

References and Notes

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Separation Rate and Neighbor Diffusivity

Abstract. Separation rates of neighboring pieces of orange peel floating on the sea were measured under fresh breeze conditions. When Stommel's equation for neighbor diffusivity (F) was applied to the data it became apparent that the F value increased by an order of magnitude whenever the time adrift increased by this amount. This is a result of the fact that the increase in spacing distance is squared while the time adrift is not. It is recommended that a standard time of 1 second be used whenever Stommel's equation is applied in neighbor diffusivity problems. Recomputation of data from the literature showed that neighbor diffusivity varied between 0.08 and 1 cm²/sec while time adrift varied between 10 and 10⁸ seconds. Further study of separation rates, as parameters of surface turbulence, is recommended.

Turbulence is one of the most important factors influencing aquatic ecology and quantitative measurements of it are needed. Hutchinson (1) has reviewed the theoretical treatment of turbulent energy relationships, stating that, if all the energy in the largest eddy of a system is considered, turbulent energy varies directly with the size of the space under consideration; thus if l is the linear dimension, average turbulent energy will be proportional to $l^{2/3}$, average eddy viscosity to $l^{1/3}$, and average velocity to $l^{1/3}$. Hutchinson also summarized the work of Richardson and Stommel on neighbor diffusivity showing that this parameter is analogous to eddy diffusivity in transport equations of the Fickian type, and reporting that neighbor diffusivity, computed from separation rates of wet pieces of paper floating on the sea, varied as the 4/3 power of the distance separating neighbor pairs. This observation would seem to recommend the neighbor diffusivity as a measure of turbulent energy and to substantiate the theoretical relationship between energy

and the linear dimensions of the space under consideration. Olson and Ichiye (2) have published a graph showing that the neighbor diffusivity (F), when computed with Stommel's (3) equation (4):

$$F = \overline{(l_1 - l_0)^2} / 2T$$

increases by approximately one order of magnitude whenever $(l_1 - l_0)$ increases by an order of magnitude. They summarized data for parsnip pieces, mimeograph paper, dye spots, drift cards, and drift bottles, in which $\overline{(l_1 - l_0)}$ varied between 10 and 10⁸ cm. I became interested in investigating neighbor diffusivity as a possible parameter of surface turbulence in aquatic environments, and carried out some experiments at the Alligator Harbor Marine Laboratory of the Florida State University (Tallahassee) during December 1959 (5). I used five pieces of orange peel which were deposited at the end of the laboratory pier, as close together as possible, and were allowed to drift ashore. Their time adrift was measured, and their distance apart in the direction perpendicular to the direction of the drift. Thus the shape of the shore line did not influence the measure of separation rate. From eight sets of data obtained under conditions of fresh breeze I obtained an average separation rate of 0.8 cm/sec. The averages from individual sets of data ranged from 0.24 to 1.2 cm/sec. If this value of 0.8 cm/sec is regarded as a reliable measure of the rate at which neighbor pairs separate when floating on the sea and I compute the neighbor diffusivity, using Stommel's equation, assuming a constant separation rate of 0.8 cm/sec operating for various times adrift, I obtain the values in column 3 of Table 1. In columns 4 and 5 I have entered data computed from the graph of Olson and Ichiye. This table shows that most of the increase of F with increasing

values of $\overline{(l_1 - l_0)}$ simply results from the fact that $\overline{(l_1 - l_0)}$ is squared in Stommel's equation, while T is not.

In private communications, Olson and Ichiye kindly provided me with sample sets of data, computations, and opinions which enabled me to verify that I have not misinterpreted the data in their graph. Column 5 in Table 1 shows that the average separation rates of neighbor pairs throughout this wide range of times adrift are all reasonably close to my experimental value of 0.8 cm/sec. If one wishes to employ an equation such as Stommel derived for neighbor diffusivity, then a standard time interval, preferably 1 second, should be used in the computation. If this is done, the F values obtained from the data in column 5 of Table 1 will range from 0.08 to 1 cm²/sec. It appears that the purported proportionality of neighbor diffusivity with distance of spacing ($F = kl^{1/3}$) (6) is a result of mathematical treatment that disappears when one uses a standard time interval in Stommel's equation. The theoretical relationship between turbulent energy and the linear dimension of the space under consideration is not confirmed by these data. If this relationship were valid, the separation rates in column 5 of Table 1 should be of the order of 100 cm/sec when $\overline{l_1 - l_0}$ equals 10⁶ cm, that is, they should vary as the cube root of the linear dimension. The data in Table 1 suggest that the separation rate and neighbor diffusivity are relatively independent of the linear dimension of the space under consideration. Olson and Ichiye emphasized the fact that the data they compiled did not meet the requirements made by Stommel in his derivation of the theoretical relationship. This fact may be responsible for the discrepancy between theoretical and observed separation rates. The most significant feature of these data is the relatively constant average

Table 1. Neighbor diffusivity values, computed from Stommel's equation, compared with the rate of separation of neighbor pairs.

Time adrift (sec)	$\overline{(l_1 - l_0)}$ assuming separation rate of 0.8 cm/sec	Computed neighbor diffusivity $\frac{\overline{(l_1 - l_0)^2}}{2T}$	Neighbor diffusivity from graph of Olson and Ichiye	Separation rate (cm/sec) computed from graph of Olson and Ichiye $\frac{\overline{(l_1 - l_0)}}{T}$
10	8	3.2	3 (6)	0.77
10 ²	80	32	15 (6)	0.55
10 ⁴	8 × 10 ³	3.2 × 10 ³	0.8 × 10 ³	0.40
10 ⁶	8 × 10 ⁵	3.2 × 10 ⁵	6 × 10 ⁵	1.1
10 ⁸	8 × 10 ⁷	3.2 × 10 ⁷	2 × 10 ⁸	1.4

separation rate obtained over such a wide range of space dimensions. My experience with individual sets of neighbor pairs, however, leads me to believe that the separation rate may be a valuable parameter of turbulent energy near the surface of aquatic habitats and that it warrants more attention than it has received. The methods are simple and inexpensive. Attempts to correlate separation rates with other environmental factors will certainly yield valuable information.

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 4. Where l_0 is the distance apart initially and l_t is the distance after T seconds. The bar indicates that the values are averages of several neighbor pairs.
 5. The Oceanographic Institute generously supplied living space for my family and research facilities for me. The work was supported in part by the Atomic Energy Commission, contract AT (11-1)-536.
 6. The least-squares line of Olson and Ichiye lies below most of Stommel's data. The values of 3 and 15 in Table 1 were obtained by drawing a line, by inspection, through Stommel's data.
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Effect of Implanted Adult Corpora Allata on That of Host in Two Species of *Drosophila*

Abstract. Experiments to show the effect of implanted adult corpora allata on that of the host have given negative results in *Drosophila melanogaster*, while the presumed compensatory effect has been verified in *Drosophila virilis*. Reasons are presented which suggest that the nature of the latter effect should be further analyzed.

Bodenstein (1) reported that implantation of corpora allata (or corpus allatum complexes) from mature *Drosophila virilis* females into freshly emerged female hosts results in a compensatory reduction in size of the host corpus allatum within 2 to 10 days. On the other hand, larval ring glands implanted into 1-day-old adult hosts have no such effect. In the stick insect, *Dixippus*, implantation of larval, but not adult, corpora allata into fifth instar nymphs is known to induce a compensatory effect (2). In view of the homologies made between the small round antero-medial cells of the *Drosophila* larval ring gland, which give rise to the imaginal corpus allatum, and the larval

corpus allatum in other insects (3), this reversal of relationships is of some interest even though caution must be taken in comparing such unrelated forms.

The compensatory effect described by Bodenstein was sought in reciprocal corpus allatum complex transplantations between homozygous *female sterile* (2) *adipose* and wild-type adult females of *D. melanogaster* (4). It was hoped that the effect of the mutant complex on the corpus allatum of the wild-type host might be used as an assay of the activity of the donor's corpus allatum, which normally hypertrophies in mated females of the mutant genotype. No effect of the implants on either the mutant or on the reciprocal wild-type hosts could be detected. In addition, some question was raised as to whether the compensatory effect could be induced even in wild-type flies with implanted wild-type corpus allatum complexes.

To further test the presumed compensatory effect, another series of transplantations has been carried out on *D. melanogaster* adult females. The flies used were hybrids between two highly inbred (originally "isogenic") wild type lines of Oregon R and Sevelen, whose egg production is known to be of a high order and less variable than is generally the case (5). Donor females were mated, aged 4 days, and their corpus allatum-complexes were removed in Waddington's *drosophila* Ringer solution. Host females were 1 to 4 hours old at the time of injection and received two complexes each; operated controls of the same ages were injected with Ringer solution. Each pair of females, host and operated control, was placed in a creamer of food with three males and aged for 6 days. Fresh food was supplied 72 and 24 hours before sacrifice. Whole mounts of host and control corpora allata were made and measured, and the results were treated statistically (6). Hosts were then fixed, sectioned, and stained in order to determine the number of successful implants. Both implants were found and were in good shape in the hosts of 12 of the 13 successful transplantations, while only one implant was found in the remaining case. A comparison of the size of the host corpus allatum to that of the operated control in each creamer pair showed no detectable difference between them (over-all mean for hosts, from planimeter readings of camera lucida outlines, = 0.44 in.²; controls = 0.43 in.²). Thus, it appears that the compensatory effect of implanted corpora allata

on that of the host, originally described for *D. virilis*, does not occur in *D. melanogaster*, at least when hosts are of the ages used.

Because of these results, it seemed appropriate to repeat Bodenstein's experiments on *D. virilis*. Another series of transplantations similar to those described above for *D. melanogaster* was set up. The experiment differed from Bodenstein's in that I used an operated control for each host. Both flies of each pair were placed in a creamer with three males, and all flies were sacrificed on the seventh day. The size of the adult corpus allatum in *D. melanogaster* is somewhat larger in mated females than in virgins (6) and it was not clear from the previous experiments on *D. virilis* whether or not virgin females had been used as hosts. Therefore, a group of unoperated controls, including both mated and virgin females (20 each), was prepared and their corpora allata were measured on the seventh day along with those of the hosts and operated controls.

Although experiments on *D. virilis* are still in progress, certain results are very clear. First, the corpus allatum of 1-week-old virgin females is smaller than that of mated females (mean of planimeter measurements for mated females = 1.35 in.²; mean for virgins = 1.06 in.²). The size difference appears to be on the order of that found in *D. melanogaster*, but in no way approaches the difference found by Bodenstein between hosts that received extra corpora allata and his unoperated controls. Second, the apparent compensatory effect previously described for *D. virilis* was again quite clearly demonstrated in the present study. The mean values for corpus allatum size in 14 successful pairs of hosts and operated controls are 0.93 in.² for the former and 1.47 in.² for the latter. (A *t*-test showed the difference to be statistically significant, $P < .01$.) The average size for eight hosts, whose paired operated controls died, is 0.74 in.²; the mean for an additional six operated controls, whose hosts died, is 1.66 in.² (Unlike low rates in *D. melanogaster*, the mortality of both hosts and operated controls is extremely high for the line of *D. virilis* used in both these and other experiments.) The corpus allatum in three of the *D. virilis* hosts showed no reduction in size, so that the difference in mean values between hosts and operated controls is even greater if these are omitted. Because of the failure to demonstrate