ders suggest that the source rock may have been layered. In addition, the boulders are on a slope and one may postulate that the source rock is somewhere uphill from the area photographed. A process of degradation is, or was, clearly operating in this area. Because of the size, this process can be referred to as the decimeter-scale degradation.

Another process of degradation must also be postulated to account for the pitted surfaces and rounded edges of the outcrops at the Venera 10 landing site. Because of the scale, this process may be referred to as the centimeter-scale degradation. From a geomorphic point of view, the landscape of the Venera 10 landing site is more mature than that of Venera 9 landing site.

It is difficult to speculate on the nature of the two degradational processes. The decimeter-scale degradation is likely to be mass-wasting, but in the absence of liquid water it is hard to visualize the activating agent. If future landers find high seismic activity, venusian quakes could be the agent.

The centimeter-scale degradation is even more puzzling. The gentle winds and the inert atmosphere cannot be the agents, unless active chemical compounds are present in as yet undetected amounts. Sporadic inputs from volcanic events, either chemically or dynamically active, may also be possible (*13*).

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# Determining the General Circulation of the Oceans: A Preliminary Discussion

Abstract. *The classical oceanographic problem of deducing the unknown constant in the dynamic method—the problem of the "level of no motion"—may be treated as a geophysical inverse problem. The unknown "barotropic" velocity may be chosen to satisfy an arbitrary number of conservation laws, subject to perfect geostrophic balance and with explicit use made of the relative errors in the observations. The solution obtained is one of minimum energy. A western North Atlantic region is used to demonstrate the power of the method.*

Most knowledge of the general circulation of the world oceans is based on the classical dynamical method. Under the assumption of geostrophic balance, one computes the vertical shear of velocity from observed horizontal gradients in the mass field. The major difficulty with this method is that there is a missing constant of integration. This missing constant, the barotropic velocity, cannot normally be determined by direct means, and over the years oceanographers have developed a variety of ad hoc methods (*1*) for determining it as a function of position. Many of these methods are based on the idea of a "level of no motion"—the assumption that somewhere at depth there is a level (pressure surface) where the velocity vanishes. If there is such a level and it can be determined, then the missing constant of integration is known and the complete flow field computed. Most such methods are based on sometimes plausible, if imprecise and arbitrary, assumptions about the behavior of chemical tracers. None of them can be considered well established or very convincing. Hidaka (*2*) attempted to determine the barotropic flow directly by conserving heat and salt within a volume of ocean. He was criticized by Defant (*3*), who showed the problem to be ill posed and hence unstable. Stommel (*4*) used specific dynamical ideas to determine the meridional component of the barotropic flow, but with mixed results.

Worthington (*5*) has recently attempted a complete synthesis of the general circulation of the North Atlantic. He nearly conserves (some small property exchange does occur) total heat and salt at various levels in the ocean and constrains the circulation to absorb supposedly known amounts of water from various sources (such as the Norwegian Sea). To close his circulation, Worthington violates the assumption of geostrophy. If one seeks the reason for this violation it is seen to follow from his arbitrary selection of a level of no motion.

In this report I show that (i) one may require that geostrophic balance be exact, (ii) conservation of an arbitrary number of properties may be required to within any predetermined accuracy, (iii) there is an infinite number of flow fields that will satisfy (i) and (ii), (iv) out of the infinite number of solutions one may rationally choose a unique field based on a simple dynamical principle, and (v) the formalism permits one to understand the relationship between the flow field actually chosen and all other acceptable fields and the degree to which the observations actually constrain the flow.

The burden of this report is that this problem is an excellent example of one for which the formalism of geophysical inverse theory (*6–8*) is suited. To be specific, I consider the sections of hydrographic stations shown in Fig. 1. These were obtained by Worthington on the R.V. *Atlantis* in 1955. The stations are such that they nearly confine a volume of ocean including the Gulf Stream. With the ocean in a (presumed) steady-state condition, one expects that, on the average, there will be conservation of mass within this volume, and that to within an excellent first approximation individual water masses will also be conserved as long as they are not in contact with the atmosphere. There are $M = 43$ usable station pairs in Fig. 1. Figure 2A shows the geostrophic velocity field for the sections with the level of no motion assumed to be at the sea floor. This choice implies that 20 sverdrups ($20 \times 10^6$ m$^3$/sec) more water leaves the volume than enters it.

Let $v_{ij}$ be the known baroclinic velocity at pressure level $i$ between station pair

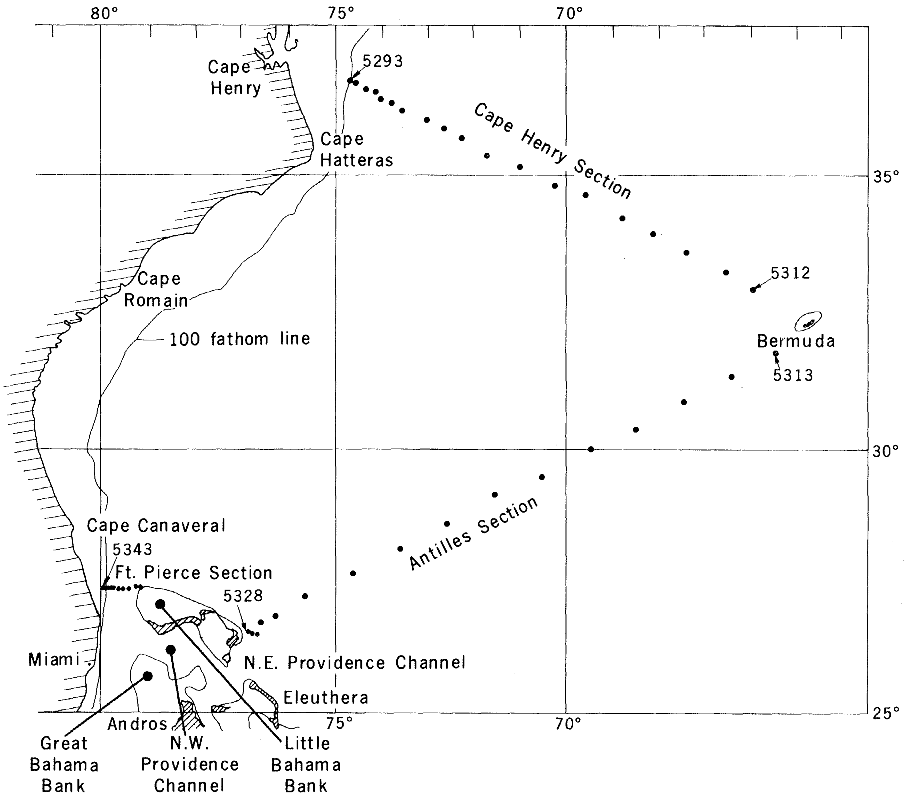

Fig. 1. Locations of *Atlantis* 215 stations used here.

$j$ computed relative to the bottom. Let $b_j$ be the unknown barotropic velocity between station pair $j$. With the present convention, this will be the bottom velocity. Let water having some characteristic property $C_k$ (such as temperature between 3° and 4°C, a particular salinity range, or simply mass) occupy a depth range $\Delta p_{kj}$ in station pair $j$ (depth is measured in pressure units), and $\Delta x_j$ be the horizontal station separation. Let $\bar{v}_{kj}$ be the average baroclinic velocity in that range; then the statement that property $C_k$ is conserved may be written

$$\sum_{j=1}^{M} (\bar{v}_{kj} + b_j)\, \Delta p_{kj} \Delta x_j = 0 \qquad (1)$$

and let there be $k = 1, \ldots, N$ such properties. Then we can combine Eq. 1 into matrix form

$$A\mathbf{b} = -\Gamma \qquad (2)$$

where $A$ is the $N \times M$ matrix of elements

$$A_{ij} = \Delta p_{ij} \Delta x_j \qquad (3)$$

$\mathbf{b}$ is the $M \times 1$ column vector of barotropic velocities, and $\Gamma$ is the $N \times 1$ column vector

$$\Gamma_i = \sum_{j=1}^{M} \bar{v}_{ij} \Delta p_{ij} \Delta x_j \qquad (4)$$

representing the imbalance of properties based on the baroclinic flow component alone. I have chosen a unit normal directed inward with the convention that the station separation $\Delta x_j$ is negative for stations in the northern Cape Henry section and positive for all parts of the southern sections. Positive velocities thus have a positive northward component.

For this example, I have chosen (following Worthington's division) to conserve the temperature ranges 12° to 17°C, 7° to 12°C, 4° to 7°C, and 2.5° to 4°C, as well as the total mass.

Equation 2 represents five equations in 43 unknowns (the total number of station pairs) and is thus underdetermined. Indeed the effective number of equations is actually less than five because some of the conservation requirements are nearly redundant (isotherm slopes tend to be parallel over the water column). It is this underdetermined nature of the problem that historically has led to arbitrary assumptions about the depth where $v_{ij} + b_j = 0$ in the water column.

Matrix $A$ has a uniquely definable inverse (*9, 10*) that allows one to select a particular solution to Eq. 2. This is the Moore-Penrose inverse

$$A^{-1} \equiv A^{\mathrm{T}}(AA^{\mathrm{T}})^{-1} \qquad (5)$$

where T denotes the transpose. A solution to Eq. 2 is

$$\mathbf{b} = A^{\mathrm{T}}(AA^{\mathrm{T}})^{-1}(-\Gamma) \qquad (6)$$

This value of $\mathbf{b}$ is the solution to Eq. 2 with the smallest possible variance (that is, $\mathbf{b}^{\mathrm{T}}\mathbf{b}$ is smaller than for any other of the infinite number of solutions); it is also the simplest solution. Equation 6 could also be obtained by least-squares minimization of $\mathbf{b}^{\mathrm{T}}\mathbf{b}$ with Eq. 2 imposed as a constraint.

In actually carrying out this procedure, some modifications are useful. Inspection of Eq. 5 shows that the greatest weight will be given to the stations with the greatest horizontal separation (largest $\Delta x_j$). This seems undesirable as an a priori consideration. To avoid this weighting we define a new diagonal matrix $W$ whose elements are the inverse station spacings $W_{jj} = \Delta x_j^{-1}$, a new matrix $A' = AW$, and a new vector $\mathbf{b}' = W^{-1}\mathbf{b}$, and then solve the new equation set

$$A'\mathbf{b}' = -\Gamma \qquad (7)$$

The Moore-Penrose inverse will minimize $\mathbf{b}'^{\mathrm{T}}\mathbf{b}'$, the mean square barotropic transport (*11*). Thus the solution obtained will have the minimum possible barotropic energy consistent with geostrophy and conservation requirements. We then obtain $\mathbf{b} = W\mathbf{b}'$.

Because the solution is determined from a minimal principle, it will depend on where in the space of all acceptable solutions the inversion procedure is started. It seems reasonable to use all available information in order to start as close to the observed state as possible. For this reason, the value of the transport through the Florida Straits section was increased to 33 sverdrups, close to the best observed value (*12*), by adding 29 cm/sec uniformly to the velocity field across the straits.

Another modification derives from recognizing that there are errors in the measurements. These are of two kinds: (i) errors of observation, such as navigational inaccuracies, and (ii) kinematic errors. The latter are probably the more important and arise from two distinct causes. The first and less important is the presence of the internal wave field, which leads to errors in the values of $\Delta p_{ij}$ and hence in $v_{ij}$. But more important, the ocean is filled with mesoscale eddies (*13*), which may be temporally or spatially aliased, and in their presence we do

Fig. 2. (A) Geostrophic velocity contours (in centimeters per second) computed with a level of no motion at the bottom. Flow violates mass and heat transport requirements. It is the starting solution used to obtain flow in (B) except that 29 cm/sec was first added to the Fort Pierce section velocities. Positive values are to the north. Areas of southward-moving water have been shaded. (B) Geostrophic velocity contours computed from the flow of (A) plus the barotropic velocity found from Eq. 8. Actual bottom speed is denoted by an underlined number. Conservation requirements are now met to the accuracy stated in the text.

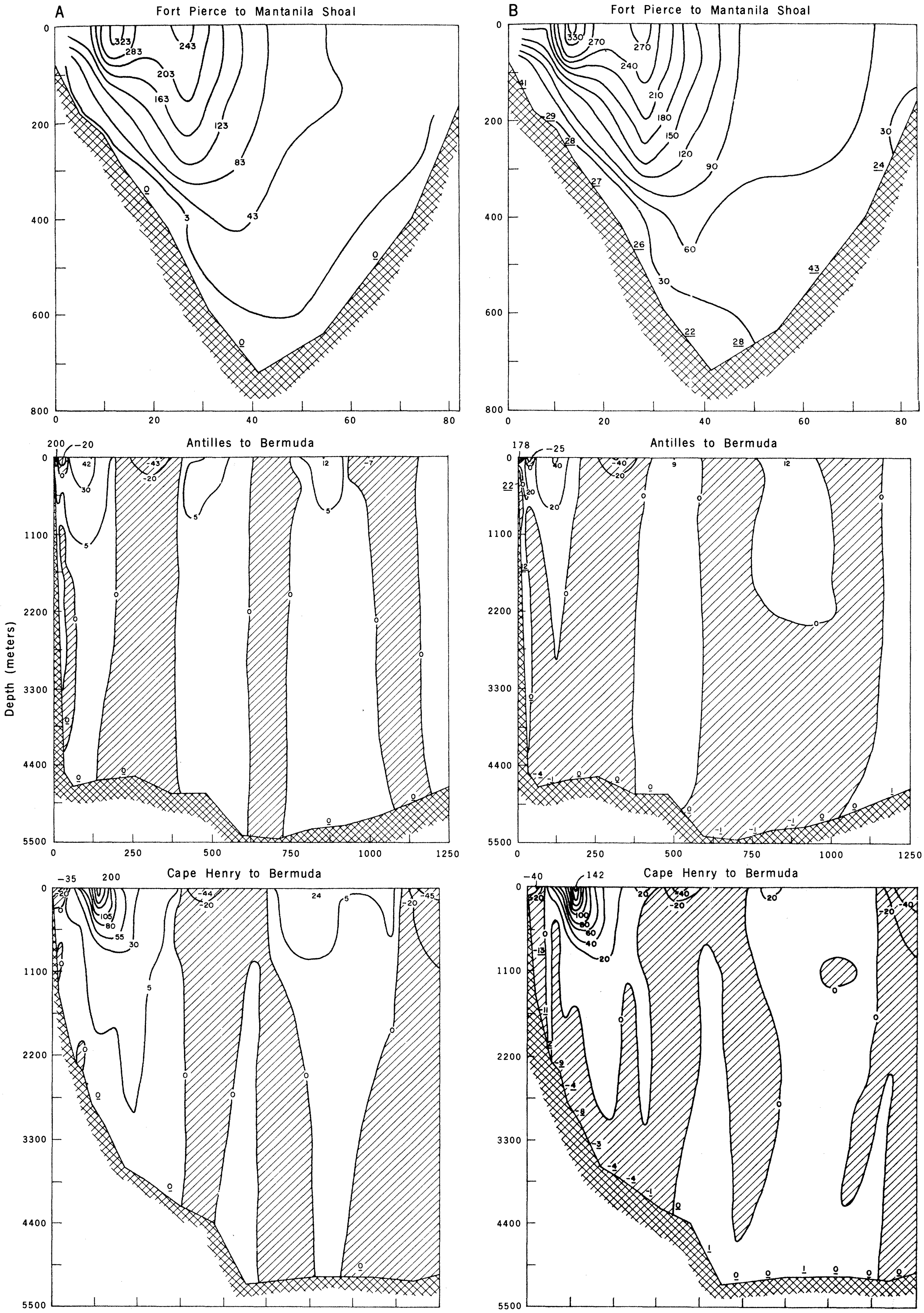
A
Fort Pierce to Mantanila Shoal
B
Fort Pierce to Mantanila Shoal
323
283
243
203
163
123
83
43
3
0
330
270
270
240
210
180
150
120
90
60
30
41
29
28
27
26
22
28
43
24
30
0
200
400
600
800
0
20
40
60
80
Antilles to Bermuda
200
−20
42
−43
−20
30
5
12
−7
178
−25
40
−40
−20
9
12
22
20
0
1100
2200
3300
4400
5500
0
250
500
750
1000
1250
Cape Henry to Bermuda
−35
200
105
80
55
30
5
−44
−20
24
−45
−40
142
100
80
60
40
20
−13
−11
−9
−4
−8
−3
−4
−1
1
0
200
400
600
800
Depth (meters)
Kilometers

Table 1. Initial and final transports through the three sections in sverdrups, rounded to the nearest sverdrup. Negative values are to the south.

| Water mass | Fort Pierce | | Antilles | | Cape Henry | |
|---|---|---|---|---|---|---|
| | Initial | Final | Initial | Final | Initial | Final |
| Total mass | 33 | 34 | 25 | 7 | 68 | 42 |
| 2.5° to 4°C | 0 | 0 | −2 | −10 | 4 | −9 |
| 4° to 7°C | 0 | 0 | 3 | 1 | 8 | 2 |
| 7° to 12°C | 5 | 5 | 10 | 6 | 13 | 10 |
| 12° to 17°C | 7 | 7 | 14 | 7 | 19 | 16 |

not expect that the conservation laws should apply instantaneously. Rather they are meant to apply as long-term averages. The required averaging interval may be years, and it is precisely for this reason that direct measurements of the mean barotropic flow are almost nonexistent; mean oceanic flows may be almost as inaccessible to direct measurement as the density within the earth's interior, the problem for which geophysical inverse theory was invented.

To recognize explicitly the existence of errors of both types, we can rewrite Eq. 7 as

$$A'\mathbf{b}' + \boldsymbol{\sigma} = -\Gamma$$

where $\boldsymbol{\sigma}$ is the vector error of observation. In practice, we here have handled this error by modifying $A'A'^{\mathrm{T}}$ through the addition of $\sigma^2 I$, where $I$ is the identity matrix, so that Eq. 6 becomes

$$\mathbf{b}' = A'^{\mathrm{T}}(A'A'^{\mathrm{T}} + \sigma^2 I)^{-1}(-\Gamma) \qquad (8)$$

It may be shown (*8*) that this modification reduces the dependence of the solution on the smaller eigenvalues of the matrix $A'$, eigenvalues which cannot, in fact, be distinguished from zero. In addition to this modification, we could weight the system (Eq. 7) by a matrix $S$ representing the uncertainty of the individual observations $\Delta p_{ij}$. For this particular example we have not done so, because the solution, Eq. 8, will be weighted by the observations that occupy the largest fraction of the water column—total transport conservation receiving the greatest weight—and this seems a reasonable first estimate of appropriate relative error. Future solutions should account for the fact that measurement errors are, in fact, correlated.

If $\sigma = 0$, the conservation requirements (*3*) are satisfied exactly, and we have computed solutions for this case; they are wildly varying and look unphysical. A study of the eigenvalues and eigenfunctions of $A'A'^{\mathrm{T}}$ suggests that the rank of $A'$ is actually little more than three or four and that perhaps only four of the conservation requirements are really independent. The solution is thus sensitive to slight changes in measurements. If the dependence on the near-zero eigenvalues is reduced by addition of a slight amount of noise $\sigma^2$ (here taken to be 0.08 percent of the trace of $A'A'^{\mathrm{T}}$) we obtain a well-behaved and stable solution (insensitive to $\sigma^2$); the conservation equations are no longer satisfied exactly, but that is as desired. The result of this computation is shown in Fig. 2B, where the full geostrophic fields of the two sections are displayed. In this solution the total mass imbalance has been reduced to 0.2 sverdrup. Table 1 lists the section transports before and after the addition of the solution $\mathbf{b}$. The worst case is the temperature range 12° to 17°C, where the mass imbalance is 2 sverdrups. This imbalance could be reduced if the $\sigma^2$ chosen is an overestimate, or it could be a real ageostrophic effect.

This first attempt at a solution is crude, but it does give something resembling the western boundary undercurrent under the Gulf Stream and a total flow through the Florida Straits not unlike that directly measured (*12, 14*). No single level of no motion emerges, but rather a complex spatial variability. Much of this variability is presumably due to the eddy field and could be reduced by using average sections—thereby reducing $\sigma^2$—or by taking advantage of the knowledge one obtains from the eigenvectors of $A'A'^{\mathrm{T}}$.

Although I have provided a particular solution to the mass flow problem for these sections, it is meant to be exemplary rather than optimal. The best choice of the error variance is still under study, as is the question of resolution; that is, which pairs of hydrographic stations are providing useful information and which are redundant or incompatible (*15*). Also, a number of crude numerical approximations have been made here that should be eliminated in a final solution.

The class of all solutions not chosen by the Moore-Penrose inverse is represented by the null space of $A$ and represents all free solutions $\mathbf{g}$, $A\mathbf{g} = 0$, which leave the conservation laws untouched. An arbitrary solution may be made up out of our particular solution and any linear combination of the null-space vectors.

At the moment, it is difficult to give anything but an esthetic argument as to why the ocean should be in a state of minimum barotropic energy (here also a state of minimum bottom velocity). But such minimal principles often emerge as dynamical consequences and one could seek such results from the equations of motion. The solutions obtained here appear to be attached to the structure of the bottom much as dynamics suggests should occur (bottom flows are expected to follow contours of $f/h$, where $f$ is the Coriolis parameter and $h$ the water depth). There is no dynamical rationale for the existence of a simple level of no motion as classically assumed.

Exploration of other minimal principles should be undertaken (perhaps minimum total energy or minimum derivatives). But the solutions I have obtained from the minimum principle used here are sufficiently close to the actual state of the ocean that it seems unlikely that a radically different requirement will be correct.

If any of the $b_i$ are known it is, of course, a simple matter to compute a new minimal solution embodying that new information. Also, additional information concerning geochemical or dynamical tracers may be assimilated to reduce the arbitrariness remaining in the solution space. A solution for the full western North Atlantic will be published elsewhere (*16*).

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17. I thank L. V. Worthington for suggesting the use of the R.V. *Atlantis* sections and for discussions of the problem, and B. Grant for computing help. Supported by NSF grant OCE 75003998 (POLYMODE). This is MODE contribution No. 85.

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# Aldehyde Oxidase Compartmentalization in *Drosophila melanogaster* Wing Imaginal Disks

Abstract. *Distribution of the enzyme aldehyde oxidase in mature* Drosophila melanogaster *wing disks may allow visualization of known developmental compartments comprising (i) presumptive dorsal and ventral wing surfaces, and (ii) the presumptive anterior wing and the presumptive posterior wing.*

Our objectives in this report are (i) to present aldehyde oxidase histological staining patterns that support the concept of developmental compartments within presumptive wing tissue of the fruit fly *Drosophila melanogaster*, and (ii) to report an upset in the distribution of the enzyme in the presence of the mutation for engrailed (*en*/*en*). Rigidly defined developmental compartments that originate early in development have been demonstrated for the *Drosophila* wing (*1, 2*). By staining for aldehyde oxidase (E.C. 1.2.3.1) during larval development, it has been observed that compartmental boundaries delineate the presumptive anterior wing blade compartment from the posterior compartment of the wing blade, as well as the dorsal from the ventral surfaces of the adult wing.

Adult *Drosophila* structures are formed primarily from groups of cells that have limited or no function during larval development. These groups of cells are referred to as imaginal disks and histoblasts. Our report concerns a single pair of imaginal disks which form the wings and some dorsal parts on the thorax. The *Drosophila* wing disk derives from about seven preblastoderm cells (*3*). Cell division proceeds until about 24 hours after the larva secretes the pupal case, at which time some 52,000 cells are present (*4*). The adult wing forms from an unfolding (evagination) and folding and extension (eversion) of the disk, primarily through cell flattening and possibly by some cellular movement (*5*).

Recently it was discovered that the *Drosophila* wing disk can be subdivided early in development into several defined areas, referred to as compartments, that are made up of small groups of founder cells (*1*). The term polyclone (*6*) is applied to descendants of these founders. Once a compartmental polyclone is formed, it may be divided into subcompartments with their founder cells. Resultant compartments may then be studied in the adult wing. Crick and Lawrence (*6*) suggest that histological staining for various enzymes in the imaginal disks may uncover biochemical compartments since cells in one compartment must biochemically differ in some way from cells of neighboring compartments. The enzyme aldehyde oxidase was chosen for study because of the relatively simple histochemical techniques involved, the highly repeatable patterns of activity that can be attained, and because we had already successfully used this histochemical technique to show abnormal aldehyde oxidase patterns in the eye portion of the eye-antennal imaginal disks of larvae possessing the homoeotic tumorous-head mutation (*7*).

The Canton-S wild-type laboratory strain, 15 other *Drosophila melanogaster* laboratory strains, a strain of flies mutant for engrailed (*8*), and an engrailed strain possessing about 2 to 4 percent of the normal amounts of aldehyde oxidase were used during the course of this study (*8*). All flies were maintained at 25°C on standard *Drosophila* medium. Third instar larvae and prepupae (from 1 to 12 hours after puparium formation) were sources for wing disks and prepupal wings. Preparation of disks and staining procedures followed those described previously (*7*).

The pattern of aldehyde oxidase activity in wing disks of late-third instars of the strains Canton-S, Oregon-R-C, and vermilion is shown in Fig. 1. Other laboratory strains analyzed showed similar aldehyde oxidase distribution in their wing disks. Areas of disk differentiation into adult wing blade, within region 1 (which includes the wing pouch), are central to our report. In Bryant's fate map of the mature wing disk (*9*), two parallel lines are shown that arc across the central portion of region 1 separating presumptive dorsal from ventral wing surfaces. Figure 1, a to c, shows that aldehyde oxidase activity follows the wing margin as outlined in Bryant's fate map (*9*).

Figure 1 also shows the developmental fate of various areas within the wing disk, while Fig. 2 shows their corresponding adult derivatives. Aldehyde oxidase appears to be a biochemical marker showing where folding at the presumptive wing margin will occur during differentiation into the dorsal and ventral surfaces of the adult wing blade.

Perpendicular to the aldehyde oxidase arc, on the left side of the disk, is activity in the form of two dark bands with a lightly stained area between them (region 1 of Fig. 1a). The entire left side of region 1 shows staining for aldehyde oxidase in the vermilion (Fig. 1c) and other laboratory strains. However, the stain does not extend to the right of the center band in the more than 200 disks studied from 16 laboratory strains. A similar but overstained aldehyde oxidase pattern has been recorded by Janning (*10*) in the Canton-S strain.

Perhaps the straight line separating the two areas represents a compartmental boundary separating the presumptive anterior portion of the adult wing blade from the posterior portion. Such a boundary must exist since Garcia-Bellido *et al.* (*1, 11*) found such a boundary in the adult wing blade. Cells from a clone are shown to divide mitotically along either side of a straight line following closely the fourth wing vein (Fig. 2) (*1, 6*). We used the homoeotic mutant engrailed, which transforms the posterior compartment incompletely into an anterior compartment, to study this compartmental boundary. Aldehyde oxidase distribution in an *en*/*en* wing disk is shown in Fig. 3, while Fig. 4 shows the triple row of bristles in the posterior compartment of *en*/*en* homozygous flies that is normally characteristic of the anterior compartment. A posterior row of hairs is normally observed in the posterior compartment (Fig. 2). Morata and Lawrence (*12*) show that the homozygous condition for engrailed (*en*/*en*) results in a breakdown of the anteroposterior compartmental line.

Apparently, function of the normal $en^+$ gene is necessary for maintenance of the compartmental boundary (*12*), and this gene controls pattern of veins and bristles (*13*). Based upon these results