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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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 by R. N. Shepard [*Psychometrika* **27**, 125 (1962); *ibid.*, p. 219] and 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).
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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.

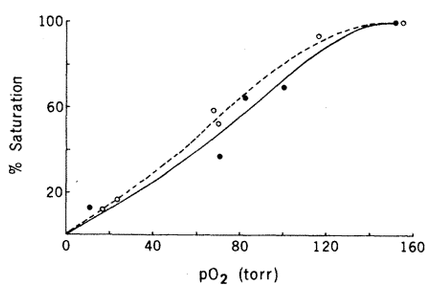

Fig. 1. Oxygen dissociation curves (at 0°C) for *Myctophum nitidulum* (●) and *Vinciguerria lucetia* (○).

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

Table 1. Blood oxygen capacities and percentages of swim bladder oxygen from fishes in the DSL and oxygen-minimum zone.

Specimens	Number sampled	Blood oxygen capacity*		Swim bladder oxygen† (%)
		Determinations	Percentage (by volume)	
Myctophidae				
Myctophum nitidulum‡	22	6	3.6	85
Lampanyctus parvicauda	6	4	1.5	75
Lampanyctus idostigma‡	5	2	1.5	§
Diaphus pacificus	3	2	2.2	90
Gonichthys tenuiculus‡	16	2	3.2	§
Melamphaidae				
Melamphaes acanthomus‡	2	1	3.0	85
Scopelogadus mizolepis bispinosus	3	2	1.6	87
Gonostomatidae				
Vinciguerria lucetia	12	4	1.5	82
Diplophos (proximus ?)‡	3	2	3.6	93

*These determinations represent replicate analyses from a single pooled sample of blood. The maximum range in the values was ± 0.2 percent (by volume). †Highest individual measurement. ‡*Myctophum nitidulum* was taken only from Station Westfall (30°N, 120°W), in the California Current where the minimum oxygen concentration was 0.26 ml/liter. *Lampanyctus idostigma* and *Gonichthys tenuiculus* were taken only from 22 °N, 111°W, a station in the frontal zone in the boundary between the transitional water of the California Current and the equatorial water of the eastern tropical Pacific, although both species have listed ranges extending through the oxygen-minimum zone of the eastern tropical Pacific (*19*). *Melamphaes acanthomus* is found from southern California to the Gulf of Panama at depths between 700 and 3500 m (*20*). Our specimens were from a single haul made at 16°N, 107°W, between 850 and 900 m; in that interval the oxygen concentrations ranged between 0.38 and 0.43 ml/liter. The taxonomy of the eastern Pacific species of *Diplophos* is quite unsettled (*21*). Thus our identification of this fish is tentative. §The swim bladder of *Lampanyctus idostigma* is regressed and fat-invested. No swim bladder was observed in *Gonichthys tenuiculus*, in agreement with the observations of Marshall (*22*), who found no trace of a swim bladder in *Gonichthys cocci* adults from the Atlantic. Hematocrits obtained from pooled blood samples of *L. idostigma* and *G. tenuiculus* were 3.9 and 12.7 percent, respectively, further substantiating the low oxygen capacities obtained on blood from these animals.

closed net was lowered to a selected depth, allowed to open, and trawled, generally in stepwise fashion, for 35 to 95 minutes until closure occurred (*7*). Because the net was open only for specified intervals of time and depth, the fishes and larger plankton sampled were uncontaminated by specimens from other depths. Within 10 minutes of closure, the net was on deck; the fishes were immediately placed in iced seawater, and blood sampling was begun. An incision was made from the ventral side into the pericardium, exposing the beating heart. Blood was obtained from the ventricle by puncture with a heparinized capillary tube fitted with a length of polyethylene tubing used for suction. Standard lengths of the fishes ranged from 25 to 100 mm.

Blood gases were determined microgasometrically (*8*) on pooled blood samples. All blood was equilibrated at 0°C in an ice slurry. Oxygen capacities were determined by air equilibration, and we constructed the dissociation curves by equilibrating blood with different air-nitrogen mixtures. The swim bladder gases were analyzed with an accuracy of 0.2 to 0.3 percent (by volume) (*9*). Blood gases were analyzed with comparable accuracy (*8*). The precision of duplicates was 0.2 percent (by volume) for both gas and blood analyses. The CO_2 tension of the blood was equal to or less than 0.3 torr.

The low oxygen capacities (Table 1) and the low affinities for oxygen demonstrated in the dissociation curves (Fig. 1) are striking. Oxygen capacity or affinity can sometimes be correlated with oxygen demand as in tunas and their relatives (*10*). Fishes in low-oxygen waters in some cases have evolved air-breathing habits and have higher blood oxygen capacities than fishes from more normally oxygenated environments (*11*). A few teleosts have blood oxygen capacities approaching those reported here, but these fishes tend to be benthic forms living in areas of comparatively high oxygen (*12*). Factors such as temperature, the partial pressure of CO_2 (pCO_2), and organic phosphates within the erythrocytes, along with physical activity and possible accessory respiratory organs, all further complicate interpretation of the oxygen dissociation curves of fish blood (*13*).

These DSL fishes, however, undertake vigorous vertical migrations of several hundred meters toward the surface at dusk and return to depth at dawn. Most of the migrations are accomplished in 1 to 2 hours, as a result of which these fishes encounter rapidly changing environmental variables, such as dissolved oxygen concentrations changing by one to two orders of magnitude, temperatures varying by as much as 20°C or more, and hydrostatic pressures increasing or decreasing by 30 to 40 atm. During daylight hours the fishes are probably inactive (*14*) and are strongly hypoxic or anaerobic.

Data available at present do not permit us to conclude that small mesopelagic fishes from less limited oxygen environments will not also have blood oxygen capacities as low as those reported here. For example, *Myctophum nitidulum* (Table 1; Fig. 1) from a station in the southern part of the California Current (30°N, 120°W) seldom encounters an oxygen minimum lower than 0.2 to 0.3 ml/liter, whereas the lower values in the area sampled on the *Minox* cruises were an order of magnitude below these. Thus, it is not yet clear whether the low capacities we report here represent an adaptation to the ultralow oxygen regime per se or are a response to a complex of factors associated with a life-style oscillating daily between relatively quiescent, hypoxic, cold episodes at depth, and active, oxygenated, warmer intervals connected with near-surface feeding at night.

Oxygen minima are a ubiquitous feature of the oceanic world, but seldom in the pelagic realm is the oxygen minimum found to be so pronounced or of so great an extent as in the region of our study. Conceivably, the complications associated with the delivery of oxygen to the tissues in an environment exhibiting such an extreme paucity of oxygen may be the factors responsible for these very low blood oxygen affinities of the teleost fishes listed here (Fig. 1). On the other hand, no more than 1 percent of the hemoglobin would be oxygenated under these circumstances while the fishes are at depth (Fig. 1), and it seems more likely that they must obtain energy by alternate pathways as suggested for other facultative anaerobes (*15*).

The swim bladder oxygen that must be resorbed into the vascular system during upward migration is also available for aerobic metabolism. The situation is reversed, however, when the fishes migrate downward and apparently resecrete some gas into their swim bladders, perhaps at least in part for buoyancy regulation (*4, 16*). The energy requirements of these activities have been studied (*17*) but can still only be approximated, because in the extreme oxygen minimum the particular physiological and biochemical processes involved are as yet poorly understood.

Adaptation to an extreme environment frequently involves changes in several aspects of a physiological system. The hemoglobin-free blood of antarctic icefishes, for instance, also has a low oxygen capacity (*18*), but the subzero habitat is well oxygenated. The low oxygen capacities of the *Minox* fishes, like the icefishes, could in part be supplemented by various cardiovascular adjustments such as increased cardiac output, increased blood volume, or circulatory shunts (*18*), but these adjustments are difficult to assess in the small fishes we examined. In light of the low blood oxygen affinities reported here, it seems to us more likely that these fishes may possess enhanced anaerobic capabilities. Future studies may reveal that many of the mesopelagic organisms from the ox-

ygen minimum of the eastern tropical Pacific have additional, perhaps heretofore undescribed, means of meeting their energy requirements in that comparatively vast area of vanishingly low concentrations of dissolved oxygen.

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2. Our observations are based on data gathered on Naval Undersea Center cruises *Minox* I (July 1970), *Minox* II (March 1972), and *Minox* III (October 1973). Some of the major findings from the *Minox* cruises and the general rationale for the *Minox* research program are described by W. A. Friedl, G. V. Pickwell, and R. J. Vent [in *Proceedings of a Symposium on the Prediction of Sound Scattering in the Oceans from Physical/Chemical/Biological Information*, N. R. Andersen, Ed. (Plenum, New York, in press)]. The low-oxygen area covered by our stations extends roughly from 13°N to 22°N, and from 100°W to 122°W. Seawater was collected in 8-liter polyvinyl chloride (Niskin) bottles. Samples for dissolved oxygen analysis were withdrawn anaerobically through rubber septa into 100-ml syringes. Fixing reagents were injected through additional rubber septa into the syringes, and we carried out an iodometric titration with a microburette, following the modified Winkler procedure of the Chesapeake Bay Instit → [J. H. Carpenter, *Limnol. Oceanogr.* **10**, 141 (1965)]. Typically, dissolved oxygen concentrations at the depths of the oxygen minimum ranged from 0.08 to 0.02 ml/liter (equivalent to an oxygen tension of approximately 1.8 to 0.4 torr). Occasionally dissolved oxygen in our 100-ml samples was undetectable by this technique. In this re → J. D. Cline and F. A. Richards [*Limnol. Oceanogr.* **17**, 885 (1972)] reported values for dissolved oxygen measured by means of a photometric technique consistently in the vicinity of 0.02 ml/liter. At DSL depths (400 m) temperatures ranged from 6.5° to 8°C and salinity averaged 34.5 per mil, whereas at the surface temperatures ranged from 18.5°C (Station Westfall, Table 1) to 28°C at the southernmost station, with corresponding surface salinities of 34.1 per mil and 32.6 to 33.5 per mil, respectively, depending on the season.
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4. Swim bladder oxygen values from a series of 15 oxygen-minimum fishes (five species) collected on *Minox* II during daytime (descended scattering layers) ranged from 57 to 88 percent. Values to 92 percent were obtained from additional specimens collected from ascended scattering layers at night [A. O. Valkirs, in *Scientific Results of the* Minox *Program*, G. V. Pickwell, Ed. (Technical Report, Naval Undersea Center, San Diego, in press)]. J. Kinzer [*Umsch. Wiss. Tech.* **22**, 733 (1967)] found myctophids and gonostomatids associated with the DSL in oxygen-depleted waters (0.08 to 0.04 ml/liter) of the eastern Arabian Sea and wondered what physiological mechanisms permitted such sojourns.
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7. Net depth was monitored throughout the haul, and the length of the towing cable was adjusted to maintain the net within the desired depth interval. Most diurnal hauls through the DSL sampled a stratum 45 to 95 m thick; nocturnal hauls in near-surface scattering layers seldom ranged over more than 50 m. Thirty-eight hauls made in the region of extremely low oxygen content were open an average of 57 ± 12 minutes, had an average velocity while open of 1.2 ± 0.1 m/sec, and filtered an average volume of 16,000 ± 3,800 m^3.
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Epoxide to Olefin: A Novel Biotransformation in the Rumen

Abstract. *Studies with an insect juvenile hormone mimic and the insecticide dieldrin have shown that enzymatic processes in the rumen reduce the epoxide moiety in these compounds to an olefin. This reaction is apparently microbial in origin and does not involve an observable intermediate. Epoxide reductions in the digestive tract of ruminants and possibly other mammals may be important in the detoxication of biologically active epoxides, including pesticides, alkylating agents, and carcinogens.*

Enzymatic detoxication reactions protect mammals against the potentially toxic effects of foreign compounds to which they are almost continuously exposed. Oxidative, reductive, hydrolytic, and conjugative reactions transform the compounds to metabolites that usually have reduced biological activity or are more readily excreted from the body. Although most detoxications occur in the liver after absorption, it is advantageous to the organism if detoxication occurs before absorption, that is, in the case of oral exposure while the compounds are still in the alimentary canal. The epoxide moiety, whose presence in organic compounds often confers high biological activity (*1*), is reduced in the rumen in appreciable quantity to an olefin, a reaction which may represent a significant detoxication mechanism.

Studies on the metabolic behavior in steers of the insect juvenile hormone mimic 1-(4′-ethylphenoxy)-3,7-dimethyl-6,7-epoxy-*trans*-2-octene (**1**) (Stauffer R-20458), labeled with ^{14}C in the phenyl ring, indicated that the compound was totally