is perceived but the object moves too rapidly to be followed as a rigid whole throughout its trajectory. In the final stage, rated "3," the two alternating views appear superimposed. There is flickering but no apparent movement.

The subject took as much time as he needed on each trial to rate the quality of the apparent movement for a given pair at a particular rate of alternation. The trials were grouped into three equal blocks by condition, with half of the depth pairs preceding and half following the block of picture-plane pairs. Each subject rated a particular pair at all nine rates of alternation before proceeding to another pair with a new angular difference. The order of the five angular differences was counterbalanced across subjects, and the order of the nine rates of alternation within each angular difference was randomized separately for each subject.

Although the subjects were not informed of either the angular difference or the randomly chosen rate of alternation for each successive trial, each subject gave consistent ratings, which generally changed monotonically with rate of alternation. Out of the 1350 ratings, there were only five violations of monotonicity. According to the subjects, the perceptual experience produced by a given rate of alternation of a given pair of views was quite distinctive and readily classified on the three-point scale.

For sufficiently slow alternations, ratings of "1" are consistently given, but beyond some critical rate, the rigid coherence of the apparent movement is lost and the ratings rather abruptly fall off toward "2" (Fig. 2A). (Some subjects exhibit a short plateau at "2," which indicates that the experience of nonrigidity or noncoherence of the motion can occur over a range of rates.) Typically, as the angular difference is reduced, the drop occurs at shorter field durations; that is, for smaller angles, the appearance of rigid rotation of the object as a whole is maintained into more rapid rates of alternation.

As a quantitative estimate of the field duration at which the appearance of coherent rigid motion breaks down for each pair of views, we took the duration corresponding to the point at which the linear rating profile, starting from the level 1, first reached the level of 1.5, halfway between the ratings for rigid and nonrigid motion. For the rating profiles shown in Fig. 2A, this crossing point occurred at durations (to within 5 msec) of 100, 140, 180, 230, and 270 msec for angles of 20°, 60°, 100°, 140°, and 180°, respectively.

Although the results for individual subjects are more variable for this task than they were in the mental rotation task of Shepard and Metzler (*1*), the mean results (Fig. 2B) are parallel. Again we find that estimated time increases linearly with angular difference; the slope is virtually the same for differences in depth and in the picture plane. Statistical analyses indicated no significant departure from linearity in either of the two functions and no significant difference between their slopes. [The fact that the absolute times were again slightly longer, overall, for the picture-plane pairs may be attributable, as in the earlier studies (*1, 2*), to properties peculiar to the particular objects and views chosen for the depth and picture-plane pairs.]

The total range of times here of only 190 msec (from about 110 msec at 0° to 300 msec at 180°) is much less than the corresponding 3500-msec range (from 1 second at 0° to between 4 and 5 seconds at 180°) in the previous mental rotation task. Whereas the earlier range corresponded to an estimated rate of mental rotation of 50° to 60° per second, the present range corresponds to a vastly greater rate of nearly 1000° per second. The similarity between the patterns of these and the earlier results is consistent with the growing body of findings that corresponding processes of visual imagery generally proceed much more rapidly when (as in more perceptual tasks) they are driven externally than when (as in purely imaginal tasks) they must be generated internally (*4*).

The finding of near equivalence between the breakdown times for apparent rotation in depth and in the picture plane adds to earlier evidence (*5*) that phenomena of apparent movement are governed by relations in an internally constructed representation of something three-dimensional rather than by distances in the purely two-dimensional retinal image.

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3. This relation is generally known as Korte's third law. Reviews of some of the classical work on apparent movement can be found in E. G. Boring [*Sensation and Perception in the History of Experimental Psychology* (Appleton-Century-Crofts, New York, 1942)] and in P. A. Kolers [*Aspects of Motion Perception* (Pergamon, New York, 1972)].
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6. Supported by NSF grant BMS 75-02806 to R.N.S. Under her former name, S. J. Huntsberger, S.A.J. presented this work at the annual meeting of the American Psychological Association in Chicago, 31 August 1975.

29 September 1975

A Line, Not a Space, Represents Visual Distinctness of Borders Formed by Different Colors

Abstract. *When observers are asked to rate the visual distinctness of borders formed by the junction of two photic stimuli, normal trichromatic subjects behave in a manner similar to that of tritanopes in a color mixture experiment. All stimuli that look the same to the tritanope produce the same border distinctness with any other stimulus. Sets of such stimuli, whose members do not form borders with each other, map as single points along a curved line, where the Euclidean distance between pairs of points representing the two stimuli is nearly proportional to the rated distinctness of the border formed between them. In the absence of luminance differences, the perception of contour apparently depends on the stimulation of only two cone types.*

Colors of equal luminance are typically conceived as being arranged in a two-dimensional space. White is at the center, spectral colors form the outer limits, complementary colors are opposite, and nonspectral colors fill the space defined by spectral colors and nonspectral purples. This representation characterizes chromaticity diagrams derived from color mixture data, and also describes purely psychological color diagrams based upon the appearance of colored chips without regard to their physical characteristics (*1, 2*).

In experiments described here, observers were required to ignore color appearance and judge instead the distinctness of a contour formed between two adjacent fields of light (*3*). In each case, before the distinctness judgment, the intensity of one field was varied with respect to the other until the border formed between them appeared minimally distinct. By this criterion of judging color pairs, we have obtained the unexpected and surprising result that all colors—spectral and nonspectral alike—can be ordered along a line.

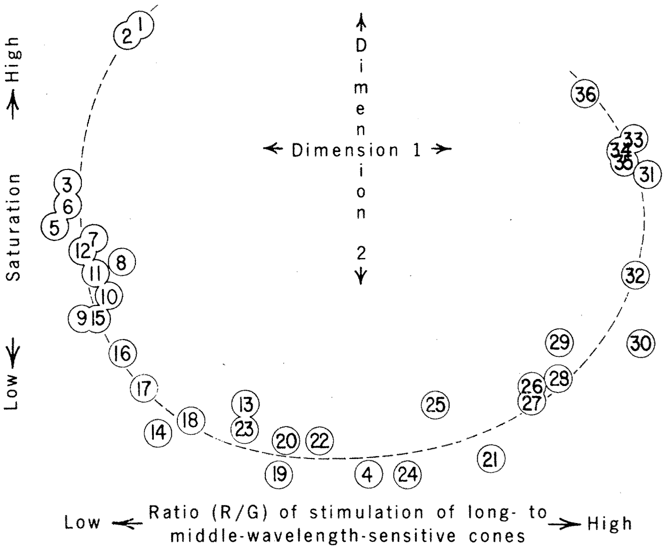

Fig. 1. Results from the multidimensional scaling of judged differences among all possible pairs of 36 nonspectral colors. Stimuli were juxtaposed and the luminance of one of the pair was adjusted so that the border between them was minimally distinct. Distinctness was then judged on an eight-point scale. Distances between points in the two-dimensional space depicted here and the initial distinctness ratings (obtained experimentally) are highly correlated (r = .98). Within the limits of experimental error, all of the points fall along a curved line schematized here by a curve fitted by eye. A second experiment (Fig. 2) demonstrated that each of these nonspectral colors is equivalent, in its border-forming properties, to some monochromatic stimulus. The wavelengths of these equivalent stimuli are given in Table 1.

We investigated 36 nonspectral colors having the chromaticities shown in Table 1. These were presented in all possible combinations as the right and left halves of a circular, 25-troland bipartite field subtending 1.35° of visual angle. The stimulus on the right served in each case as a reference field. Each of the 36 stimuli had been previously adjusted in intensity to form a minimally distinct border (MDB) with a white reference field; thus the entire experiment was done at a constant luminance (*4*). The other 35 stimuli were presented in turn to the left field.

Our first task as observers was to adjust the intensity of the left field until an MDB was formed between it and the reference field. After doing this, we rated the perceived distinctness of the border on an eight-point scale, where 0 corresponded to no perception of a border, 1 meant a just-perceptible border, and 7 represented a very distinct border.

The data of the experiment were arranged in a 36 × 36 half matrix representing all possible pairs of different colors. There were four entries in each cell—two for each subject times two for the right-left positioning of otherwise identical pairs. The averages of these sets of four distinctness ratings comprised 630 entries into a multidimensional scaling program (*5*). The purpose of the scaling procedure was to find a representation of the 36 stimuli as 36 points in a space of the least number of dimensions such that the experimentally obtained distinctness ratings were approximately monotone or, preferably, nearly porportional to corresponding distances. For example, points representing stimuli that formed very distinct borders (rating of 7) should be far apart on such a diagram whereas those for stimulus pairs rated 0 should coincide. Although degree of monotonicity improves with the number of dimensions in the solution, the validity and interpretability of the configuration becomes more uncertain so that it is generally advisable to attempt to find a solution in as few dimensions as possible (*6*).

The result of this analysis is schematized in Fig. 1. The correlation of Euclidean, straight-line distances between points in this configuration and the distinctness ratings is .98, which indicates that this arrangement of the stimuli well represents the perceived distinctness of borders formed between them. Spectral and nonspectral colors are intermixed along the line in a systematic way. Stimuli that are located at the same point on the line should form 0-rated borders with one another, and any one of these should be equivalent to any other when tested with a color that plots elsewhere on the line. It should be emphasized, contrary to previous reports, that this figure clearly does not represent a chromaticity diagram or color mixture diagram (*7*). The space in which the line rests can only be viewed from the standpoint of the subjects' task—the rating of border distinctness. Thus, it is not possible to "mix" two stimuli together to produce a point that plots somewhere other than on the line, for within experimental error, all stimuli fall on its locus.

In an attempt to understand this result, we then asked the question: How are sets of stimuli arranged in chromaticity space, so that members of these sets map onto a single point along the line? An initial inspection of the chromaticity of stimuli that plotted close together on the line suggested that the points within such clusters would probably be confused by tritanopic observers—members of that rare class of dichro-

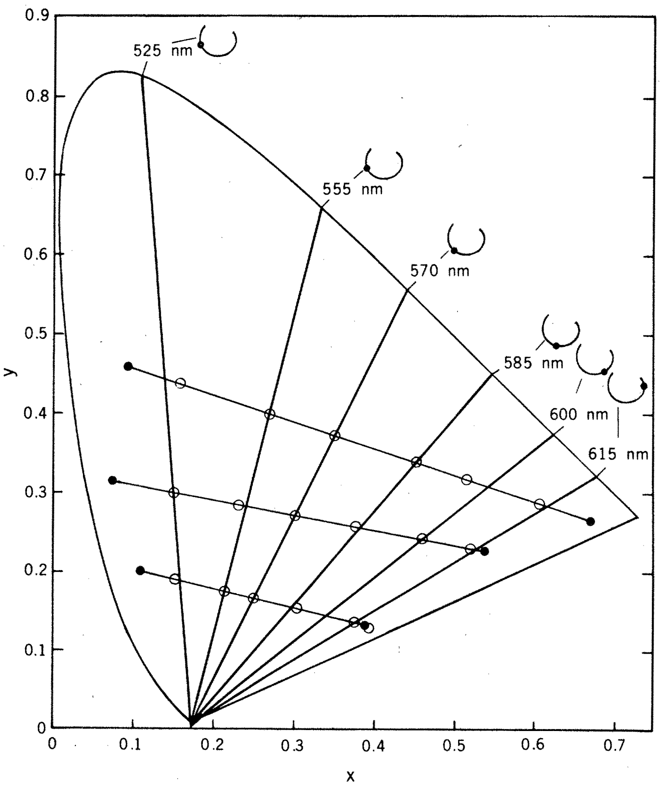

Fig. 2. In this experiment, monochromatic stimuli of the wavelengths shown in this C.I.E. chromaticity diagram were juxtaposed with mixtures of nonspectral primaries. There were three sets of these, defined by the connected solid points. Subject B.W.T. adjusted the ratio of the primaries at constant luminance until an MBD was formed between the mixture and the monochromatic stimulus beside it. In most such cases the border disappeared entirely. The residual border was otherwise always very indistinct and was never visible to the other subject. The chromaticities of the mixture points, as determined by the method of vector colorimetry, were determined and are shown by the open circles. An additional experiment that permitted exact matches to be made under a condition of artificial tritanopia yielded identical results. The straight lines converging toward the blue corner of the diagram are the tritanopic confusion lines. All of the chromaticities which fall along these lines collapse to single points on the line at approximately the locations shown.

mat believed to lack the cones sensitive to short wavelengths (*8*). We confirmed this in two further experiments. In the first, the experimenter set a monochromatic light of fixed intensity into the left field. The observer then adjusted the chromaticity and luminance of the light in the right field (which fell somewhere along the lines defined by the solid end points shown in Fig. 2) until he had minimized the distinctness of the border. Subject R.M.B. could always find a unique setting that produced an MDB of 0; subject B.W.T. could always produce a unique setting, but sometimes weak borders were seen.

The results of this experiment (Fig. 2) defined lines that converge toward the tritanopic copunctal point, which represents the missing receptors sensitive to short wavelengths. This finding was tested directly in another experiment. Each observer was exposed for 5 minutes to an intense blue light (436 nm, 10^5 trolands) and continued to view it throughout the session except for the periods required to make instrument settings. The purpose of the adapting light was to create and maintain a state of artificial tritanopia (*9*) by suppressing the sensitivity of cones sensitive to short wavelengths more than that of the other two types. Subject R.M.B. was wholly successful in doing this: at the match point the field appeared as a circular spot of homogeneous color.

Data from the two experiments were identical within experimental error (*10*). For subject R.M.B., this means that if the effects of adaptation to the blue light are allowed to wear off, the color difference that emerges between the halves of the previously uniform field does not produce a discriminable border (*11*). Subject B.W.T.'s results are consistent with this except that he sometimes perceived a slight color difference under artificial tritanopia. These findings suggest that the cones that mediate the perception of blueness in trichromatic observers do not contribute to the perception of contour (*12*). This means that any two stimuli that activate cones sensitive to long and middle wavelengths equally will fail to support a contour at their junction. Consequently, any observer with only one of these latter two types of cones should see no contour when the remaining cones are equally activated on both sides of the field, and borders rated 0 should therefore occur for any two chromaticities provided that adjustment of the relative intensity of one of them is allowed. This leads to the prediction that protanopes and deuteranopes, who are believed to lack cones sensitive to long and middle wavelengths, respectively, but who have normal cones sensitive to short wavelengths, should show no sensitivity to borders formed by any two chromaticities at an MDB because they lack one of the two mechanisms required for border perception in the absence of luminance differences (*13*). The tritanope, who lacks cones sensitive to short wavelengths, should make the same setting as the normal trichromatic observer. These results have led us to consider the question of the underlying structure of the initial scaling study reported here. From the latter experiments it seems clear that the activities of the cones sensitive to long and middle wavelengths can be posited as the major underlying mechanism contributing to these results. We have tentatively labeled the axes of Fig. 1 with this in mind; further experimentation is needed to determine more thoroughly the shape of the line. The abscissa can be seen to relate to the ratio of the activities of the two cone types under consideration while the ordinate may relate to some aspect of saturation.

Our results may have important implications for attempts to understand color metrics by using MacAdam ellipse data as the empirical base against which to test color discrimination theory. MacAdam's original observer attempted to match colors along various meridia in chromaticity space (*14*). The dispersion of his settings was used as an index of perceived color difference in the direction of the variable stimulus. MacAdam's fields were juxtaposed, but not perfectly so, such that the border between them did not completely disappear after the observer made a color match. It is therefore possible that the observer may have confounded two different criteria in making settings: (i) just-noticeable differences in color appearance and (ii) minimally perceptible border distinctness. Our results indicate that these two criteria of judgment depend upon very different mechanisms (*15*).

Table 1. 1931 Commission Internationale d'Eclairage (C.I.E.) chromaticity coordinates of the 36 stimuli used in the initial experiment. Also shown is the wavelength of a monochromatic light that a tritanopic observer should confuse with the stimulus.

Stimulus	*x*	*y*	λ (nm)
1	.16	.02	455
2	.16	.04	503
3	.17	.18	532
4	.17	.03	533
5	.23	.74	540
6	.21	.45	541
7	.23	.38	546
8	.24	.32	552
9	.30	.65	552
10	.26	.48	552
11	.26	.30	558
12	.30	.45	558
13	.21	.10	563
14	.31	.38	563
15	.27	.24	566
16	.26	.20	567
17	.31	.30	567
18	.39	.49	567
19	.22	.11	567
20	.41	.50	569
21	.20	.05	573
22	.25	.12	578
23	.33	.24	578
24	.24	.10	578
25	.34	.20	586
26	.35	.20	588
27	.33	.16	592
28	.47	.30	592
29	.59	.39	594
30	.26	.08	594
31	.36	.13	608
32	.64	.30	614
33	.40	.14	617
34	.51	.20	619
35	.64	.25	635
36	.73	.27	660

In chromaticity space, one can trace out many paths from one color to another along a graded series of colors. Although a straight line does not necessarily represent the smallest number of just-noticeable differences between two such points, there is at least no problem about varying chromaticity along such a straight-line path. The representation of stimuli in two-dimensional border distinctness space has very different properties because there is only one path that can be followed in a continuous series leading from one color to another, and this is the curved path along the line in Fig. 1. Yet the measure of sensory difference between two stimuli juxtaposed and compared in this way is not the length of that curved path, but rather the length of the straight line connecting the points representing the two stimuli—a line along which no real colors lie. This provides an unusually clear example of how integrating just-noticeable differences can lead to incorrect conclusions about the size of large sensory differences.

Some of the 36 stimuli tested in our initial experiment lie on the spectral locus of chromaticity space, and are thus equivalent in chromaticity to spectral colors. It is an unorthodox notion that spectral and nonspectral colors can be represented together for any purpose along a single line. It may help to recall that this does occur in the one-dimensional chromaticity diagrams of dichromats, and because we deal here not with color appearance but border distinctness, normal observers behave like tritanopes. Thus, the fan of lines in chromaticity space—each representing a set of colors all of which are seen as the same by a tritanope—can be used to determine which spectral color is equivalent to any given nonspectral color with respect to contour-producing ability.

Along the curved line, white is located near the center and other colors appear to be graded according to increasing imbalance of the activity of the cones sensitive to long and middle wavelengths. One direction from white indicates the relative increase in the activity of the long-wavelength cones while the other direction indicates relative increase in the activity of the middle-wavelength cones. Whereas representation of the same stimuli in chromaticity space shows which colors are equivalent when used as members of an MDB pair, representation in border-distinctness space shows how all possible sets of such stimuli map along the line, which in turn predicts their ability to form contours with other colors.

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3. R. M. Boynton and P. Kaiser, *Science* **161**, 366 (1968).
4. The juxtaposition of the photometric fields was done with unusual care. An achromatizing lens whose prescription has been given (*1*, p. 212) is used to minimize the effects of axial chromatic aberration. The fields are so precisely aligned that, if there is no perceptible color difference, the border between them disappears completely at equal luminance and for a range of a few percent on either side of this which constitutes the threshold of contrast perception. See R. M. Boynton [*J. Opt. Soc. Am.* **63**, 1037 (1973)] for a review of experiment and theory concerned with the minimally distinct border, and for further references.
5. We used nonmetric multidimensional scaling methods of the sort developed → R. N. Shepard [*Psychometrika* **27**, 125 (1962); *ibid.*, p. 219] → J. B. Kruskal [*ibid.* **29**, 1 (1964)]. Essentially identical best-fitting solutions were obtained in two dimensions by using Kruskal's M-D-SCAL (version 5M) with random initial configurations and the more recent program KYST (derived from the names Kruskal, Young, Shepard, and Torgerson), which incorporates Young and Torgerson's method for generating a rational initial configuration.
6. R. N. Shepard [*Psychometrika* **39**, 373 (1974)] cautions against the extraction of more dimensions than can be provided with reasonable and meaningful interpretations. Although our initial choice for a solution was a helical line in three dimensions, a curved line in two dimensions well represents the basic properties of the findings. Also, at this point we can offer no compelling interpretation for a third dimension. The two-dimensional solution was retained in preference to the one-dimensional one here because it permitted an appreciably closer approximation to a proportional relation between distinctness ratings and distance and because both dimensions were susceptible to plausible interpretation.
7. R. M. Boynton and H. G. Wagner, in *Color Metrics*, Proceedings of the 1971 International Color Symposium on Color Metrics, J. J. Vos, L. C. F. Friele, P. L. Walraven, Eds. (Institute for Perception, TNO, Soesterberg, Netherlands, 1972), pp. 26–35; R. Ward and R. M. Boynton, *Vision Res.* **14**, 943 (1974).
8. As a result, there are lines of color confusion for a tritanope that plot on the chromaticity diagram for a normal observer. These lines converge toward a point just outside the "blue" corner of the space of real colors (Fig. 2). This point defines the spectral sensitivity of the short-wavelength-sensitive cones as altered by the absorption of the preretinal media [P. L. Walraven, *Vision Res.* **14**, 1339 (1974)]. Walraven also presents tabular data describing the spectral sensitivities of the three trichromatic cone types whose sensitivities peak at about 570, 540, and 440 nm, respectively.
9. G. S. Brindley, *J. Physiol. (London)* **122**, 332 (1953). We thank D. I. A. MacLeod for suggesting this experiment to us.
10. The end points of the color mixture lines are shown in Fig. 2. In none of the experimental cases did the difference between the mean of five settings under the trichromatic condition differ significantly from the mean of five settings under the artificial tritanopia condition. The degree of relationship between the wedge settings of these two experimental conditions is very high (r = .995 for both subjects).
11. It is difficult to describe the appearance of a field that differs in its two parts where color is concerned, there being nevertheless no clear contour separating them. Perhaps the best description is to say that one field seems to "melt" into the other [R. M. Boynton and T. S. Greenspon, *Vision Res.* **12**, 495 (1972)].
12. The residual contour for B.W.T. may have been due to chromatic aberration, as the achromatizing lens does not seem to correct his eye as well as it does that of R.M.B. Under conditions of normal trichromacy, for subject B.W.T., there was no one position of the achromatizing lens which could be used to bring all wavelengths of light in the two stimuli to perfect juxtaposition. Thus, when the long- and middle-wavelength components of the stimuli were aligned, the short-wavelength components were not. This misalignment of the short-wavelength component could differentially stimulate cones sensitive to long and middle wavelengths on either side of the border, thus contributing to the residual border perception.
13. In initial studies of two deuteranopes and three protanopes, tentative evidence in support of this prediction has been obtained. It has not been possible to evaluate these observers in the same experimental paradigm reported here, however, and because of this we are cautious with respect to the conclusions. Additionally, the prediction also implies that the spectral sensitivity of cones sensitive to middle and long wavelengths for the protanope and deuteranope, respectively, could be determined with the MDB technique. Tentative evidence in support of this notion has also been obtained (B. W. Tansley, in preparation).
14. D. L. MacAdam, *J. Opt. Soc. Am.* **32**, 247 (1942).
15. For example, if two fields were perfectly juxtaposed and the observer used the criterion of a just-discriminable border, none would be seen if the chromaticity varied along a tritan confusion line. F. Parra [in *Color Metrics*, Proceedings of the 1971 International Color Association Symposium on Color Metrics, J. J. Vos, L. C. F. Friele, P. L. Walraven, Eds. (Institute for Perception, TNO, Soesterberg, Netherlands, 1972), pp. 88–92] has reported results that support this idea. We observe that the color difference between the halves of such a field is definitely enhanced if there is a separation between them. On the other hand, when chromaticity is varied in a direction perpendicular to a tritanopic confusion line, a small variation in chromaticity produces a very discriminable border. In this case, if the fields were separated slightly so that the color appearance became the only cue for perception, sensitivity might well be reduced.
16. We thank R. N. Shepard for his helpful comments regarding the multidimensional scaling procedures used in this study. Supported by NIH grants No. EY 00187-20 and EY 01541-01 to R.M.B.

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Fishes in Oxygen-Minimum Zones: Blood Oxygenation Characteristics

Abstract. *Teleosts living in some mid-water pelagic regions of the Pacific are hypoxic or anaerobic during most of the day and become aerobic only during their diurnal migrations to and from the sea surface. The blood oxygen capacities of these fishes are among the lowest ever reported, and the oxygen dissociation curves show a very low affinity for oxygen.*

The oxygen-minimum zone in the northeastern tropical Pacific is the largest open-ocean area exhibiting well-developed hypoxic or anaerobic features (*1*). In the eastern extremes of this ocean off the coast of central and southern Mexico, the depth of the oxygen minimum (the dissolved oxygen content is generally less than 0.1 ml per liter of seawater) extends from approximately 100 to 900 m with relatively little variation throughout the year, or from year to year (*2*).

Biologically, however, the eastern portion of the low-oxygen region is characterized by surprisingly abundant populations of metazoans, living in the oxygen-impoverished water at least during daylight hours, and often associating in deep scattering layers (DSL) (*3*). These populations, particularly the fishes, make a diurnal migration to the surface at dusk and return to depth just prior to sunrise in the classical DSL pattern characteristic of these species. The vertical migrations amount to 300 m or more.

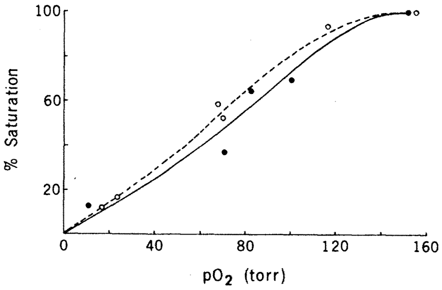

Fig. 1. Oxygen dissociation curves (at 0°C) for *Myctophum nitidulum* (●) and *Vinciguerria lucetia* (○).

Paradoxically, the fishes present in the low-oxygen region often have gas-filled swim bladders with high percentages of oxygen (Table 1) (*4*). The means by which such diverse groups as fishes, squids, crustaceans, and others survive in the condition of low oxygen are poorly understood, but in the case of some crustaceans and at least one fish they include adaptations permitting regulation of oxygen consumption in environmental oxygen concentrations dropping as low as 0.2 ml per liter of seawater (*5*). We report here some physiological parameters of the blood of representative fishes from this region.

Fishes were collected with a Tucker net (*6*) equipped with a timer-actuated, opening-closing mechanism, an acoustic depth-indicating pinger, and a digital flowmeter mounted within the body of the net. The