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Reduced oxygen at high altitude limits maximum size

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The trend towards large size in marine animals with latitude, and the existence of giant marine species in polar regions have long been recognized, but remained enigmatic until a recent study showed it to be an effect of increased oxygen availability in sea water of a low temperature. The effect was apparent in data from 12 sites worldwide because of variations in water oxygen content controlled by differences in temperature and salinity. Another major physical factor affecting oxygen content in aquatic environments is reduced pressure at high altitude. Suitable data from high-altitude sites are very scarce. However, an exceptionally rich crustacean collection, which remains largely undescribed, was obtained by the British 1937 expedition from Lake Titicaca on the border between Peru and Bolivia in the Andes at an altitude of 3809 m. We show that in Lake Titicaca the maximum length of amphipods is 2–4 times smaller than other low-salinity sites (Caspian Sea and Lake Baikal).

Keywords: size limits; oxygen availability; gigantism; temperature; amphipod

Studies investigating the limits set by physical factors on animal size require many species inhabiting a given area. A large number of species living proximally causes selective pressures to drive some close to their maximum potential size. Amphipods meet these criteria better than most other taxa, and the existence of giant species at high latitude is well known (Saintemarie 1991; Poulin & Hamilton 1995). Until recently, only 11 species of amphipod crustaceans had been described from Lake Titicaca (Dejoux 1992). However, a minimum of 93 additional unnamed distinct morphotypes have been described from the 1937 expedition and at least 104 species clearly inhabit the lake (Crawford *et al.* 1993). The oxygen content of the water in Lake Titicaca is reduced because of its high altitude, and because its salt content is slightly higher than in most lakes (Iltis *et al.* 1992). The largest amphipod species present has a maximum length of 22 mm, and is yet to be named. This compares with the 90 mm *Acanthogammarus grewingkii* from Lake Baikal (salinity of 0 psu (practical salinity units)) and the 42 mm *Gammaracanthus loricatus* from the Caspian Sea (salinity of 13 psu). In their analysis of amphipod size variations in varying salinity and temperature sites, Chapelle & Peck (1999) used the threshold size separating the smallest 95% of species from the largest 5% (hereafter termed TS95/5) as the measure of large size to overcome any potential sampling bias. For Lake Titicaca we measured the largest individuals of the 10 largest morphotypes, and used the threshold between species 5 and 6 as the TS95/5, which is 15.2 mm. This result falls very close to the overall relationship linking TS95/5 for amphipods and water oxygen content (Chapelle & Peck 1999) (figure 1). Thus, high altitude has a similar effect on size to high salinity and temperature because it reduces oxygen availability.

It has been argued by Spicer & Gaston (1999) that the oxygen content of water should not affect size in aquatic organisms. They attributed to temperature the trends towards increased size with latitude, and pointed out that oxygen uptake depends on gas partial pressure differences that remain constant in all shallow waters at sea-level. However, unlike the variation of oxygen concentrations in sea water with latitude, both oxygen partial pressure and concentration decrease with altitude. If Spicer & Gaston (1999) were correct then, at 12 °C, Lake Titicaca should contain amphipods of at least 40 mm long. In fact, the largest amphipods found there are approximately half of this length, and are four times smaller than amphipods from Lake Baikal at 6 °C. This clearly shows that oxygen availability rather than temperature is the limiting factor for maximum size.

Spicer & Gaston (1999) also argued that partial pressure is the driving force for oxygen uptake across respiratory surfaces and, because this does not vary in the sea with latitude, that oxygen uptake will also be constant. However, the mass of oxygen transferred across a respiratory surface for a given partial pressure difference varies with gas solubility (Dejours 1973; Peck & Chapelle 1999), and temperature and salinity both affect solubility (figure 2). Atmospheric partial pressure of oxygen is *ca.* 159 mm Hg. For blood passing across a respiratory surface with a partial pressure of 40 mm Hg, 360 μmol kg^{-1} of oxygen passes to the blood in fresh water, but only 146 μmol kg^{-1} passes from sea water, and this is the effect of differing solubility. Oxygen solubility in sea water varies with temperature, and is 1.82 times higher at 0 °C than at 30 °C. Antarctic marine species thus receive 1.82 times as much oxygen as tropical species for the same partial pressure difference across respiratory surfaces. For Lake Titicaca, the external partial pressure of oxygen is only 95 mm Hg compared with 159 mm Hg for lakes at sea-level. Because of this, the amount of oxygen delivered across a respiratory surface where blood has a partial pressure of 40 mm Hg is 160 μmol kg^{-1}, compared with the 360 μmol kg^{-1} for sea-level lakes. Thus the oxygen available to Titicaca amphipods is, at most, only 40% that of amphipods in low-altitude lakes. The concept of partial pressure driving oxygen across respiratory surfaces, but being affected by solubility, is analogous to an electrical current where voltage drives the current, but resistance also affects the amount of current that is passed.

Essentially, the mass of oxygen available to an organism dictates the mass of sustainable tissue. In this context, recent work on temperature and oxygen effects on growth and development in fruitflies, *Drosophila melanogaster*, by Frazier *et al.* (2001) is of interest. Their data demonstrated a strong effect of oxygen on size, with markedly reduced size obtained in low oxygen treatments. Male *Drosophila* from 10% oxygen treatments had 30% smaller

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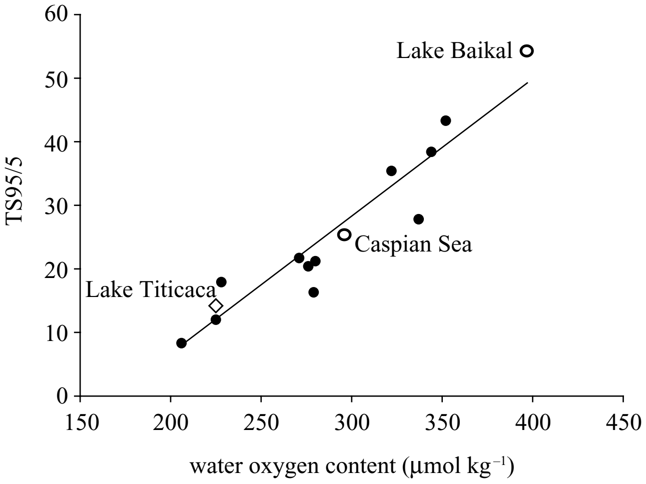

Figure 1. Plot of TS95/5 (mm) against water oxygen content (μmol O_2 kg^{-1}) from 13 sites worldwide and Lake Titicaca. Since the publication of Chapelle & Peck (1999), the data have been updated for the five Southern Ocean sites and South African coast data have been added. Oxygen solubility in water varies with temperature and salinity, described by the relationship: $\ln k_{o,s} = 3.718 + 5596/T - 1049668/T^2 + S(0.0225 - 13.608/T + 2565.68/T^2)$ (where $k_{o,s}$ is the Henry coefficient for the solubility in water of varying salinity and temperature, T is temperature (in °C) and S is salinity (in psu)). Regression line: $Y = 0.216x - 36.5$ ($r^2 = 0.90$). Oxygen and lake temperature (12 °C) data for Lake Titicaca are from direct measurements (Iltis *et al.* 1992).

body mass than normoxic flies at 27.5 °C. They also showed an interactive effect on growth, where elevated temperature and low oxygen had the most marked effect on size, indicating oxygen stress as a major factor in delimiting the possible envelope for adult size. Low oxygen and low temperature both slowed development rate, but had opposite effects on size. Varying environmental oxygen concentration affects cell size in a similar fashion to the way it affects whole animals; lowering ambient oxygen reduces cell size in the fruitfly *Drosophila melanogaster* (L. S. Peck and S. H. P. Maddrell, personal observation).

The analyses here are based around amphipod crustaceans, which have very low levels of blood pigment carrying oxygen around the body (Wolvekamp & Waterman 1960). This probably makes the oxygen effect clearer. However, size limits set by oxygen availability should be widespread, and in this context it is interesting that giant sea spiders and isopods occur in high-oxygen-availability sites, and that giant dragonflies existed in the Carboniferous when atmospheric oxygen levels were 30–35% (Graham *et al.* 1995).

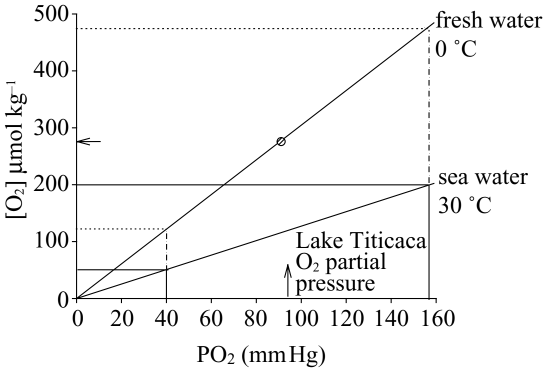

Figure 2. The effect of solubility on oxygen transport. The relationships between water oxygen concentration ([O_2], μmol kg^{-1}) and oxygen partial pressure (PO_2, mm Hg) are shown for freshwater at 0 °C (broken lines) and for 35 psu sea water at 30 °C (solid lines). For an animal respiring in 0 °C fresh water, a partial pressure difference of 120 mm Hg across its respiratory surfaces would deliver 360 μmol O_2 kg^{-1}, whereas the same partial pressure difference would deliver 160 μmol O_2 kg^{-1} to an animal in 30 °C sea water. O_2 delivery is limited in Lake Titicaca by the reduced external PO_2 (95 mm Hg), and for an animal with an internal PO_2 of 40 mm Hg only 145 μmol kg^{-1} is delivered across the respiratory surfaces.

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