Minimal Dissolved Oxygen Requirements of Aquatic Life with Emphasis on Canadian Species: a Review

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Preface

Originally, some of the material in this report was prepared for the National Research Council of Canada Environmental Secretariat under the title "Waterborne Dissolved Oxygen Requirements and Criteria With Particular Emphasis on the Canadian Environment." That document was published in 1975 as part of N.R.C.'s special publication series under the auspices of the Associate Committee on Scientific Criteria for Environmental Quality. The emphasis in the N.R.C. document was on development of oxygen criteria which were defined as cause and effect interrelations based on a scientific evaluation of environmental harm caused by low oxygen in water. The content of the N.R.C. report was, of necessity, limited to matters considered the mandate of the N.R.C. environmental secretariat.

This report, although similar in many ways to the N.R.C. report, is intended to serve more as a review document to persons interested in oxygen requirements of Canadian aquatic species. Where criteria are discussed, suggestions are made as to how criteria might be implemented. It must be stressed that the suggestions herein are the author's opinions and are not the opinions of N.R.C. whose mandate does not include recommendations on criteria implementation. Readers should be very careful to distinguish between the content and positions taken when making reference to these two reports.

Abstract

DAVIS, J. C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J. Fish. Res. Board Can. 32: 2295–2332.

This article reviews the sensitivity, responses, response thresholds, and minimum oxygen requirements of marine and freshwater organisms with strong emphasis on Canadian species. The analysis attempts to define low dissolved oxygen thresholds which produce some physiological, behavioral, or other response in different species.

Oxygen availability is discussed with reference to seasonal, geographical, or spatial variation in dissolved oxygen. Factors affecting availability of dissolved oxygen include atmospheric exchange, mixing of water masses, upwelling, respiration, photosynthesis, ice cover, and physical factors such as temperature and salinity. Dissolved oxygen terminology is summarized and tables are included for both fresh and saltwater O_2 solubility at different temperatures.

Incipient O_2 response thresholds are used in a statistical analysis to develop oxygen criteria for safeguarding various groups of freshwater and marine fish. These include mixed freshwater fish populations including or excluding salmonids, freshwater salmonid populations, salmonid larvae or mature salmonid eggs, marine anadromous and nonanadromous species. Criteria are based on threshold oxygen levels which influence fish behavior, blood O_2 saturation, metabolic rate, swimming ability, viability and normal development of eggs and larvae, growth, circulatory dynamics, ventilation, gaseous exchange, and sensitivity to toxic stresses. The criteria provide three levels of protection for each fish group and are expressed as percentage oxygen saturation for a range of seasonal temperature maxima.

Oxygen tolerances and responses of aquatic invertebrates to low oxygen are reviewed for freshwater and marine species according to habitat. No invertebrate criteria are proposed owing to the capacity for many invertebrate species to adopt anaerobic metabolism during low O_2 stress. It is suggested that the criteria proposed for fish species will provide a reasonable safeguard to most invertebrate species. It appears likely, however, that a change in oxygen regime to one of increased O_2 scarcity will probably influence invertebrate community structure.

It is suggested that criteria for protection of aquatic life be implemented by groups of experienced individuals. The group should consider the natural oxygen regime for a specific water body and its natural variability, the aquatic life therein and its value, importance, relative O_2 sensitivity, and the possibility of interactions with toxicants and other factors that may compound the stress produced by low O_2 on aquatic life. Each water body and its aquatic life should be considered as a unique situation and criteria application should not encompass diverse areas, habitats, or biological associations as if they were identical.

Résumé

DAVIS, J. C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J. Fish. Res. Board Can. 32: 2295–2332.

Dans cet article, l'auteur passe en revue la sensibilité, les réponses, les seuils de réponse et les exigences minimales en oxygène d'organismes marins et dulçaquicoles, avec accent particulier sur les espèces canadiennes. Il y définit les seuils minimums d'oxygène dissous qui déclenchent des réponses physiologiques, de comportement ou autres chez différentes espèces.

Il analyse la disponibilité d'oxygène en relation avec la variation géographique ou spatiale de l'oxygène. Les facteurs affectant la disponibilité de l'oxygène dissous sont, entre autres, les échanges avec l'atmosphère, le mélange des masses d'eau, la remontée d'eaux profondes, la respiration, la photosynthèse, la couverture de glace et des facteurs physiques tels que la température et la salinité. Il donne un résumé de la terminologie de l'oxygène dissous et des tables de solubilité de l'oxygène, tant en eau douce qu'en eau salée, à différentes températures.

Il utilise les seuils de début de réponse à l'oxygène dans une analyse visant à mettre au point des critères de sauvegarde des divers groupes de poissons de mer et d'eau douce. Ces groupes comprennent des populations mixtes de poissons d'eau douce, incluant ou excluant les salmonidés, des populations de salmonidés d'eau douce, des larves ou des œufs mûrs de salmonidés, et des espèces marines anadromes et non anadromes. Ces critères sont fondés sur les niveaux de seuil d'oxygène affectant le comportement des poissons, la saturation du sang en O_2, le taux métabolique, l'aptitude à la nage, la survivance et le développement normal des œufs et des larves, la croissance, la dynamique de la circulation, les échanges gazeux et la sensibilité aux stress toxiques. Les critères fournissent trois paliers de protection pour chaque groupe de poissons et sont exprimés en pourcentage de saturation d'oxygène sur une gamme de maximums saisonniers de température.

L'auteur passe en revue la tolérance à l'oxygène et les réponses d'invertébrés aquatiques à de bas niveaux d'oxygène, pour des espèces dulçaquicoles et marines, selon l'habitat. Il ne propose aucun critère pour les invertébrés à cause de l'aptitude de plusieurs espèces à adopter un métabolisme anérobie au moment d'un stress causé par un bas niveau d'O_2. Les critères suggérés pour les espèces de poisson fourniraient une sauvegarde raisonnable pour la plupart des espèces

d'invertébrés. Il est probable, cependant, qu'un changement de régime d'O₂ en direction d'une plus grande rareté d'O₂, affecte la structure des communautés d'invertébrés.

L'auteur suggère que les critères de protection de la vie aquatique soient appliqués par des groupes d'individus expérimentés. Ces groupes devraient étudier le régime naturel d'O₂ d'un plan d'eau particulier et sa variabilité naturelle, la sensibilité relative à l'O₂ et la possibilité d'interactions avec les toxiques et autres facteurs qui peuvent s'ajouter au stress causé par un bas niveau d'O₂ sur la vie aquatique. Chaque plan d'eau et la vie aquatique qu'il contient devraient être considérés comme situation unique, et l'application des critères ne devrait pas englober des régions, des associations biologiques et des habitats différents comme s'ils étaient identiques.

Introduction, Rationale, and Objectives

THE purpose of this paper is to review available information on the oxygen requirements of aquatic organisms as a basis for formulating water oxygen quality criteria that provide a reasonable assessment of hazard for Canadian aquatic resources. A large body of literature exists on the general subject and some excellent reviews have appeared (Doudoroff and Shumway 1970; Warren and Shumway 1964; Warren et al. 1973). This paper attempts to arrive at a consensus of opinion on low oxygen sensitivity of fish and invertebrates. Results of this review are used to develop water quality criteria based on the best available cause and effect information relating to aquatic life.

In preparing this paper it was not intended to reiterate much of the information summarized by other reviewers. Instead, this report attempts to concentrate mainly on aquatic organisms found in Canadian waters, relying on the reader to consult other sources relevant to geographic areas outside Canada. Some considerable attention has been given to defining low oxygen effects on aquatic organisms, identifying oxygen response thresholds, and examining physiological responses to low oxygen under different conditions.

In reviewing the literature it was evident that numerous and often contradictory results have been reported for critical oxygen levels for the same aquatic organisms. This lack of clarity has made it extremely difficult for reviewers to decide the levels of oxygen that are critical as a basis for criteria recommendations. Part of the problem appears to be one of definition. Much of the literature deals with determining lethal levels of dissolved oxygen (see table 1 in Doudoroff and Shumway 1970). In contrast, some workers have defined critical oxygen levels as that point when fish lost equilibrium (e.g. Townsend et al. 1938; Townsend and Earnest 1940; Townsend and Cheyne 1944) or exhibited "respiratory distress" (Wilding 1939). It should be recognized that each of these responses reflects some degree to which the animal responds to low oxygen. Thus there is an entire range of responses to hypoxia (lowered oxygen) which may

be exhibited by the test species, and the response varies with the severity of hypoxia. Attempts to arrive at critical oxygen levels, based on data gathered under differing experimental conditions and with varying approaches and experimental criteria, are bound to be frustrating.

The present approach has been to scan the literature and extract information on dissolved oxygen levels where sublethal responses to hypoxia first became apparent (i.e. the incipient sublethal threshold). By extracting this sort of information one becomes aware of the oxygen level where some physiological, behavioral, or other stress-induced response occurs. It is then that the animal indicates at what point energy must be expended or adjustments made to counteract hypoxia. When such a stress is a chronic occurrence, it is an important determinant factor in the long-term survival of an organism.

Some readers may take exception to the above approach, citing the ability of animals to adjust or regulate to altered conditions. A later section will deal with acclimation phenomena, and other sections will explain the significance of observed sublethal responses. It is my belief that we should look for "no-effect" levels in setting water quality criteria that assure the long-term survival of aquatic organisms. Any departure from this level assumes a degree of risk which increases with the severity of hypoxia present. The degree of risk accepted becomes a matter of judgement based on the economic value of an individual aquatic population or an entire aquatic community, assessed against such factors as industrial needs or the aesthetics of unpolluted waters — none of which can be satisfied by scientific criteria.

Physical Considerations

At 19 C fresh water contains 7.93 ml/liter oxygen, roughly 0.8% of its volume, when exposed to air at sea level. Air at the same temperature and pressure, in contrast, holds approximately 209 ml/liter oxygen, roughly 26 times as much oxygen as water. Aquatic organisms have evolved within the physical constraints of their relatively oxygen-scarce environment and many

possess high specialized gas exchange systems which permit maximal utilization of available oxygen supplies.

Aerobic organisms utilize the process of diffusion to move oxygen into their systems by means of an internal–external O_2 pressure gradient. The exchange process is often facilitated by a delivery system (e.g. branchial and opercular pumps in fish) and a transport system (e.g. internal circulatory system) to distribute oxygen within the body. In all aerobic organisms, movement of oxygen to the tissues for metabolism is fundamentally via tension gradients, both within and without the body. Thus, it is the oxygen tension gradient between tissues and the external medium that is critical to the gas exchange process.

Air at sea level contains about 20.9% oxygen. Under standard conditions dry air exerts a pressure equivalent to 760 mm Hg. The oxygen tension can be calculated:

$$PO_2 = (\text{Atmos. Press} - H_2O \text{ vap. press.}) \times \%O_2 \quad (1)$$

where: Atmos. Press. = Atmospheric pressure in millimeters Hg

H_2O vap. press. = water vapor pressure in millimeters Hg at test temperature

$\%O_2$ = percentage oxygen in atmosphere

PO_2 = oxygen partial pressure, millimeters Hg

For the above example at 10 C (assuming Atmos. Press. = 760 mm Hg):

$$PO_2 = (760 - 9.2) \times 20.946\% = 157.3 \text{ mm Hg} \quad (2)$$

Water equilibrated with atmospheric air at sea level usually has an oxygen partial pressure of about 154–158 mm Hg. Thus organisms exposed to fully saturated water under those conditions exist with an external oxygen pressure of 154–158 mm Hg. In fish the internal oxygen tension (ca. 50–110) is lower than the external tension. Oxygen therefore diffuses across the gills into the blood down an O_2 gradient of 40–100 mm Hg (Randall 1970). A drop of external PO_2 reduces this gradient or depresses arterial PO_2 levels. If the oxygen depression is severe, insufficient O_2 tension will occur at the tissue level.

For practical purposes the PO_2 of water can be calculated from the above cited equation (1), when the barometric pressure is known. Water vapor pressure can be obtained from tables (e.g. Table 1) for purposes of calculation.

It is more conventional for water quality or oceanographic purposes to express water oxygen levels in terms of their concentration rather than partial pressure. Thus one speaks of oxygen in terms of milliliters O_2/liter or mg O_2/liter (parts per million). All the terms can be interrelated such that a sample of air-equilibrated fresh water at 10 C at sea level has 11.33 mg O_2/liter (ppm),

TABLE 1. Saturated water vapor pressure and oxygen partial pressures in relation to water temperature in water exposed to fully oxygen-saturated air at 760 mm Hg air pressure.

Temp (C)	Saturated water vapor pressure (in mm Hg)	Oxygen partial pressure for 100% air saturation at 760 mm Hg pressure in water (in mm Hg)
−5	3.0	158.6
−4	3.4	158.5
−3	3.7	158.4
−2	4.0	158.4
−1	4.3	158.3
0	4.6	158.3
+1	4.9	158.2
+2	5.3	158.1
+3	5.7	158.0
+4	6.1	157.9
+5	6.5	157.9
+6	7.0	157.8
+7	7.5	157.6
+8	8.0	157.5
+9	8.6	157.4
+10	9.2	157.3
+11	9.8	157.2
+12	10.5	157.0
+13	11.2	156.9
+14	12.0	156.7
+15	12.8	156.5
+16	13.6	156.4
+17	14.5	156.2
+18	15.5	156.0
+19	16.5	155.8
+20	17.5	155.6
+21	18.6	155.3
+22	19.8	155.1
+23	21.0	154.8
+24	22.4	154.5
+25	23.7	154.3
+26	25.2	153.9
+27	26.7	153.6
+28	28.3	153.3
+29	30.0	152.9
+30	31.8	152.6

7.93 ml O_2/liter (1 mg O_2 = 0.7 ml O_2) and from (2) has a partial pressure of 157.3 mm Hg. If that sample were only 50% saturated, it would have 11.33/2 = 5.67 mg O_2/liter, 7.93/2 = 3.82 ml O_2/liter, and a PO_2 of 157.3/2 = 78.65 mm Hg.

As temperature and salinity increase, oxygen content decreases. Tabulated values (Tables 2 and 3) and well-known formulae (Gameson and Robertson 1955; Truesdale and Gameson 1957) enable easy calculation of oxygen content of water at different temperatures and salinities. As temperature increases, oxygen content drops

TABLE 2. Solubility of oxygen in fresh water at different temperatures when water is exposed to an atmosphere containing 20.9% oxygen at a pressure of 760 mm Hg (including water vapor pressure) (derived from Whipple 1914).

Temp (C)	Parts per million	Cm³ per liter (at 0 C and 760 mm)	Temp (C)	Parts per million	Cm³ per liter (at 0 C and 760 mm)
0	14.62	10.23	16	9.95	6.96
1	14.23	9.96	17	9.74	6.82
2	13.84	9.68	18	9.54	6.68
3	13.48	9.43	19	9.35	6.54
4	13.13	9.19	20	9.17	6.42
5	12.80	8.96	21	8.99	6.29
6	12.48	8.73	22	8.83	6.18
7	12.17	8.52	23	8.68	6.07
8	11.87	8.31	24	8.53	5.97
9	11.59	8.11	25	8.38	5.86
10	11.33	7.93	26	8.22	5.75
11	11.08	7.75	27	8.07	5.65
12	10.83	7.58	28	7.92	5.54
13	10.60	7.42	29	7.77	5.44
14	10.37	7.26	30	7.63	5.34
15	10.15	7.10			

owing to reduced solubility, while oxygen partial pressure drops only slightly owing to increased molecular activity. Thus a fish breathing warm water must pump more water over the gills than in cold water to deliver a given volume of oxygen/unit time, because of the reduced oxygen content of inspired water. This is necessary even though the O_2 tension gradient between blood and water is little changed at high temperatures. Severe respiratory problems can result from a combination of high temperature (low O_2 content) and reduced oxygen tension (water not fully saturated) as both availability and the gradient for oxygen diffusion are reduced. Associated with this phenomenon is the fact that higher temperatures usually increase the metabolic demand for oxygen. It is likely that the stimulatory effect of increased temperature on metabolism is the most important of all these factors owing to the magnitude of its effect. It is largely for these reasons that fish kills related to low oxygen levels often occur in warmwater periods. Obviously, meaningful oxygen criteria should consider the critical oxygen content and oxygen tension as well as temperature effects on metabolism in order to provide a full measure of protection.

Natural O_2 Regimes in the Aquatic Environment

Bodies of fresh water often show large variations in dissolved oxygen, both seasonally and geographically. Welch (1952) attributed to photosynthesis values of oxygen supersaturation as high as 364.5% in the upper portion of a Wisconsin lake. Tarzwell and Gaufin (1953) described a location in a southern Ohio creek polluted with sewage where dissolved oxygen was 19.4 mg O_2/liter one afternoon and 0.7 mg O_2/liter the next morning. Oxygen concentrations in ponds and lakes exceeding 30 mg O_2/liter have been reported (Wiebe 1933; Woodbury 1942). Servizi and Burkhalter (1970) reported oxygen levels close to saturation on the surface of the Thompson and Fraser rivers in 1963 and 1966, prior to operation of pulp mills on the upper reaches of the rivers. Seasonally low levels of oxygen in freshwater bodies can lead to "winter kills" resulting from decay of organic materials under ice cover without replenishment of oxygen from the atmosphere. Summer kills can result from high water temperatures, reduced water oxygen solubility, and large oxygen demands from planktonic and bacterial respiration.

In the sea, oxygen levels in the photic zone may rise to 130% saturation or higher, owing to photosynthetic processes (Fairbridge 1966). As well as the contribution from photosynthesis, oxygen enrichment occurs in water by atmospheric exchange. The rate of enrichment is dependent on the rate of "turnover" of the system. In deep marine waters, oxygen levels are generally lower than at the surface owing to reduced atmospheric exchange and to conditions where respiration exceeds photosynthesis. Fairbridge (1966) reported that Atlantic bottom water generally does not fall below 60% saturation, while oxygen levels in deep Pacific water may be somewhat lower. In

TABLE 3. Solubility of oxygen in sea water of salinity 35‰, in milligrams per liter, from a normal atmosphere saturated with water vapor at a total pressure of 760 mm of mercury from -2 to $+40$ C. ΔC_1 is the change in solubility for a change of 1‰ in salinity (from Truesdale and Gameson 1957). (This table can be used to calculate oxygen content of water at various temperatures and salinities.)

Temp (C)	.9	.8	.7	.6	.5	.4	.3	.2	.1	.0	ΔC_1
-2										11.86	
-1	11.82	11.79	11.76	11.72	11.69	11.66	11.63	11.59	11.56	11.53	-0.088
-0	11.50	11.47	11.44	11.41	11.37	11.34	11.31	11.28	11.25	11.22	-0.085

Temp (C)	.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	ΔC_1
$+0$	11.22	11.19	11.16	11.13	11.10	11.07	11.04	11.01	10.98	10.95	-0.083
1	10.92	10.89	10.86	10.83	10.80	10.78	10.75	10.72	10.69	10.66	-0.080
2	10.64	10.61	10.58	10.55	10.52	10.50	10.47	10.44	10.41	10.39	-0.078
3	10.36	10.33	10.31	10.28	10.26	10.23	10.20	10.18	10.15	10.12	-0.076
4	10.10	10.07	10.05	10.02	10.00	9.97	9.95	9.92	9.90	9.87	-0.073
5	9.85	9.82	9.80	9.78	9.75	9.73	9.70	9.68	9.66	9.63	-0.071
6	9.61	9.58	9.56	9.54	9.52	9.49	9.47	9.45	9.42	9.40	-0.069
7	9.38	9.36	9.33	9.31	9.29	9.27	9.25	9.22	9.20	9.18	-0.067
8	9.16	9.14	9.12	9.10	9.07	9.05	9.03	9.01	8.99	8.97	-0.065
9	8.95	8.93	8.91	8.89	8.87	8.85	8.83	8.81	8.79	8.77	-0.063
10	8.75	8.73	8.71	8.69	8.67	8.65	8.63	8.61	8.59	8.58	-0.061
11	8.56	8.54	8.52	8.50	8.48	8.46	8.45	8.43	8.41	8.39	-0.059
12	8.37	8.36	8.34	8.32	8.30	8.29	8.27	8.25	8.23	8.22	-0.058
13	8.20	8.18	8.17	8.15	8.13	8.12	8.10	8.08	8.06	8.05	-0.056
14	8.03	8.02	8.00	7.98	7.97	7.95	7.94	7.92	7.90	7.89	-0.055
15	7.87	7.86	7.84	7.83	8.81	7.80	7.78	7.76	7.75	7.73	-0.053
16	7.72	7.70	7.69	7.67	7.66	7.65	7.63	7.62	7.60	7.59	-0.052
17	7.57	7.56	7.54	7.53	7.52	7.50	7.49	7.48	7.46	7.45	-0.051
18	7.43	7.42	7.41	7.39	7.38	7.37	7.35	7.34	7.33	7.31	-0.049
19	7.30	7.29	7.27	7.26	7.25	7.23	7.22	7.21	7.20	7.18	-0.048
20	7.17	7.16	7.15	7.13	7.12	7.11	7.09	7.08	7.07	7.06	-0.047
21	7.05	7.03	7.02	7.01	7.00	6.99	6.97	6.96	6.95	6.94	-0.046
22	6.93	6.92	6.90	6.89	6.88	6.87	6.86	6.85	6.84	6.82	-0.045
23	6.81	6.80	6.70	6.78	6.77	6.76	6.75	6.73	6.72	6.71	-0.044
24	6.70	6.69	6.68	6.67	6.66	6.65	6.64	6.63	6.62	6.61	-0.044
25	6.60	6.59	6.57	6.56	6.55	6.54	6.53	6.52	6.51	6.50	-0.043
26	6.49	6.48	6.47	6.46	6.45	6.44	6.43	6.42	6.41	6.40	-0.042
27	6.39	6.38	6.37	6.36	6.35	6.34	6.33	6.32	6.31	6.30	-0.042
28	6.29	6.28	6.27	6.26	6.25	6.24	6.23	6.22	6.21	6.20	-0.041
29	6.19	6.18	6.17	6.16	6.15	6.14	6.13	6.12	6.12	6.11	-0.041
30	6.10	6.09	6.08	6.07	6.06	6.05	6.04	6.03	6.02	6.01	-0.041
31	6.00	5.99	5.98	5.97	5.97	5.96	5.95	5.94	5.93	5.92	-0.040
32	5.91	5.90	5.89	5.88	5.87	5.86	5.85	5.84	5.83	5.82	-0.040
33	5.82	5.81	5.80	5.79	5.78	5.77	5.76	5.75	5.74	5.73	-0.040
34	5.72	5.71	5.70	5.69	5.68	5.68	5.67	5.66	5.65	5.64	-0.040
35	5.63	5.62	5.61	5.60	5.59	5.58	5.57	5.56	5.55	5.54	-0.040
36	5.53	5.52	5.51	5.51	5.50	5.49	5.48	5.47	5.46	5.45	-0.040
37	5.44	5.43	5.42	5.41	5.40	5.39	5.38	5.37	5.36	5.35	-0.041
38	5.34	5.33	5.32	5.31	5.30	5.29	5.28	5.27	5.26	5.25	-0.041
39	5.24	5.23	5.22	5.21	5.20	5.19	5.18	5.17	5.16	5.15	-0.041
40	5.14										

coastal Atlantic inlets such as Bedford Basin (Krauel 1969) and Petpeswick Inlet (Platt and Irwin 1972), surface water is close to saturation on a year-round basis while bottom water can have seasonally low oxygen levels of 40 and 0% saturation in the two areas, respectively.

Pickard (1961, 1963) provided a comprehensive study of the oceanographic characteristics of a number of mainland British Columbia and Vancouver Island inlets. These areas are important to commercial and recreational fisheries. They are also attractive as sites for location of oxygen-depleting industries such as pulp mills. In general, oxygen levels are high in the surface waters of

these inlets, whereas the deep inlet water is often low in oxygen.

In Vancouver Island inlet studies, Pickard encountered considerable variability in dissolved oxygen. He found vertical stratification related to temperature and salinity variance. Horizontal oxygen stratification was due to pockets of photosynthesis, or respiration and decay or organics. At depths greater than 100 m, oxygen levels were usually less than 4 ml O_2/liter (5.7 mg/liter) and in many instances they were below 1 ml O_2/liter (1.4 mg/liter).

Mainland B.C. inlets receive considerable freshwater runoff of varying volume flow, chiefly from glaciers. On this topic, Pickard (1961) has stated: "Generally the large-runoff inlets show less variable dissolved oxygen values along an inlet at any depth than do small runoff inlets. Supersaturation of the upper layers is common and there is often an oxygen maximum just below the halocline of the larger-runoff inlets. A few small-runoff inlets have a mid-depth oxygen minimum in which the lowest values are at the inlet head. Dissolved oxygen values of less than 2 ml/1 are not common in any mainland inlets and zero values have not been definitely recorded."

Useful dissolved oxygen profiles for B.C. inlets are shown in Pickard (1961, 1963).

Oxygen Requirements of Fish

A summary of literature values of incipient oxygen response thresholds for Canadian aquatic life appears in Table 4A–D. A detailed description of the summarized responses and the rationale for including each of them follows.

BLOOD OXYGEN DISSOCIATION CURVES

The process of diffusion of oxygen into the blood depends on a partial pressure difference, describing a gradient between blood and water. In many fish the respiratory pigment hemoglobin has a high affinity for oxygen which enables it to act as an oxygen transport mechanism. The blood oxygen dissociation curve for fish relates the percentage saturation of the blood to the oxygen partial pressure (PO_2) applied. The hemoglobin curve maintains the gradient between water and blood, and blood and tissues, and therefore promotes a high rate of gas transfer.

Figure 1 illustrates that rainbow trout blood remains nearly 100% saturated with oxygen until PO_2 drops below 80 mm Hg. These data also indicate how an increase in either temperature or CO_2 tension shifts the curve to the right. Arterial blood in fish has a low PCO_2 owing to the high water solubility of CO_2 and ease of CO_2 loss

via the gills (Randall 1970). In the tissues, higher CO_2 levels shift the blood curve to the right causing release of oxygen.

The oxygen tension where the blood ceases to be fully oxygen saturated is indicative of a limiting oxygen condition for fish. Under these conditions more circulatory and ventilatory work must be done to meet the oxygen requirements of the tissues. Indeed, even at PO_2's above the point where arterial blood ceases to be saturated as PO_2 drops, a critical point is reached owing to the need to maintain a gradient between water and blood to drive oxygen into the blood. Jones et al. (1970), on the basis of data for rainbow trout at 5 C, suggested that a PO_2 of 118 mm Hg was necessary to maintain a proper gradient for oxygen uptake. Randall (1970) calculated that the internal–external gradient for trout should be 20 mm Hg PO_2. C. M. Wood (unpublished data) noted physiological signs of hypoxia 20 mm Hg PO_2 above the point where the blood ceased to be fully saturated. This relationship was related to the shape of the blood curve such that when it shifted with temperature so did the PO_2 threshold for hypoxia responses.

VENTILATION, CIRCULATION, AND RESPIRATORY DEPENDENCE

Ventilatory and circulatory changes have been observed in a number of fish species in response to hypoxia. Rainbow trout (Holeton and Randall 1967a, b) and carp (Garey 1967) show elevations in both rate and amplitude of breathing and decreased heart rate in response to low oxygen. In trout the stroke volume output of the heart also increases, thus maintaining cardiac output as heart rate decreases. The gill transfer factor for oxygen (a measure of the ability of the gills to transfer oxygen per unit gradient) increases, gill water flow goes up, and venous oxygen tension drops. All these factors operate to maintain oxygen uptake in the face of reduced oxygen availability.

In understanding effects of low oxygen on metabolism, it is useful to refer to Fig. 2 which embodies the classical concepts of Fry (1957). Metabolic rate (oxygen uptake rate) is shown plotted against oxygen tension. Standard metabolic rate was defined by Brett (1962) as the minimal metabolic rate accompanying the energy cost of maintenance, measured under laboratory conditions. It is close to, but slightly higher than, the term "basal metabolic rate" used by other workers. The point at which available oxygen level coincides with the oxygen needs for bare maintenance of bodily functions is termed the

TABLE 4. The incipient oxygen response thresholds for various fish groups and habitats gathered from the literature with emphasis on Canadian species. The rationales for choosing the reported response and its significance are reported in the following pages 2301–2311. In most instances, oxygen response thresholds were found in only one form of terminology (e.g. column 6 — mg O_2/liter and the others in the table were calculated. Calculations for freshwater fish made use of the reported temperature and the O_2 solubility data in Tables 1 and 2 while those for nonanadromous fish in sea water used the data in Table 3 and an assumed salinity of 28‰. It is stressed that the response levels reported are incipient oxygen levels where effects first become apparent thus providing a "biological indication" of the onset of hypoxic stress. A) Freshwater species, B) Marine nonanadromous species, C) Anadromous species, D) Eggs and larvae (freshwater and marine species).

Species	Size	Temp (C)	Level of dissolved oxygen				Response to oxygen level	Reference
			PO_2-mm Hg	ml O_2/liter	mg O_2/liter	% Satn.		
A. Freshwater species								
Arctic char, *Salvelinus alpinus*	—	2 ± .05	25	1.53	2.18	15.8	"signs of asphyxia and loss of equilibrium"	Holeton (1973)
brown bullhead, *Ictalurus nebulosus*	43–127 g	9–10	60	4.87–4.76	6.95–6.80	38.0	onset of oxygen — dependent oxygen uptake	Grigg (1969)
Rainbow trout, *Salmo gairdneri*	682–1136 g	20	78	3.20	4.59	50	below this level blood is not fully saturated with oxygen	Irving et al. (1941)
" "	120–250 g	8.5–15	80–100	3.63–5.14	5.18—7.34	50.7–63.7	circulatory changes occur, including a slowing of heart	Randall and Smith (1967)
carp, *Cyprinus carpio*	77–350 g	10	50	2.51	3.59	31.7	standard oxygen uptake elevated (depressed at lower levels)	Beamish (1964)
	30–600 g	20	80	3.29	4.71	51.3		
" "	235–785 g	13.3–25	80	2.74–3.04	5.39–4.34	50.9–51.6	blood ceased to be fully saturated with O_2 below this level	Itazawa (1970)
Walleye, *Stizostedion vitreum*	2 yr-old	22	35.2–70.4	2.8–1.4	4–2.0	45.3–22.7	loss of negative phototaxis (light avoidance behavior)	Scherer (1971)
			70.4–96.8	3.85–2.8	5.5–4.0	45.3–62.3	increased mobility, "darting" behavior	
Largemouth bass, *Micropterus salmonides*	5–9 cm	—	—	3.15	4.5	—	some indication of avoidance behavior	Whitmore et al. (1960)
				1.1	1.5	—	marked avoidance	(1960)
Brook trout (speckled trout) *Salvelinus fontinalis*	682–1136 g	20	77.95	3.21	4.59	50	blood ceases to be fully satd. with O_2 below this level	Irving et al. (1941)
" "	17–65 g	5	100	5.66	8.09	63.2	onset of O_2-dependent metabolism	Graham (1949)
		8	80	4.19	5.99	50.7	reduced cruising speed	
		20	154	6.34	9.06	98.8	onset of O_2 dependent metabolism	
		5–20	116.9–118.7	6.72–4.82	9.6–6.88	75	reduced activity, all temps.	
" "	56–140 g	10,15	80	4.03–3.63	5.75–5.18	50.7–51.0	standard oxygen uptake reduced below this level	Beamish (1964)
Brown trout, *Salmo trutta*	682–1136 g	20	77.95	3.21	4.59	50	blood ceases to be fully satd. with O_2 below this level	Irving et al. (1941)
Rainbow trout, *Salmo gairdneri*	13.3 ± 1.4 cm	17 ± .5	156.6	6.82	9.74	100	any reduction in oxygen led to more rapid death in cyanide	Downing (1954)
" "	20 mos old	8–10	78.85–79.95	4.16–3.97	5.94–5.67	50	43% reduction in maximum swimming speed	Jones (1971b)
		21–23	77.85–77.6	3.15–3.04	4.50–4.34	50	30% reduction in maximum swimming speed	
" "	235–510 g	2.3–13	100	6.11–4.71	8.73–6.74	63.1–63.6	blood is not fully satd. with oxygen below this level	Itazawa (1970)
" "	—	15	78.45	3.55	5.08	50	altered respiratory quotient, little capacity for anaerobic metabolism below this level	Kutty (1968a)
	—	15	80–100	3.63–4.53	5.18–6.47	51.0–63.7	changes in oxygen transfer factor and effectiveness of O_2 exchange occur	Randall et al. (1967)

TABLE 4. (Continued)

Species	Size	Temp (C)	Level of dissolved oxygen PO$_2$-mm Hg	ml O$_2$/liter	mg O$_2$/liter	% Satn.	Response to oxygen level	Reference
" "	400–600 g	13.5	80	3.74	5.35	51.0	breathing amplitude and buccal pressure elevated	Hughes and Saunders (1970)
" "	approx. 300 g	10,15, 20	80	3.30–4.03	4.71–5.75	50.7–51.3	below this level blood is not fully satd. with oxygen	Cameron (1971)
" "	1–11 g	17.5	93.8	4.05	5.78	60	toxicity of zinc, lead, copper, phenols increased markedly below this level	Lloyd (1961)
Largemouth bass, Micropterus salmoides	juvenile	25	92.3–110.7	3.5–4.2	5–6	59.7–71.6	final (maximum sustained) swimming speed reduced below this level	Dahlberg et al. (1968)
Bluegill, Lepomis macrochirus	5–9 cm	—	—	2.1	3.0	—	some avoidance behavior	Whitmore et al. (1960)
				1.1	1.5	—	strong avoidance	
B. Marine nonanadromous species								
Pile perch, Rhacochilus vacca	adults	11	80	3.19	4.56	50.8	blood ceases to be fully O$_2$ saturated below this level	Webb and Brett (1972)
Dogfish, Squalus suckleyi	2.5–6.0 kg	10	115	4.68	6.69	72.92	blood ceases to be fully O$_2$ saturated below this level	Lenfant and Johansen (1966)
Dogfish, Scyliorhinus canicula[a]	150–600 g	12–14	80	3.12–2.95	4.46–4.20	50.8–51.0	Oxygen-dependent metabolism begins below this level	Hughes and Umezawa (1968a)
Dragonet, Callionymus lyra[a]	70–140 g	11–12	125	4.98–4.88	7.12–6.97	79.4	Oxygen-dependent metabolism below this level	Hughes and Umezawa (1968b)
			100	3.97–3.90	5.67–5.58	63.5	altered heart rate	
Dragonet, Callionymus lyra[a]	80–120	—	80	—	—	—	increased ventilatory muscle activity below this level	Hughes and Ballintijn (1968)
Ratfish, Hydrolagus colliei	—	11	150	5.98	8.54	95.2	blood ceases to be fully O$_2$ saturated below this level	Hanson (1967)
Atlantic cod, Gadus morhua	1.14–2.33 kg	5	158.2	7.14	10.20	100	any reduction in ambient O$_2$ level produces rise in ventilatory water flow	Saunders (1963)
C. Anadromous species								
Steelhead, Salmo gairdneri — see freshwater species								
Sockeye salmon, Oncorhynchus nerka	50 g	20–24	155.9–154.9	6.42–5.97	9.17–8.53	100	available oxygen level appears to limit active metabolism and maximum swimming speed	Brett (1964)
" "	1579 g	13	100	4.72	6.74	63.6	blood ceases to be fully O$_2$ saturated below this level	Davis (1973)
" "	1.5–1.7 kg	15	78.45	3.55	5.07	50	elevated blood and buccal pressure and breathing rate increased	Randall and Smith (1967)
Coho salmon, Oncorhynchus kisutch	6.3–11 cm	"summer temperatures"	—	3.15	4.5	—	erratic avoidance behavior	Whitmore et al. (1960)
	5.1–14.8 cm	12 ± 1	130.8	6.3	9.0	83.1	below this level acute mortality in kraft pulpmill effluent increased	Hicks and DeWitt (1971)
" "	Juvenile	10–20	157.7–155.9	7.93–6.42	11.33–9.17	100	reduction of O$_2$ below saturation produced some lowering of maximum sustained swimming speed	Davis et al. (1963)
" "	" "	20	155.9	6.42	9.17	100	as above	Dahlberg et al. (1968)
" "	" "	" "	136–67.9	5.6–2.8	8.0–4.0	87.2–43.6	growth rate proportional to oxygen level with best growth at 8.0 mg/liter, lowest at 4.0 mg/liter	Hermann (1958)

TABLE 4. (Concluded)

Species	Size	Temp (C)	Level of dissolved oxygen				Response to oxygen level	Reference
			PO$_2$-mm Hg	ml O$_2$/liter	mg O$_2$/liter	% Satn.		
Chinook salmon, Oncorhynchus tshawytscha	6.3–11 cm	"summer temps"	—	3.15	4.5	—	marked avoidance of this level in summer	Whitmore et al. (1960)
		"fall temps"	—	—	4.5	—	little avoidance of this level in fall	
" "	Juveniles	10–20	157.7–155.9	7.93–6.42	11.33–9.17	100	reduction of O$_2$ below saturation produced some lowering of maximal sustained swimming speed	Davis et al. (1963)
Atlantic salmon, Salmo salar	87–135 g	15	69.6	3.15	4.5	44.33	Salmon stop swimming at a speed of 55 cm/s at O$_2$ levels below this. Faster swimming requires more oxygen	Kutty and Saunders (1973)
American shad, Alosa sapidissima	—	—	—	1.75–2.1	2.5–3.0	—	threshold for migration through polluted areas	Chittenden (1973)
				2.8	4.0	—	necessary for spawning areas	
D. Eggs and larvae								
Rainbow trout, larvae, Salmo gairdneri	1+8 day old larvae	10+1	100	5.03	7.18	63.4	elevated heart and breathing rates below this level. Bradycardia (heart rate slows) sets in at lower O$_2$ levels	Holeton (1971)
Chum salmon eggs, Oncorhynchus keta	early stage eggs	10	13.9	.7	1	8.8	retarded development, deformities, mortality, respiratory O$_2$-dependence	Alderdice et al. (1958)
	pre-hatch eggs	10	>97.4	>4.9	>7.0	>61.8	oxygen level required for normal development and non O$_2$-dependent metabolism	
" "	5 day eggs	8.0–8.2	22.2	1.17	1.67	14.07	critical oxygen level for supply of oxygen demand and non O$_2$-dependent metabolism	Wickett (1954)
	(eyed) 85 day eggs	3.6–4.9	>60.3[b]	>3.5[b]	>5.0	>38.1[b]		
Atlantic salmon, Salmo salar	early eggs near hatching	5.5	9.62	.53	0.76	6.09	As above	Lindroth (1942) (from Wickett 1954)
	hatching	5	71.7	4.06	5.80	45.31		
	hatching	17	160.8	7.0	10.0	102.67		
Atlantic salmon, Salmo salar	eyed hatching	10	43.14	2.17	3.1	27.36	critical O$_2$ level for supply of O$_2$ demand and non O$_2$-dependent metabolism	Hayes et al. (1951) (from Wickett, 1954)
	hatching	10	98.83	4.97	7.1	62.67		
Northern pike, Esox lucius	from fertilization to feeding larvae	15,19	>5.18–5.66	>2.16–2.35	>3.35–3.09	>33.0	necessary O$_2$ level for proper hatching, survival and development	Siefert et al. (1973)
Mummichog,[c] Fundulus heteroclitus	fertilization to hatching	20	101.2	3.15	4.5	64.9	reduced hatching at this level compared to 7.5 mg/liter O$_2$	Voyer and Hennekey (1972)
Pacific cod, Gadus macrocephalus	fertilization to hatching	3–5			>2–3		oxygen level required for optimal hatching at 15‰ salinity	Alderdice and Forrester (1971)

[a]European species — representatives of this family found in Canadian Atlantic waters.
[b]Calculations based on 4 C.
[c]Estuarine fish — calculations based on salinity of 30‰.

"incipient lethal tension." Below this level organisms resist for a time but eventually die. The point at which metabolic rate ceases to be dependent on available oxygen is termed the "incipient limiting tension." It is identical with the critical oxygen tension of Prosser and Brown (1962), termed Pc, and is frequently given in Tables 4A–D as the "no-effect oxygen threshold" that affords good protection for fish species. This relationship seems to hold for a variety of species, from fish eggs to invertebrates, and will be frequently referred to in this paper. In animals tolerant of low oxygen, the curve in Fig. 2 is pushed to the left, while in animals requiring
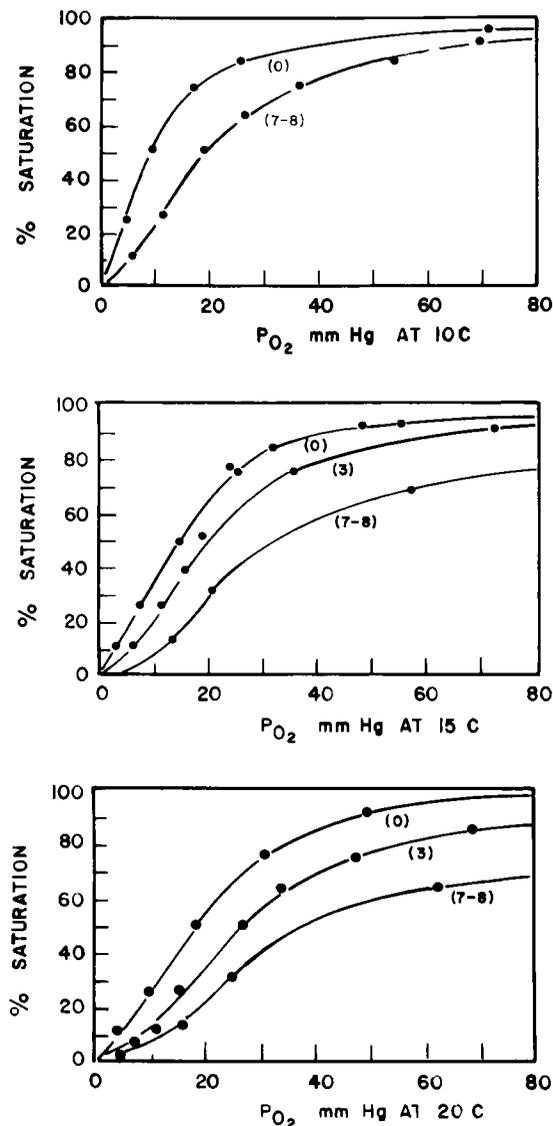
FIG. 1. Blood oxygen dissociation curves for rainbow trout (*Salmo gairdneri*) blood, plotted as O_2 tension vs. percentage oxygen saturation in the blood at three temperatures. CO_2 tensions accompanying each curve are indicated below it in parentheses (from Cameron 1971).

considerable oxygen the curve shifts right. Thus the oxygen tension that produces respiratory dependence varies with species.

Different species of teleosts (bony fish) vary in ability to regulate oxygen uptake over a range of available oxygen tensions. Elasmobranchs (cartilaginous fish) are apparently less able to regulate oxygen uptake in this way (Randall 1970). It should be remembered that levels of hypoxia

severe enough to provoke the above responses occur at oxygen levels well above those acutely lethal to fish.

The responses of fish to hypoxia represent some form of compensation or adjustment of bodily processes. Fish can resist or tolerate reduced levels of oxygen for short periods. The success of tolerance depends on species, the oxygen levels, and on environmental factors, particularly temperature. Use of regulatory or compensatory mechanisms requires energy expenditure and will consequently reduce energy reserves for swimming, feeding, avoiding predators, and other activities.

ENERGETICS AND LOW OXYGEN

Considerable work has been done on the oxygen requirements of quiescent fish under laboratory conditions. Much of the earlier work on harmful or lethal oxygen levels is of this nature. Fry (1957) recognized that the respiratory dependence phenomenon should be studied in relation to active metabolism, i.e. the level of oxygen uptake accompanying maximal swimming activity. Brett (1964) studied oxygen uptake and swimming performance of young sockeye salmon and obtained evidence that available oxygen levels may limit active metabolic rate above 15 C (Fig. 3). Brett (1970) also determined the oxygen requirements for fingerling sockeye salmon at 20 C during various important activities:

Activity	O_2 Cost of energy expenditure	% active metabolic rate
feeding — max. ration	450 mg/kg per h	55.4%
feeding — maintenance ration	300 mg/kg per h	37.3
migrating up vigorous river	625 mg/kg per h	75.0
aggression	180 mg/kg per h	22.9

In light of the above data, examination of Fig. 3 indicates that a reduction in oxygen to 50% saturation would severely limit energy expenditure for migrating or maximum feeding at the higher temperatures. Fry (1957) stated:

"Any reduction of the oxygen content below the level where the active metabolic rate begins to be restricted is probably unfavorable to the species concerned. From the ecological point of view this 'incipient limiting level' (the critical level under conditions of activity) can be taken as the point where oxygen content becomes unsuitable."

In a theoretical analysis, Jones (1971a) proposed that for salmonid fish at low temperatures (5 C) the oxygen cost of the cardiac pump limits
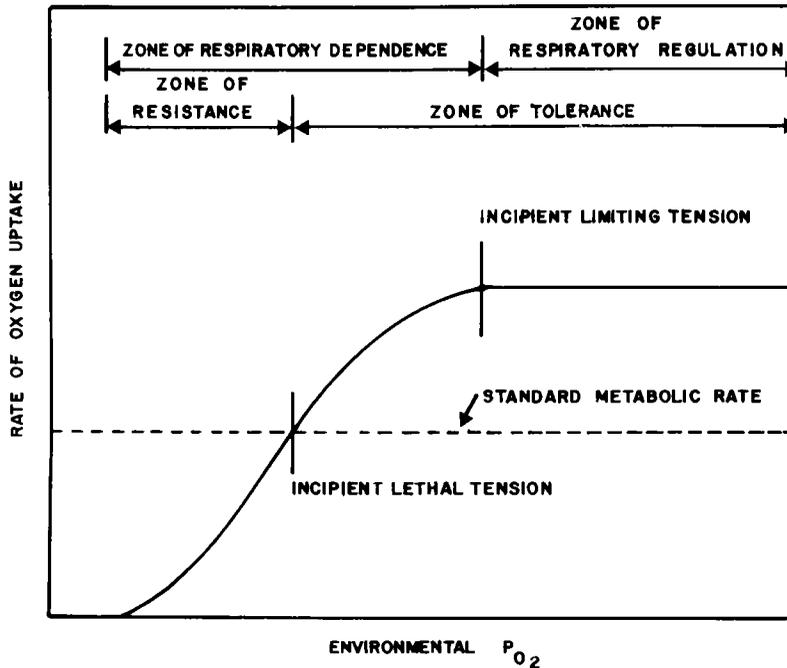
FIG. 2. Relation between standard and active (maximum) oxygen uptake rates at different environmental oxygen concentrations (from Hoar 1966).
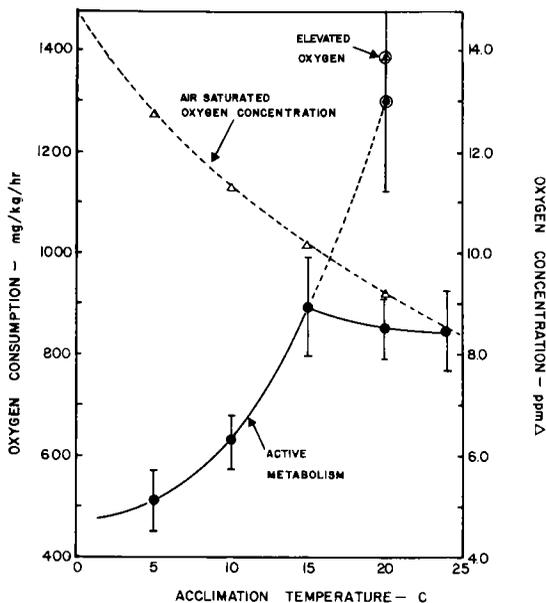

FIG. 3. Active metabolism of yearling Sockeye salmon (*Oncorhynchus nerka*) (heavy line) tested at air-saturated oxygen levels (dotted line). Mean ± 2 SE metabolic rate for elevated oxygen (13.9 ppm) determined at 20 C (circled points) (from Brett 1964).

maximal oxygen uptake during swimming; but at high temperatures (25 C) the oxygen cost of the branchial pump becomes limiting. Reductions of maximal swimming speed in rainbow trout of 30 and 43% resulted when environmental oxygen fell to 50% of saturation at 21–23 C and 8–10 C, respectively (Jones 1971b).

It should be emphasized that swimming ability in reduced oxygen may be affected by season and temperature. For example, Katz et al. (1959), reported that 6-cm largemouth bass, *Micropterus salmoides*, could resist a water current of 25 cm/s at 25 C in September even at O_2 levels of 2.0 mg/liter. However, in December at 15–17 C they were apparently unable to do so even when oxygen content was 5.0 mg/liter. In contrast, Davis et al. (1963) reported that any reduction from ambient oxygen at 10–20 C usually reduced maximum sustained swimming speed in coho and chinook salmon.

BEHAVIORAL RESPONSES TO HYPOXIA

Literature records of altered behavior of fish in low oxygen are often contradictory owing perhaps, in part, to varying experimental conditions and methods applied in studying fish
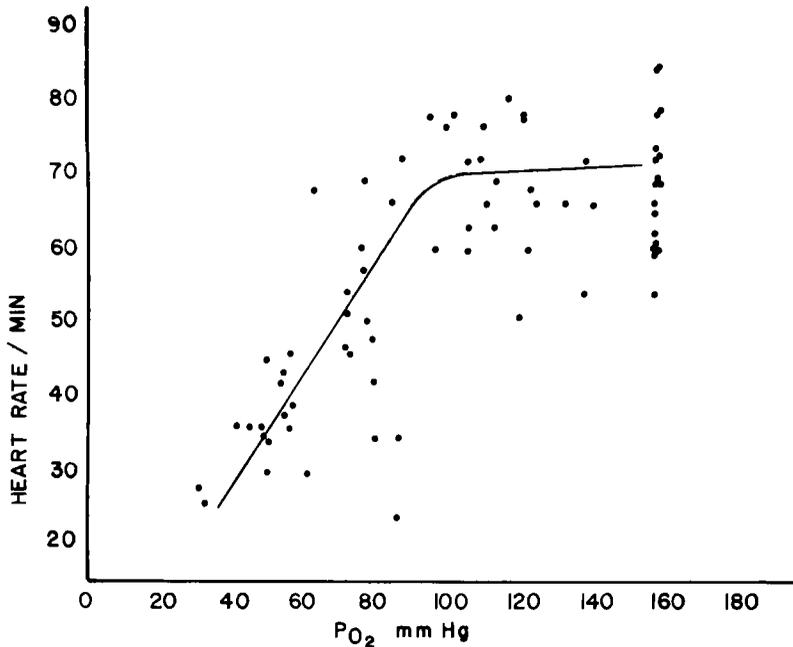
FIG. 4. Onset of bradycardia (slowing of heart beat rate) in rainbow trout in response to water oxygen tension. Solid line was fitted following a statistical analysis of the data (from Randall and Smith 1967).

behavior. It has often been stated that fish generally become more active in hypoxic water and attempt to move away from the low oxygen region (Randall 1970). Avoidance behavior has been reported for a number of species, although the reported O_2 threshold for a given response often varies considerably. For example, Whitmore et al. (1960) observed that juvenile chinook salmon (*Oncorhynchus tshawytscha*) showed marked avoidance of 1.5–4.5 mg O_2/liter in the summer at high temperatures but showed little avoidance of 4.5 mg O_2/liter in the fall. As described earlier, problems of hypoxia may develop at high temperatures where reduced water O_2 content and elevated metabolic rates would prevail. Thus a seasonal variability in behavioral sensitivity to dissolved oxygen does not seem unreasonable.

A number of other behavioral responses to hypoxia have been reported. Scherer (1971) described loss of normal avoidance of high light intensities (negative phototaxis) in walleye (*Stizostedion vitreum*) when O_2 fell to 2–4 mg/liter. Shepard (1955), studying speckled trout, *Salvelinus fontinalis*, reported "a violent burst of activity involving all the individuals in a sample" with evident "attempts to surface" when oxygen deficient water was introduced to test chambers. He further reported that fish held

at O_2 levels slightly above incipient lethal levels (1.75–1.9 mg O_2/liter) "were sluggish in their movements, fed poorly and were susceptible to disease."

It is not clear whether avoidance behavior in response to low oxygen constitutes a highly directed form of behavior. It may result simply from increased locomotor activity with more random movement, which is satisfied by discovery of improved oxygen conditions. It seems likely that avoidance behavior in low oxygen would have survival value and that the presence of this behavior pattern suggests that fish periodically may benefit from it.

Implicit in a behavioral response to low oxygen would be some means of detecting low oxygen water. The physiological responses to hypoxia are rapid, consisting of circulatory and ventilatory changes in trout and tench within a few seconds of the onset of hypoxia (Eclancher 1972; Randall and Smith 1967; Fig. 4). Such rapid responses suggest the presence of an oxygen receptor system on or near the gills. The precise location of this is not yet clear. The response is rapid enough to suggest that a reflex mechanism is involved (Dejours 1973).

It is also possible that behavioral responses to low oxygen are triggered by the circulatory and ventilatory changes necessary to compensate for
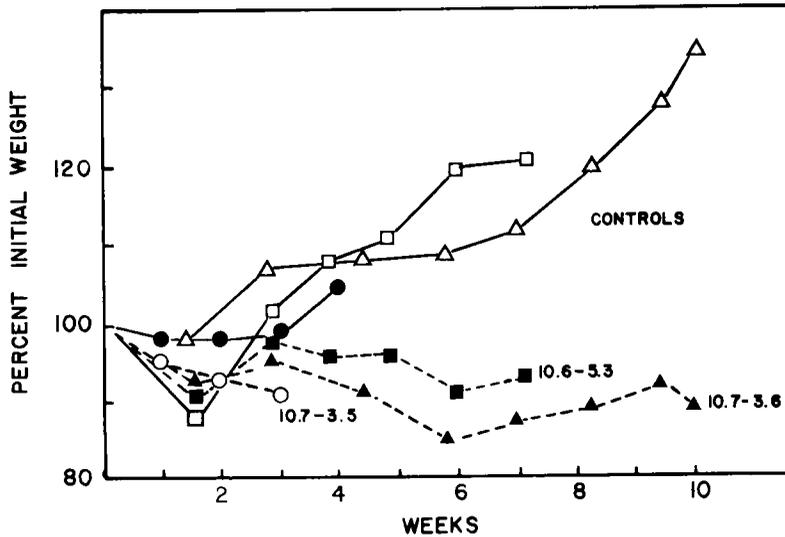
FIG. 5. Growth rate in yearling eastern brook trout (*Salvelinus fontinalis*) in constant high (solid lines — controls) and various daily fluctuating levels of oxygen (broken lines with O_2 range in mg O_2/liter) (from Fry 1970).

hypoxia. Such a mechanism would help to explain the varied behavioral thresholds reported for hypoxia, since the response might be triggered at a higher O_2 level when metabolic needs are large (for swimming, feeding, high temperatures, etc.) but not when they are minimal.

GROWTH IN REDUCED OXYGEN

High environmental oxygen levels seem to encourage growth rates in experimental fish. Stewart et al. 1967) reported that growth rate and food consumption in juvenile largemouth bass, *Micropterus salmoides*, at 26 C increased markedly as oxygen increased to near air-saturation levels and then decreased above those levels. Herrmann (1958) obtained similar results for juvenile coho salmon at 20 C as follows:

constant O_2 level — mg O_2 liter	21–27 day weight gain
4	56%
5	68%
6	88%
8	92%

He concluded that at temperatures around 20 C the "minimal oxygen concentrations to which juvenile coho salmon may be exposed for relatively long periods without markedly affecting growth, feeding, food conversion, and general activity, lie within the range of four to six milligrams per liter." Lozinov (1956) gave the opti-

mum oxygen level for growth of young sturgeon fry as 5.0–5.5 mg O_2/liter. Davison et al. (1959) observed that juvenile coho salmon at 20 C or less in the summer or fall fed well and gained weight at 2.9 mg/liter, but concluded that their fish were "probably somewhat affected."

Exposure to cycling oxygen levels appeared to reduce growth of largemouth bass juveniles at 26 C (Stewart et al. 1967). Food conversion efficiency was reduced at oxygen concentrations below a constant O_2 level of 4.0 mg/liter. Similarly, Whitworth (1968) observed loss of weight in brook trout exposed to daily fluctuations in oxygen (Fig. 5).

ACCLIMATION TO LOW OXYGEN

There are a number of indications that fish can acclimate, to some degree, to lowered oxygen levels. Shepard (1955) showed that the lethal O_2 level for brook trout, *Salvelinus fontinalis*, could be reduced with low oxygen acclimation. He suggested that adjustments might be made in the oxygen carrying capacity of the blood, thus increasing the ability to extract O_2 from the water. MacLeod and Smith (1966) showed that fathead minnows, *Pimephales promelas*, increased hematocrit (packed volume of red blood cells) in response to low oxygen, thus making more hemoglobin available for O_2 transport in the blood. However, Cameron (1970), in assessing hematological responses of pinfish, *Lagodon rhomboides*,
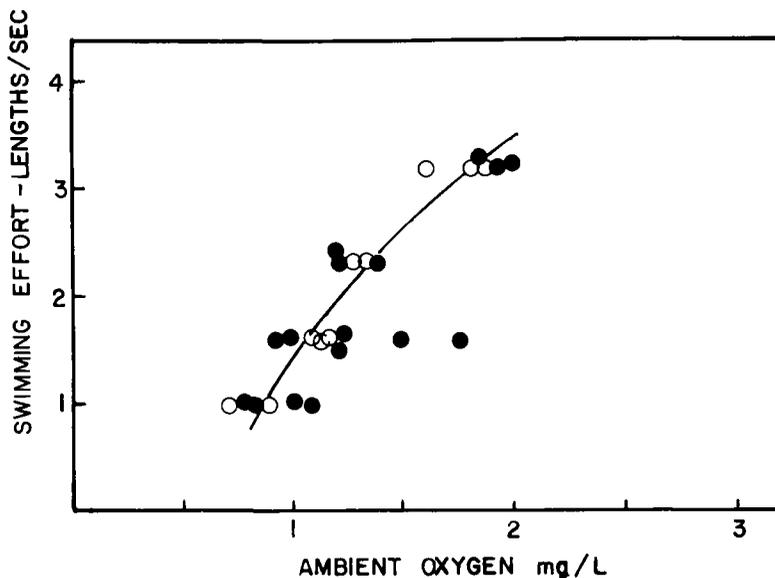
FIG. 6. Swimming ability vs. oxygen availability in goldfish (*Carassius auratus*). Open circles denote fish acclimated to air-saturation O_2 levels; closed circles indicate fish acclimated to 15% oxygen saturation. Acclimation to low oxygen did not appear to enhance swimming ability in low oxygen water under these conditions (from Kutty 1968).

and striped mullet, *Mugil cephalus*, concluded that changes in blood oxygen capacity induced by low oxygen acclimation were small and of slight significance to respiration, rather than the extensive compensatory hemoglobin production previously proposed for goldfish (Prosser et al. 1957).

As well as resulting in blood oxygen capacity changes, acclimation could be behavioral in nature. It is possible that considerable energy could be expended by a nonacclimated fish reacting behaviorally to low oxygen conditions. Acclimation could lower the magnitude of these reactions and might thus enable conservation of energy under oxygen stress.

Acclimation that enhances survival at near-lethal conditions may not always aid active processes. Kutty (1968b) found no difference in swimming speed at limiting oxygen levels in goldfish acclimated to both low and air-saturation oxygen levels (Fig. 6). In addition, he observed that reduced oxygen consumption existed in low O_2-adapted fish at a given swimming speed compared to fish held at high oxygen levels.

There is a scarcity of field data to show that ability to acclimate to low O_2 markedly improves survival chances of fish populations. Any such ability to adapt to low oxygen should be useful to some degree, especially if the transition to a low oxygen regime is slow enough to enable acclimation to occur without severe physiological stress. However, the mechanism would be of little help to fish suddenly encountering low-oxygen water. Acclimation ability can be considered as a built-in safety factor for some species encountering low oxygen conditions. I consider that there is insufficient evidence to warrant modification of oxygen criteria to include acclimatory ability of fish.

INTERACTION OF LOW OXYGEN AND TOXIC AGENTS

Areas polluted with industrial waste, sewage, and other contaminants frequently have both a low oxygen and a toxicity problem. Often a number of different wastes are discharged into a body of water from various sources. The effects of these discharges can be additive. Alderdice and Brett (1957) observed an apparent increase in toxicity of kraft pulpmill waste to young sockeye salmon in the presence of low oxygen. Townsend and Cheyne (1944) reported a similar toxic interaction of low oxygen and elevated hydrogen ion concentrations to coho salmon. Markedly increased toxicity of ammonia solutions, salts of zinc, lead, and copper and a mixture of monohydric phenols, was evident in

rainbow trout when oxygen levels fell below 60% saturation at 17.5 C (Lloyd 1961). Lloyd felt that toxicant delivery to the gills, and its rate of uptake, was enhanced by the increased respiratory flow necessary to counteract hypoxic conditions. Presumably high water temperatures, hyperactivity, or some other metabolism-stimulating condition elevating respiratory activity, would produce a similar result.

EGG AND LARVAL DEVELOPMENT IN LOW OXYGEN

There are several studies on the dissolved oxygen requirements of developing fish eggs and larvae. Like fish, eggs also show respiratory dependence (Fry 1957) (Fig. 7). Alderdice et al. (1957) reported a gradual increase in the dissolved oxygen requirements of chum salmon eggs, *Oncorhynchus keta*, as development progressed. Eggs at early stages of incubation required about 1 mg O_2/liter, while those about to hatch required over 7 mg O_2/liter. Eggs held at low oxygen tensions showed reduced growth and retarded development. Deformities in embryos exposed to hypoxia were observed, with mortality occurring at the stage when the circulatory system develops. Other workers report similar increased oxygen requirements of eggs as development proceeds (Guilidov 1969; Hayes 1949; Lindroth 1942; Wickett 1954).

Larval fish, like eggs, are affected by reduced oxygen. The oxygen demand of larval fish increases markedly with age (Sharmardina 1954). Nikiforov (1952) reported complete yolk sac
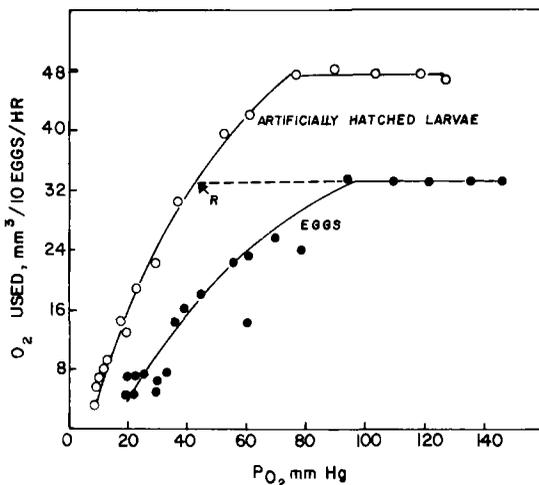

FIG. 7. Oxygen uptake rates in eggs and larvae of Atlantic salmon, *Salmo salar*, at 10 C, illustrating respiratory dependence and the influence of the egg capsule (from Fry 1957).

absorption and better growth in 5-day-old *Salmo salar* larvae reared for 25 days at 6.8–7.5 mg O_2/liter, compared to those reared at 4.5–5.0 mg O_2/liter. The latter group weighed less than one half of the high-oxygen reared group and had one third of the yolk sac unabsorbed.

Circulatory and ventilatory responses of fish larvae to low oxygen have been described. Holeton (1971) observed that oxygen tensions below 100 mm Hg stimulated heart rate and breathing rate in 1-day-old rainbow trout larvae. Similar, but more marked responses, were seen in 8-day-old larvae. In these older larvae, PO_2 levels of 45–50 mm Hg produced reduced breathing rate and increased depth (amplitude) of breathing.

There is very little information on the dissolved oxygen requirements of marine fish eggs. It seems likely that marine eggs, when close to hatching, require fairly high oxygen levels similar to eggs of freshwater species. Conceivably, an oxygen level acceptable to adult marine fish may be unsuitable for marine eggs — a factor that could easily be overlooked!

Summary of Oxygen Requirements of Fish

Reduction in the level of available oxygen has a marked effect on many physiological, biochemical, and behavioral processes in fish. The oxygen level where such effects first become apparent — i.e. the incipient oxygen response threshold, has been used throughout this report in the derivation of oxygen criteria selected to assess adverse effects on fish.

Restriction in the supply of oxygen available for metabolic processes including swimming, migrating, and feeding are likely caused by hypoxia. Adequate oxygen levels for such activities are necessary for survival of healthy fish populations. Oxygen requirements of fish are noticeably influenced by season, temperature, and activity. The oxygen tension where respiratory dependence begins is considered an important lower limit for tolerable available oxygen. Effects of hypoxia on metabolic processes and swimming ability, as well as O_2 levels causing the onset of respiratory dependence, are thus considered good indicators of the incipient sublethal effect threshold for low oxygen.

The blood oxygen dissociation curve delineates the water oxygen tension where the blood ceases to be fully oxygen saturated. For optimal gas exchange, water PO_2's, preferably 20 mm Hg above that saturation point are required in trout to maintain the necessary oxygen gradient at the gills. Oxygen dissociation curves, therefore, provide an indication of the point where available

oxygen limits or influences respiratory and circulatory functions. The shape of the blood curve and position of the limiting O_2 tension are influenced by temperature and CO_2, such that increases in these factors elevate the PO_2 required to fully saturate the blood. Limiting oxygen tensions, therefore, can be derived from blood curves and are useful for defining low oxygen effects on fish. In addition, oxygen response thresholds for circulatory and ventilatory systems have been described.

Low oxygen levels have been shown to influence growth rate, food conversion efficiency, and feeding in some species. In some cases, cycling oxygen levels appear to adversely affect growth under laboratory conditions. As growth is an expression of the net product of metabolic functions, it is a good indicator of an overall effect of low oxygen. Therefore, adverse effects of low O_2 on growth constitute a useful criterion for permissibly low oxygen levels.

Avoidance behavior has been reported for a number of species in response to low oxygen, although reports of O_2 thresholds to initiate this behavior vary considerably. Observed behavior patterns in low O_2 include increased activity, poor feeding behavior, and altered phototaxis. Avoidance behavior is likely a useful protective mechanism that enhances the survival of some species.

It is apparent that low oxygen in the presence of some toxicants enhances the lethal effect of those toxicants on some fish. Low oxygen levels producing metabolic stress could lower the ability of fish to resist toxicants as well as increase toxicant uptake rate via elevated ventilatory water flow. For these reasons the need for sound scientific dissolved oxygen criteria should be obvious, especially in geographical areas polluted by discharges toxic to fish.

Some fish show ability to acclimate to lowered ambient oxygen. However, the degree of advantage gained is not clear. Acclimation can enhance blood oxygen capacity and oxygen utilization somewhat but may not aid active swimming performance. This acclimation phenomenon may be useful to fish subjected to gradual reductions in oxygen levels, but would be of little advantage when encountering reduced oxygen levels for the first time, especially if the O_2 depression was severe. For these reasons, the application of acclimation phenomena to water oxygen criteria for fish protection has not been attempted in a subsequent section of this report and can be considered only as a possible safety factor enhancing the fish's resistance to low oxygen.

Developing fish eggs and larvae show a number of responses to low oxygen including respiratory dependence, retarded growth, reduced yolk sac absorption, developmental deformities, and mortality. As development proceeds, the oxygen requirements of both eggs and larvae increase. Trout larvae exhibit circulatory and respiratory effects of low oxygen. Most data on the effect of low oxygen on fish eggs and larvae are confined to freshwater species, particularly salmonids, and there is little informatiton for marine eggs and larvae.

It is particularly evident that much of our knowledge of low O_2 effects on fish tends to be confined to freshwater species, particularly salmonids. There is a great lack of knowledge available on the oxygen requirements and tolerances of nonsalmonid species and their eggs and larvae. The need for more research in this area is strongly emphasized.

Oxygen Requirements of Aquatic Invertebrates

There is extensive literature pertaining to measurement of metabolic rate (oxygen uptake) of aquatic invertebrates under various environmental conditions such as temperature, salinity, pH, CO_2 tension, etc. Indeed, a considerable body of knowledge is available on the interaction of environmental oxygen availability, oxygen uptake, and ventilation rates for many freshwater, marine, and estuarine organisms. The following is an attempt to summarize some of the general findings of this rather extensive literature. Unlike the fish section of this report, this section is not mainly confined to a discussion of purely Canadian species. Wherever possible, however, attention is given to reporting results from work with Canadian species. In my opinion, knowledge of invertebrate community oxygen requirements is too incomplete to warrant the setting of definite "ecologically safe" oxygen criteria for invertebrate communities. The following discussion was designed to review current general knowledge and attempts to arrive at some general recommendations that can be followed by those attempting to define safe oxygen levels for prolonged survival of invertebrate communities.

AEROBIC AND ANAEROBIC METABOLISM

Most aquatic organisms can utilize several metabolic pathways as a means of obtaining energy. These processes can be aerobic (utilizing oxygen) or anaerobic. Anaerobic processes yield energy in the absence of oxygen. An excellent discussion of the various metabolic pathways, their evolution, and relationship to oxygen availability can be found in Hochachka and Somero (1973).

TABLE 5. Summary of A) oxygen independent (regulated O_2 uptake) and B) oxygen dependent (O_2 conforming) groups of organisms (from Prosser and Brown 1962).

A) Oxygen independent

Most protozoa — *Tetrahymera, Paramecium, Trypanosoma*

Coelenterates — *Hydra* between 10 and 100%. O_2 in the gase phase

Annelids — *Tubifex, Lumbricus*, the leeches *Glossiphonia* and *Hirudo*, larvae of some polychaetes, Pc = 40 to 50 mm

Echinoderm eggs — *Arbacia*, unfertilized, Pc = 40; fertilized, Pc = 50 mm Hg

A few parasitic worms — *Trichinella*, Pc = 8 mm; *Nematodirus, Haemonchus, Rhabditis elegans*, Pc = 121 mm; *Rhabditis strongloides*, Pc = 58.5 mm

Molluscs — clam *Mya*, Pc = 40 to 50 mm; oyster, Pc = 100 mm; snail *Ancylus*, Pc = 80 mm; snail *Australabrus*, Pc = 30 mm; *Mytilus*, Pc = 50% air saturation

Crustacea — copepod *Calanus*, Pc = 204 ml O_2/liter; crayfish, Pc = 40 mm; crab *Pugettia*, Pc = 70 mm; *Uca pugilator* and *Uca pugnax*, Pc = 4 mm

Insects — termite *termopsis*, Pc = 38 mm; diapausing cecropia pupae, Pc = 23 to 28 mm; several chironomid larvae, Pc = 55 to 68 mm

Most aquatic vertebrates, Pc = 30 mm Hg

Crucian carp — 30 mm Hg at 5 C

All terrestrial vertebrates; probably all terrestrial insects

B) Oxygen dependent

Protozoa — *Spirostomum*

Numerous coelenterates — actinians, *Cassiopea*

Free-living worms — *Sipunculus, Urechis*, leeches *Piscicola* and *Erpobdella, Nereis*

Most parastic worms — trematodes — *Fasciola, Schistosoma*, cestode *Diphyllobothrium*, nematodes *Ascaris, Litomosoides, Limax*, strongyles larvae

Some molluscs and crustaceans — *Limes, Limulus, Homarus*, series of marine crustaceans daphnid *Simocephalus* fifth instar conforms over environmental range 14.6 to 1.1 cm^3 O_2/liter

Echinoderm adults — starfish, sea urchins

Some aquatic insects — *Ephemera, Anatopynia, Tanytarsus*

Few vertebrates — toadfish, *Triturus pyrrhogaster*, cutaneous respiration

The degree to which organisms can utilize anaerobic processes varies considerably and thus determines the tolerance of individual species to low oxygen conditions. Anaerobiosis is common in parasites and some, such as the intestinal flagellates of termites, may be poisoned by small amounts of oxygen (Prosser and Brown 1962). Others such as mud-dwelling tubificid worms can live for long periods in water nearly devoid of oxygen. Many organisms are normally aerobic but can survive many hours without oxygen (e.g. frogs, earthworms, cockroaches, aquatic snails) by utilizing anaerobic means of energy production. In contrast, many aerobic animals are highly dependent on oxygen. Typically, these animals can build up only a brief oxygen debt (accumulated metabolic products of anaerobic metabolism, such as lactic acid, or other compounds, which must be later oxidized), particularly in their muscles. Examples of these organisms are birds, mammals, many adult insects, and cephalopod molluscs (Prosser and Brown 1962). In general, animals with high metabolic rates are less tolerant of low O_2 than sluggish forms; early eggs and cysts and small organisms are often tolerant of low oxygen, as are hibernating or behaviorally-inactive organisms.

It should be emphasized that anaerobic processes yield less energy per unit glucose metabolized compared to aerobic processes (Lehninger 1965). The utilization of anaerobic pathways is therefore accompanied by some reduction of available energy. This is likely not a serious consequence for small, relatively inactive species but would be problematical to larger, active species. A reduction in available oxygen would therefore most seriously affect the more active, high-energy utilizing members of a community. These generalizations will be discussed in the following sections on animals inhabiting different environments.

RESPIRATORY DEPENDENCE IN INVERTEBRATES

Earlier it was pointed out that the phenomenon of respiratory dependence (a correspondence of the rate of oxygen uptake with available oxygen level) occurs in many fish as well as in their eggs and larvae. Often there is a critical oxygen tension for invertebrates as well (Pc — Prosser and Brown 1962) below which respiratory dependence begins. Prosser and Brown describe organisms whose oxygen uptake rate is independent of available O_2 level above the Pc level (Table 5A) and

others (Table 5B) whose O_2 uptake rate conforms to the available O_2 level.

It can be seen from Table 5 that many aquatic invertebrates possess the ability to regulate oxygen uptake over a range of oxygen tensions, while many others show conformity (dependence). Furthermore, the level of Pc varies considerably, sometimes even between closely related forms. Nicol (1967) suggested that a number of factors determine whether an animal is dependent or independent of the environmental oxygen level. These factors include size, existence of a circulatory system, diffusion distances, temperature, degree of locomotor activity, ability to regulate external respiration, and the existence of respiratory pigments.

Examples of respiratory dependence and independence will be discussed in the following sections.

OXYGEN REQUIREMENTS OF SOME FRESHWATER INVERTEBRATES

The oxygen-sensitivity and oxygen uptake rates of many freshwater organisms appear to reflect the habitat in which they live. For example, Fox et al. (1937) reported the following results with mayfly nymphs:

Genus	Habitat	O_2 uptake at air satn. (mgO$_2$/g/h)	Pc (ml O$_2$/liter)	Pc (mg O$_2$/liter)
Baetis	swift streams	2.8	12.0	17.00
Leptophlebia	lake	2.1	2.5	3.60
Cloean	pond	1.3	2.0	2.86

Von Brand et al. (1950) reported that Lymnaeidae and Physidae groups of freshwater snails could withstand 6 h of anaerobiosis, while Planorbidae and Operculate snails survived at least 24 h. *Donacia* larvae (Chrysomelidae: Coleoptera) survived 168 h in closed bottles that had only 0.26 ml O_2/liter (0.37 mg O_2/liter) at the start of the test (Hoffman 1940). Also, Cole (1926) reported that freshwater clams, *Anadontoides ferrussacianus*, could live for several days in the absence of oxygen. These species inhabit muddy bottoms where oxygen may be periodically low. Sprague (1963) observed 50% mortality in 24 h in the isopod *Asellus intermedius* at 0.03 mg O_2/liter, and mortality thresholds of 0.7, 22, and 4.3 mg O_2/liter for the amphipods, *Hyalella azteca*, *Gammarus pseudolimnaeus*, and *Gammarus fasciatus*, respectively. Of these, *A. intermedius* is often found in polluted and deoxygenated water, whereas records of *G. fasciatus* inhabiting deoxygenated water are scarce.

Moshiri et al. (1970) reported dependent respiration in the crayfish, *Pacifastacus leniusculus*. At 20 C over a range of 2–7 ml O_2/liter oxygen utilization was elevated below 4.0 ml O_2/liter (=5.7 mg/liter) and ventilation depressed below 2.5 ml O_2/liter (=3.6 mg/liter). Larimer and Gold (1961) found similar respiratory dependence in the crayfish, *Procambarus simulaus*, and a stimulation of ventilation when oxygen levels dropped. Hoglund (1961) showed that the crayfish, *Astacus fluviatilus*, responded to oxygen gradients by moving from low to high O_2 concentration. Berg (1952) compared related freshwater snails, *Ancylus fluviatilus*, and *Acroloxus lacustris*, and noted that *Acroloxus* could survive much longer anaerobic exposure than *Ancylus*. Berg suggested this difference could be related to *Acroloxus'* preference for stagnant conditions.

Various responses of freshwater organisms to low or declining oxygen levels have been described. Chironomid larvae and the leech, *Erpobdella testacea*, are able to regulate oxygen uptake and lower their Pc following acclimation to low oxygen. *Daphnia* produce hemoglobin and turn red after stimulation with low oxygen for about 10 days (Prosser and Brown 1962). *Donacia* larvae become inactive in low oxygen water and resume activity when oxygen levels rise (Hoffman 1940). *Daphnia magna* show a preference for fully saturated water over that only 15% saturated, although more than an hour is required for the response to develop (Fig. 8) (Ganning and Wulff 1966). *Gammarus pulex* (Costa 1967) increases its pleopod movement in low oxygen and moves out of low oxygen water. A slowly developing avoidance reaction to oxygen contents up to 7 mg O_2/liter was demonstrated (Fig. 9). Freshwater snails, *Ancylus fluviatilus*, climb to-
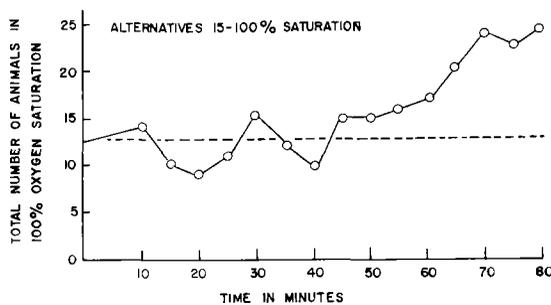

FIG. 8. Oxygen preference test with *Daphnia magna* taken from a laboratory culture kept in 80% O_2-saturated water. Dotted line refers to a 50–50% distribution of animals in the two choice O_2 saturations (from Ganning and Wulff 1966).
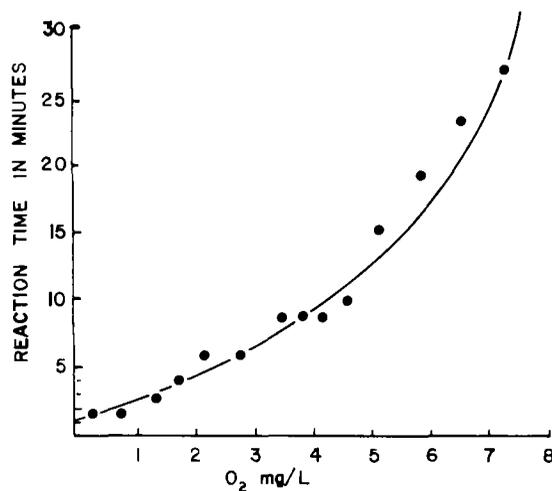
FIG. 9.   Time for the onset of avoidance behavior to low oxygen water by *Gammarus pulex* at 14–15 C (from Costa 1967).

wards the surface of the water when dissolved oxygen drops (Berg 1952). Chironomids suspend feeding when oxygen drops to 5–7.5% of saturation (Prosser and Brown 1962).

OXYGEN REQUIREMENTS OF SOME INTERTIDAL MARINE INVERTEBRATES

During the night at low tide, oxygen levels in pools and animal burrows may drop substantially, depending on community respiration rates, population density, organic decomposition, and other factors. The lugworm, *Arenicola marina*, cannot tolerate oxygen in water above 4% of saturation. Fully O_2-saturated water is slowly toxic, reflecting this species' tolerance and specialization for periodic anoxic conditions. In contrast, *Sabella pavonina*, a tubicolus polychaete normally dwelling in well-aerated water, tolerates 10% O_2 saturation but dies in 4 days at 4% (Nicol 1967). The polychaete *Nereis diversicolor* reduces its rate of water pumping in low O_2, as does *Arenicola*, possibly to conserve energy. *Gammarus oceanicus* from Nova Scotia tide pools avoid experimental anoxic conditions and become more active (Cook and Boyd 1965). Oysters, *Ostrea virginica*, survive exposure for at least a week to water containing less than 0.5 mg O_2/liter (Mitchell 1912). Similarly, the mussel, *Mytilus edulis*, can survive several weeks without oxygen (Moore 1964).

Nematodes and mites, inhabiting large coastal sea weeds (*Fucus, Ascophyllum*) which collapse at low tide and consume oxygen from tide pools, can survive anaerobic conditions for 16 h at 25 C (Wieser and Kanwisher 1959). Marsh crabs,

Uca pugnax and *U. pugilator*, show respiratory independence down to a PO_2 of 40–50 mm Hg, and can withstand anaerobic conditions for at least 1 wk (Teal and Carey 1967).

Pacific sea urchins provide a good example of utilization of various degrees and modes of respiration related to O_2 availability and demands of metabolism. *Strongylocentrotus drobachiensis, S. franciscanus,* and *S. purpuratus* show respiratory dependence below 60–70 mm Hg PO_2 (Fig. 10), and below that level, oxygen tensions in water and coelomic fluid show close correspondence (Fig. 11). Indeed, these urchins appear able to reduce their internal coelomic fluid PO_2 even in well-aerated water, possibly utilizing energy-saving mechanisms in doing so (Johansen and Vadas 1967). Furthermore, urchins can survive up to 15 h exposure to moist air. The gas exchange occurring under these conditions is enough to support an oxygen uptake rate ½–⅕ of the maximum rate observed in aerated water.

Some amphipods, frequently found under rocks, logs, and algae on Pacific shores can tolerate low oxygen. Waldichuk and Bousfield (1962) observed numerous *Allorchestes angustus* and some *Anisogammarus pugettensis* in surface water containing 0.3–0.89 mg O_2/liter (near a Sulphite pulp mill). C. D. Levings (unpublished cruise report — Ocean Falls Harbour, B.C.) lowered baskets of *Anisogammarus confervicolus* into a low oxygen layer 40 m deep. All the amphipods survived 24 h exposure to 0.52–1.25 ml O_2/liter (0.74–1.8 mg O_2/liter) but died after 36 h.

OXYGEN REQUIREMENTS OF BENTHIC MARINE ORGANISMS AND COMMUNITIES

Marine benthos are often exposed to low oxygen conditions due to oxidative processes occurring in or near the sediments that deplete water of oxygen. The severity of the depletion depends upon many factors including geographical position, depth, tides and currents, population structure, settlement rate of organic matter, and aerobic respiration of organisms.

In many instances the oxygen level most suitable for benthic dwellers can be related to their life habits. The amphipod *Corophium arenarium* inhabits aerobic sediments, while *Corophium volutator* is found in anaerobic sediments. Behavior experiments showed that *C. arenarium* has a significant preference for oxygenated water, while *C. volutator* is indifferent (Gamble 1971).

Numerous responses of benthic invertebrates to declining oxygen levels have been reported. The octopus, *Octopus dofleini*, exhibits lowered arterial blood oxygen levels and elevated cardiac output when O_2 partial pressure falls below 120 mm Hg
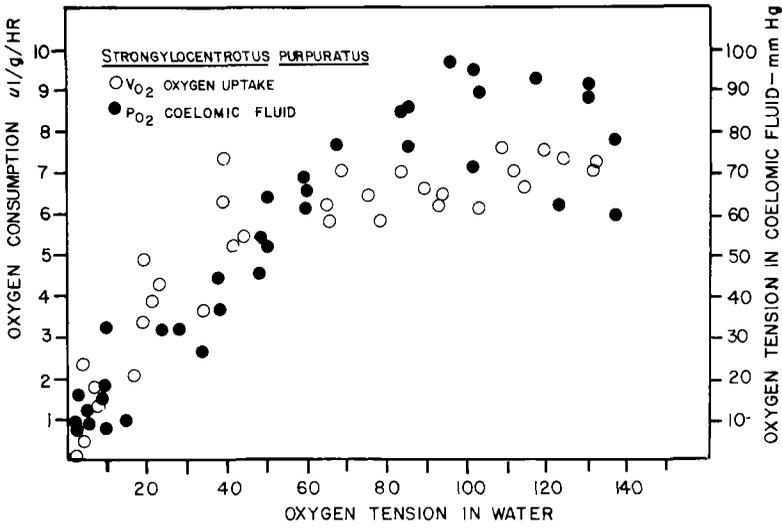
FIG. 10. Oxygen uptake (left ordinate, open circles) and coelomic fluid PO$_2$ (right ordinate, closed circles) vs. partial pressure of ambient water in the Pacific sea urchin *Strongylocentrotus purpuratus* (from Johansen and Vadas 1967).
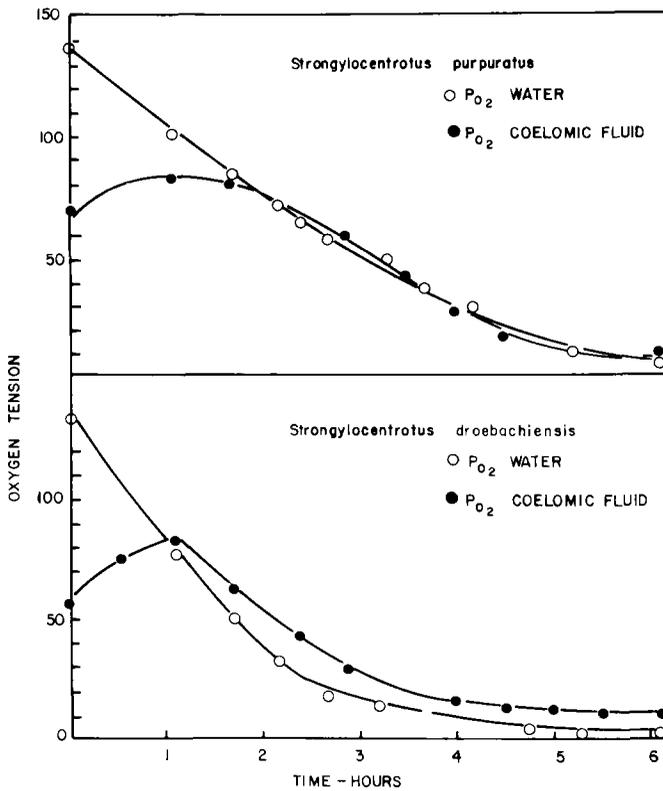
FIG. 11. Oxygen tension in water and coelomic fluid to two species of Pacific urchins observed when the urchins were in a closed respiration chamber (from Johnsen and Vadas 1967).
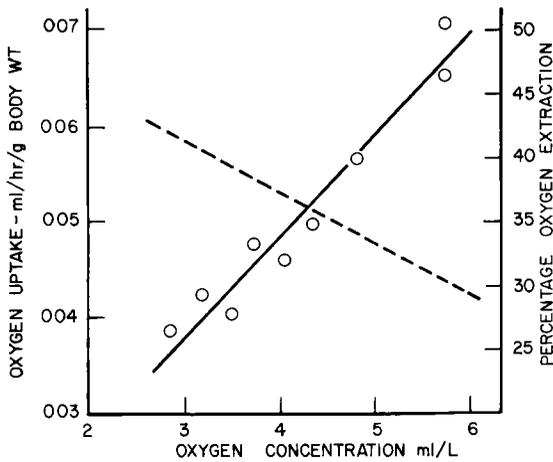
FIG. 12. Effect of water oxygen content on oxygen uptake, and percentage oxygen extracted by the gills of a 332-g European lobster, *Homarus vulgaris*. Solid line depicts oxygen uptake and the dotted line denotes percentage extraction (from Thomas 1954).
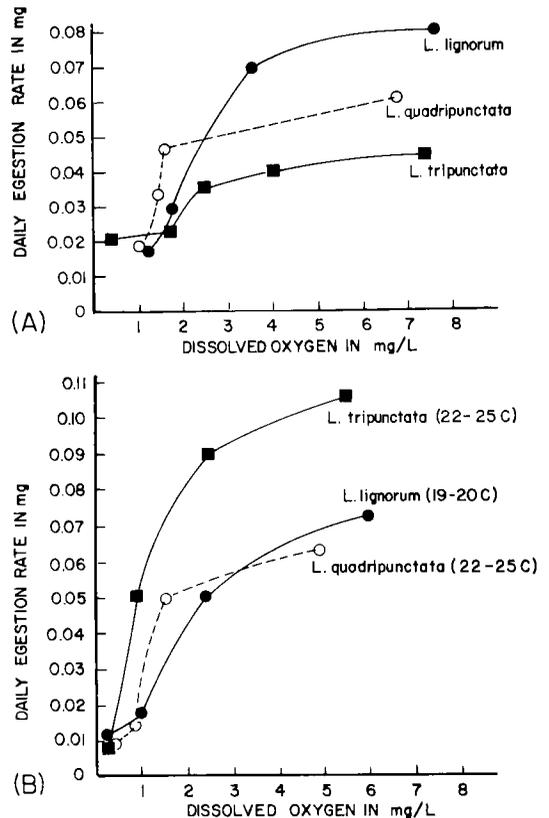

FIG. 13. Daily egestion rates of three species of *Limnoria* at different dissolved oxygen concentrations at A) 15 C and B) the temperatures indicated (from Anderson and Reish 1967).

PO_2 (Johansen and Lenfant 1966). Some tendency for oxygen-dependent respiration is evident in the lobster, *Homarus vulgaris* (Fig. 12) and crab, *Cancer productus*, especially at high temperatures when oxygen availability falls (Belman and Childress 1973). Burrowing activity in wood of three marine isopods, *Limnoria lignorum*, *L. quadripunctata*, and *L. tripunctata*, (Fig. 13) appears directly related to available oxygen tension (Anderson and Reish 1967). Twenty-eight days MTL's for survival of these three species tested at three temperatures range from 0.6 to 1.18 mg O_2/liter. The calcareous tube-building polychaete, *Hydroides norvegica*, may show reduced larval settlement in low oxygen conditions (Reish 1961) as well as in low temperatures. Estuarine shrimps, *Crangon vulgaris*, are asphyxiated below 20% air saturation (21 C, 23‰ salinity), and are stimulated to swim vertically at dissolved oxygen levels between 22 and 35% of saturation (Huddard and Arthur 1971). The authors suggest that this vertical swimming response may allow the shrimps to be horizontally displaced by currents and so reach areas of improved oxygen conditions where they passively sink to the bottom. The anemonae *Actinia* moves to the surface when O_2 falls below 2 ml O_2/liter (2.8 mg O_2/liter), but if this movement is prevented it closes up and "enters a latent period of life," (Nicol 1967).

Ventilatory activity is often affected by O_2 level. *Arenicola* and *Nereis diversicolor* reduce their rate of water pumping in burrows, while another polychaete, *Chaetopterus variopedatus*, increases its pumping rate. The lobster *Homarus*

vulgaris shows increased oxygen utilization and respiratory dependence at 15 C, in response to declining oxygen levels. Atlantic lobster kills are suspected to be sometimes related to low dissolved oxygen (Young 1973), although McLeese (1956) reported survival of American lobsters for 48 h in 1.1 mg/liter of oxygen. Crustacea often show elevated respiratory movements in low oxygen, as seen in the stomatopod, *Squilla mantis*, the prawn, *Pandalus borealis* and the crab *Carcinus maenas* (Johnston 1936).

The respiratory dependence phenomenon, exhibited by many invertebrates, can be demonstrated for benthic communities. The log of sediment oxygen uptake from a variety of benthic communities appears correlated significantly with temperature (Fig. 14A). Thus, in terms of their oxygen requirements, benthic communities of diverse geographical location appear similar. When oxygen levels fall below 6.0 mg O_2/liter, the rate of sediment-community O_2 uptake may decline (Fig. 14B). The sediment community appears to
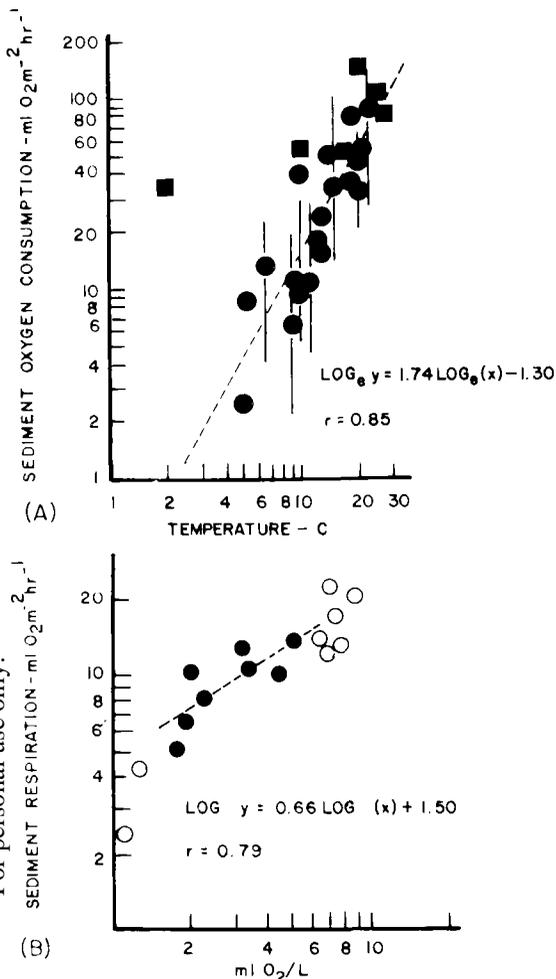
FIG. 14. A, Oxygen uptake by a variety of benthic communities, both marine and fresh water, in relation to temperature. Values are given as individual points or as ranges if the data permit, each point or range signifying a different study; B, Relationship between the sediment oxygen uptake rate and the oxygen content of overlying water at 15 C in Marion Lake, B.C. Open circles are not included in the regression calculation (from Hargrave 1969).

exhibit the respiratory dependence phenomenon, likely because of the response of the individuals composing the community. It follows that the degree of hypoxia tolerated by a community will depend on the ability of individuals within the community to withstand low oxygen. Thus, if a prolonged low oxygen regime is imposed on a community, the tolerant members will survive while the less resistant will die off and may be replaced by more tolerant forms from within or outside the community.

A comprehensive documentation of the effect of periodic anaerobic conditions on benthic community structure was made by Hoos (1973). Her study dealt with Petpeswick Inlet, Nova Scotia, where the deeper water becomes anoxic in late summer and fall. Hoos found that species diversity of benthos decreased with depth, and varied seasonally according to the available dissolved oxygen level. Below 15 m, *Nephtys incisa, Mytilus edulis, Mya arenaria, Capitella capitata,* and copepods were the dominant organisms when sufficient oxygen was present to support life. In the deep basin, species diversity declined to zero in September–November, 1971. When basin turnover occurred, the major recolonizers included adult *Yoldia limatuloides, Nephtys incisa, Polydora quadrilobata, Corophium* sp., phyllodocid polychaetes, and nematode worms. Hoos reports that her findings are similar to those of several authors, working elsewhere, who listed organisms best able to survive periods of deoxygenation that included *Nephys* sp., *Nereis* sp., *Scoloplos* sp., *Capitella capitata, Mytilus edulis, Mya arenaria, Corophium volutator,* harpacticoid copepods, and nematodes. Similar studies and reports of sensitivity of benthos to low oxygen in other parts of the world were made by Emery and Hulsemann (1962), Heegaard (1944), Rhoads and Morse (1971), and Tulkki (1965).

Substantial benthic communities often exist under low oxygen conditions. For example, C. D. Levings (unpublished data) examined the oxygen content and community structure below 150 m depth in two areas in the north end of Howe Sound near Vancouver, B.C. Seasonal oxygen levels at these two sample areas taken 5 m above the bottom were:

Date	Basin station (x, range, n) ml O_2/liter	Woodfibre station (x, range, n) ml O_2/liter
June 1972	2.24, 2.10–2.57, 4	2.25, 1.87–2.63, 2
Sept. 1972	5.65, 4.08–7.16, 3	5.86, (identical), 2
Nov. 1973	2.79, 2.32–3.11, 4	2.54, 2.22–2.86, 2
Jan. 1973	3.03, 2.30–3.32, 7	2.42, 2.41–2.43, 2
Feb. 1973	2.84, 2.71–2.93, 4	2.71, 2.57–2.86, 2

Summaries of the polychaete worm species retained on a 0.5-mm sieve at each station are presented in Table 6. It can be seen that a variety of taxa exist in deep water where only 2–3 ml O_2/liter (2.9–4.3 mg/liter) is commonly found. The large differences in number of taxa between the two communities may be related to the presence of wood waste and/or chemical contamination at Woodfibre station, or other factors, as yet unknown.

A thriving mixed invertebrate community was described by Levings and McDaniel (1974) who examined benthos attached to an undersea cable spanning the Strait of Georgia, B.C. The cable was retrieved from deep water where the oxygen levels are between 2 and 4 ml O_2/liter (2.9 and 5.7 mg/liter). Levings and McDaniel observed "a wide variety of epifaunal invertebrates including sponges, anemones, gorgonians, polychaetes, and starfish attached to the cable retrieved from water 300–350 m deep."

OXYGEN TOLERANCES AND REQUIREMENTS OF MARINE PLANKTONIC AND PELAGIC ORGANISMS

Organisms that swim freely in the sea, float, or are passively transported in some way, could encounter a variety of oxygen conditions. Generally, surface waters are well oxygenated while deeper layers tend to be lower in oxygen content, although there are numerous exceptions due to upwelling, river outflows, decomposition, respiration, photosynthesis, and pollution influences.

The oxygen requirements, oxygen-related behavior and physiology of pelagic fish have been reviewed previously. Pelagic invertebrates in many instances show some similar responses. The squid *Loligo* is reported to avoid oxygen-deficient water (Prosser and Brown 1962), and observations of other planktonic species' availability in low oxygen conditions are recorded. For example, Hoos (1970) observed a variety of species inhabiting an oxygen-minimum deep layer (approximately 0.4 ml O_2/liter = .57 mg/liter) in a B.C. inlet (Table 7). Hoos found that some vertically migrating species such as *Euphasia pacifica* did not enter the oxygen-minimum layer, while others such as *Calanus plumchrus* tended to remain there. In contrast, Marshall et al. (1935) concluded:

"*Calanus* are unaffected by an increase in the oxygen content of the water, but are sensitive to low oxygen tensions. Below a concentration of about 3 ml/l the respiration decreases. At concentrations between 1 & 2 ml/l they are killed. They are more resistant at 5°C than 15° and stage V are more resistant than adults at both these temperatures." (Fig. 15)

Summary of Oxygen Requirements of Aquatic Invertebrates

From the foregoing discussion it is obvious that a great range of tolerances, responses, and requirements for oxygen exist amongst aquatic invertebrates. Separate aquatic communities are also likely to differ in sensitivity to oxygen, and a range of susceptibility to low O_2 is often found amongst the individuals of a community. Oxygen tolerance tends to be correlated with habitat, so that individuals normally living in well-oxygenated water are less tolerant of low dissolved oxygen than those encountering it periodically. Furthermore, there is some evidence that oxygen-dependent respiration may apply to oxygen uptake relations of communities, as well as to individuals.

Difficulty is encountered in determining safe levels of dissolved oxygen for aquatic invertebrates because of i) the wide range of responses reported, ii) the ability of many organisms to inhabit low oxygen regimes and obtain energy anaerobically, and iii) by a lack of understanding of the physiological effects of low O_2. Survival in continuous levels of low oxygen depends on ability to produce energy continuously anaerobically, or the capacity to extract oxygen from an environment low in oxygen. Also, the ability of organisms to cope with oscillating oxygen levels is very poorly known or understood. Obviously, the tolerance of the species involved and the duration of low oxygen condition are of prime importance to survival. Utilization of anaerobic metabolism could satisfy the energy needs of many aquatic invertebrates for long periods, particularly the smaller, sluggish forms with a typically low oxygen demand. The larger, more active

TABLE 6. Polychaete taxa retained on a 0.5-mm seive from benthic samples taken at two Howe Sound, B.C. stations in 1972 by C. D. Levings (unpublished data).

Taxa at basin stations	Taxa at woodfiber stations
Polychaeta (Families)	Polychaeta (Families)
Ampharetidae	Capitellidae
Capitellidae	Cirratulidae
Cirratulidae	Nereidae
Flabelligeridae	Nephytidae
Glyceridae	Paraonidae
Lumbrineridae	
Maldanidae	Σ 5 taxa
Nephytidae	
Nereidae	
Opheliidae	
Oweniidae	
Paraonidae	
Pectinariidae	
Phyllodocidae	
Polynoidae	
Sabellidae	
Spoinidae	
Syllidae	
Sternaspidae	
Terebellidae	
Σ 20 Taxa	

TABLE 7. Pelagic invertebrate species inhabiting an oxygen minimum layer (approx. 0.4 ml O_2/liter = 0.57 mg/liter) in Saanich Inlet, B.C. (from Hoos 1970).

| Phylum	Species	Abundance[a]
Cnidaria	*Aglantha digitals*	seasonally abundant
	Aequorea aequorea	rare
	Phialidium gregarium	common
	Aegina rosea	rare
Ctneophora	*Pleurobrachiia pileus*	seasonally abundant
	Beroe cucumis	rare
Annelida	*Tomopteris renata*	rare
Chaetognatha	*Sagitta elegans*	rare
Mollusca Pteropoda	*Clione limacina*	rare
	Limacina helicina	common
Arthropoda Copepoda	*Calanus plumchrus*	very abundant
	Calanus cristatus	rare
	Pseudocalanus minutus	abundant
	Eucalanus bungii bungii	common
	Euchaeta japonica	abundant
	Metridia lucens	abundant
Mysidacea	*Neomysis rayii*	rare
Amphipoda	*Parathemisto pacifica*	abundant
	Euprimno abyssalis	rare
	Cyphocaris challengeri	abundant
	Orchomenella obtusa	abundant
Euphausiaceae	*Euphausia pacifica*	abundant
	Thysanoessa longipes	common
	Thysanoessa raschii	common
	Thysanoessa spinifer	rare
Decapoda	*Spirontocaris sica*	rare
	Munida quadrispina	common

[a]Terms described by Fulton (1968).
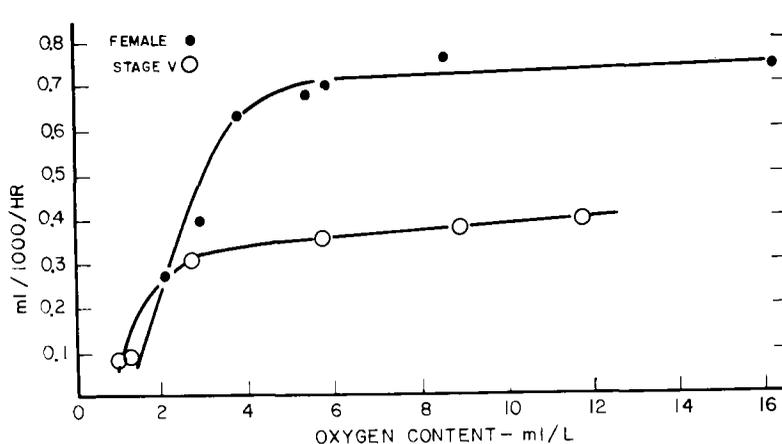
FIG. 15. Effect of oxygen content on the oxygen consumption of female and stage V *Calanus*, at 15 C (from Marshall et al. 1935).

forms are likely to be more affected by low O_2 and thus may be the most sensitive members of the community. Thus, a change from an adequate oxygen regime to one of relative O_2 scarcity may result in loss of the more sensitive organisms and a restructuring of the community. New species, tolerant to low oxygen, could move into the community; or those already present in the community could become more numerous to replace the intolerant species. Alternatively, no replacement could take place, leading to a net reduction in biomass and/or alteration of species composition of the community.

In conclusion, and on a common-sense basis alone, it seems likely that any depression of natural oxygen conditions can result in a change in an aquatic invertebrate community. The severity of this change will be related to the species composition, the species sensitivity of low oxygen, the degree of oxygen depression, and other factors acting on the community, such as temperature. Whether a change in an invertebrate community is necessarily bad from an ecological point of view may be very difficult to determine. It may be that a change from one type of community to another may not be necessarily deleterious. On the other hand, if major food chain constituents drop out, the change could be considered deleterious.

Insufficient evidence exists presently to formulate definite dissolved oxygen criteria concerning aquatic invertebrate communities. However, a reasonable basis will probably be assured by following the recommendations for fish populations given here, particularly as many invertebrates are able to temporarily withstand periods of low oxygen. It must be remembered, however, that any change in dissolved oxygen will likely affect invertebrate communities in some way. Ideally, we need a good knowledge of community structure in areas threatened by pollution so that important sensitive species are identified and protected. In addition, knowledge of the seasonal oxygen minima for specific areas is required to identify periods when further oxygen depression poses a hazard to aquatic life.

Development of Oxygen Criteria for Fish Populations

The incipient oxygen response levels for fish populations were presented in Tables 4A–D. These tables yield:

1. Oxygen response thresholds for freshwater fishes including nonanadromous salmonids (as the steelhead is a variant of the rainbow trout, it was considered a nonanadromous species for the purpose of this paper).

2. Oxygen response thresholds for marine fishes, including both anadromous and nonanadromous species. All the species of salmon (except rainbow trout and steelhead) are included in this section although they spend some portion of their life in fresh water.

3. Thresholds of oxygen response for salmonid eggs and larvae at various stages of development.

These groupings can be further broken down by including or excluding the salmonids, to thereby derive criteria for nonsalmonid freshwater or marine species.

STATISTICAL TREATMENT OF DATA FOR DEVIATION OF CRITERIA

The data of Table 4A–D were analyzed by averaging the incipient threshold levels of PO_2, milliliters O_2 per liter, milligrams O_2 per liter, and percent saturation for various fish groups within the tables. The data-groups analyzed appear in Table 8. For each group, the mean average incipient threshold oxygen level was calculated and reported with its standard deviation, standard error, and number of observations. Averaging the data in this way assumes that results will be unaffected by different experimental conditions, fish tested, and factors such as temperature. Variations due to differing experimental conditions should be minimized by the large sample size in most instances.

The effect of temperature on the incipient oxygen threshold was examined to test the validity of the averaging procedure. For the largest body of data (Table 4A), all results showing the incipient oxygen level in milligrams O_2 per liter (Fig. 16) and percent saturation (Fig. 17) were plotted in relation to temperature. From these figures it can be seen that the oxygen content threshold, in milligrams O_2 per liter, is relatively unaffected by temperature; although, higher percentage saturation levels are required at higher temperatures. This is logical since the oxygen content drops as temperature increases. Thus, progressively higher percentage saturation is required at high temperatures to fulfil the oxygen requirements of fish. For the analysis then, oxygen content data (milligrams per liter) rather than percentage saturation data were used in the derivation of criteria.

From the data in Table 8, major fish groups (only those with a large number of observations) were selected (Table 9) for criteria purposes. These groups encompass both salmonid and nonsalmonid species in fresh and salt water, as well as larvae and mature eggs of salmon. Owing to the fact that oxygen levels often fluctuate in

TABLE 8. Mean thresholds of incipient oxygen response thresholds listed in Table 4A–D. Values are means ($\bar{x}$) shown with ± 1 standard deviation (SD), $\pm$ standard error (SE), and the number of observations (*n*).

Averaged Group		PO$_2$-mm Hg	Mg O$_2$/liter	% Satn.
Freshwater species	$\bar{x}$	85.56	5.26	54.62
including salmonids	SD	27.37	2.01	17.53
	SE	5.37	0.37	3.44
	n	26	30	26
Freshwater species	$\bar{x}$	72.56	3.98	46.53
excluding salmonids	SD	18.83	1.65	12.34
	SE	7.12	0.50	4.66
	n	7	11	7
Freshwater salmonids	$\bar{x}$	90.35	6.00	57.60
	SD	28.84	1.84	18.47
	SE	6.62	0.42	4.24
	n	19	19	19
Marine, nonanadromous	$\bar{x}$	111.03	6.72	73.25
	SD	31.54	2.12	19.72
	SE	11.15	0.80	7.45
	n	8	7	7
Marine anadromous	$\bar{x}$	122.86	6.43	78.49
species, including	SD	35.86	2.57	23.03
salmonids	SE	11.95	0.69	7.68
	n	9	14	9
Marine anadromous	$\bar{x}$	—	3.38	—
species, excluding	SD	—	—	—
salmonids	SE	—	—	—
	n	—	2	—
Marine anadromous	$\bar{x}$	122.86	6.94	78.49
salmonids	SD	35.86	2.39	23.03
	SE	11.95	0.69	7.67
	n	9	12	9
Early eggs, freshwater	$\bar{x}$	15.24	1.14	9.65
salmonids	SD	6.40	0.47	4.06
	SE	3.69	0.27	2.34
	n	3	3	3
Mature eggs,	$\bar{x}$	76.47	5.93	48.40
prehatching salmonids	SD	19.00	1.01	12.15
	SE	10.97	0.58	7.01
	n	3	3	3
Hatching eggs and	$\bar{x}$	119.88	8.09	76.26
larval salmonids	SD	35.45	1.65	22.88
	SE	20.46	0.95	13.21
	n	3	3	3
Eggs, fertilization	$\bar{x}$	77.45	3.86	48.95
to hatching, non-	SD	—	—	—
salmonids	SE	—	—	—
	n	2	2	2

natural waters, the levels of protection selected were defined as MINIMUM oxygen levels in a body of water SEASONALLY (fall, winter, spring, and summer). Three levels of protection were devised to provide flexibility in interpretation:

Level A — This level is 1 SD above the mean

average incipient oxygen response level for the group. The rationale is that few members of a fish population, or fish community, will likely exhibit effects of low oxygen at or above this level. Level A represents more or less ideal conditions and permits little depression of oxygen from full saturation. It represents a level that

OXYGEN CONTENT RESPONSE THRESHOLDS IN RELATION TO TEMPERATURE FOR FRESHWATER FISH
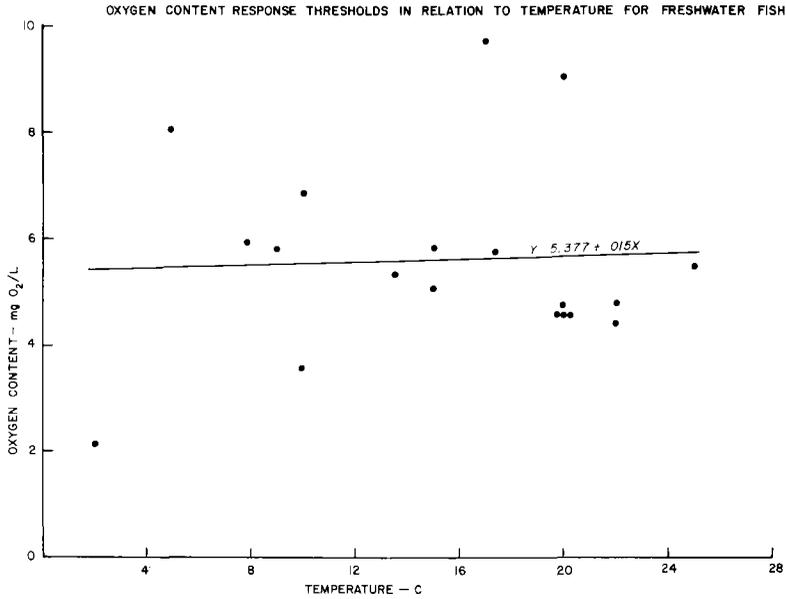

FIG. 16. Incipient sublethal oxygen response thresholds vs. temperature for all the freshwater fish data in Table 4, plotted in terms of oxygen content. The plot is similar to Fig. 17 and shows that the relationship between response threshold is not as clearly related to temperature as when plotted in terms of percentage saturation.

OXYGEN % SATURATION THRESHOLDS IN RELATION TO TEMPERATURE FOR A MIXED GROUP OF FRESHWATER FISH
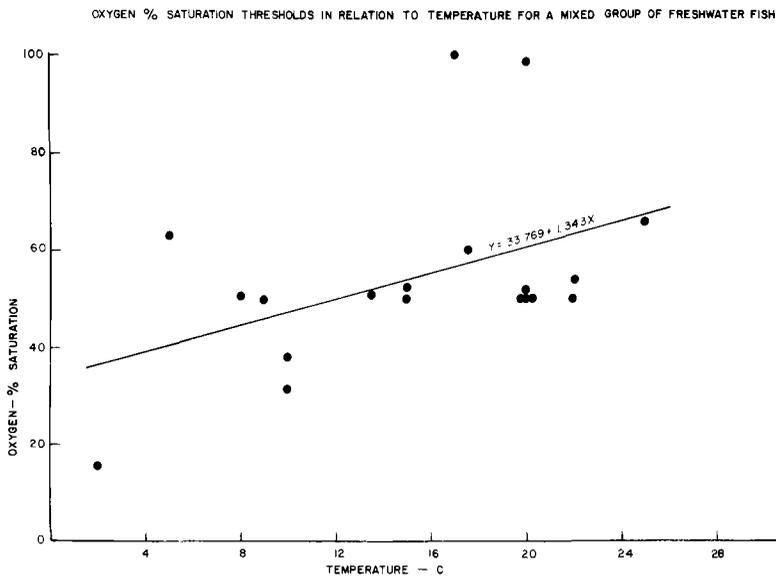

FIG. 17. Incipient sublethal response thresholds vs. temperature for all the freshwater fish data from Table 4, plotted as percentage oxygen saturation. The linear regression line and equation are given. This graph illustrates the effect of temperature on the response threshold expressed in percentage saturation O_2. (Note — As regression of percentile data is a questionable statistical procedure, the regression analysis was repeated following arcsine transformation according to Snedecor (1965). This analysis reduced the slope of the regression line somewhat; however, more slope was present than for the data of Fig. 16.)

TABLE 9. Incipient dissolved oxygen response thresholds selected from Table 8 for derivation of oxygen criteria. These selections were made to give a good representation of fish groups in both fresh and salt water for criteria purposes. Levels of protection A, B, or C (see text) are given. The average temperature, extracted from Tables 4A–D, which corresponds with the average incipient oxygen threshold (in mm Hg PO₂) is indicated in parentheses.

Group	Protection level	PO$_2$	mg O$_2$/liter
Mixed freshwater fish	A	113	7.27
population including	B	86 (15 C)	5.26
salmonids	C	58	3.25
Mixed freshwater fish	A	92	5.63
population with no	B	73 (18 C)	3.98
salmonids	C	54	2.33
Freshwater salmonids	A	119	7.84
(including steelhead)	B	90 (15 C)	6.00
	C	61	4.16
Salmonid larvae and	A	155	9.74
mature eggs	B	120 (9 C)	8.09
	C	85	6.44
Marine, nonanadromous	A	143	8.84
species	B	111 (11 C)	6.72
	C	80	4.60
Marine, anadromous	A	159	9.00
species, including	B	123 (17 C)	6.43
salmonids	C	87	3.86
Anadromous salmonids	A	159	9.33
in sea water	B	123 (17 C)	6.94
	C	87	4.55

assures a high degree of safety for very important fish stocks in prime areas.

Level B — This level represents the oxygen value where the average member of a species in a fish community starts to exhibit symptoms of oxygen distress. These values are derived from the class mean averages from Table 8. Some degree of risk to a portion of fish populations exists at this level if the oxygen minimum period is prolonged beyond a few hours.

Level C — At this level a large portion of a given fish population or fish community may be affected by low oxygen. This deleterious effect may be severe, especially if the oxygen minimum is prolonged beyond a very few hours. The values are 1 SD below the B level, or class average, for the group. This level should be applied only if fish populations in an area are judged hardy or of marginal significance, or of marginal economic importance and, as such, are dispensible (i.e. in the socioeconomic sense).

The use of standard deviations to recommend levels of protection is based on the statistical concept that, in normally distributed data, approximately 68% of the values lie with ± 1 SD of the mean. Thus, the recommended levels span the range of responses that include both sensitive and insensitive animals, both within and between species.[1] Analysis of the data for the freshwater fish group, including salmonids, indicates that these data are normally distributed about the mean and yields a typical cumulative frequency curve about the mean (Fig. 18).

The criteria values of Table 9 based on oxygen content in milligrams O₂ per liter and PO₂ were rounded off and entered in Table 10. This table constitutes the final derivation of the recommended criteria. Oxygen content values in milliliters O₂ per liter were calculated from the values for milligrams O₂ per liter in Table 10, and per-

[1] A weaker form of these criteria could be adopted by setting the value of A or B level as the average 24-h O₂ value and the minimum O₂ concentration over any 24 h equal to the next lower criteria level. For example, the value of A would represent the average 24-h O₂ level and at no time should it be allowed to fall below the value of B. Adoption of this scheme could risk serious damage to fish populations at level B. Objections to the use of average values are discussed in Warren et al. (1973).
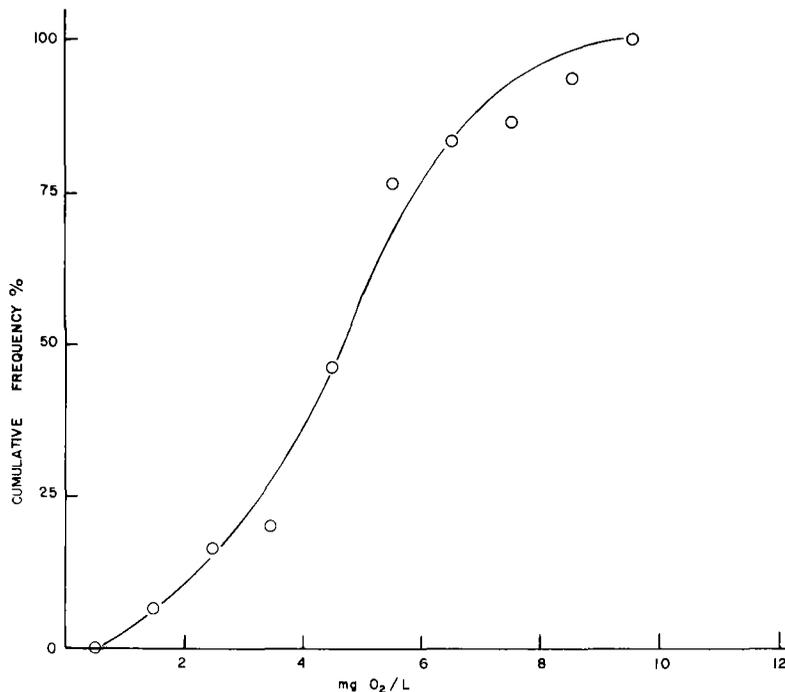
FIG. 18. Frequency distribution of oxygen response thresholds for the largest data group — that for the freshwater fish in Table 4, illustrating that the thresholds follow a more-or-less normal distribution.

cent saturation was calculated for a range of 0–25 C from the desirable PO_2 and content data. Calculations of percent saturation in sea water were based on a salinity of 28‰ (this detailed account of procedures used to derive criteria is given so that others may use the same data to derive their own criteria in another way, if so desired).

It must be emphasized that, as pointed out earlier in this report, fish require both the correct oxygen tension gradient to move O_2 into the blood and sufficient oxygen (per unit volume of water breathed) to fulfill the requirements of metabolism. Therefore, the criteria have been derived to provide both these essential requirements of fish. They are expressed as percentage saturation values over a range of temperatures. At the lower temperatures where water solubility of oxygen is high, the criteria were set using the PO_2 values in Table 10 to ensure that a percentage saturation value consistent with the required PO_2 gradient was present. At the higher temperatures, higher percentage saturation values were necessary to provide the oxygen content requirements dictated by the milligrams O_2 per liter values in Table 10.

A major criticism of these criteria might be that they are heavily biased towards the oxygen requirements of salmonids, which tend to be higher than some other species. This results from much key work being confined to salmonids. With this possible criticism in mind, the criteria recommended in Table 10 for nonsalmonid species in fresh and salt water are lower than for salmonids; however, they are based on fewer data. It must be stressed therefore, that although these criteria are based on best-available knowledge to date, they are tentative and should be subject to revision when new information arises.

A key point in application of the criteria presented above is that daily, seasonal, or periodic low oxygen levels may occur naturally in many water bodies. These natural levels may be near or below recommended criteria levels A, B, or C. In such cases, judgement and caution must be exercised in applying criteria to these naturally oxygen-deficient waters. A standard could be imposed which would be impossible to meet owing to natural fluctuations in dissolved oxygen. Also, if natural depression of oxygen occurs in waters that are to receive wastes with a significant oxygen demand, even a relatively small discharge could reduce oxygen below critical levels. One method of assessing the severity of hazard would

TABLE 10. Oxygen criteria based on percentage saturation values derived with three levels of protection as outlined in the text. PO$_2$'s and values of mg O$_2$/liter were extracted from Table 9 and rounded off for use here. The values shown for milliliters O$_2$/liter were calculated from the values of milligrams O$_2$/liter in this table.

The criteria essential for protection of aquatic fish populations are expressed as percentage saturation values at various temperatures. They were derived from both PO$_2$ and mg O$_2$/liter values, as both oxygen tension and oxygen content are critical factors. At the lower temperatures, the percentage saturation value was determined using the PO$_2$ values essential for maintaining the necessary oxygen tension gradient between water and blood for proper gas exchange. Higher percentage saturation values are necessary at the higher temperatures to provide sufficient oxygen content to meet the requirements of respiration as defined by the mg O$_2$/liter values.

Percentage saturation values are defined as "oxygen minima" at each level of protection. Graphical presentation of the results is found in Fig. 19. The temperatures corresponding to the percentage saturation criteria are defined as "seasonal temperature maxima."

Group	Protection level	PO$_2$	ml O$_2$/liter	mg O$_2$/liter	% Satn. at C for criteria					
					0	5	10	15	20	25
Freshwater mixed	A	110	5.08	7.25	69	70	70	71	79	87
fish population	B	85	3.68	5.25	54	54	54	57	54	63
including salmonids	C	60	2.28	3.25	38	38	38	38	39	39
Freshwater mixed fish	A	95	3.85	5.50	60	60	60	60	60	66
population with	B	75	2.80	4.00	47	47	47	47	47	48
no salmonids	C	55	1.75	2.50	35	35	35	35	35	36
Freshwater salmonid	A	120	5.43	7.75	76	76	76	76	85	93
population (including	B	90	4.20	6.00	57	57	57	59	65	72
steelhead)	C	60	2.98	4.25	38	38	38	42	46	51
Salmonid larvae and	A	155	6.83	9.75	98	98	98	98	100	100
mature eggs of	B	120	5.60	8.00	76	76	76	79	87	95
salmonids	C	85	4.55	6.50	54	54	57	64	71	78
Marine, nonanadromous	A	140	6.13	8.75	88	88	95	100	100	100
species[a]	B	110	4.73	6.75	69	69	74	82	90	98
	C	80	3.15	4.50	50	51	51	55	60	65
Anadromous marine	A	160	6.30	9.00	100	100	100	100	100	100
species, including	B	125	4.55	6.50	79	79	79	79	87	94
salmonids[a]	C	90	2.80	4.00	57	57	57	57	57	58

[a]Percentage saturation calculations based on salinity of 28‰.

be to calculate the expected oxygen depression for the receiving water and then subtract this depression from the naturally occurring O$_2$ minimum value(s). The severity of hazard could then be estimated by reference to Table 10, after conversion of the data to percentage saturation (see also Fig. 19).

Guidelines for Low Oxygen Tolerance of Aquatic Invertebrates

Owing to considerable lack of knowledge of effects of low oxygen on the physiology of marine invertebrates, oxygen criteria cannot be proposed for these organisms at this time. It is reasonable to assume, however, that the levels proposed in Table 10 for fish would provide good protection for most aquatic invertebrates. Indeed, many invertebrates can withstand a much more severe oxygen lack for a longer period than can fish.

Regarding aquatic invertebrates and aquatic ecosystems generally, the following recommendations are proposed:

1. Any change in the dissolved oxygen regime will likely have some effect on the ecosystem and the magnitude of that effect will depend on the severity and duration of the change.

2. A guide to sensitivity of the system could be based on knowledge and study of the area in question. Open ocean coasts, swift-flowing freshwater streams, or other well-aerated bodies of water are likely to contain more low oxygen-intolerant species than poorly aerated water bodies. Thus the habitat and its physical features would serve as an index of the degree of sensitivity of the system.

3. Wherever possible, knowledge of the natural seasonal oxygen *minima* conditions should be available as a guide to implementing criteria.

4. Where seasonal oxygen minima are identified, it is suggested that the potential depression

of water oxygen caused by a discharge be calculated. In this way, further reduction in oxygen level, imposed on the natural condition, could be predicted.

Relationship of Proposed Criteria to Other Documents

Davis (1975) summarized the findings of other oxygen criteria documents. The reader should consult that reference for a detailed comparison of various points of view. A number of the other documents are based on the comprehensive review of Doudoroff and Shumway (1970).

This report was written entirely without consulting other criteria documents prior to derivation of the criteria, hopefully, to avoid bias. I was generally aware, however, of the findings of other reviewers and it was partly for this reason that the foregoing statistical methods were used to derive cause/effect criteria for the present report. I was also aware that Doudoroff and Shumway (1970) had recommended various "levels of protection" in compiling oxygen criteria and that full acknowledgement must be given to their sensible concepts.

In general, the O_2 criteria formulated in this report, and derived specifically for Canadian aquatic life, incorporate a number of considerations identified as critical in other oxygen criteria documents. The herein-presented criteria include the concept of seasonal oxygen minima, allow consideration of temperature, and contain three levels for assessment of potential risk: Level A provides a high safeguard for very important aquatic populations; with Level B, there is some possibility of moderate risk to aquatic organisms, because it allows some degree of oxygen depression; with Level C, it is possible that a large portion of a given fish population or fish community may be severely affected by low oxygen, especially on a "chronic exposure" basis.

These criteria, unlike most others, present oxygen levels as percentage saturation. This was
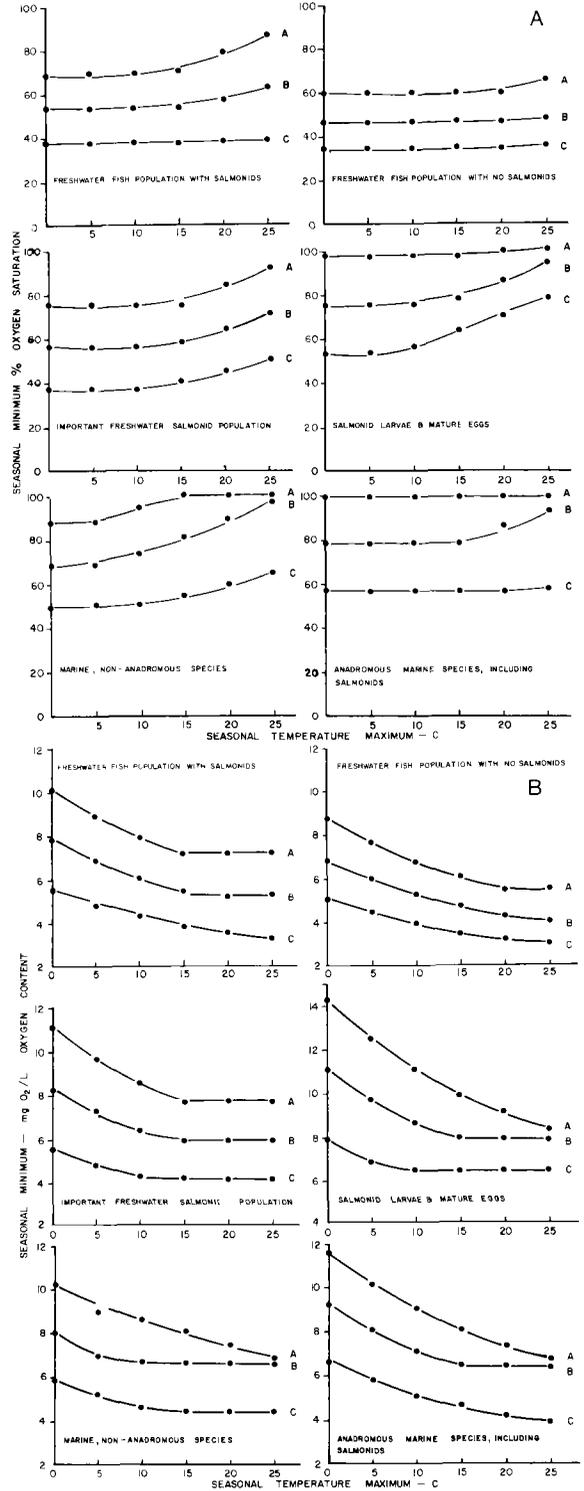

FIG. 19. A, Oxygen criteria, expressed as seasonal minima in percent saturation, at various seasonal temperature maxima. Three levels of protection, A, B, and C, are given as defined in the text. Values used in derivation of the criteria are summarized in Table 10; B, Oxygen criteria, expressed as oxygen minima in mg O_2/liter (ppm), at various seasonal temperature maxima. Three levels of protection, A, B, and C, are given as defined in the text. These values were calculated from the percentage saturation values illustrated in (A) and summarized in Table 10.

done partly because the concept is easily understood and can be assessed conveniently. In addition, the criteria, expressed as percentage saturation, incorporate both the necessary oxygen content and partial pressure essential for fish respiration over a range of temperatures. The values can be easily converted to other units such as milligrams O_2 per liter.

Unlike other criteria, the present oxygen criteria include consideration of marine fish, based on actual data. These data are admittedly somewhat scanty; thus, there is a need for more extensive data on all aspects of pollution research with marine fish.

Lacking current knowledge of oxygen requirements for aquatic invertebrates, oxygen requirements for assessment of harm to these organisms have not been specifically proposed. For protection of aquatic invertebrates, adoption of the criteria relating to fish populations is recommended, for reasons given in this report. Much more work is needed in this particular area, to elucidate the effects of low oxygen on invertebrate communities and ecosystems, especially those in the sea.

Suggestions for Implementation of Criteria

Criteria should only be implemented in keeping with a thorough knowledge of the specific area in question and the aquatic life inhabiting it. In my opinion, use of a single oxygen level, or group of oxygen levels, applied to all waters on a national basis is an unrealistic and potentially questionable practice. A sensible approach would be to form regional panels, whose members have expertise in diverse fields such as fisheries biology, ecology, oceanography, limnology, and industrial pollution. The duty of the panels would be to review existing information, initiate studies to seek new knowledge and implement criteria (such as those suggested here) once sufficient knowledge on the relevant area was amassed. The panel should try and establish:

1) What fish and invertebrates species reside in or move through the area, their relative O_2 sensitivity, and what their economic, recreational, or biological importance is.

2) The seasonal natural oxygen regime for the area.

3) Physical factors that affect dissolved oxygen levels such as temperature regimes, water circulation patterns, and "turnover" of water masses.

4) Existing oxygen-depleting factors, either natural or man-made such as industrial or domes-

tic waste discharge, respiration, upwelling of deep O_2-deficient water, decomposition, etc.

5) Occurrence of toxicants in the water mass which, in combination with low oxygen, may lead to a potentiation stress responses on the part of aquatic organisms.

If such a panel implements oxygen criteria in keeping with the above considerations, there is considerable assurance that the criteria will be realistically applied to the area in question according to the best current available knowledge. The proposed criteria should be considered subject to revision as new knowledge comes available.

Glossary of Terms

Acclimation — compensatory change or adjustment of a bodily function (e.g. metabolism) in response to a single environmental factor, such as temperature, in the laboratory (Prosser and Brown 1962).

Aerobic — process that proceeds in the presence of oxygen such as aerobic respiration (respiration requiring and utilizing oxygen).

Anaerobic — process that proceeds in the absence of oxygen, such as anaerobic respiration (energy production from metabolites without oxygen utilization).

Anadromous — term applied to an animal, usually a fish, that spends part of its life in fresh water and part in salt water, necessitating some movement (migration) from one media to the other.

Blood oxygen dissociation curve — experimentally derived curve describing the saturation kinetics of blood in relation to available oxygen tension. The curve indicates percentage saturation of the blood at different oxygen tensions, illustrating the oxygen level required to saturate the blood and how the blood carries oxygen and delivers it to the tissues.

Criteria — set of rules or guidelines based strictly upon a scientific assessment of environmental harm. Oxygen criteria are derived from a study of cause and effect interrelations involving the responses of organisms to reduced oxygen.

Food conversion efficiency — efficiency with which a given quantity of food consumed is converted to body mass.

Hypoxia — a condition when oxygen availability is low. A fish reacting to low oxygen can be said to be hypoxic.

Incipient — just beginning. The incipient oxygen response threshold can be defined as the oxygen level where some organism just starts to respond in some way to reduced oxygen availability.

Metabolism — chemical process involving enzyme reactions in the body whereby energy is made available for bodily work. Metabolic reactions may be both oxidative and nonoxidative in nature.

Metabolic rate — rate at which metabolism proceeds, usually expressed as oxygen consumption rate, caloric heat produced or rate of CO_2 liberation. In many instances, fish and aquatic invertebrate metabolic rate is measured in terms of oxygen uptake rate.

Oxygen concentration (content) — the concentration, measured in terms of milligrams O_2 present in a given body of water, usually 1 liter, at a specified temperature, pressure, and salinity. The amount of oxygen present per unit water breathed by an aquatic animal governs, in part, the oxygen availability to the organism.

Oxygen partial pressure (PO_2) —oxygen tension measured in millimeters Hg, in a solution. Oxygen diffuses down a concentration gradient across the respiratory surface. The magnitude of the gradient is conveniently determined by measuring oxygen partial pressure on either side of the exchange surface and considering solubility coefficients of oxygen in water and blood.

Phototaxis — directed behavioral response of an organism to light. Phototaxis may be positive (directed towards) or negative (directed away) to the light stimulus.

Respiration — process of gaseous exchange across the respiratory surface via diffusion. Often respiration rate (gas exchange rate) is confused with ventilation rate (rate of breathing movements).

Respiratory dependence — condition exhibited by many animals where, under certain conditions of oxygen availability, respiration rate (and thus aerobic metabolic rate) show a direct correspondence to the available oxygen level. Animals whose oxygen uptake rate increases as oxygen availability increases are thus termed conformers.

Respiratory independence — many animals maintain their oxygen uptake rate independent of available oxygen over a wide range of environmental oxygen concentrations. These animals are said to exhibit respiratory independence and may, in some instances, regulate their oxygen uptake rate. In most cases, however, when available oxygen declines to a certain critical level, oxygen uptake rate declines dramatically, indicating the presence of a limiting situation. Animals that maintain their metabolic rate independent of available oxygen are termed regulators.

Salinity — total salt content of water expressed in parts per thousand (‰).

Standard deviation — statistical term that measures the spread, or deviation, of individual measurements from the center (usually the mean average) of normally distributed data.

Standard error — statistical term describing the standard deviation of sample means for samples drawn from a parent population — i.e. a measure of the reliability of the mean average.

Ventilation rate — breathing rate of an organism denoting the number of ventilatory movements per unit time.

List of Symbols

D.O. — abbreviation for dissolved oxygen level.

H_2O vap. press. — water vapor pressure, in millimeters Hg.

mg O_2/liter — concentration of oxygen in milligrams per liter of water (1 mg O_2/liter = 1 ppm).

ml O_2/liter — concentration of oxygen in milliliters per liter of water (0.7 ml O_2/liter = 1.0 mg O_2/liter = 1 ppm).

n — the number of individual data used in a computation

PCO_2 — partial pressure of carbon dioxide in millimeters Hg.

PO_2 — partial pressure of oxygen in millimeters Hg.

ppm — abbreviation for parts per million concentration term.

SD — standard deviation (statistical terminology).

SE — standard error of the mean (statistical terminology).

MTL — median tolerance limit in terms of dosage or concentration of a substance that is lethal to half of the organisms in a bioassay test over a specified test time — usually 96 h.

‰ — parts per thousand (used for expressing salinity of water).

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