.0	58.9	75.4	100.0
<i>Ephemerella funeralis</i> and <i>E. dorothea</i>	65.9	62.7	82.5	93.5
<i>Isoperla holochlora</i> and <i>I. similis</i>	56.9	56.9	85.4	93.2
<i>Rhyacophila minima</i> and <i>R. vibox</i>	69.2	60.7	81.1	96.3
<i>Ameletus</i> "A" and <i>Ameletus</i> "B"	62.7	48.8	66.3	81.1
<i>Ameletus</i> "A" and <i>Ameletus</i> "C"	88.6	63.2	98.7	99.2
<i>Ameletus</i> "B" and <i>Ameletus</i> "C"	66.0	53.0	94.7	95.5
<i>Lepidostoma</i> "A" and <i>Lepidostoma</i> "B"	93.7	93.7	97.6	98.5
<i>Lepidostoma</i> "A" and <i>Lepidostoma</i> "C"	78.5	61.2	81.7	90.3
<i>Lepidostoma</i> "B" and <i>Lepidostoma</i> "C"	95.6	95.6	95.8	98.3
* <i>Amphinemura wui</i> and <i>Ostrocerca albidipennis</i>	95.9	85.1	96.2	98.6
<i>Amphinemura wui</i> and <i>Soyedina vallicularia</i>	42.3	33.7	88.3	94.5
<i>Ostrocerca albidipennis</i> and <i>Soyedina vallicularia</i>	96.3	89.8	98.6	99.5
$\bar{x} \pm 2S\bar{x}$	77.82 ± 10.28	65.64 ± 11.16	87.87 ± 5.64	

**Amphinemura*, *Ostrocerca*, and *Soyedina* are different subgenera of the genus *Nemoura* (Ricker 1952).

reduces the level of the significance of the time data ($P < 0.01$), but does not alter the results. The importance of temporal separation is thus demonstrated.

Conclusions

We conclude that ecological separation of closely related species by habitat is relatively weak in these species. If the intergrades between the discrete habitats had been sampled as well, our coefficients of ecological separation by habitat may have been even smaller. Williams (1951*b*), after analyzing data of congeneric terrestrial organisms, also came to the conclusion that segregation by habitat was infrequent, although this is not without dispute (Hairston 1964). On the other hand separation by time is considerably greater. Hynes (1961)

noticed a similar separation among stream insects in Wales, and there are plenty of published lists of data showing the same (e.g. Macan 1957; Tebo and Hassler 1961; Sprules 1947; Svensson 1966; Ulfstrand 1967, 1968).

These findings suggest that congeneric species of stream insects live in much the same habitats, being adjusted to them with similar adaptive systems, including patterns of resource exploitation. Within this framework, natural selection has favored a difference in the time at which the maximum impact upon the resources is made by each species, i.e. the maximum energy flow through them is temporally staggered. If true, the corollary should be true also. Where pairs of species are not able to segregate by time or space (large or medium scale) their coexistence is dependent upon different exploitation patterns, which will be reflected in the structures most intimately associated with the exploitation. More detailed information, particularly on diet and microspatial (within habitat) distribution, is needed.

We turn now to the case of *Ameletus* A and B which, in showing a substantial degree of temporal overlap, appears to be exceptional. Size data show that, despite the large temporal overlap, coexisting animals of the two species are almost always of different size (Fig. 1). The small temporal separation is sufficient to produce a nearly complete size separation owing to the approximately equal growth rates. The size data that we have for other pairs of species suggest that size differences are even greater among these.

A temporal separation places the two species in environments which differ not only in food but in temperature, flow rate, predators, etc. Natural selection will act on the fitness of members of each species in relation to all aspects of the environment. We cannot assess the importance of these other factors, but see no reason at present why they should be of overriding importance and thus obscure our principal result. For instance, there is no obvious avoidance of predation gained by one species occurring at a particular time of year.

Discussion

We have used the coefficient of separation as a measure of ecological incompatibility, but it

TABLE II

χ^2 analysis of the coefficients of separation

	Station	Habitat	Time
χ^2 for 1sts ^a	2.53	4.30*	13.79***
2nds	8.94**	1.82	4.30*
3rds	1.82	12.06***	2.53
$\sum\chi^2$	13.29	18.18	20.62
d.f.	2	2	2
P	<0.005	<0.001	<0.001

^a1sts refer to the number of times the coefficient is greater than the coefficients for the other two categories; 2nds and 3rds refer to the intermediate and smaller coefficients.

*5% level of significance, **1% level of significance, ***0.1% level of significance.

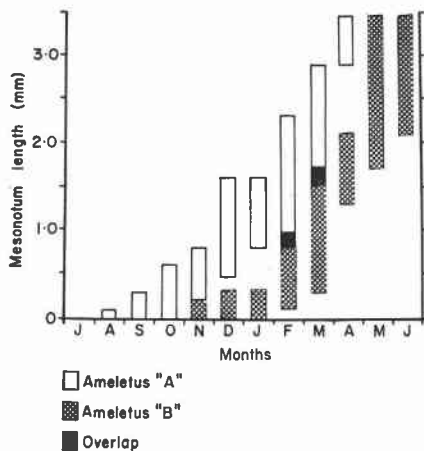


FIG. 1. The size and temporal separation of *Ameletus* "A" and "B". The bars represent size range only.

is likely that under certain conditions it will be inadequate. For example, marked differences in body size between animals of equivalent age (not a problem in this study) will render numerical comparisons almost meaningless. The most serious source of concern is that in some cases numerical differences between species may be quite unrelated to interactions (in the broad sense) between them, but be governed by environmental factors which have no bearing upon the coexistence function. If this was a common phenomenon, however, we would not expect the analysis to yield the consistent results it did, unless some biasing error was operating in a systematic way, and we have no knowledge of what that error might be.

In our method of analysis no account is taken of sampling variation because rarely did we have more than one sample per category subdivision, and this is a serious limitation. More samples, and data analyzed by methods developed by Morisita (1959) and elaborated by Horn (1966) would be highly preferable. Also more sampling is desirable because it allows a greater variety of environment types to be surveyed, and the avoidance of human bias in the selection of types of habitat.

It would be interesting to compare the nature and degree of ecological separation between congeneric species and between heterogeneric species. This could not be attempted in the present study because of a lack of sufficiently closely related species with which to compare congeners. Most appealing is the possibility of using the same methods, such as those of 'numerical taxonomy,' to assess both the morphological and ecological similarity of species. This could be done with homogeneric and with heterogeneric species. It would provide a useful means of exploring the contention that systematically closely related species show adaptations to the avoidance of interspecific competi-

tion more strongly than do distantly related species.

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ERRATUM

Equations (2) and (3) (p. 692) should read as follows:-

$$(2) \quad E_s = 100(\sum nY / \sum nX)$$

$$(3) \quad G_s = 100 - E_s = 100 - 100(\sum nY / \sum nX)$$

The coefficients presented in Table I were calculated using the above formulae, and are therefore correct.