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Antarctic and Baikal Amphipods: A Key for Understanding Polar Gigantism

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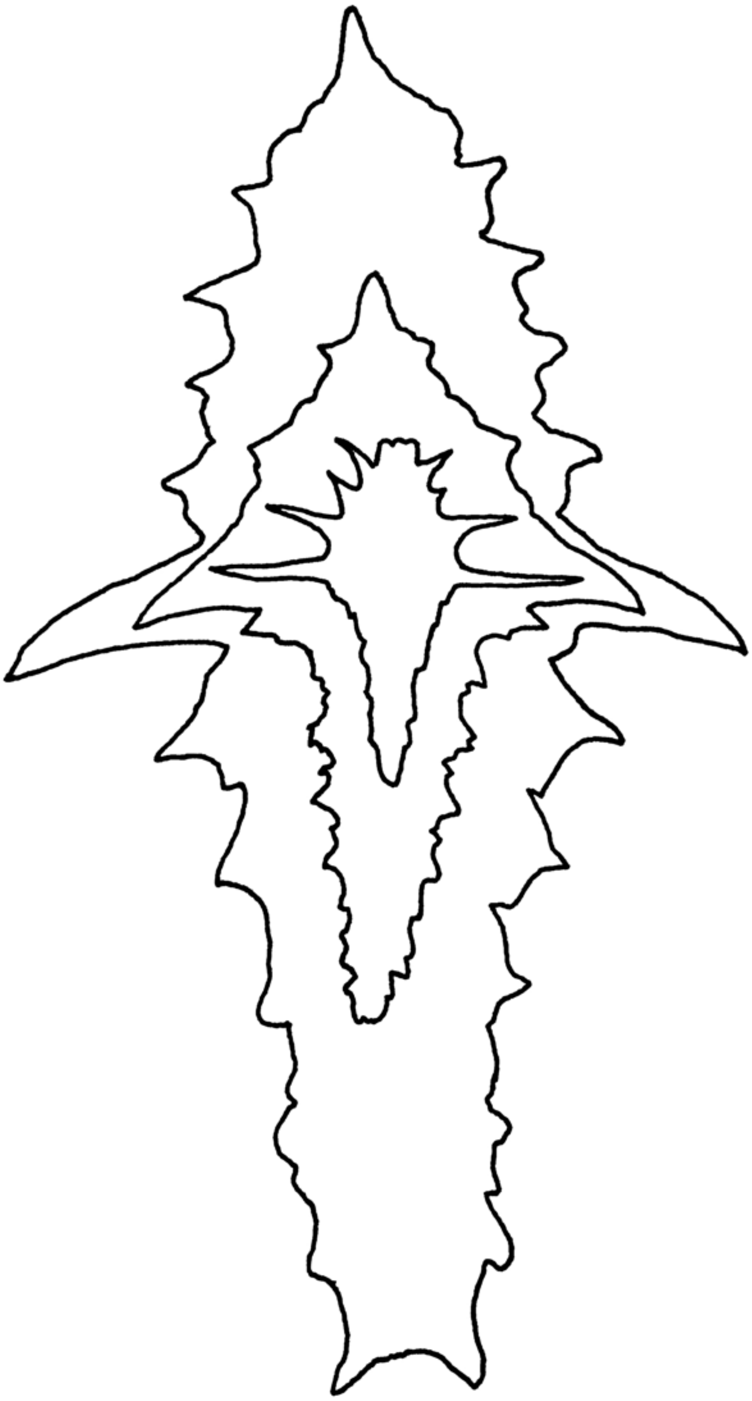

Cover legend : Size range and morphological convergences between “armored” amphipods : from the largest to the smallest, *Propachygammarus maximus* (Garjajew, 1901), 67 mm, from Lake Baikal; *Epimeria pulchra* (Coleman, 1990), 29 mm, from Antarctica and *Hyalella armata* (Faxon, 1876), 9mm, from Lake Titicaca. Redrawn by Judith Reymann.

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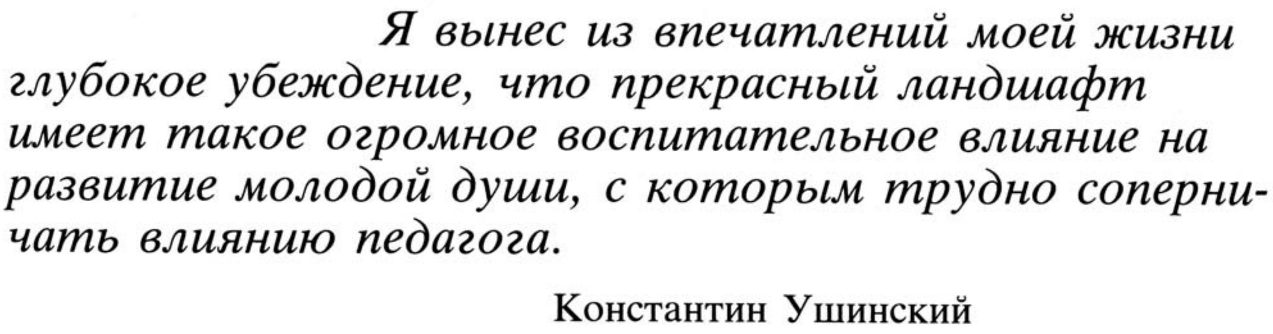


Я вынес из впечатлений моей жизни глубокое убеждение, что прекрасный ландшафт имеет такое огромное воспитательное влияние на развитие молодой души, с которым трудно соперничать влиянию педагога.

Константин Ушинский

2. *“ From my own impressions in life I have arrived to a profound conviction that a beautiful landscape has such an enormous educational effect on the development of a young soul that the pedagogue’s influence will find it hard to compete with it.”*

Konstantin Ushinsky

Contents

Résumé

La tendance que montrent de nombreux invertébrés benthiques à posséder une plus grande taille sous les hautes latitudes - le "gigantisme polaire" - n'est pas encore bien comprise, bien qu'elle ait été souvent attribuée aux basses températures et leur effet sur le métabolisme. Toute étude approfondie du phénomène du gigantisme doit pouvoir s'appuyer sur des groupes taxonomiques riches en espèces, largement distribués dans le monde, avec un nombre suffisant de sites où ils ont été répertoriés en détail.

Pour cette étude, nous avons analysé les mesures de longueur de plus de 2000 espèces de crustacés amphipodes benthiques, répartis dans 15 localités géographiques, depuis les tropiques jusqu'aux pôles, en eaux douces comme en eaux marines. Cette analyse a mis en évidence le rôle déterminant exercé sur la taille par l’oxygène bien plus que par la température.

En effet, grâce à la comparaison des spectres de taille obtenus pour chaque site géographique, nous avons tout d'abord montré la relation étroite y existant entre la taille des amphipodes gammaridiens présents et la concentration absolue moyenne en oxygène des eaux de surface. Il apparait que lorsque cette concentration s'élève, l'augmentation de taille est légère pour les petites espèces, plus prononcée au milieu du spectre, et maximale pour les plus grandes.

L'hypothèse retenue pour expliquer cette relation se base sur deux facteurs physiologiques. Le premier est le caractère essentiellement passif de la respiration chez les crustacés amphipodes. Le second consiste en la diminution du rapport surface/volume lorsque la taille des animaux augmente, ce qui entraîne la fixation d'une limite supérieure au-delà de laquelle la surface respiratoire ne suffit plus pour approvisionner en oxygène le volume des tissus métaboliquement actifs.

Cette relation a ensuite été progressivement étendue aux rangs taxonomiques moins élevés. Ainsi la taille moyenne des espèces au sein de chaque superfamille, famille et genre étudiés a pu être corrélée de façon significative avec la concentration en oxygène par une régression linéaire. La pente de cette régression varie d'un taxon à l'autre, et ce sont les taxons les plus sensibles à l'oxygène qui dominent les hautes latitudes par leur diversité et leur richesse en grandes espèces.

De même, la concentration en oxygène agit également au sein de chaque espèce, dont la taille augmente en moyenne de 0,03 mm par µmole d'oxygène et par kg d'eau. Ce résultat suggère que chaque espèce tend à ajuster sa taille le plus finement possible aux coûts métaboliques de la respiration, eux-mêmes liés à l'oxygène disponible dans le milieu.

En conclusion, cette recherche montre que la disponibilité en oxygène se comporte non pas comme une pression de sélection en faveur des grandes tailles, mais bien comme un plafond limitant la taille maximale potentielle que peuvent atteindre les amphipodes gammaridiens. Par contre, la taille minimale, proche de la taille modale, est probablement liée au *bauplan* des amphipodes et dépend de la taille minimale viable de l'oeuf unique pondu par les plus petites espèces.

Des premières données montrent que la relation entre oxygène et taille maximale s'applique au moins à d'autres groupes d'arthropodes marins, voire au-delà, comme l'indiquent les libellules géantes du Carbonifère à une époque où la concentration atmosphérique de l'oxygène atteignait 30 à 35%. Leur disparition concomitante à une chute de cette concentration, tout comme les résultats de cette recherche, constituent une première justification du gigantisme en tant que spécialisation, ainsi que de la plus grande vulnérabilité évolutive des espèces les plus grandes de chaque groupe.

Mots clés: crustacés - amphipodes - benthos - gigantisme polaire - taille - respiration - concentration en oxygène - Antarctique - Lac Baïkal

Summary

The trend shown by numerous benthic invertebrates towards acquiring a larger size at high latitudes –"the polar gigantism"– is still poorly understood, although it was often attributed to low temperatures and their effect on metabolism. All thorough studies on the phenomenon of gigantism must be based on taxonomic groups rich in species, having a broad worldwide distribution, with a sufficient number of areas where there were recorded in detail.

In this study, we have analysed length measurements of more than 2000 species of benthic amphipod crustaceans, divided over 15 geographical localities from the tropics to the poles, in both fresh and marine waters. This analysis has highlighted the key-role played by oxygen, much more than by temperature, in the size of animals.

Indeed, thanks to the comparison of size spectra obtained in each geographical area, we were able to show, in the first place, the narrow relationship existing between the size of gammaridean amphipods present in a particular location and the mean absolute oxygen concentration of the surface waters there. Our results show that, with the increase of this concentration, the increase in size is slight in small animals, more pronounced in the middle of the spectrum and maximal in the largest animals.

The privileged hypothesis for explaining this relationship is based on two physiological factors. The first one is the essentially passive nature of respiration in amphipod crustaceans. The second consists in the decrease of the surface/volume ratio with the increasing size of the animals, which leads to the setting of an upper threshold beyond which the respiratory surface becomes insufficient for supplying in oxygen the volume of metabolically active tissues.

This relationship was subsequently extended to lower taxonomical ranks. Thus, the average size of the species of each superfamily, family and genus could be significantly correlated with oxygen concentration, with a linear regression. The slope of this regression varies from one taxon to another, and the taxa which dominate in high latitudes by their diversity and richness in large species are those which are the most sensitive to oxygen.

In the same way, the action of oxygen concentration is also felt within each species, the size of which increases, on the average, by 0.03 mm per µmole of oxygen and per kg of water. These results suggest that each species tends to adjust its size as narrowly as possible to the metabolic costs of respiration, the latter themselves depending on the oxygen available in the environment.

In conclusion, this study shows that the availability in oxygen acts not as a selection pressure in favour of large sizes, but as a ceiling limiting the maximum potential size which gammaridean amphipods can reach. On the other hand, the minimum size, close to the modal size, is probably related to the *bauplan* of amphipods and depends on the minimum viable size of the unique egg laid by the smallest species.

Preliminary data show that the relationship between oxygen and maximum size is valid at least for other groups of marine arthropods, or even beyond them, as indicated by giant dragonflies of the Carboniferous, at a time when oxygen concentration in the atmosphere amounted up to 30-35%. Their extinction, which coincided with the drop in this concentration, and the results of our investigations, may represent a first evidence of gigantism as a specialization, as well as of great evolutionary vulnerability of the largest species of each zoological group.

Keywords: crustaceans – amphipods – benthos – polar gigantism – size – respiration – oxygen concentration – Antarctica – Lake Baikal

Samenvatting

De trend in talrijke benthische invertebraten om grotere lichaamsafmetigen te bekomen op hogere breedtegraden – het polaire gigantisme – is tot op heden slecht begrepen, niet tegenstaande het (fenomeen) vaak in verband werd gebracht met de lage omgevingstemperaturen en het effect hievan op het metabolisme. Alle diepgaande studies over het fenomeen van gigantisme moeten gebaseerd zijn op taxonomische groepen met een grote soortenrijkdom die een zo groot mogelijke verpreiding op wereldvlak vertonen en waarvan nauwkeurige gegevens voorhanden zijn uit een aannemelijk aantal gebieden.

In deze studie, werd de lichaamslengte van meer dan 2000 soorten benthische Amphipoda, afkomstig van 15 geografische gebieden gelegen tussen de tropen en de polaire gebieden, en zowel uit het mariene als het zoetwater milieu, geanalyseerd. De analyse toont duidelijk aan dat zuurstof, en in veel mindere mate temperatuur, de sleutelrol speelt in de bepaling van de grootte van de dieren.

Vergelijking van de grootte-spectra uit elk geografisch gebied, toonde het nauwe verband aan tussen grootte van de gammaride Amphipoda en de gemiddelde absolute zuurstofconcentratie van het oppervlaktewater. Uit de resultaten blijkt dat bij stijging van de zuurstofconcentratie, de stijging van de afmetingen klein is bij kleine dieren, meer uitgesproken is bij dieren uit de middelste groottegroep, en maximaal is in de groep met de grootste dieren.

De hier naar voor gebrachte hypothese wordt ondersteund door twee fysiologische faktoren. Als eerst wordt verwezen naar de van nature passieve ademhaling van Amphipoda. De tweede faktor staat in relatie met de vermindering van de verhouding oppervlakte/volume bij vermeerdering van de lichaamsgrootte, wat automatisch leidt tot een limit waarboven de oppervlakte dat instaat voor de ademhaling ontoereikend wordt om het weefselvolume van zuurstof te voorzien.

De relatie werd vervolgens verder onderzocht voor lagere taxonomische niveau’s. De gemiddelde grootte van elke soort binnen een superfamilie, familie en genus bleek significant, en lineair, gecorreleerd met de zuurstofconcentratie. De hellingsgraad van de regressielijn varieert naar gelang het taxon, en het blijkt dat de taxa die de grootste sensibiliteit voor de zuurstofconcentratie vertonen, domineren in hogere breedtegraden door hun diversiteit en rijkdom aan grote soorten.

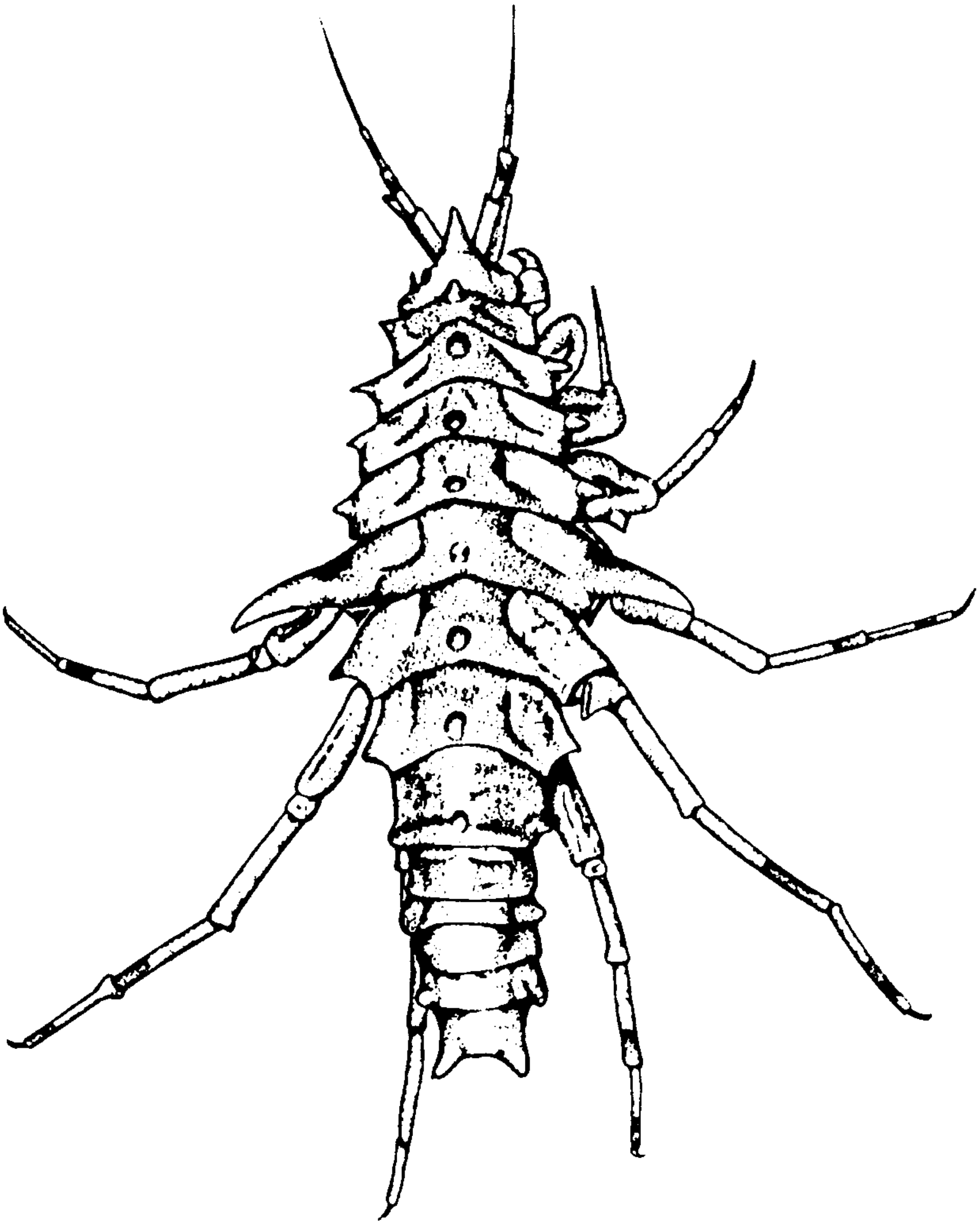
Verder blijkt dat de zuurstofconcentratie ook rechtstreeks inspeelt binnen de soort als de grootte stijgt, met gemiddeld, 0,03 mm per µmol zuurstof en per kg water. Dit resultaat laat vermoeden dat elke soort haar grootte zo optimaal mogelijk zal aanpassen in funktie van de metabolische kost voor ademhaling, met dit laatste afhankelijk van het in het milieu beschikbare zuurstof.

Deze studie toont aan dat de beschikbaarheid van zuurstof geen rol speelt als een selectie-mechanisme in het voordeel van grote afmetingen, maar als een waarde dat de potentiële maximumgrootte van gammaride Amphipoda begrensd. Anderzijds, de minimale grootte, dat nauw aanligt bij de modale afmetingen, verwijst mogelijks naar het *bauplan* van de Amphipoda en de minimale afmetingen voor de levensvatbaarheid van het enige ei dat afgelegd wordt door de meeste van de kleine soorten.

Voorlopige data tonen aan dat de relatie tussen zuurstof en maximale grootte ook geldt voor andere mariene schaaldieren, en zelfs voor andere diergroepen, zoals de reuzenlibellen uit het Karboon, toen de atmosferische zuurstofconcentratie 30-35% bedroeg. Het verdwijnen van deze laatste, dat samenviel met de afname van de zuurstofconcentratie in de lucht, en de resultaten van de hier aangebrachte gegevens, zijn mogelijk de eerste aanwijzingen van gigantisme als specialisatie, maar ook van de evolutionaire kwetsbaarheid van de grootste soorten binnen elke diergroep.

Sleutelwoorden: Crustacea – Amphipoda – benthos – polair gigantisme – grootte – respiratie – zuurstofconcentratie – Antarctica – Lake Baikal

Introduction



One of the largest Baikalian amphipods, *Propachygammarus maximus* (Garjajew, 1901), 67 mm, picture from the author, redrawn by K. Martens.

Introduction

Importance of Crustacea in aquatic biota

As well for non-biologists as for most biologists, the word "crustaceans" will first bring to the mind the edible groups, such as shrimps, prawns, crabs, lobsters or crayfish. All of these animals belong to the decapods (Order Decapoda), which with 10,000 species, constitute one of the most speciose groups of crustaceans.

Nevertheless, many other groups - mostly unknown to the large public - make a significant contribution to aquatic communities. *Euphausia superba* (Order Euphausiacea), the Antarctic "krill", is the key species of the Southern Ocean food web, and contends with *Homo sapiens* for the position of having at world scale the heaviest total biomass for a single species. The copepods (Subclass Copepoda), with 9,000 described species and many more undescribed, can be found in virtually all aquatic environments, and constitute one of the main groups of zooplankton and meiobenthos. The ostracods (Subclass Ostracoda), another widespread group of 2,000 species, are best known to paleontologists as biostratigraphic markers. Finally, the peracarids (Super Order Peracarida) bring together, among a handful of small orders, two other very diversified groups: the isopods (Order Isopoda), with 4,000 species (Brusca & Brusca, 1990), including the most successful terrestrial crustaceans (e.g. the wood lice), and the amphipods (Order Amphipoda), with around 8,000 described species, to which this study is devoted.

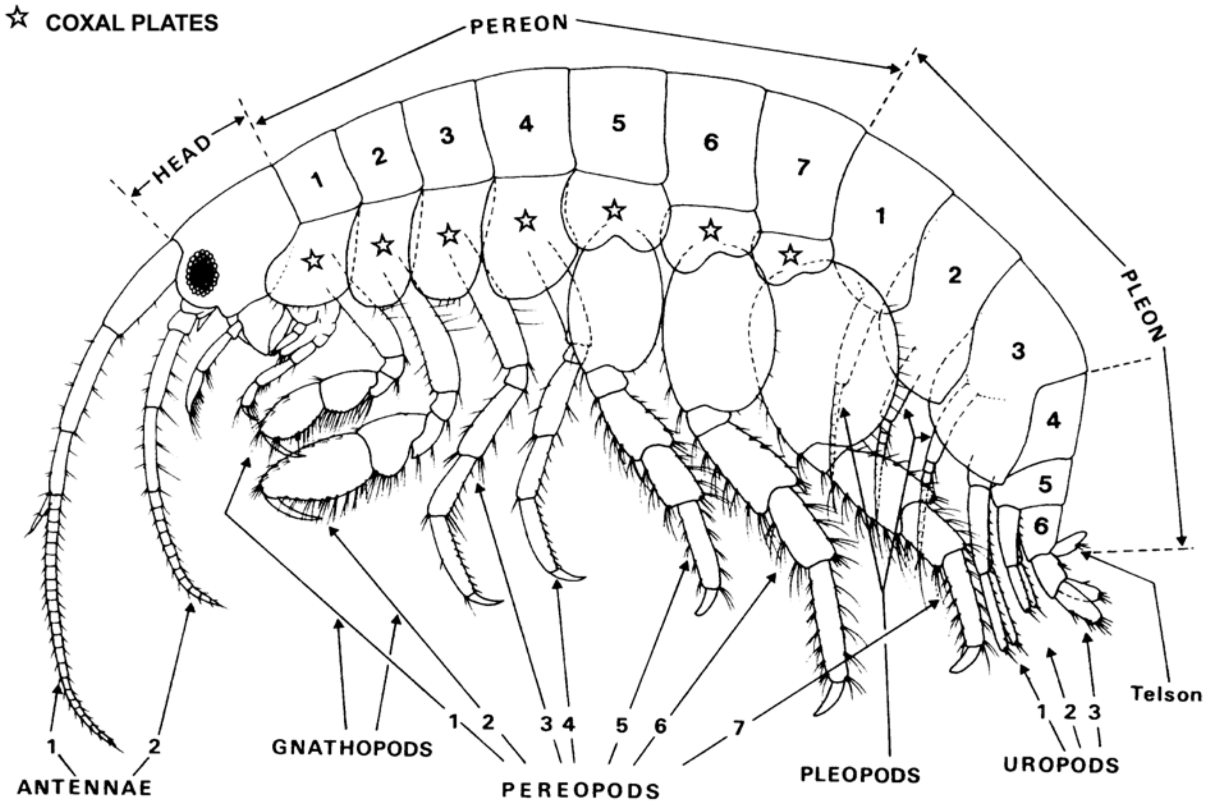


Fig. 1 – Basic morphology of gammaridean amphipod. Redrawn from Lincoln (1979)

What is an amphipod ?

Like all peracarids, amphipods carry their eggs in a ventral brood pouch, the "marsupium". Unlike isopods, they hatch at an advanced stage of development as miniature amphipods. Although much morphological variation exists within the order, a typical amphipod can be described as a small crustacean, of around 10 mm, with an arched and laterally compressed body divided in three parts (Fig. 1): the head, the 7-segmented pereon and the 6-segmented pleon (Bellan-Santini, 1999). The pereon bears seven pairs of pereopods, three directed to the rear and four directed to the front respectively, hence their name "Amphi - poda". The first two pairs are usually modified to gnathopods. The coxae of the pereopods are usually flattened as coxal plates and constitute the disto-lateral expansions of the pereon segments. The pleon classically bears another six pairs of appendices and a telson.

Diversity of the Amphipoda

As for copepods, ostracods or isopods, the Amphipoda inhabit nearly all aquatic habitats. They can be encountered in the hot vents of the deep sea or beneath the polar sea ice, in mountain streams or in caves, in the interstitial water of aquifers or on the bottom of the deepest abyssal trenches, on the skin of cetaceans or inside jellyfish, in the shell of hermit crabs or on the shell of sea turtles, under decaying algae on every beach or in the litter of some rain forests... and greenhouses. This habitat diversity is coupled to an equally diverse trophic spectrum; amphipods comprise specialized predators, herbivores, scavengers or detritivores as well as many opportunistic omnivorous species.

Amphipoda are divided in four suborders; the mainly benthic Gammaridea, the interstitial Ingolfiellidea (sometimes considered as belonging to Gammaridea), the rod-shaped and benthic Caprellidea (including the Cyamidae, parasites of cetaceans) and the exclusively marine and planktonic Hyperidea.

With more than 6,000 species, Gammaridea are by far the most speciose of this group. To avoid a possible influence of the mode of life, pelagic and/or deep species have been excluded from our study, which will focus on benthic species living on the continental shelf. However, it should be noted that the question raised by the two largest amphipods, both abysso-pelagic species, is discussed in Chapter 3.

Size of amphipods

For a marine biologist or a scuba diver, the most conspicuous crustaceans of the temperate or tropical benthos are mainly decapods, and very rarely peracarids. Although numerous amphipod species occur at temperate latitudes, their usual size is around 10 mm, while their most visible representatives seldom exceed 30 mm in length, and never attain 50 mm. In the same biota, the decapods' size spectrum extends much further, with a great diversity of species measuring between 100 and 450 mm.

The polar giants

But when during the XIXth century, the first antarctic research expeditions were made, a very different story was revealed: peracarids, and especially isopods and amphipods were the dominating crustacean taxa from the macrofauna, both in terms of abundance and size. Indeed, most bottom samples would yield numerous colorful amphipod specimens belonging to many species in excess of 30 mm, as well as several with length between 50 and 90 mm, sometimes quite abundant, and with a significant effect on amphipod mean size (Barnard, 1962). At the same time, only a few shrimp species and virtually no crabs could be found. This of course raised the question of possible competition between decapods and peracarids; the demise of the former could have allowed, or alternatively been caused by an increase in size of the latter.

Nonetheless, competition with decapods was not sufficient to explain polar gigantism, since on the other side of the planet, the Arctic seas contained various crabs and shrimps side by side with a number of giant amphipods and isopods. Furthermore, the gigantism displayed around the Antarctic continent was not restricted to the peracarids. As pointed out by Arnaud (1974) and other authors, exceptionally large species also existed within groups as different as Porifera, Nematoda, Nemertea, Polychaeta, Pycnogonida, Cirripeda, Ostracoda, Copepoda and Ascidiacea. Other factors to explain polar gigantism were thus necessary, and Arnaud (1977) proposed the usually slow growth linked to low temperature and low predation pressure on certain species as the main candidates. De Broyer (1977) added to the list the trophic type and the possible role of the abundance of phytoplanktonic resources during summer.

Amphipods of the "Siberian Sea"

Nevertheless, the origin of the present study is to be found in the presence of giant amphipods in a completely different ecosystem: Lake Baikal (Bazikalova, 1948). It is only the seventh largest lake in terms of surface area (more than 30,000 km^2), but great depths make the "Pearl of Siberia" the world's largest lake in volume (23,000 km^3). It accounts for one fifth of the liquid surface fresh water on Earth (Kozhova & Izmestieva, 1998).

With not far from 300 described species, Lake Baikal harbors the same proportion (20%) of the world's freshwater amphipods (Takhteev, 2000). From these, about 60 species are bigger than 30 mm, and another 5 are above 70 mm (Bazikalova, 1945). The Baikalian record of 90 mm is held by the spiny *Acanthogammarus grewingkii* (Dybowski, 1874) and will become the maximum size recorded in our world data set. After the polar regions, Lake Baikal provided an additional thoroughly known amphipod fauna for investigating gigantism, without the complicating depth factor which would have been included in any comparison with the poorly known marine abyssal fauna.

Different or not ?

Although they have very different salinity regimes, Baikal and Antarctic waters share more characteristics than could be expected at first thought. Both environments are highly oxygenated (mostly above 70% of saturation), cold (mean temperature of 6 and 0°C respectively) and ice-covered during winter. This temperature is also very stable during the year: annual variations in the entire water column do not exceed 3°C in the Antarctic (Clarke, 1983), while in Lake Baikal, they attain 8°C at 50 m depth and 3°C at 200 m (Kozhov, 1963). Oligotrophy occurs year-round in Lake Baikal but only in winter in the Antarctic.

Another very important similarity between Lake Baikal and Antarctica concerning the evolution of amphipod faunas is the age of each ecosystem, as both became isolated at least 10 million years ago. Finally, in parallel with the previously mentioned antarctic absence and scarcity of crabs and shrimps respectively, no decapods at all occur in Lake Baikal, with potential effects on niche availability through reduced predation and competition.

Objectives and overview of the thesis

It is this intriguing combination of similarities and differences between these two environments and biota which brought up the initial question of this thesis: **What is the reason for the existence of giant amphipods in Antarctica and Lake Baikal and their scarcity in other shelf and shallow areas ?**

To attempt to answer this question, we first wanted to situate these giants in their environment, and among the other coexisting amphipod species. We will start with **amphipods from Antarctica** in **Chapter 1**, by evaluating the importance of the giant species through a comparison of the size spectra of Antarctic and subantarctic amphipods respectively.

Chapter 2 will explore the unique fauna constituted by **the amphipods of Lake Baikal**. Four trips to Siberia have allowed the collection of a significant collection of the large amphipod species, as well as many of the papers devoted to Baikalian amphipods. As an introduction to an extensive list of papers on this topic (see Annex B), we will outline the data collected in the past regarding the size and thus question again the importance of the largest species using size spectra.

Having highlighted the difficulty of defining giant species in the study of these two areas, we will extend the scope of this study to other amphipod fauna throughout the world in **Chapter 3**. A first paper will examine the variations between 12 **size spectra** from the tropics to the poles, allowing the comparison between two important factors possibly acting on size, temperature **and oxygen**. In a second paper, we will consider in more detail the physiological basis of these two factors. Finally, in a third paper, unexpected data from another ancient lake, Lake Titicaca, will offer an opportunity to test the respective effects of temperature and oxygen.

In **Chapter 4**, we will analyze **the effect of oxygen on mean species size** at lower taxonomic ranks, namely **for superfamilies, families and genera**.

Chapter 5 will deal with the same question **at the intraspecific level**, providing additional information about the underlying mechanisms.

Chapter 6 will return to the **size spectra**, with the addition of data from three other areas, bringing **new insights in the relationship between size and oxygen** in the light of the two previous chapters before concluding.

To sum up, the main aim of the whole work is to dissect out the major factors controlling size and the occurrence of gigantism in amphipods. These factors are likely to also be of importance for other groups.

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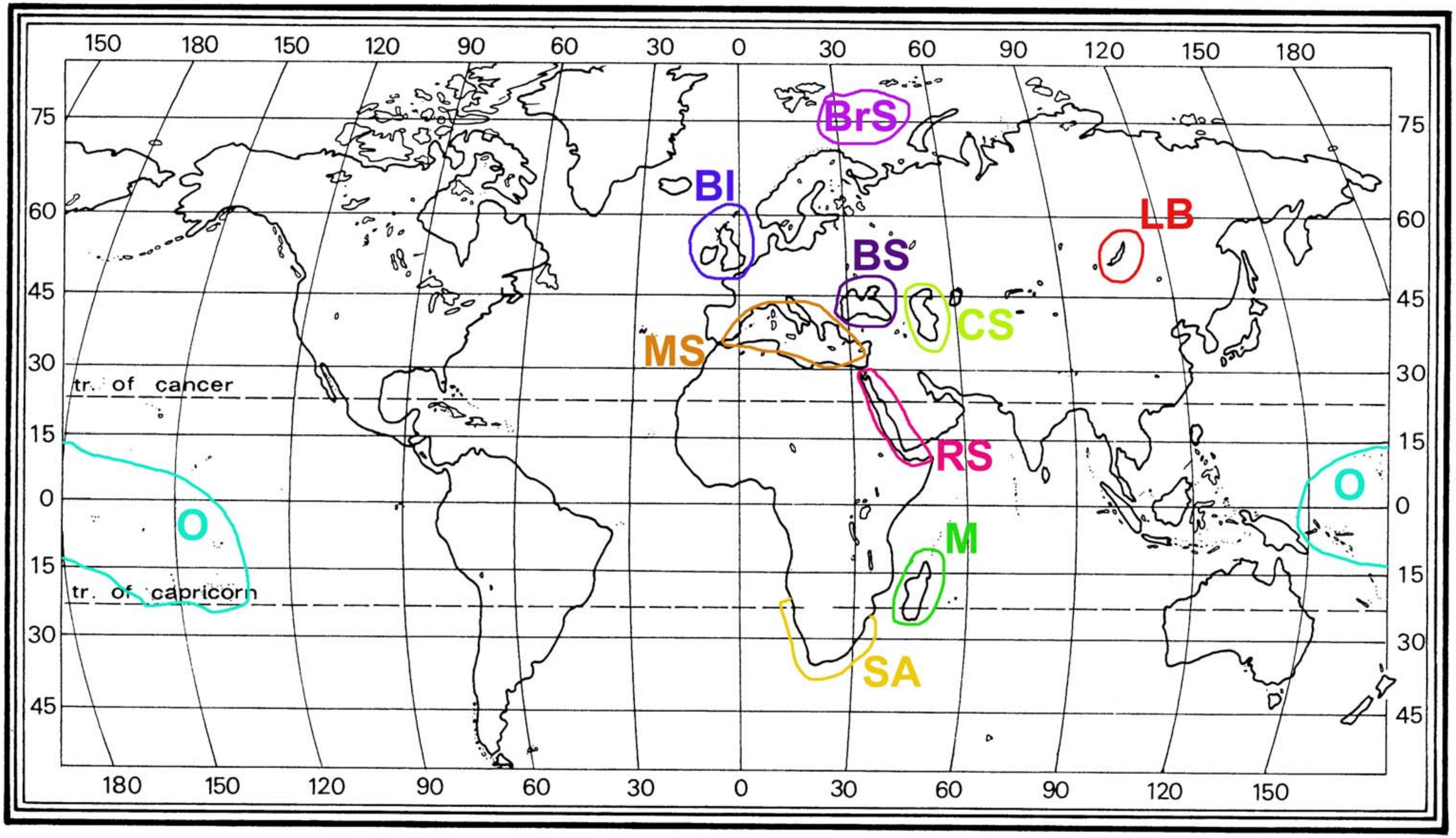
Geographic areas

Throughout this work, amphipod size data compiled from the literature (see Annex A) from 15 areas worldwide will be used extensively. The geographical situation of these areas is shown on the two following maps (Fig 2 & 3).

Fig. 2 - World map: from the North to the South,
BrS = Barents Sea
BI = British Isles
LB = Lake Baikal
BS = Black Sea
CS = Caspian Sea
MS = Mediterranean Sea
RS = Red Sea
O = Oceania (Micronesia, Bismarck, Samoa, Society & Fiji Islands)
M = Madagascar
SA = South Africa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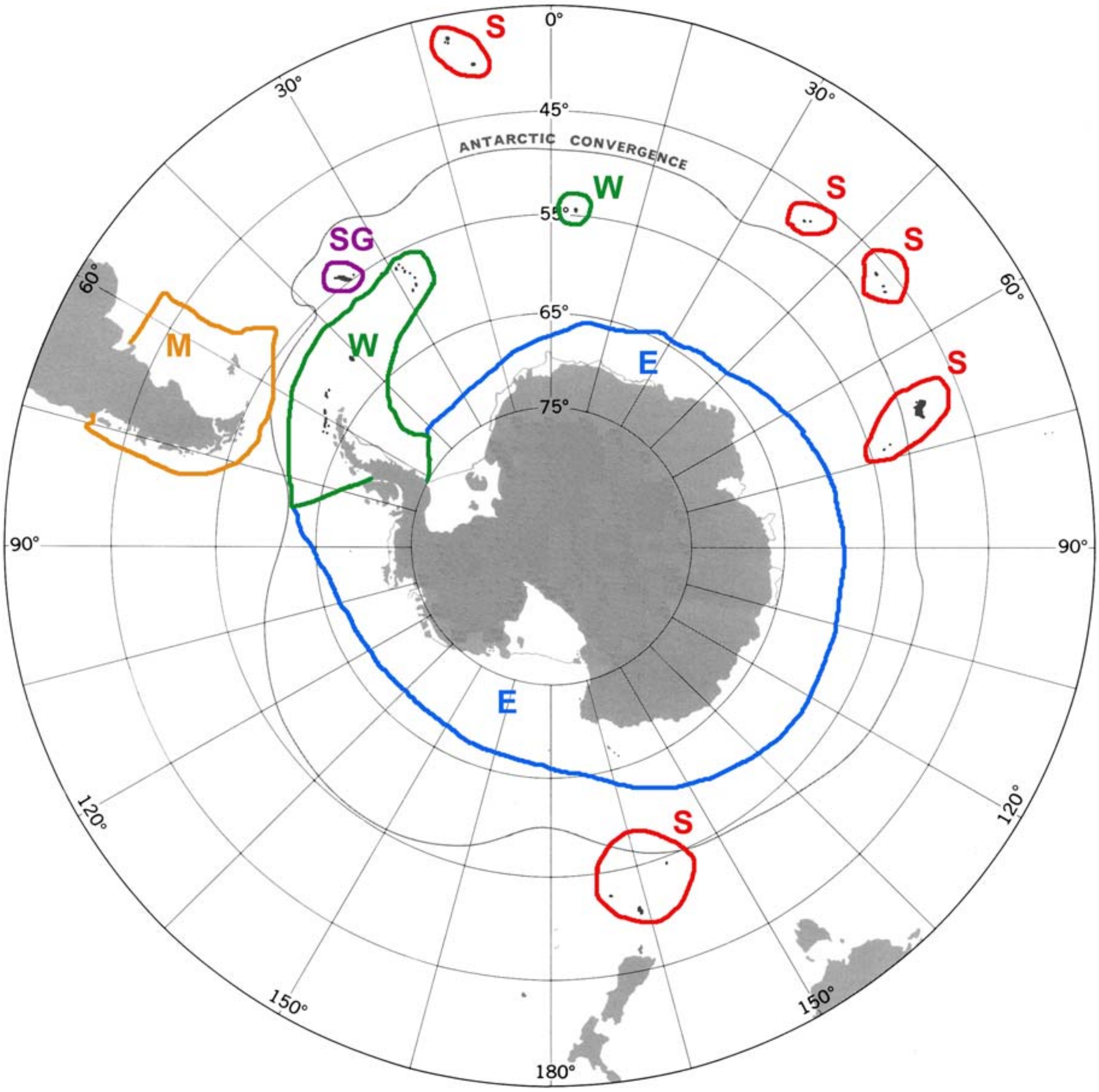


Fig. 3 - Southern Ocean: from the North to the South,
S = Subantarctic islands
M = Magellanic region
SG = South Georgia
W = West Antarctica
E = East Antarctica

Chapter 1: The Antarctic amphipods

One of the largest Antarctic amphipods, *Epimeria rubrieques* (De Broyer & Klages, 1991), 69 mm. Picture T. Schickan.

> *"...Relativement à leur volume considérable déjà, combien paraissait petit notre navire dont certains icebergs dominaient la mâture ! ...la variété des grandeurs se doublait de celles des formes, différenciées à l'infini. L'effet était merveilleux, lorsque ces enchevêtrements dégagés des brumes, réverbéraient, comme d'énormes cabochons, les rayons solaires. Parfois, les strates se dessinaient en couleurs rougeâtres, sur l'origine desquelles on n'est pas exactement fixé, puis se coloraient des nuances du violet et du bleu..."*
>
> "Le Sphynx des glaces", Jules Verne

Oediceroides emarginatus (Nicholls, 1938), from the family Oedicerotidae ; size up to 55 mm.

This large amphipod is found on sandy bottoms, half-burrowed with head and upper pereon emerging. Although its diet remains unclear, this species is likely to feed opportunistically on both small living and dead preys.

Maxilliphimedia longipes (Walker, 1906), from the family Iphimedidae ; size up to 43 mm.

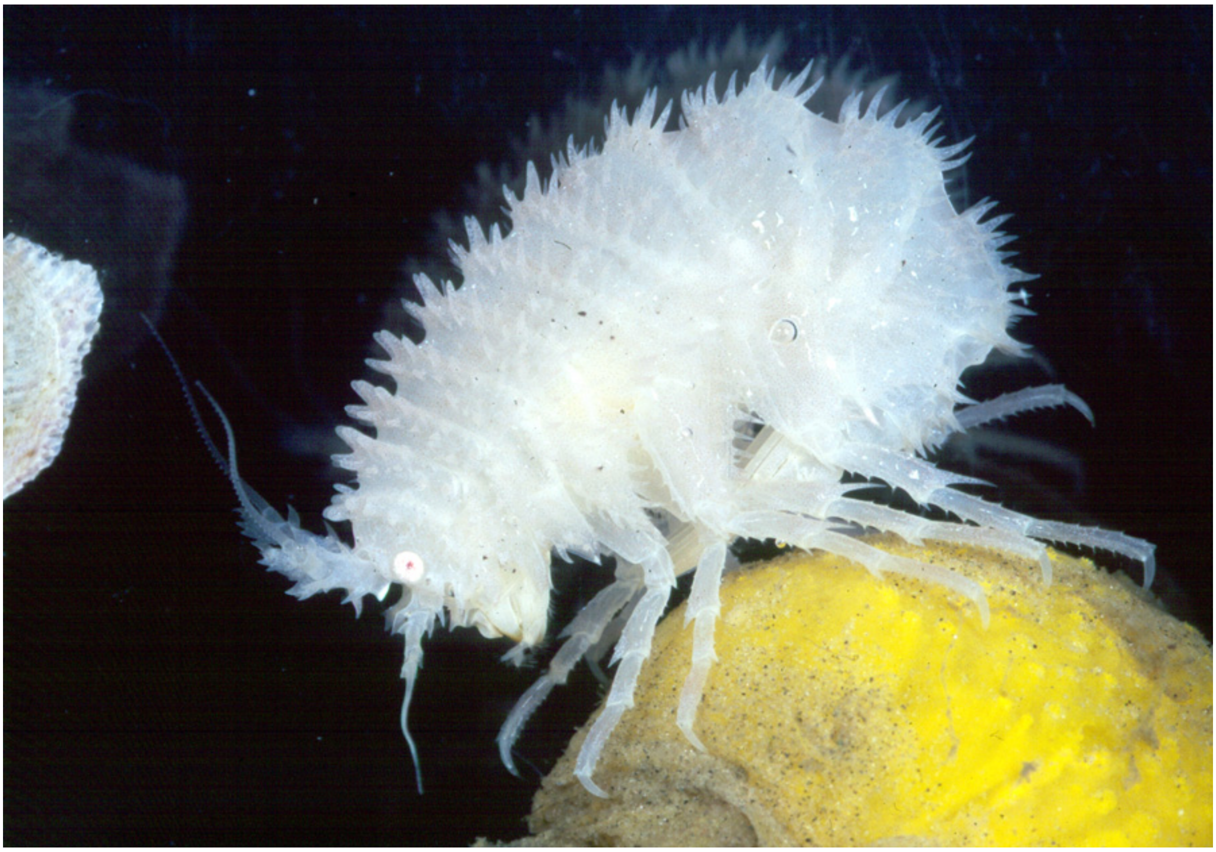
Like many other species from this family, this strong and calm amphipod is a rather specialised micropredatory browser, in its case on sessile cnidarians.

Waldeckia obesa (Chevreux, 1905), from the superfamily Lysianassoidea ; size up to 35 mm.

This common species has a wide circum-Antarctic distribution. It is a typical necrophage very frequently caught by hundreds in baited traps.

Paraceradocus gibber (Andres, 1984), from the family Hadziidae ; size: up to 63 mm.

Among the largest gammarids from the Antarctic, it uses to shelter in crevices or to burrow in the sand. It is mainly a deposit-feeder, but should also be able to catch small living crustaceans. The picture shows two specimens, the white colour of the lower one being unusual.



Echiniphimedia hodgsoni (Walker, 1906), from the family Iphimediidae ; size: up to 40 mm.

Like *Maxilliphimedia*, the « white hedgehog » is also a specialized browser. Its diet is almost exclusively constituted by sponge tissues.

Abyssorchomene rossi (Walker, 1903), from the superfamily Lysianassoidea ; size up to 40 mm.

This species is an opportunist macro-feeder, both predator and scavenger, which can also been caught in big numbers in baited traps. This specimen is an ovigerous female, with its purple eggs visible through the coxal plates.

Chapter 1: The Antarctic amphipods

1. Antarctic giants

In Antarctica, sampling benthos to collect amphipods is a fascinating experience. The first surprise arises when a bottom trawl is emptied on the deck of the ship. Considered from a human perspective, the environmental conditions - especially the temperature, permanently near or below 0°C, and the extensive ice cover - do not prepare us to the astonishing abundance of benthic life: glass sponges, soft corals, ascidians, sea anemones, bryozoans, starfish, sea cucumbers, shrimps, fish, - or algae when the bottom is shallow enough - make even the biggest amphipods difficult to spot at first sight.

However, once sorted from the catch and allowed to settle down in our aquaria, these crustaceans reveal their remarkable variety in shape and colors; the massive, orange and half-buried *Oediceroides emarginatus* (Nicholls, 1938), the square-headed chocolate *Maxilliphimedia longipes* (Walker, 1906), the plump *Waldeckia obesa* (Chevreux, 1905), the *Epimeria rubrieques* (De Broyer & Klages, 1991), aptly nick-named "Red Knight", the lazy *Paraceradocus gibber* (Andres, 1984) hiding between bryozoans debris, *Echiniphimedia hodgsoni* (Walker, 1906), the white hedgehog, the energetic and colorful *Abyssorchomene rossi* (Walker, 1903) and many others not only constitute a wonderful living fresco, but their size also appears to confirm the existence of "polar gigantism".

The aim of this chapter is to further substantiate the gigantism of Antarctic amphipods. After a brief introduction of their environment, we will use the main tool of this study by presenting the size spectrum of all benthic Antarctic species, and compare it to the one established for the Subantarctic region.

2. The Antarctic continental shelf: a unique ecosystem

The most obvious physico-chemical characteristic of the Antarctic coastal and shelf ecosystem (ACSE) is the year round cold temperature of its waters. For example, temperature close to the sea bed varies annually between 0 and 3°C in South Georgia (54° S), -1.8 and 2°C in the South Orkney Islands (West Antarctic, 61° S), and -1.9 and -1.8°C at McMurdo Sound (East Antarctic, 78° S) (Clarke, 1983).

This low and very stable temperature in comparison with temperate waters has important biological consequences. One is due to the inverse relationship between gas solubility and temperature, making the Antarctic seas the highest oxygen content marine waters in the world. Also, the low temperature allows a reduced basal metabolic rate, and therefore, some life strategies which would be difficult if not impossible in warmer waters (Clarke, 1983). For example, extended longevity is a trait shared by many Antarctic benthic organisms, often leading to high densities and biomass (Knox & Lowry, 1977; Mülenhardt-Siegel, 1988).

Another major characteristic of the ACSE is the highly seasonal character of the primary production (Clarke, 1988). This primary production relies mainly on phytoplankton, not only in the shelf waters, but also in the intertidal and shallow subtidal areas, due to the paucity of macroalgae resulting from the negative impact of little bergs, brash ice and solid ice during winter on the macroalgae (Clarke, 1996a). Compared to warmer latitudes, this primary bloom is also more decoupled from the grazing bloom of the zooplankton, ensuring an important phytoplanktonic input to the bottom fauna (Gray, 2001).

As pointed out by Grassle (1989), the patchiness of this settlement of material is greatest in polar regions, and it could partly account for the high diversity of the Antarctic benthos, together with the still controversial link between energy input and diversity (Gage & Tyler, 1991; Roy et al., 1998; Gray, 2001).

Also important is the stochastic, but depth related physical disturbance from icebergs. This adds to the heterogeneity of the environment and increases niche diversity (Arntz et al., 1997).

Another factor responsible for this higher diversity in comparison to the Arctic is the long evolutionary history of the Southern Ocean (Clarke, 1996b). When the first has only been isolated for 2-3 million years, separation of the Antarctic occurred at least 20 million years ago (Dunton, 1992; Dayton et al., 1994; Clarke & Crame, 1997).

Irrespective of its origins, this high species richness can be shown both for the sessile suspension-feeder fauna, such as bryozoans, sponges, ascidians or anthozoans, and the vagile fauna, best represented by polychetes, mollusks, echinoderms and peracarid crustaceans (De Broyer & Jazdzewski, 1996; Arntz et al., 1997; Orejas, 2001). This is also reflected in the complex 3-dimensional structure of some benthic communities, as described for a range of localities of the Antarctic shelf (e.g. Dayton et al., 1974; Voss, 1988; Galeron et al., 1992; Gutt & Starmans, 1998), providing a rich choice of micro-habitats for motile organisms like amphipods (De Broyer et al., 2001).

On the other hand, beside this diversity of the main marine groups, decapod crustaceans are noticeably scarce in the ACSE. Only one anomuran crab and a handful of benthic shrimps exist, and it could be of importance for amphipod size regarding competition (Sieg & Wagele, 1990; Klages et al., 1995; De Broyer & Jazdzewski, 1996).

3. The amphipods

With more than 1000 described species, the peracarid crustaceans are by far the most diverse group of the Antarctic macrobenthos, ahead of the 650 polychete species recorded (De Broyer & Jazdzewski, 1996). Benthic amphipods represent nearly a half of the peracarids, comprising 11 Caprellidea and 451 Gammaridea (including 264 genera), and were also found to be the most speciose group at the local scale in the only study of this type (Jazdzewski et al., 1996; De Broyer & Jazdzewski, 1993).

It is always difficult to estimate the percentage of undescribed species in a given area. 26% of the Southern Ocean amphipod fauna have been described during the last two decades, and 17% only in the last decade. This gives credit to the speculated figure of 2,000 species for the Antarctic only (including Antarctic deep sea), as extrapolated from the world total (Bousfield, 1979) by De Broyer & Jazdzewski (1996).

The diversity encountered at the species level also exists for higher taxonomic ranks, as most of the classical marine superfamilies and families are represented in Antarctica, even if the amphipod fauna is dominated by the Eusiroidea, Iphimedioidea, Lysianassoidea and Stenothoidae (De Broyer & Rauschert, 1999). The ancient geographic as well as thermal isolation of the ACSE has led to an important endemism, attaining 78 and 27% for species and genera respectively (De Broyer & Jazdzewski, 1996).

This species richness is also reflected in the trophic and habitat diversity. For instance, amphipods of the Eastern Weddell Sea have been ascribed to six main groups, including the endobenthic species living in the sediment, the highly diversified epibenthic fauna, dwelling on all kinds of substrata, the specialized cryopelagic species living on the lower surface of sea-ice as well as the various groups swimming more or less permanently in the water column (De Broyer et al., 2001).

Diversity of the trophic types is also high, as most potential food sources are exploited by one species or another. Macropredators, micropredatory grazers, suspension and deposit feeders, scavengers are amongst the types described for East Antarctica (Dauby et al., 2001), while macroherbivores are common in West Antarctica within the macroalgal zone and even below (De Broyer & Jazdzewski, 1996).

4. Gigantism and size spectra

The exceptional sizes attained by Antarctic amphipods have been often mentioned (e.g. Arnaud, 1974; Klages, 1993), but rarely studied in the past. While investigating abyssal amphipod size, Barnard (1962) has calculated the average size of a range of amphipod faunas. According to his data, the polar faunas are ahead of all the others, with a mean size of 13 mm and 17 mm for the Antarctic and Arctic amphipods respectively.

In the only paper exclusively devoted to Antarctic gigantism in amphipods, De Broyer (1977) confirmed the high relative frequency of Antarctic giant species by comparing the maximum size of each Antarctic or Subantarctic species to the genus mean size, calculated by pooling the size of all world representatives. A species was called giant when its size measured at least twice the genus mean size (g.m.s.).

However, by comparing only species belonging to genera with representatives both outside and inside the Southern Ocean, this major study did not encompass genera endemic to the Antarctic, thus excluding polar giants like *Paraceradocus, Gnathiphimedia, Maxilliphimedia* and *Echiniphimedia*.

A second problem arose because of the definition chosen for giant species. Indeed, genera having speciated mainly in Antarctica and produced a majority of large species, like *Epimeria* had already a very high genus mean size. Hence even the largest did not reach the threshold of twice the g.m.s. and could not be categorized as giants, even if they were clearly much larger than amphipods from elsewhere.

To overcome these problems, and because of the difficulty to distinguish giant species from the others, we decided to build size spectra for the entire amphipod fauna from the Antarctic and Subantarctic regions, and compare them with other zoogeographical areas.

Maximum adult length was also retained as the measuring parameter, since it is the most commonly reported size measure, whereas weight data remain the exception. Female mean size at maturity, as used by Sainte-Marie (1991) in his review of reproductive bionomics, would have been another potential metric. However, this would have excluded too many species, since up to 38% of the Southern Ocean gammaridean amphipods are known only from the original material (De Broyer & Jazdzewski, 1996).

The Southern Ocean fauna has been subdivided in two distinct data sets, for the Subantarctic and Antarctic regions respectively, as defined by De Broyer & Jazdzewski (1993), and benthic amphipod length data have been gathered by checking all the relevant references of the two existing checklists (Lowry & Bullock, 1976; De Broyer & Jazdzewski, 1993; see the Annex A for the full list). Species with length measures reported only for immature specimens were discarded and to avoid bathymetric bias, only the species living on the continental shelf were used to establish the size spectra.

These size spectra are already quite informative (Fig. 1). Both display a distribution skewed to the right, showing the predominance of small species. The main difference lies in species longer than 30 mm, much scarcer in the Subantarctic region, although they still represent only a low proportion of the total number of Antarctic species. Interestingly, the mean size value for Antarctic species is 15 mm, thus a bit higher than the 13 mm reported by Barnard (1962). Comparisons with other geographical areas will be presented in Chapter 3.

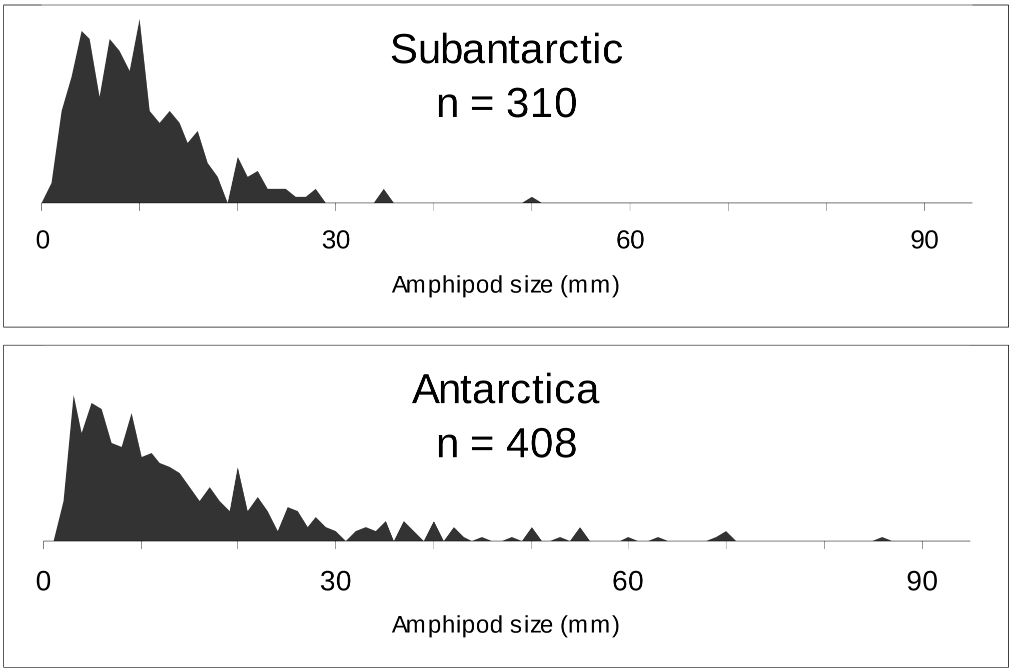


Fig. 1 - Gammaridean amphipod size spectra for the Southern Ocean: the X-axis is for the maximum length of each species (mm); Y-axis gives the number of species of that size. The number of species n is provided for each area.

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Chapter 2: The Baikalian amphipods

One of the largest Baikalian amphipods, *Propachygammarus maximus* (Garjajew, 1901), 67 mm, picture from the author.

> *"... une immense nappe d'eau se déroulait aux pieds de Michel Strogoff. C'était le Lac Baïkal...*
> *... Sa longueur est environ de neuf cents verstes, sa largeur de cent. Sa profondeur n'est pas connue. Mme de Bourboulon rapporte, au dire des mariniers, qu'il veut être appelé "Madame la Mer". Si on l'appelle "Monsieur le Lac", il entre aussitôt en fureur..."*
>
> "Michel Strogoff", Jules Verne

Pallasea cancellus (Pallas, 1776), from the family Pallaseidae ; size up to 65 mm.

This opportunist predator can be found in very shallow waters, usually under stones. It is a very resistant species in captivity : one individual died after 4 years, while several specimens were still in excellent shape after 3 years in the aquaria of the Institute.

Abyssogammarus swartschewskii (Sowinsky, 1915), from the family Gammaridae ; size up to 55 mm.

Abyssogammarus swartschewskii has never been caught above 350 m, although he remains to date the shallowest species from this specialised deep genus. Sometimes caught in baited traps, it is thus a permanent inhabitant of the 3-4°C water mass.

Odontogammarus calcaratus (Dybowsky, 1874), from the family Gammaridae ; size up to 35 mm.

This opportunist scavenger makes often the bulk of trap catches above 150 m. Four subspecies are known of this widely distributed species.

Acanthogammarus victorii (Dybowsky, 1874), from the family Acanthogammaridae ; size up to 67 mm.

One of the most specacular representative of its genus, it can be taken by hundreds in shallow trawls. The taxonomy within this species remains unclear : this specimen belongs to the North form of the subspecies *maculosus*, but is likely to be completely distinct from the population inhabiting the « Maloye More » (shallow part between Olkhon Island and the northern side of the lake).

Ommatogammarus albinus (Dybowsky, 1874), from the family Gammaridae ; size up to 25 mm.

It can be caught by hundreds in traps, down to the deepest parts of the lake, and is the commonest species of this highly specialised necrophagous genus, ecologically analogous to the marine superfamily Lysianassoidea. In contrast to its antarctic counterparts, it poorly survives in aquaria.

Parapallasea puzyllii (Dybowsky, 1874), from the family Pallaseidae ; size up to 50 mm.

Rather widely distributed throughout the lake, it is restricted to the upper 250 m. The specimens of its shallower populations are distinctively smaller.

Chapter 2: Baikalian amphipods

1. Baikalian giants

Our expectations were quite high when came the time of our first Baikalian expedition. On the one hand, we had already some experience of the Antarctic benthos and its large amphipods; on the other, we knew about Baikalian giants mainly from sparse mentions in the literature and from a few fixed and discolored specimens. But nothing had really prepared us for what we found in our first "deep" trawls (200 m) in Lake Baikal.

The first obvious difference with the Antarctic was regarding the abundance of amphipods relatively to the rest of the catch: except for a few huge flatworms, some thin-shelled gastropods and many Cottoid fish, nothing else than amphipods ! A first sorting often produced one or two buckets full of a bright orange (or pink, or whitish with increasing depths) mass of large amphipods belonging to about ten species, even more impressive at first sight than their Antarctic relatives. Or in shallower water, similar quantities would be dominated by a single spiny species, beside some specimens of less common and smoother giants.

Distinguishing the different species with the help of our Russian colleagues, and as in Antarctica, observing the amphipods in aquaria allowed us to get acquainted with the most common species and to appreciate their own peculiar style; the greenish and resistant *Pallasea cancellus* (Pallas, 1776), the long and pale *Abyssogammarus swartschewskii* (Sowinsky, 1915), the red and white jewel-like *Odontogammarus calcaratus* (Dybowsky, 1874), the huge, spiny and long-legged *Acanthogammarus grewingkii* (Dybowsky, 1874), the plump *Ommatogammarus flavus* (Dybowsky, 1874), the chocolate and flattened bronze-crested *Parapallasea puzyllii* (Dybowsky, 1874), or the long-antenned and half-blind G*arjajewia sarsi* (Sowinsky, 1915), were amazing discoveries. Moreover, they seemed to seriously threaten the unicity of polar gigantism.

The aim of this chapter is to examine Baikalian amphipods gigantism before confronting it to other world locations in the following ones. A summary of the characteristics of this unique environment and the amphipods living in it will be given. Finally, gigantism and the size spectrum of the Baikalian amphipod fauna will be presented.

Compared to the Antarctic fauna, Baikalian amphipods offered the additional challenge of the access to the relevant literature, nearly exclusively in Russian before the nineties. Throughout these years, we have collected most, and had translated in English, many of the papers devoted to that group. In order to show the full value of this work, and to make it more easily accessible to interested colleagues, an extensive list of all the collected papers was produced and can be found at the end of this thesis (Annex B).

2. Lake Baikal: the "Sacred Sea"

Nestled in the heart of Eastern Siberia, Lake Baikal cumulates superlatives. Its dimensions already speak for themselves. A surface of more than 31,500 km^2, a length of 640 km and a maximum width of 80 km already place it amongst the biggest fresh water bodies (Martin,1994). But what distinguishes Lake Baikal from other big lakes is an exceptional combination of depth and water circulation pattern. With a record measurement of 1642 m in the central basin, Lake Baikal is the deepest freshwater lake on Earth, slightly ahead of Lake Tanganyka (1470 m) and Malawi (785 m). At the same time, a very particular water regime constantly provides 75% oxygen saturation down to the deepest parts of the lake, unlike in other deep lakes where the lower waters are anoxic from the bottom down to depths varying from 70 to 200 m (Martin, 1994; Martin et al., 1998; Coulter, 1994; Ribbink, 1994). Oxygen even penetrates very deeply into the sediments (up to 50 mm; Martin et al., 1993).

Furthermore, with at least 25 million years of age, Lake Baikal is also the most ancient lake on Earth (Mats, 1993). The rift in which it appeared is still active today, preventing the sediments (already 7 km thick !) to fill up the lake. This coupling of a long history and the occurrence of oxygen down to the bottom has allowed the first invaders of Lake Baikal to create an amazing variety of niches in the water column and on the bottom, and gave also birth to the only specialized deep fresh water ecosystem.

Lake Baikal is frozen during winter, and the one-meter-thick ice layer is present from January to May (Martin, 1994), accompanied by a cryophilic community of non specialized algae, ciliates, rotifers and copepods (Timoshkin, 1999). While below 250 m the temperature is always between 3.2 and 4°C, the upper layer experiences much higher variations, from 0 to 16°C for the open lake, and up to 22°C in the most sheltered bays (Martin, 1994). Temperature regime and the low mineral content of the water are probably responsible for the low annual primary productivity (Kozhov, 1963). Its highly marked seasonality has led many organisms to concentrate juvenile release in the summer months, including most of the studied amphipods (Bazikalova, 1941; 1951; Gavrilov, 1949).

The result is a highly diversified fauna (2565 species) with a noticeable more than 50% endemism (Timoshkin, 1997). For the macrofauna, the most important groups in terms of diversity and abundance are sponges, turbellarians, oligochetes, gastropods, trichopterians, chironomids, cottoid fish, and finally, amphipods (Kozhov, 1963; Martin, 1994; Kozhova & Izmestieva, 1998). Crustacean groups of similar size are either very scarce in the case of Isopoda (five uncommon species) or totally absent in the case of Decapoda.

3. The amphipods

Pallasea cancellus (Pallas, 1776), the first Baikalian amphipod to be described, is already one of the biggest species (Pallas, 1772). Although some other species were described in the meantime by Gerstfeldt (1859), it took the famous Polish researcher Dybowsky to fully recognize and illustrate the outstanding richness of the Baikalian amphipod fauna (Dybowsky, 1874). Subsequently, the most important contribution was brought by Bazikalova between 1941 and 1975, in particular with her monograph "Amphipods of Lake Baikal" (Bazikalova, 1945), the only book, so far, allowing determination of most genera.

With 272 species and 76 subspecies described nowadays, Baikalian amphipods represent 10% of the total number of aquatic animals and are the second most speciose group of Lake Baikal beside the protozoans (Takhteev, 2000b). As there are 1000 freshwater amphipod species worldwide, including 400 in subterranean and karstic waters, the Baikalian species represent as much as 45% of the amphipod diversity in the surface freshwater bodies of our planet (Takhteev, 2000b). All of them belong to the superfamily of Gammaroidea *sensu* Barnard & Barnard (1983).

This huge diversity is coupled to an astonishing endemism of more than 95% (Martin, 1994). From the remnant 5%, 10 species are considered non endemic for having successfully colonized the effluent river system, some of them penetrating as far as the complex lake system surrounding the Yenisei estuary on the shore of the Arctic Ocean (Kozhov & Tomilov, 1949; Greze, 1951). These eurythermal species have been (too) successively introduced in numerous reservoirs and lakes of the former USSR as additional food for fish (e.g. Bekman & Bazikalova, 1951; Timm & Timm, 1993). The only species with no direct origins from Lake Baikal itself, the palearctic *Gammarus lacustris* (Sars, 1863), is restricted to the warmest parts of the most sheltered bays (Bekman, 1954).

It is presently hotly debated about the exact age of the Baikalian amphipod fauna. On one hand, and based on the inferred age of the symbiotic ciliophores of many amphipod species, some investigators considered it as rather young, because the former fauna was wiped out following a still hypothetical disaster some 2 to 3 million years ago (e.g. Yankovsky, 1982). Using molecular genetics, others have proposed a polyphyletic origin for Baikalian amphipods, with the colonization of the lake occurring 28 million years ago (Sherbakov, 1999; Sherbakov et al., 1999; for discussion see Timoshkin, 1999).

Futhermore, Pleistocene paleoglacial studies have recently made the debate even more complex. They established the existence, along the edge of the receding Eurasian ice sheet, of large proglacial lakes interconnected in a Trans-Eurasian meltwater drainage system including Lake Baikal, Aral, Caspian and Black Seas to be finally discharged in the Eastern Mediterranean Sea, and later also in the Baltic Sea (Grosswald, 1988).

This could explain the disputed attribution of some Iberic freshwater gammarids to the supposedly endemic Baikalian genus *Eulimnogammarus* (Stock, 1969; Pinkster & Stock, 1972; Karaman, 1977), as well as the numerous convergences between the Caspian and Baikalian amphipod faunas (Bazikalova, 1940; Starobogatov, 1994). Similarly, after having been removed from its original genus by Barnard & Barnard (1983), the amphipod *Pallasea quadrispinosa* (Sars, 1867), a freshwater glacial relict widely distributed in the Northern Palearctic (Segestrale, 1957), was found to be nested within the Baikalian *Pallasea* radiation (Väinölä et al., 2000).

Whichever the correct hypothesis, the Baikalian amphipod richness probably reflects successive levels of diversification. Beside the obvious differences between genera (more than 40; Takhteev, 2000b), allozyme analyses often indicate a species distinction for taxa previously considered as subspecies, and a number of vicariant sibling species have been detected amongst morphologically stable species, leading to speculation of a putative total of 1,000 species for Baikalian amphipods (Väinölä & Kamaltynov, 1999).

As in Antarctica, the Baikalian amphipods display a great diversity of habitats. Nearly all types of substrate are used by more or less specialized species, from silt to sand, from sponges (very common in the lake) to algae (Kamaltynov et al., 1993; Takhteev, 2000b). There is also a complete sequence from the purely pelagic *Macrohectopus branicki* (Dybowski, 1874) (95% of the amphipod biomass in the lake) to species living permanently in various layers of the sediment, including many more ways of life more or less connected with the water column (e.g. Takhteev, 1997).

Amongst this diversity, some groups deserve a special mention, such as the rich "abyssal fauna", a unique phenomenon for freshwater, which includes several giant species (Takhteev et al., 1993; Takhteev & Mekhanikova, 1996). Equally exceptional is the species-flock of 16 *Pachyschesis*, host-specific parasites found in the brood pouch of most large species (Takhteev & Mekhanikova, 1993; Takhteev, 2000b).

Although still poorly known, a certain trophic diversity has also been described in Baikalian amphipods. Beside a number of littoral species feeding mainly, if not exclusively, on filamentous algae, many species seem to have a rather eclectic diet (Bazikalova, 1962; Morino et al., 2000), including the giant opportunist predator *Acanthogammarus grewingkii* (Dybowski, 1874) (Bazikalova, 1954a). The only known specialized groups are the already mentioned oophagous and parasitic *Pachyschesis* on the one hand, and the benthopelagic scavengers, mostly found in deep waters on the other hand (Takhteev, 1995; Tahkteev, 2000b; Mekhanikova et al., in press). This last group, mainly represented by the genus *Ommatogammarus*, has been shown to be ecologically analogous to the scavengers belonging to the marine superfamily Lysianassoidea. Other such convergences between some Baikalian and marine amphipods have been thoroughly investigated (Takhteev, 1995; 2000a,b).

4. Gigantism and size spectra

In the only paper on gigantism in Baikalian amphipods produced prior to this work, Bazikalova (1948) proposed gigantism (and dwarfism) as the result of predation pressure, mainly by the Cottoid fish. A thorough study of stomach content from these fish dismissed that claim by showing that amongst the 18 amphipod species reported, 15 and 12 were larger than 20 and 30 mm respectively (Sideleva & Mekhanikova, 1990). However, this hypothesis could be partly relevant to some species at least, since the same fish study revealed a marked preference for smooth amphipod species, together with a very low occurrence in the fish stomachs of the most heavily armoured genus, namely *Acanthogammarus*. Furthermore, Bazikalova (1954b) had shown that in this very genus, the growth rate of lateral teeth was higher than the one calculated for the rest of the body, till the total width would reach that of the fish' mouth.

On the other hand, beside this particular case, no satisfactory explanations had been put forward for the rest of the fauna, while no attempt had been made to quantify gigantism at all. It is in this context that the size spectrum was established, using Bazikalova's monograph (1945) as the source of the length data. In order to obtain valid comparison with marine data, only the species living from 0 to 250 m depth were used (Fig. 3).

Like the Antarctic one, the Baikalian size spectrum again illustrates how little important the large species are relatively to the much more numerous small ones. However, the right end of the Baikalian size spectrum extends further than the Antarctic, bringing factual support to the first impressions gathered during the expeditions, and the consequences of this difference will be discussed in the next chapter.

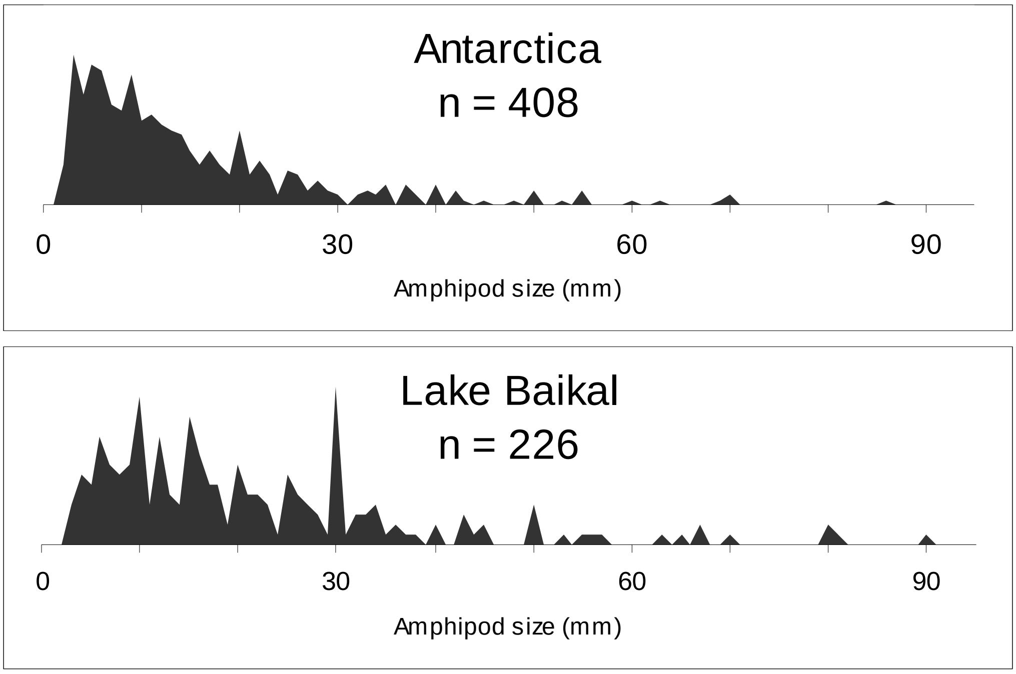

Fig. 1 - Comparison between Antarctic and Baikalian gammaridean amphipod size spectra: the X-axis is for the maximum length of each species (mm); Y-axis gives the number of species of that size. The number of species n is provided for each area.

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Chapter 3: Amphipod maximum size and oxygen content

Contents

1. Polar gigantism dictated by oxygen availability (Publication I)

First (long) version of: CHAPELLE, G.& PECK, L.S. 1999. Polar gigantism dictated by oxygen availability. *Nature*, 399: 114-115.

2. Amphipod gigantism dictated by oxygen availability?

2.1. Publication II :

SPICER, J.I. & GASTON, K.J., 1999. Amphipod gigantism dictated by oxygen availability? (provided for easier understanding)

PECK, L.S. & CHAPELLE, G. 1999. Amphipod gigantism dictated by oxygen availability?: reply – *Ecology Letters*, 2:401-403.

2.2. The case of the two "supergiants": an abyssal gigantism in amphipods ?

3. Lake Titicaca amphipods confirm oxygen limits maximum size. (Publication III)

CHAPELLE, G & PECK, L.S., submitted. Lake Titicaca amphipods confirm oxygen limits maximum size. *Oikos*.

Publication I

Polar gigantism dictated by oxygen availability

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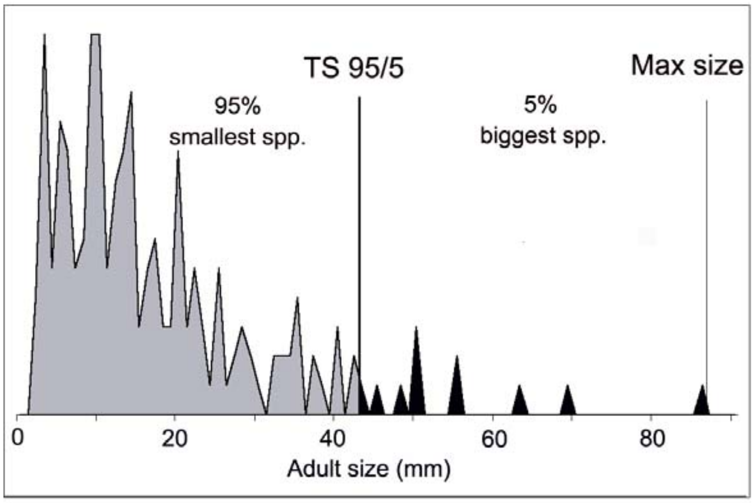
Nature, 399: 114-115.

Important notice to the reader :

The paper published as a scientific correspondence in Nature was a shortened version of the initially submitted « Letter to the Editor ». We have taken advantage of the publication of the whole thesis to present this first and extensive version, as it allowed to rescue a number of themes which were dropped in the final paper (available in most scientific libraries).

In the following paper, we have introduced a key parameter of this research too briefly, due to the reduced format imposed by the journal. This parameter is aimed at quantification of gigantism in each area, i.e. the upper part of each size spectrum. Instead of using maximum size, which is sensitive to sampling bias, we have defined the 95% / 5% threshold size ***-TS95/5*** *- as* ***the size separating the 95% smallest species from the 5% largest species****. This method, which will be used in all 6 papers, enabled us to reduce each site to a single size value, as shown here for East Antarctica.*



Polar gigantism dictated by oxygen availability

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Nature, version submitted as a "Letter to the Editor"

The factors regulating maximum size in animals are still poorly understood. This is especially true for gigantism in the fossil record and extremely large size in marine ectotherms at high latitudes. Examples are Antarctic sea spiders with diameters >30 cm and Carboniferous dragonflies with wingspans >70 cm. Suggested limiting factors are both physiological and ecological and include temperature, growth rate, resource availability, predation pressure and mortality (Atkinson, 1996 ; Atkinson & Sibly, 1997). Because gigantism is associated with low temperature in the sea, marine taxa have received considerable attention, but thorough analyses are still scarce and controversial (Arnaud, 1974 ; Clarke, 1996).

Using data for 1853 species of benthic amphipod from 12 sites worldwide we show that gigantism is part of a wider scale trend to large size at low temperature and is also associated with reduced salinities. However, environmental oxygen availability, rather than temperature or salinity is the principal factor influencing Maximum Potential Size (MPS). Furthermore our data indicate that carrying capacity of circulating haemolymph and reduction in metabolism with temperature (Atkinson, 1994) are not major factors.

Investigating latitudinal or temperature related gigantism with confidence requires widely distributed taxa with extensive species representation at many well-studied sites. Amphipods meet these criteria and have large sized representatives at high latitudes (Barnard, 1962 ; De Broyer, 1977). We analyzed length data for 1853 amphipod species and produced detailed size spectra for sites from polar to tropical and marine to freshwater environments. Only benthic species were included and at marine sites, analyses were restricted to the continental shelf.

At all sites size spectra are right skewed, however, skewedness increases as temperature decreases. Thus, mode, mean and maximum size all increase with decreasing temperature whereas minimum size does not change (correlation coefficient= -0.019, P=0.952).

To analyse gigantism a focus on the right hand extreme of the distribution is needed. However, maximum size itself is not used because of potential sampling bias at some sites. Instead, the threshold size separating the 95% smallest species from the 5% largest (TS95/5) has been used. When plotted against mean water temperature for marine sites, the TS95/5 increases curvilinearly as temperature decreases (Fig.1a).

However, reduced salinity sites do not fit this pattern. Lake Baikal (0), and less conspicuously, the Caspian (13) and Black Sea (17), lie above the relationship for marine sites, and the discrepancy increases as salinity decreases. The Lake Baikal TS95/5 is x1.8 the marine value for the same temperature.

Replotting the TS95/5 values against water dissolved oxygen content removes the discrepancy between marine and reduced salinity environments (Fig.1b). The relationship produced covers all sites, is linear and accounts for >98% of the variance in the data:

$TS95/5 = -46.2 + 0.252\ AE2$ $(N = 12; r2=0.98; F=51.69; P<0.0001)$ (1)

This indicates the underlying factor controlling TS95/5 is oxygen availability. When data (not shown) for TS90/10, TS80/20, TS50/50 and TS20/80 are regressed against mean environmental oxygen the fit of the relationships improves as TS value increases, indicating that oxygen becomes more important and other ecological factors reduce in effect as size increases. Furthermore the relationship between TS95/5 and temperature for marine sites in Fig 1a is curvilinear, reflecting the fact that the relationship between seawater oxygen content and temperature is non-linear.

TS95/5 in equation 1 reaches zero when mean environmental oxygen is at 183 $\mu mol.kg^{-1}$. This could indicate an environmental limit for amphipods. A variety of hot and/or highly saline conditions could produce 183 $\mu mol.kg^{-1}$ of oxygen (e.g. 30°C and 40 salinity or 40°C and 20). No amphipods are found in such hot brine areas which are inhabited by organisms including brine shrimp and ostracods (Ruffo, pers. comm.).

Surprisingly, minimum size does not vary significantly, either with temperature (Pearson correlation coefficient (PCC)=-0.019, P=0.952), or environmental oxygen (PCC=0.402, P=0.195). Clearly oxygen availability is not an overall selective pressure towards increased size for all species, but sets upper limits to maximum attainable size for the largest species (MPS).

If modal size corresponds to optimal size for a given body design, then optimal amphipod size increases with oxygen availability. However, minimum size is independent of environmental oxygen, temperature or salinity within the ranges investigated. Thus MPS increases dramatically with oxygen, modal size increases less and minimum size not at all, and the overall effect widens the size spectrum.

Having established that MPS in amphipods is tightly linked to environmental oxygen we now examine underlying mechanisms potentially underpinning this limitation: 1) the metabolic rate relationship with temperature. 2) haemolymph oxygen carrying capacity and 3) external oxygen availability.

1. Ectotherm metabolic rate rises with temperature (Ivleva, 1980 ; Clarke, 1991). The cost of maintaining body tissue (mass specific metabolism), therefore decreases with reduced temperature. This suggests large size at low temperature is a consequence of reduced maintenance cost allowing greater mass per unit resource, or a temperature effect on trade offs between tissue synthesis and resource loss through catabolism (Von Bertalanffy, 1960 ; Perrin, 1995 ; Atkinson & Sibly, 1997). This argument is contradicted by our data. Although a clear inverse relationship between size and temperature exists for marine sites, the largest amphipods were not found in our coldest site (high Antarctic, 0°C) but in Lake Baikal (+6°C), and these were ~50% longer than the largest marine species. Furthermore increased osmoregulation requirements for freshwater amphipods provide extra metabolic costs. The metabolic costs hypothesis would produce the largest MPS at Antarctic marine sites. Our data are also not consistent with maximum size being limited by trade-offs between anabolism and catabolism. To produce the observed increase in MPS between marine and freshwater sites in the face of enhanced osmoregulatory costs for freshwater species would require an unlikely increase in resource acquisition.

2. Oxygen is transferred into amphipod blood via the gill, and crustacean gills have low efficiencies for oxygen transfer. Data suggest transfer efficiencies are as low as 50% (Wolvekamp & Waterman, 1960). Two mechanisms exist for transporting oxygen around the body: by passive diffusion, or bound to respiratory pigments. Relative amounts carried depend on blood oxygen solubility and the quantity of pigment present (Dejours, 1981). Amphipods use haemocyanin, the commonest crustacean pigment. From the limited data available fully marine amphipod haemolymph contains 10-20 mg cm^{-3} of haemocyanin (Spicer, 1993). This is much lower than other crustaceans (21-116 mg cm^{-3}) (Lynch & Web, 1973). Amphipod haemocyanin may have an osmoregulatory function (Mangum, 1983 ; Hagerman et al., 1997) combined with a reduced oxygen transport role (Hagerman et al., 1997). Some respiratory function is evident during extreme oxygen stress, and in large species under prolonged activity (Lynch & Web, 1973), or short periods of hypoxia (Hagerman et al., 1997). No data exist on proportions of bound and unbound oxygen in the haemolymph of amphipods from different environments, although dissolved oxygen is most important in the Baltic amphipod *Monoporeia affinis* (Lindström, 1855) (Hagerman et al., 1997). The Antarctic giant isopod *Glyptonotus antarcticus* (Eigths, 1852) has one of the lowest haemocyanin contents of non-amphipod crustacea (20.5 mg cm^{-3}), and 55-60% of the oxygen in its haemolymph is dissolved (Whiteley et al., 1997). Isopods and amphipods are closely related, both being peracarid Crustaceans, and probably have similar functioning haemocyanins. Thus, for similar haemolymph dissolved oxygen levels, Antarctic amphipods would carry 60-70% of their circulating oxygen as dissolved oxygen, whereas for tropical species this would be 40%. Lake Baikal amphipods would also carry ~60-70% as dissolved oxygen, because although they inhabit a completely freshwater environment most have haemolymph osmotic concentrations around 340-360 mOsm (Zerbst-Boroffka, pers. comm.). This reduces the haemolymph dissolved oxygen content of Baikal amphipods at 6°C to similar levels to marine species at 0°C. Thus Antarctic amphipods should be around x1.5 to x2 larger than Madagascar species, and Lake Baikal and Antarctic species should be similar sizes. The TS95/5 for Baikal amphipods is 54.4 mm, for Antarctic species it is 43.6 mm, and for Madagascar it is 8.3 mm. Thus calculated differences in circulating haemolymph oxygen levels do not

match the observed size differences. Accounting for haemocyanin does not affect this conclusion, because haemolymph total oxygen content (dissolved and bound) is less than 3% different in Lake Baikal and Antarctica. This suggests saturation levels of haemolymph dissolved oxygen must increase from tropical to polar, and marine to freshwater environments, and the critical factor dictating MPS is gill efficiency.

3. Environmental oxygen concentration and amphipod MPS are linearly related. However, oxygen uptake by aquatic organisms is usually considered in terms of transfer of oxygen across permeable surfaces, e.g. gills. This process is governed by Fick's diffusion law:

$$M = K(F/G)P_{w\text{-}b} \qquad (2)$$

where the key parameter is the partial pressure difference between the external medium and the circulating haemolymph ($P_{w\text{-}b}$), which drives oxygen across the gill surfaces. Here external partial pressures do not vary from site to site, as all are within the same depth ranges. Hence the rate of transfer in the gills where minimum haemolymph oxygen content opposes maximum seawater content will be similar at all sites. However, the concentration of oxygen in the water changes in line with changes in solubility. Consequently for the same gill efficiency a greater mass of oxygen can pass into the blood at sites where the external concentration is higher, although partial pressure differences remain constant. Thus the saturation levels and absolute concentrations of oxygen in the blood will be higher at low temperature and salinity sites and amphipod MPS will reflect this in the way observed.

The above arguments indicate MPS is limited by oxygen concentration in the external water, mediated by a less than 100% efficient gill. Thus large size will occur at high concentrations, because a greater mass of oxygen will pass across the gills, increasing the possible path length for oxygen in the circulatory system.

The strong relationships we obtained were between external oxygen concentration and length, not body mass. However amphipods, like other groups showing large size at low temperatures (e.g. pycnogonids and nemerteans) have a restricted circulatory system with few lateral branches. In other groups a stronger relationship with body mass would be expected. Whether MPS is reached will depend on several factors. In any environment with many species selection pressures will drive them into as many niches as possible and both large and small size will be exploited.

Oxygen supply has been suggested as the reason for Carboniferous insect gigantism, because during this period atmospheric oxygen was 30-35% (Graham et al., 1975). Their demise when oxygen content fell could indicate that large species are susceptible to such change and the giant amphipods described here would disappear first following elevated temperatures or other global oxygen reducing events. Being close to the critical limit for MPS in a given oxygen environment may be a specialization making giant species more prone to extinction over geological time.

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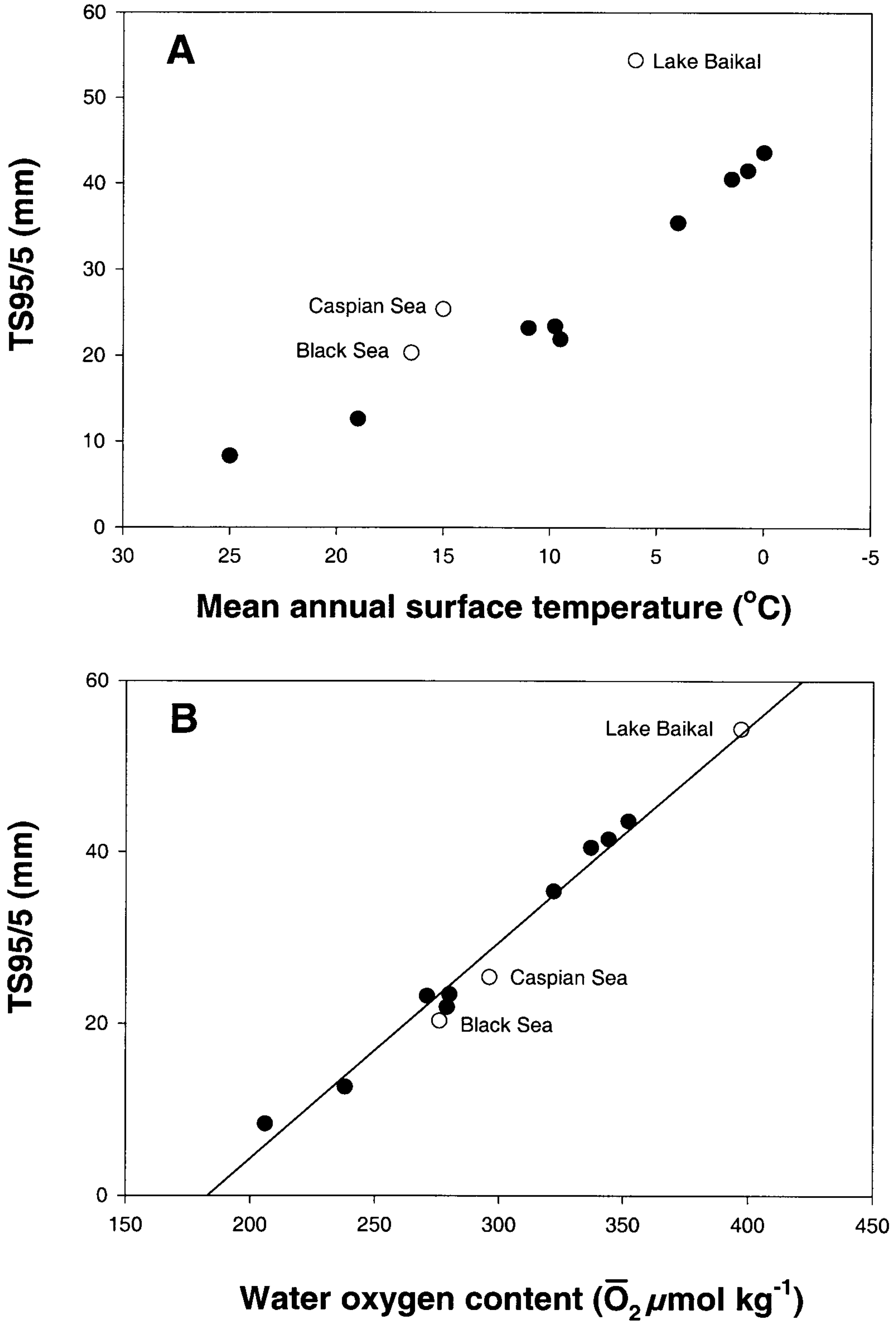
A
Lake Baikal
Caspian Sea
Black Sea
TS95/5 (mm)
60
50
40
30
20
10
0
30
25
20
15
10
5
0
-5
Mean annual surface temperature (°C)
B
Lake Baikal
Caspian Sea
Black Sea
TS95/5 (mm)
60
40
20
0
150
200
250
300
350
400
450
Water oxygen content (O$_2$ µmol kg^{-1})

Fig. 1

Fig. 1 - Effects of (A) temperature and (B) oxygen availability on the biggest amphipod crustacean sizes for 9 marine ( ) and 3 reduced salinity sites (O). (A) 95%/5% threshold size (TS95/5) vs mean annual water temperature (inverted scale). (B)TS95/5 vs calculated dissolved oxygen content at saturation (AE2 *mol kg-1), based on the surface water mean temperatures and salinity. Although not every habitat in the considered sites will experience permanent high oxygen saturation, this 100% value represents the optimal conditions for species to attain large size.

Publication II

Amphipod gigantism dictated by oxygen availability?

A reply to Spicer and Gaston.

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REPORT

Amphipod gigantism dictated by oxygen availability?

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Abstract

A recent study of gigantism in amphipods proposes a novel mechanism which could be used to explain Bergmann's rule, namely differences in environmental O_2 concentration. Consideration of the respiratory biology of this group indicates significant flaws in this proposal. Nonetheless, it is not unreasonable to predict a relationship between ectotherm body size and O_2 partial pressure (pO_2) in some systems, where the partial pressure gradient is steep, either in time (comparison of Carboniferous and Permian atmospheres) or space (animals inhabiting oceanic O_2 minimum layers, and, particularly in freshwaters, living at high altitude). Animal gigantism can be correlated with periods of very high environmental pO_2 over geological time. Unfortunately, data for present day spatial patterns are scant.

Keywords
Amphipoda, Bergmann's rule, body size, gigantism, oxygen, respiratory physiology

Ecology Letters (1999) 2: 397–403

BERGMANN'S RULE

It is commonly held that body size tends to increase with increasing latitude, both between and within animal species. The interspecific pattern, and in some quarters the intraspecific one, is known as "Bergmann's rule" (Bergmann 1847), although whether in either case the balance of support and refutation is appropriate for a "rule" remains questionable (see Blackburn *et al.* 1999). Where it does occur, the reasons for an interspecific latitudinal gradient in body size for ectotherms, in particular, remain obscure, with discussion centring on the possible role of the need for greater starvation resistance of animals at higher latitudes (Cushman *et al.* 1993; Blackburn *et al.* 1999; Chown & Gaston 1999). Mechanisms suggested to explain intraspecific gradients for ectotherms centre on the effects of temperature (through acclimation and/or adaptation) on cell size and/or number or on patterns of whole organism mortality (Yampolsky & Scheiner 1996; Mousseau 1997; Partridge & Coyne 1997; Van Voorhies 1997).

AMPHIPOD GIGANTISM

Amphipods are one ectotherm group known to exhibit a marked interspecific latitudinal gradient in body size (Poulin & Hamilton 1995). A recent study by Chapelle & Peck (1999), in which almost 2000 benthic species from 12 sites encompassing polar to tropical environments were examined, found that the maximum body size of amphipod species (expressed not as absolute maximum size, but as threshold size, $TS_{95/5}$; the size separating the smallest 95% of species from the largest 5%) was strongly correlated ($r^2 = 0.98$) with O_2 concentration ($[O_2]$); minimum size and $[O_2]$ were not significantly correlated. The authors conclude that maximum potential size (MPS) is limited by O_2 availability. If correct, this may be of major importance as it provides a novel approach to understanding Bergmann's rule. As the authors note it could also explain the occurrence of insect gigantism during the Carboniferous period as a result of elevated atmospheric $[O_2]$ at that time.

OXYGEN PARTIAL PRESSURE, NOT CONCENTRATION, DRIVES GAS EXCHANGE

That there is a good relationship between maximum body size and $[O_2]$ for benthic amphipods is not in doubt. And, as the authors point out, that relationship is noticeably stronger than the one observed for maximum body size and average sea temperature. However, significant problems arise in invoking mechanistic explanations of this pattern. Given that the central issue is O_2 availability, it is necessary to understand the features that determine the amount of O_2 that will enter an animal from the environment. This is relatively easy to model using a derivation of the Fick equation. The quantity of oxygen (QO_2) diffusing per unit time across a respiratory surface, of thickness L and area A, can be calculated as

$$QO_2 = DO_2 \frac{A \Delta PO_2}{L}$$

where ΔpO_2 is the difference in gas partial pressure across the respiratory gas exchange surface(s) and DO_2 is the permeability coefficient of the material(s) comprising that surface.

Hence, if MPS of benthic amphipods is limited by O_2 availability, one would expect MPS to scale with O_2 partial pressure (or tension) (pO_2) and not with $[O_2]$. There may be more O_2 in a given volume of polar sea water than tropical sea water as a result of the marked temperature-sensitivity of O_2 solubility ($\alpha O_2 = O_2$ solubility coefficient) in sea water, but nevertheless pO_2 is likely to be similar for both. The value for αO_2 will also be influenced by the salinity of the water, but again the pO_2 of air equilibrated water is likely to be similar whatever its salinity. This is important as it is only the pO_2 gradient across the gas exchange surfaces that drives the movement of respiratory gases between media of different O_2 capacitances (βO_2 = change in the $[O_2]$ per unit pressure change or $\Delta[O_2]/\ \Delta pO_2$. If the haemolymph contains a respiratory pigment $\beta O_2 > \alpha O_2$). Thus, in such cases the $[O_2]$ is almost irrelevant except for severely hypoxic or relatively small, enclosed systems (e.g. the O_2 minimum layer and isolated tide pools; Morris & Taylor 1983; Childress & Seibel 1998); here, when $[O_2]$ in the water declines as a result of respiration it does so markedly and there is a concomitant decrease in pO_2. If gas exchange *was* driven by $[O_2]$ then O_2 would actually leave the animal, as, due to the presence of Hc in the haemolymph, the $[O_2]$ of arterialized haemolymph in crustaceans (Mangum 1997), including amphipods (Spicer & McMahon 1994), is usually considerably greater than that found in the environment. This is even the case in those amphipod species that display some of the lowest concentrations of respiratory pigment (haemocyanin [Hc]) within the Crustacea (Spicer & McMahon 1992; Spicer 1993).

Chapelle & Peck (1999) state that saturation levels of dissolved O_2 in the (presumably arterialized) haemolymph will increase from tropical to polar environments. They may be correct, but the bearing this has on O_2 supply to the tissues is entirely dependent on knowing the [Hc] and HcO_2 binding properties present in temperate and tropical amphipods. Currently we only have such information for temperate species (Spicer 1993; Spicer & Taylor 1994a; Hagerman *et al.* 1997). In these, Hc is only essential for O_2 transport under certain conditions (e.g. activity, environmental hypoxia) and, as is certainly the case for all other crustaceans (Mangum 1997; contrary to Chapelle & Peck 1999), there are few grounds for suggesting that these molecules are more important for osmoregulation than O_2 transport. In conclusion, it is difficult to envisage how aquatic $[O_2]$ *per se* could limit MPS.

Apart from the generation of a pO_2 gradient, the area, thickness and composition of the gas exchange surfaces are all features that, if altered, could change the capacity for O_2 uptake. Chapelle & Peck (1999) assume that the gills of amphipods are the main sites of gas exchange and are relatively inefficient, the latter being a critical factor in determining MPS. It is not yet known if gill areas, thicknesses or compositions vary with latitude, the only published studies concentrating on temperate aquatic species (Milne & Ellis 1973; Moore & Taylor 1984). However, perhaps more importantly, there is good evidence for extrabranchial gas exchange in amphipods and, in some cases at least, the gills are unlikely to be the main areas of O_2 uptake (Graf & Magniez 1969; Spicer & McMahon 1994; Spicer & Taylor 1994b). Until it is possible to partition the relative importance of gills and extrabranchial surfaces, any question of gill efficiency is premature. With regards to Chapelle & Peck's (1999) comments on "restricted circulatory systems" in amphipods being the reason that $[O_2]$ scales with body length rather than body mass, as data on amphipod cardiovascular function are virtually nonexistent, it makes such speculation unhelpful. It is still possible that the value for the permeability coefficient (DO_2) of the gas exchange surfaces may differ in individuals or species kept at different environmental temperatures, thus altering the rate of O_2 diffusion into the body. Unfortunately accurate measurements of DO_2 are difficult to obtain and the effect of temperature acclimation of exchange surfaces on such values almost totally unstudied. Even replacing DO_2 with the biological coefficient KO_2 (a product of αO_2 and DO_2) introduced by Krogh, only complicates matters further. For although αO_2 increases by about $1.6\%\,^{\circ}C^{-1}$ with decreasing temperature, at the same time DO_2 decreases by almost twice that amount, $3\%\,^{\circ}C^{-1}$. Consequently a decrease in temperature should result, theoretically, in a net decrease in KO_2 of about $1.4\%\,^{\circ}C^{-1}$. Thus, and in sum, there is currently little evidence for limitation of O_2 availability imposed by gas exchange surfaces (whatever their identity) or circulatory systems in amphipod crustaceans.

In their study, Chapelle & Peck (1999) observe that $TS_{95/5}$ reaches zero when $[O_2] = 183\ \mu mol\ kg^{-1}$ and note that waters characterized by such conditions are not inhabited by amphipods. However, one of us has collected the freshwater amphipod *Hyallella azteca* Sauss from hot mountain springs in the Canadian Rockies ($T = 33^{\circ}C$) where the water $[O_2]$ is substantially below this proposed lower limit (J.I. Spicer, unpublished data). What is more, individuals from the hot springs were characterized by body sizes not dissimilar from those recorded from sites with considerably greater $[O_2]$ (maximum body length, 7 mm). Perhaps even more spectacularly there exist some giant deep-sea amphipods inhabiting waters characterized by $[O_2]$ below the "lower limit" proposed by Chapelle & Peck (1999) (J.J. Childress, personal communication).

GIGANTISM IN GEOLOGICAL TIME

The parallel drawn by Chapelle & Peck (1999) between the relationship between $[O_2]$ and amphipod body size, and gigantism in Carboniferous insects is also an interesting, if misleading, one. During the Carboniferous period there was an increase in atmospheric $[O_2]$, while nitrogen concentration stayed approximately constant. Consequently there was a significant increase in pO_2, which has been estimated to have been as high as 30 kPa (approximately 50% greater than today) (Berner & Canfield 1989). Thus there was an increase in the partial pressure gradient across the gas exchange surfaces of terrestrial, and also presumably aquatic, animals, with O_2 diffusion increasing by about as much as 67% (Dudley 1998). In insects a limit to maximum body size has been shown to be imposed by tracheal diffusion and so an increase in atmospheric pO_2 would enhance metabolism and so enable a larger body size to be achieved (Graham *et al.* 1995). Gigantism during the Carboniferous period also extended to other arthropod groups and to the early tetrapods (Dudley 1998). During the Permian, atmospheric pO_2 plummeted to values approximately two-thirds of those prevalent today, and it is thus not surprising that hypoxia has been blamed for the extinction of many such gigantic forms at that time. Chapelle & Peck (1999) conclude their article by speculating that giant amphipods may be amongst the first species to disappear if global temperatures are increasing. They may be right, but we suggest, perhaps for the wrong reasons.

IF NOT O₂, WHAT?

Although the mechanisms proposed by Chapelle & Peck (1999) to explain the latitudinal gradient in amphipod body size are likely to be incorrect, the relationship between MPS and $[O_2]$ remains, and requires explanation. The question then becomes whether there are environmental factors with which aquatic $[O_2]$ is a covariant. Notwithstanding its dismissal by Chapelle & Peck (1999), the strongest candidate is still probably environmental temperature. While for their data the amphipods of Lake Baikal are admittedly a definite outlier (but arguably not the Caspian or Black Sea assemblages, as implied by Chapelle & Peck), excluding that one datum there is a very strong relationship between MPS and temperature (Fig. 1; $TS_{95/5} = 41.0–1.39T°C$, $r^2 = 92.1\%$, $F_{1,9} = 105.52$, $P < 0.0001$). While the relationship between MPS and $[O_2]$ may be tighter, unlike the relationship between MPS and temperature, it lacks the explanatory power of a viable mechanism.

OXYGEN TENSION AND BODY SIZE?

Although the idea of implicating water O_2 content as responsible for the clinal variation in body size of animals is both a novel and an interesting one, in this particular case the proposed mechanism does not seem to work. However, it is pertinent to ask if there are large scale geographical patterns in pO_2 of a sufficient magnitude as to potentially limit the body sizes of animals. Ideally we should prefer examples where O_2 and temperature do not covary or if they do, where they would have opposite effects with regards to body size (i.e. decreasing temperature with a decrease in pO_2).

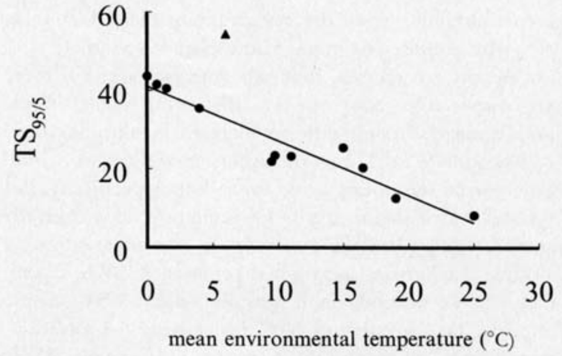

Figure 1 Maximum amphipod body size (as $TS_{95/5}$; the size separating the smallest 95% of species from the largest 5%) expressed as a function of mean environmental sea temperature at a number of different geographical locations. Data are taken from Fig 1 in Chapelle & Peck (1999). Equation of the line of best fit (excluding Lake Baikal amphipods = triangular symbol) $TS_{95/5} = 41.0–1.39T°C$, $r^2 = 92.1\%$, $F_{1,9} = 105.52$, $P < 0.0001$.

There are zones of stable and often severely hypoxic waters found at intermediate depths (400–1000 m) in many of the world's oceans; such O_2 minimum layers are characterized by their own distinctive faunas (Sewell & Fage 1948; Childress & Seibel 1998). Unfortunately, to our knowledge no formal comparisons of body size distributions of related species living both within and without these zones have been published. According to J.J. Childress (personal communication), who has considerable experience in the study of inhabitants of the O_2 minimum layer, there is no obvious difference in the body sizes of midwater fish and crustaceans down to a pO_2 of approximately 0.6 kPa.

It is also well known that pO_2 decreases with altitude, e.g. there is a 50% reduction with an increase in altitude from sea level to 5500 m (Jones 1972). There is also a reduction in temperature with increasing altitude. Thus one might suggest that if the effect of temperature was paramount in determining body size then we should see an increase in ectotherm body size with increasing altitude, and if pO_2 was paramount the opposite pattern. Such effects would be particularly acute in aquatic environments across an altitudinal range (e.g. freshwater lakes), although given the magnitude of the reduction in pO_2 with altitude one might also expect to see an effect in nonaquatic ectotherms. Relevant data are rare, but there are some. The body size of the land snail ***Arianta arbustorum*** decreases with an increase in altitude (Baur & Raboud 1988). This is the opposite of what we would expect from Bergmann's rule applied intraspecifically, but is consistent with a theory of O_2 limitation. However, for another snail (*Neohelix major*) body size increases with altitude (Emberton 1995) and in yet another (*Helix aspera*) there is no relationship (Lazaridou *et al.* 1994). Some interspecific comparisons have been made for Lepidoptera; however, here too the picture is inconsistent. While pierid species are smaller at high altitudes, papilionids are larger at high altitudes, nymphalids are largest at mid-altitudes, and riodinids show no relationship between body size and altitude at all (Hawkins & DeVries 1996). Data for body size distributions of aquatic species over an altitudinal gradient are difficult to find, and clearly there is an interesting comparison to be made of the body size distribution of aquatic ectotherm species across a pronounced altitudinal gradient. Such a study is probably one of the best hopes of determining if any mechanistic relationship between body size and pO_2 exists outside of large temporal changes in pO_2 over a geological timescale.

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BIOSKETCH

John I. Spicer is interested in the ecological implications of physiological diversity.

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REPLY

The main criticism that Spicer and Gaston have of our finding that maximum potential size in amphipods is limited by oxygen availability is based on the assertion that the quantity of oxygen entering an animal is controlled solely by the difference in partial pressure, when permeability of the respiratory surface is constant. They state that this is modelled by a derivation of the Fick equation:

$$QO_2 = DO_2\frac{A\Delta PO_2}{L} \tag{1.1}$$

However, as pointed out by Fenn & Rahn (1964) and Dejours (1981), when the Fick equation is modified to deal with activity or partial pressure gradients instead of concentration, it is necessary to introduce the solubility coefficient α, and the Fick equation correctly becomes:

$$QO_2 = \alpha DO_2\frac{A\Delta PO_2}{L} \tag{1.2}$$

Differences in solubility can give marked differences in the quantity (mols, mass) of oxygen transferred into the animal. Thus, for the same partial pressure difference, doubling the solubility of the gas will double the mass of oxygen supplied. It is because of the marked differences in solubility between seawater at high and low temperatures and between seawater and water of low salinity that differing masses of oxygen are available to amphipods in different environments. This is modelled in Fig. 1, where the relationship between oxygen concentration and partial pressure is shown for seawater (35 p.s.u.) at 30°C and freshwater at 0°C. For a partial pressure difference of 90 mm Hg (130–40 mm Hg) the amount of oxygen supplied per kg of 0°C freshwater is 280 μmol, the equivalent figure for 30°C seawater is 115 μmol. The mass of tissue that an amphipod species can sustain will depend on the quantity of oxygen available per unit time, which is a product of partial pressure gradient and solubility. As stated in our paper, if other factors are equal (including partial pressures and permeability of respiratory surfaces) the amount of oxygen supplied will depend on solubility, and hence the concentration of oxygen is important. We argue that in areas where many species have been present over evolutionary significant periods, selection pressures will have acted to push some species to large size. These pressures will also have selected in favour of optimising gas exchange surface characteristics.

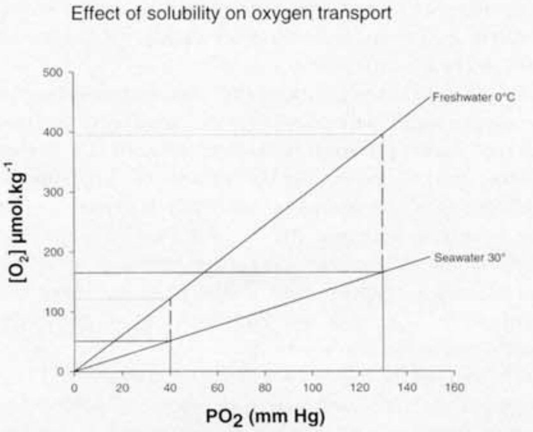
Effect of solubility on oxygen transport

Figure 1 The effect of solubility on oxygen transport. The relationships between water oxygen concentration ($[O_2]$, μmol kg^{-1}) and oxygen partial pressure (PO_2, mmHg) shown for freshwater at 0°C and for 35 p.s.u. seawater at 30°C. For a partial pressure drop from 130 to 40 mm Hg 0°C freshwater delivers 280 μmol O_2 kg^{-1} (broken lines), whereas the 30°C seawater delivers 115 μmol O_2 kg^{-1} (solid lines).

In the discussion of the importance of gills as the site for gas exchange it should be emphasised that there are very few data on this measure. The references cited by Spicer and Gaston are also only partially relevant. Spicer and McMahon (1994) and Spicer and Taylor (1994) deal primarily with semiterrestrial species, and in these cases gas exchange at gills can be expected to be dramatically reduced. The third reference, Graf and Magniez (1969), only states that gas exchange could occur at other sites, and makes no reference to relative contributions. Allowing for oxygen transfer into amphipods at other sites than the gill does not invalidate the point that oxygen transfer is inefficient, because other sites will be less efficient suppliers of oxygen than gills. Also using data for terrestrial species or semiterrestrial species in an analysis of physiological constraints in fully aquatic species should only be done with extreme care.

Spicer and Gaston also state that there is no mechanism for oxygen supply to set limits for maximum size, and that the mechanism preferred is the limitation of cell size or number by temperature. On the contrary the limitation of body mass by the amount of available resource, in this case oxygen, is a mechanistic explanation of the observed phenomenon. There is no mechanism proposed by Spicer and Gaston to explain how temperature can limit cell number or size, and we are unaware of any such mechanism in the literature.

The issue of the importance of Hc *versus* dissolved O_2 in amphipod haemolymph needs clarification, Spicer and Gaston state that "O_2 supply to the tissues is entirely dependent on knowing the [Hc] and HcO_2 binding properties present." They later say "Hc is only essential for O_2 transport under certain conditions (e.g. activity, environmental hypoxia)". This is an area with insufficient data; however, we agree with the latter statement and from that assert that under the majority of normal conditions and for most of their lives amphipods are primarily dependent on dissolved O_2. The extra importance of dissolved O_2 in amphipods makes the relationships between maximum potential size and oxygen availability clearer. In species where pigment bound oxygen was of greater importance it is unlikely that a relationship between oxygen availability and maximum size would be as clear, although it would still be an underlying factor.

Regarding a threshold of 183 μmol kg^{-1} for amphipod survival, Spicer and Gaston cite collection of amphipods from a hot mountain spring at 33°C. Saturated freshwater at 33°C contains 225 μmol kg^{-1} of oxygen. On our calculations this would allow a TS95/5 for amphipods of 10 mm, with the largest species being well in excess of that. Using a single species observation to test the minimum oxygen concentration we calculated needs careful analyses of meaures of water oxygen content combined with assessments of amphipod behaviour to indicate the conditions where most time is spent, as opposed to anecdotal unpublished observation.

We agree there should be more interest in investigating why a few deep sea amphipod species attain very large size. We can find no data indicating these species live in low oxygen conditions. They are mobile, and we are not aware of data showing they are restricted to conditions of low oxygen availability. There is generally a dearth of information on physiology of deep sea species to contribute to debates of this type. It is not possible to say whether adaptation to high pressures facilitates evolution towards large size in a few taxa. Also our study compared like with like and the presence of large deep sea species of unknown physiological attributes is not necessarily contrary to our finding.

The reevaluation of our size data asserting that it fits a temperature relationship well needs to be addressed. Spicer and Gaston produce a relationship between TS95/95 and temperature with a correlation coefficient of 0.92. To obtain this result data for Lake Baikal has to be excluded. If it is included the correlation falls to 0.72. Including all the data the fit with $[O_2]$ is 0.98. Clearly the fit to oxygen is far superior, and Occums razor would fall heavily in our favour in proposing oxygen as the underlying factor of importance. Spicer and Gaston also fail to comment that when only fully marine sites are considered the relationship between TS95/5 and temperaure is curvilinear in a similar fashion to the relationship of oxygen solubility and temperature in seawater.

Finally, we agree that investigations of aquatic environments at altitude would be a good test of the hypothesis that oxygen availability is important in limiting amphipod MPS. However, we have been careful in our analyses to only use environments where enough species have been present over evolutionary time to allow selection to drive some species to large size. Comparisons without such rigour can be of little value. If we do not know that a selected species at a given site is likely to be near the maximum possible for that type of organism then a comparison with larger or smaller species in another set of conditions is of little relevance. Oxygen availability only sets limits to the maximum size that can be attained, and there is no reason why any given species should become large without other pressures. Spicer and Gaston appear often to have missed the point that oxygen availability only sets upper limits for maximum size, it does not mean all species will be larger or necessarily that overall size of a group will increase.

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2.2 The case of the two "supergiants": an abyssal gigantism in amphipods ?

From the very beginning of this study, we have been intrigued by the size of two well-known abyssal species, the very widespread *Eurythenes gryllus* (Lichtenstein, 1822) and the poorly known and size record holder *Alicella gigantea* (Chevreux, 1899), with a maximum length of 140 and 340 mm respectively (Ingram & Hessler, 1983; Barnard & Ingram, 1986; De Broyer & Thurston, 1987), hence it was no surprise to find them mentioned in the paper criticizing our oxygen approach (Spicer & Gaston, 1999). Although we tentatively answered this question in our reply (Peck & Chapelle, 1999), the additional information gathered since the paper was submitted deserves to be discussed. We will first present the few data about the influence of depth on size distribution, and then focus on these two unique "supergiant" species.

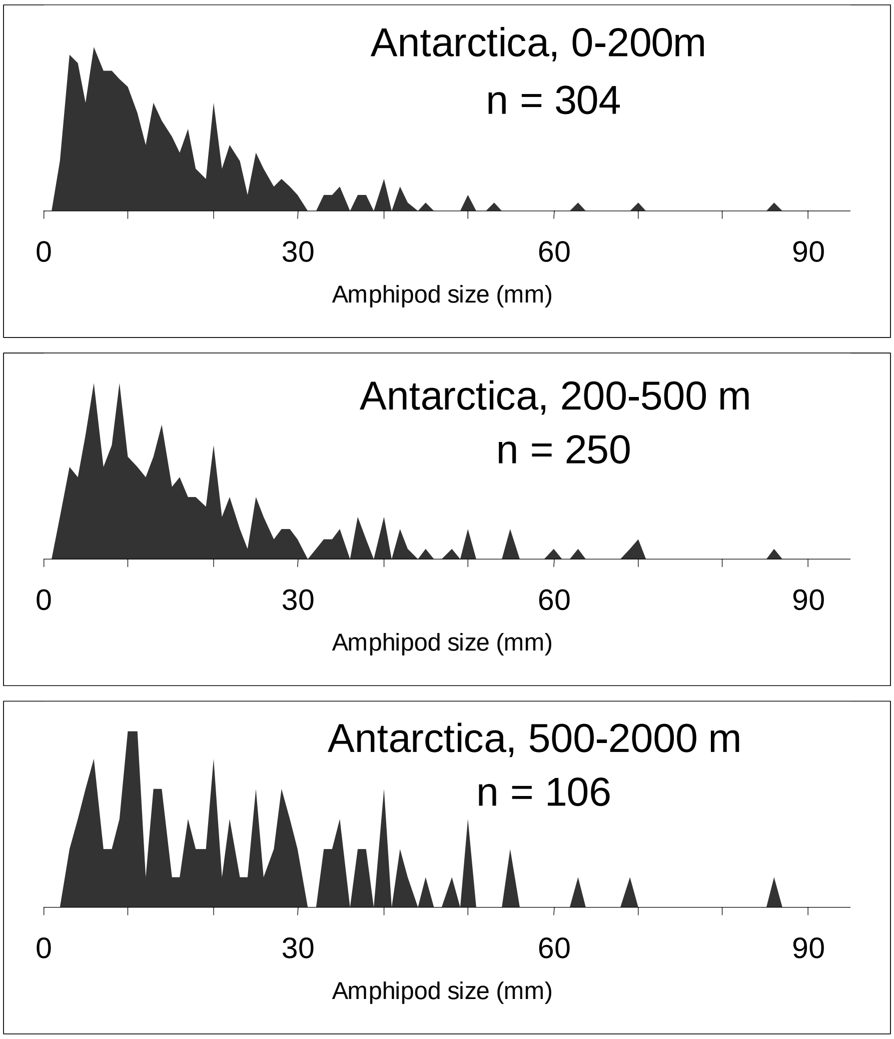

Fig. 2 - Gammaridean amphipod size spectra versus depth in the Antarctic: the X-axis is for the maximum length of each species (mm); Y-axis gives the number of species of that size. The number of species n is provided for each depth.

Depth and pressure were sometimes cited as possible factors contributing to gigantism (e.g. Wolff, 1956; Gage & Tyler, 1991), and we have therefore tested their environmental significance on size distribution in Antarctic amphipods. The size spectra suggest no depth effect on benthic amphipod size distribution (Fig. 1), although the lack of sufficient data for the abyssal fauna precludes any definite conclusions. This seems consistent with the "oxygen hypothesis", since in the almost total absence of a thermal gradient along the water column, no major differences in oxygen content should exist between depths.

On the contrary, "deep" water layers of Lake Baikal (below 250 m) are on average colder than the surface waters, and the proportion of species larger than 30 mm doubles from shallow to deep locations (24 to 47%).

Beside the Antarctic fauna, further indications for marine species are given by Barnard (1962), who showed that the mean adult size of abyssal species did not exceed 9 mm, the value calculated for the shallow water fauna of the South African coasts. This is well below the East Antarctic and Baikalian values, of 16 and 21 mm respectively. This would rather suggest a general trend to an abyssal dwarfism, supposedly related to low resource availability per individual (e.g. Madsen, 1961; Gage, 1978; for the Baikalian species, see also Starobogatov & Sitnikova, 1992; Takhteev, 1997, 2000) and was later supported by an intrageneric analysis, showing a high abyssal incidence of dwarf species when compared to the average genus size in shallow waters (De Broyer, 1977). It is also noteworthy that the maximum size of abyssal scavengers is comparable to their Antarctic counterparts (Hessler et al., 1978), with the exception of the two supergiant scavengers *Eurythenes gryllus* (Lichtenstein, 1822) and *Alicella gigantea* (Chevreux, 1899) on which we will now focus.

The first particularity of these two species is that they have a bathypelagic mode of life, making them ecologically closer to other pelagic specialists than to the hyperbenthic scavengers with which they compete for carrion. It should be noted that large size is not uncommon amongst Antarctic pelagic gammaridean amphipods and in the exclusively pelagic Hyperidea. With a length of 140 mm, *Cystisoma magna* (Woltereck, 1903) is the largest species of this latter group (Vinogradov et al., 1996), suggesting that the possible threshold set by oxygen on body size is somewhat higher in organisms permanently swimming above the usually oxygen impoverished bottom waters (Martin et al., 1998; Nybakken, 1988).

Both species also possess gills with anatomical peculiarities. On one hand, *Alicella gigantea* (Chevreux, 1899) has the accessory lobes of gills 5 and 6 with their proximal part dilated (Barnard & Ingram, 1986; De Broyer & Thurston, 1987). *Eurythenes gryllus* (Lichtenstein, 1822) on the other hand bears folds on the lateral and medial surfaces of the gills, supposedly to increase the gill surface “because body volume increases as the cube and body surface only as the square of the linear dimension” (Bowmann & Manning, 1972).

Finally, thanks to a very high lipid content, at least *Eurythenes gryllus* (Lichtenstein, 1822) is neutrally buoyant (Thurston, pers.comm.), allowing him to probably reduce significantly his basal metabolism, hence its oxygen requirements.

When, as in the deep sea, only a small amount of food reaches the bottom, it seems that mainly two evolutionary responses can be brought to this constraint. The first, as witnessed by most benthic poorly mobile species (Barnard, 1962; De Broyer, 1977), is to become smaller, in order to decrease the amount of energy needed per individual. The other possibility is to move actively in search of food, which was adopted by many scavenging amphipods. This strategy has been led close to the upper limit for *Eurythenes gryllus* (Lichtenstein, 1822), as its powerful swimming abilities (Chapelle & De Broyer, pers.obs.) enable him to intercept food falls up to 1800 m above the bottom, and this, to outdistance the other smaller scavengers (Thurston & Bett, 1995). This proximity with the hypothetic Maximum Potential Size might explain why *Eurythenes gryllus* (Lichtenstein, 1822) is also a highly stenothermal species, never found at temperatures above 5°C throughout his world wide distribution (Thurston, pers.comm.).

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Publication III

Lake Titicaca amphipods confirm oxygen limits maximum size.

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Oikos : submitted

3. Lake Titicaca Amphipods Confirm Oxygen Limits Maximum Size

We recently proposed a novel mechanism to explain polar gigantism in marine invertebrates based on oxygen availability rather than the widely cited temperature and metabolism (Chapelle and Peck, 1999). Data supporting the hypothesis came from amphipod crustacean size spectra from 12 sites worldwide: East and West Antarctica, South Georgia, the subantarctic islands, the Magellanic region, Madagascar, the Mediterranean, Black and Caspian Seas, the British islands, the Barents Sea and Lake Baikal. Maximum size at cold sites was x5 larger than warm locations and freshwater sites x2 larger than marine habitats. However, temperature and oxygen solubility covary in water, and strong debate and criticism of the hypothesis have arisen based on physiological supply mechanisms (Spicer and Gaston 1999). Oxygen uptake depends on gas partial pressure differences and these remain constant in all shallow waters at sea level. However, the mass of oxygen transferred for a given partial pressure difference varies with gas solubility (Dejours, 1973), and hence temperature and salinity (Peck and Chapelle, 1999).

The best test for the oxygen limitation hypothesis is to evaluate species from a site where water oxygen content is markedly affected by another physical factor, such as pressure. Here we present data for Lake Titicaca, which has greatly reduced water oxygen content because it is at high altitude (3809m) and has a salt content slightly higher than most lake environments (sodium chloride, sulfate and calcium ions) (Iltis et al., 1992). The data obtained confirm the limiting effect of oxygen availability on maximum potential size. The data have also been updated for the five sites of the Southern Ocean, and a new site, South Africa (based mainly on Barnard, 1916; 1925; 1932; 1955; Griffiths, 1976) has been added to the data set.

Until recently, the described amphipod fauna of Lake Titicaca consisted of 11 species (Dejoux, 1992), which we considered too few to include previously. However, exceptionally rich material was obtained but never described by the British 1937 expedition. A minimum of 93 additional morphotypes awaits description (Crawford et al., 1993), and over 100 species clearly exist in the lake. As previously the TS95/5 value (threshold size separating the smallest 95% of species from the largest 5%) was used to avoid sampling errors (Chapelle and Peck, 1999), which was obtained from measures of the maximum size of the biggest morphotypes. When plotted with the other sites versus mean temperature (fig 1a, left axis), the Titicaca TS95/5 falls in the lower range for the marine environments data and corresponds to a hypersaline site. Other low salinity sites like Caspian Sea or Lake Baikal, in contrast, are in the higher range or well above the marine relationship (Fig 1a). Indeed when calculated oxygen contents for fresh, brackish, marine and hypersaline waters (Fig 1a right axis) are coplotted with TS95/5 against temperature most other sites (which are at sea level) match expectations from oxygen contents of the relevant salinity level. When plotted versus the oxygen content (fig 1b), the Titicaca TS95/5 fits closely the linear relationship previously produced for low altitude sites ($TS_{95/5} = - 36{,}5 + 0{,}216\ O_2$; $n = 13$; $r^2 = 0.89$). These data from a high altitude lake thus confirm the close link between oxygen availability and maximum potential size in amphipod crustaceans.

Acknowledgments

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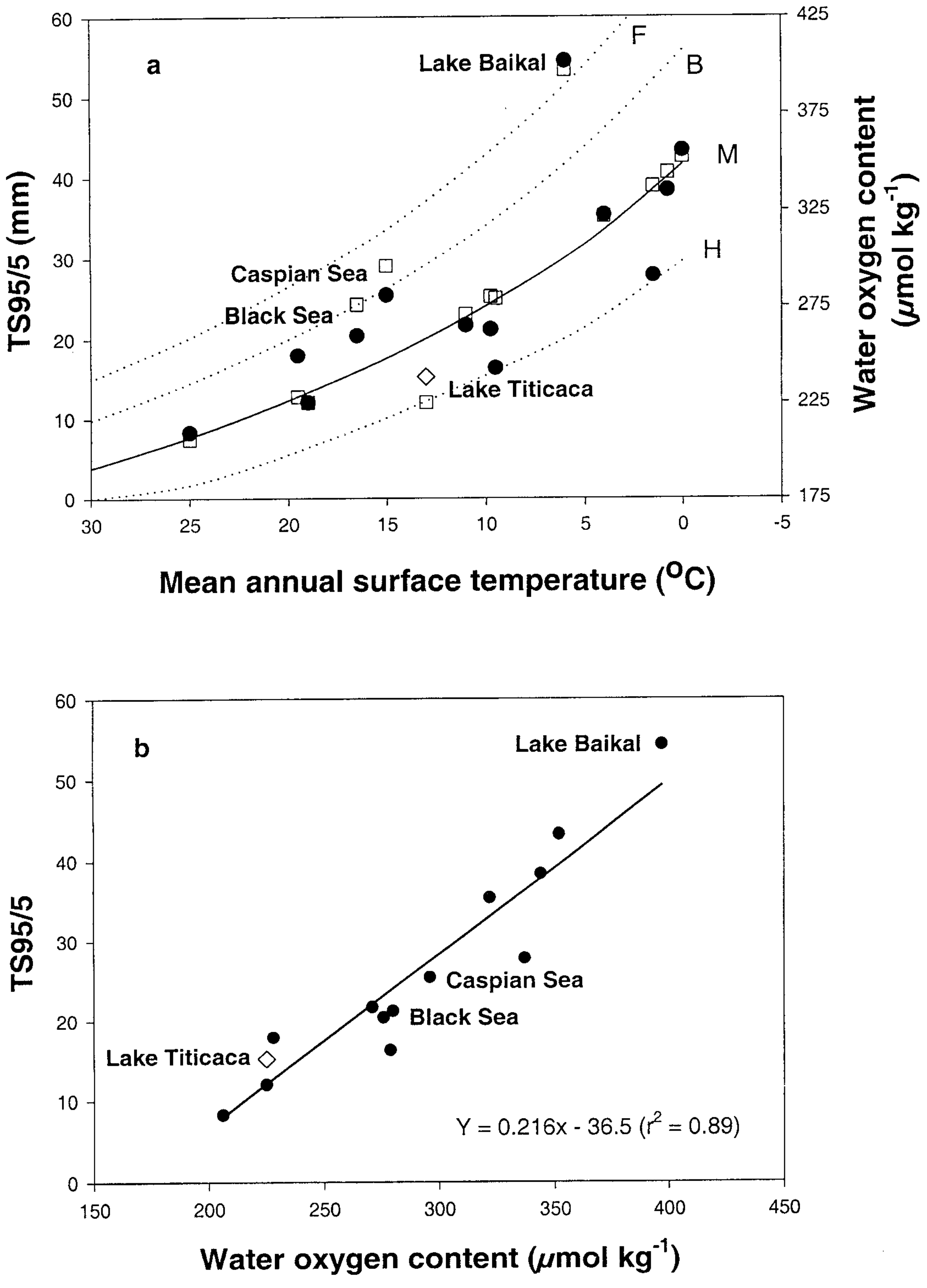
a
Lake Baikal
F
B
M
H
Caspian Sea
Black Sea
Lake Titicaca
TS95/5 (mm)
60
50
40
30
20
10
0
30
25
20
15
10
5
0
-5
Mean annual surface temperature (°C)
425
375
325
275
225
175
Water oxygen content (µmol kg⁻¹)
b
Lake Baikal
Caspian Sea
Black Sea
Lake Titicaca
Y = 0.216x - 36.5 (r² = 0.89)
TS95/5
60
50
40
30
20
10
0
150
200
250
300
350
400
450
Water oxygen content (µmol kg⁻¹)

Fig 1

Fig. 1 - a. Dual plot of the amphipod TS95/5,or threshold size separating the smallest 95% of species from the largest 5% (•) and water oxygen content (·) vs temperature in 13 different sites and Lake Titicaca. Oxygen solubility in water varies with temperature and salinity, described by the relationship: $\ln k_{o,s} = 3.718 + 5596.17/T - 1049668/T^2 + S(0.0225 - 13.608/T + 2565.68/T^2)$. Plotting dissolved oxygen content at saturation from that relationship brings our 13 sites (fig 1a, right axis) close to the three curves linking respectively the freshwater (F, 0 p.s.u., Lake Baikal), brackish (B, 15 p.s.u., Caspian and Black Seas) and marine ecosystems (M, 35 p.s.u., all the others). Lake Titicaca is close to the oxygen curve for hypersaline environments (H, 55 p.s.u.) because the oxygen content of its water is reduced by its altitude.
b. Plot of TS95/5 against water oxygen content. All data, including Lake Titicaca, closely fit the relationship. Oxygen data for Lake Titicaca from direct measurements (Iltis et al. 1992). The fit of the regression between TS95/5 and oxygen is $r^2=0.90$ ($r^2=0.85$ for the marine sites only), the equivalent relationship between TS95/5 and temperature (fig 1a) is $r^2=0.59$ ($r^2=0.80$ for the marine sites only).

Chapter 4: Effect of oxygen at superfamily, family and genus level

Contents

Publication IV

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Relationship between size and oxygen availability in amphipod crustaceans at the superfamily, family and genus level

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in prep.

Abstract

Maximum potential size in benthic gammaridean amphipods has been shown to be limited by oxygen availability. The present paper investigates the validity of this relationship for lower taxonomic ranks. 2600 length data of 14 amphipod faunas worldwide were compiled from the literature. Size distribution within each studied superfamily, family and genus are right-skewed. For a majority of taxa, the mean size for each area is linearly correlated to oxygen concentration. Slopes of these regressions vary from one taxon to another, and the highest values belong to superfamilies and families dominating the higher latitudes in terms of diversity, and rich in large species. Our results show that the existence of polar gigantism at the suborder level is partly due to a similar effect of oxygen at lower taxonomic levels, and partly to an increase in diversity of the superfamilies and families with many large species at high latitudes.

Introduction

Polar gigantism is often cited (see for example Arnaud, 1974), but still remains poorly studied and controversial (Brey & Clarke, 1993 ; Clarke, 1996). However, after the first demonstrations of its existence, at least for gammaridean amphipods (Barnard, 1962; De Broyer, 1977; Poulin & Hamilton, 1995), we have recently shown that the size of the biggest amphipods at any site is closely related to ambient oxygen availability (Chapelle & Peck, 1999 ; Peck & Chapelle, 1999). Indeed, oxygen absolute concentration increases with decreasing temperature and salinity, and so does the amphipod maximum size from tropical to polar latitudes, and from marine to freshwater areas.

For each study area, we compiled the maximum size of every species and then produced the local size spectrum (Chapelle & Peck, submitted). All spectra are right skewed, and skewedness increases when temperature and/or salinity decreases. Thus maximum potential size increases dramatically, mean and modal size increase less, and minimum size remains nearly constant when oxygen content rises, and the total effect is a gradual widening of the size spectra. This analysis also indicates that only a minority of species were able to develop the necessary adaptations allowing very large sizes.

Once demonstrated for gammaridean amphipods, polar gigantism needed further investigation to make its origins understood. A first hypothesis suggested that its very existence at the suborder level may reflect what happens at lower taxonomic level (Barnard, 1962). This was partly confirmed by De Broyer (1977), who investigated Antarctic gigantism through relative size at the intrageneric level. However, this paper contained no attempt to quantify the role of oxygen or any other physico-chemical factor on size.

Furthermore, the selected methodology did not allow the analysis of an alternative - and non exclusive - hypothesis, that polar gigantism could also find its basis in a predominance of superfamilies and families rich in large species at high latitudes and the reverse at low latitudes.

The main objective of this paper is to assess the effect of oxygen on the size distribution of several taxonomic ranks of the suborder Gammarida, viz. superfamilies, families and genera. Comparisons between the various taxa also offer the opportunity to test the alternative hypothesis that the oxygen rich waters of high latitudes select for superfamilies, families and genera with many giant species.

Material and Methods

Length data for the benthic gammaridean amphipods (from the tip of the rostrum to the tip of the telson) obtained from 14 geographical areas worldwide were compiled from the literature (Table 1). For each site, we restricted the analysis to the species inhabiting the continental shelf down to 250 m depth, except for the East and West Antarctica data which included species to 500 m, because of continental shelf depression by the Antarctic icecap.

Regarding taxonomy, attribution to superfamilies and families follows the index compiled by De Broyer et al. (2000), itself based on the last synthesis on the subject (Barnard & Barnard, 1983 ; Bousfield, 1983 ; Barnard & Karaman, 1991 ; Bousfield & Shih, 1994 ; Lowry, unpublished).

Analyses were carried out for superfamilies, families and genera. Contrarily to species, these hierarchical levels are not biologically defined and the two first are still subjects of regular changes within the Amphipoda. So far no major molecular phylogenetic studies exist and all proposed phylogenies rely solely on morphological characters. From the very few studies based on cladistic analysis (e.g. Lowry & Myers, 2000), the two most extensive (Berge et al., 2001; Lowry, unpublished) exclude the freshwater species, and hence most of the still putative « Gammaroidea » group.

Following the Talitroidea erection by Bulysheva (1957), another 10 superfamilies have been proposed within the suborder Gammaridea (Bousfield & Shih, 1994). Nine of these 11 units (Table 2) have been kept in this study. Pontoporeioidea has not been used due to an insufficient number of species in our sites sampled.

On the other hand, because of the freshwater origins of Gammaroidea, many of its species are restricted to the lowest salinity locations within areas such as the British Isles, the Mediterranean and Black Seas, while not in others like Madagascar, due to a predominance of different groups within the superfamily. As the mean oxygen content value used to establish the correlations with size could not reflect in every area the particular conditions experienced by Gammaroidea, this superfamily was also excluded from the analysis.

In the first analysis, size spectra have been constructed by pooling for each taxon (superfamily, family and genus) the species from all 14 areas. For this first analysis, only taxa with 40 species or more were used, thus 9 superfamilies, 13 families and 2 genera. Furthermore, we used only the biggest size of each species reported in more than one area.

The second analysis investigates the effect of oxygen on size distribution within each superfamily, family and genus. In this case, several size data were used for any species found in more than one site, corresponding to the maximum size recorded in each local population. In our previous work for the entire Suborder Gammarida (Chapelle & Peck, 1999), we have used the TS95/5, defined as the Threshold Size separating the 95% smallest species from the 5% biggest. Furthermore, it appeared subsequently that the mean size was also strongly linked to the oxygen level, although with a lower amplitude.

Because the number of species at a given site is often low, mean size has been chosen for this analysis. This parameter is less sensitive to sampling bias than the TS95/5, while also integrating the whole size spectrum.

For statistical robustness, we have used only superfamilies and families present at a minimum of 5 different sites with at least 6 species per site. For genera, this minimum was 3 species per site.

Results

As already stated, the benthic gammaridean species show right skewed size spectra, both when separated between different sites or when pooled all together (Chapelle & Peck, 1999; in prep). Thus as size increases, very few minute species quickly give way to the mass of species approaching the modal size. The decrease to the right of that peak is initially abrupt, but then gradually slows down towards the scarce big species, producing right skewedness.

All 24 spectra (established for 9 superfamilies, 13 families and 2 genera) show the same strongly right-skewed curve (fig 1), but had different minimum (1 to 3 mm), modal (3 to 7 mm), mean (4 to 17 mm) and maximum sizes (7 to 87 mm). This suggests a similar evolutionary pattern from the suborder level (gammaridean amphipods) down to the generic level.

For the analysis testing the effect of oxygen on size distribution, 8 of 9 superfamilies display a (highly) significant increase in mean size with oxygen (Table 2, fig. 2). At the family level, the analysis provides the same conclusion, with 3 non significant slopes from a total of 13 tested families (6 highly significant) (Table 3, fig 3). Finally, although calculated on a somewhat lower number of species per site, the trend is still clear within genera; only 4 slopes are not significant (with 3 of them very close) from the 13 examined genera (4 highly significant) (Table 4, fig 4).

Discussion

The trend towards large size in amphipods at low temperatures has been mentioned by several authors (for example Barnard, 1962 ; Arnaud, 1974 ; Nelson, 1980a; Poulin & Hamilton, 1995). At the superfamily level, it has been noted for Lysianassoids (Steele, 1983), although surprisingly only between tropical and temperate faunas, whereas there was reportedly no difference between temperate and Antarctic species.

Finally, the occurrence of polar gigantism down to the generic level has been established in the only paper specifically devoted to it in amphipods (De Broyer, 1977). This was made by comparing the maximum size of each Antarctic or

Subantarctic species to the genus mean size (g.m.s.), calculated by pooling the size of all world representatives. A species was called giant when its size measured at least twice the genus mean size.

However, by comparing only species belonging to genera with representatives both outside and inside the Southern Ocean, this major study did not encompass genera endemic to the Antarctic, thus excluding polar giants like *Paraceradocus, Gnathiphimedia, Maxilliphimedia* and *Echiniphimedia*.

A second problem arose because of the definition chosen for giant species. Indeed, genera having speciated mainly in Antarctica and produced a majority of large species, like *Epimeria*, had already a very high g.m.s.. Hence even the largest of them did not reach the threshold of twice the g.m.s. and could not be categorized as giants, even if they were clearly much larger than amphipods from areas outside the Southern Ocean. This type of problem did not occur in the present study, as it encompasses most of the species for which length has been recorded in the 14 selected areas.

The significant increase in mean size with oxygen obtained in our analysis (Tables 2 to 4) agree with the results of De Broyer (1977). It also supports the first proposed hypothesis, which suggests that the existence of polar gigantism at the suborder level (Chapelle & Peck, 1999) may reflect what happens at a lower taxonomic level.

No previous work has specifically addressed the second hypothesis, namely taxa with larger species have greater representation at high latitudes (and its possible counterpart : a reduced presence of taxa with small species). However, some necessary data were already available from studies devoted to reproductive patterns of gammaridean amphipods : both Nelson (1980b) and Sainte-Marie (1991) gave mean size values of a range of families and superfamilies, although they did not analyze them in relation to latitudinal gradients.

To establish this second hypothesis at the higher level, data for many taxa were needed both for size distribution and latitudinal distribution, before trying to correlate the two factors.

In the analysis of the relative importance of each taxon in our data set, we only used superfamilies and families which accounted for more than 5% of the fauna in at least one site. The 13 selected families and superfamilies have been assigned to three groups according to their covariation with latitude (Fig 5A, B, C) :

1. Six taxa dominating the low latitudes : the Amphilochoidea, Corophioidea, Dexaminidae, Hadzioidea, Leucothoidae and Talitroidea.
2. Five taxa dominating the high latitudes : the Eusiroidea, Iphimedioidea, Lysianassoidea, Oedicerotoidea and Stenothoidae.
3. Two taxa displaying no trend in this matter : the Ampeliscidae and Haustorioidea.

In a second step, we pooled all species from the 14 areas together in one general size spectrum (Fig 1) in order to distinguish the taxa particularly well represented in the upper 10 % size classes, i.e. the largest size classes. This choice is completely arbitrary. However, by this way we selected all species larger than the TS90/10 of 23 mm, itself 5 times larger than the modal size of 4.5 mm of the general size spectrum. The number of species greater than this overall TS90/10 value of 23 mm of each superfamily or family was divided by the total number of species belonging to each of these taxa, and this allowed to distinguish between superfamilies and families over- or underrepresented in the largest size classes. The results in Table 5 (column 1) designate the Iphimedioidea, the Ampeliscidae and the Eusiroidea as the three groups with a percentage higher than 10, and thus as the most important taxa concerning gigantism.

To enhance the understanding of each taxa's position, two other parameters of the size distribution were selected, and the 13 taxa ranked accordingly (column 2 & 3, Table 5) ; the mean size of each taxon, which should select for taxa rich in large species, and the slope of the regression lines on the relationship between mean size in each area vs oxygen water content (first calculated in Table 2 and 3), which yields how much length increases with each extra unit of oxygen, and gives an indication of the « growth potential » of each taxon.

With these data in hand, we can now analyze all 13 taxa, from the smallest to the largest (using mean size as the criterion). Validity of the second hypothesis would be established by the presence of taxa with many large species and a greater representation at high latitudes, and/or of taxa with many small species and a greater representation at low latitudes.

1. The Amphilochoidea has no species with a size over the TS90/10 (which is also true for taxon 2, 3 and 4). They can really be considered as the dwarf taxon, combining the smallest mean size and a very smooth (non significant) slope. As a typical tropical group, they support the second hypothesis.

2. Stenothoids are also always small and differ from Amphilochoidea by having no discernible trend to greater size in oxygen rich sites. In addition, they differ from the previous group by an enhanced presence at high latitudes, mainly in the Southern Hemisphere. Their effect on the overall size distribution can be considered as neutral.

3. Leucothoids are usually larger than the Amphilochoidea. However, they are even more restricted to the tropical localities. They support the second hypothesis.

4. The Haustorioidea contains mainly small and burrowing species. The slope of their size relationship to oxygen is low, but highly significant. Furthermore, they show no clear latitudinal diversity gradient. Their effect on the overall size distribution can be considered as neutral.

5. The Corophioidea is the most speciose taxa in our study, however very few species reach the TS90/10 of the overall relationship. Their low but significant slope, their low mean size and their mainly tropical distribution put them together with the Amphilochoidea and Leucothoidea ; they also support the second hypothesis.

6. The Dexaminidae constitutes a rather widespread family, with a slightly higher occurrence in warm waters. Their effect on the overall size distribution can be considered as neutral.

7. The Talitroidea is very similar to the Corophioidea in our criteria, except for having a steeper slope. However, this potential for giant size is limited by their scarcity at

high latitudes. Their effect on the overall size distribution can be considered as neutral.

8. The Oedicerotoidea represents the first of the cold waters taxa and they are also rather speciose in the bathyal regions beyond shelf depths (Thurston, 2001). However, they are less diverse in warm continental waters. They have only small representation above the TS95/5. Their effect on the overall size distribution can therefore be considered as neutral.

9. The Lysianassoidea is very similar to the Oedicerotoidea according to our criteria. They have a very high polar diversity which compensates for their lower slope and explains their rather large mean size. However, their ranking regarding to TS90/10 is inferior to Oedicerotoidea and their effect on the overall size distribution is also neutral.

10. The Hadzioidea presents a rather unusual situation. They are much more common in tropical waters. However, the few species present in cold waters are predominantly very large, and this explains the steep slope of the relationship with oxygen. This is particularly the case in the Southern hemisphere with the genus *Paraceradocus*, which is distributed exclusively from South Georgia to the High Antarctic. The 6 described species of *Paraceradocus* range in size from 42 to 70 mm, with a mean of 61 mm, making it the most « giant specialized » genus of our data set. This is also far ahead of the Baikalian *Parapallasea* (50 mm) and *Acanthogammarus* (44 mm). Although it is not representative of its superfamily, which is characterized by having many small tropical species, the genus *Paraceradocus* is one of the best examples of giant taxa restricted to highly oxygenated waters.

11. Ampeliscidae is the first of 3 taxa which have more giant species then would be expected from the all species curve for the TS90/10. Their steep slope for the size vs oxygen relationship is caused as much by the presence of large species at high latitudes as by the lack of small ones in the same place. However, the constancy of their occurrence through latitudes makes their effect on the overall size distribution neutral.

12. Regarding size, the Eusiroidea is much like the Ampeliscidae, with comparable values for columns 1 and 2 (Table 5). One difference lies in their lower slope, which is due to the presence of both large and small species in cold waters. Also, the Eusiroidea is especially speciose in the Southern Hemisphere. They represent a typical cold water group, being found in all oceans below the continental shelf. This is particularly the case for the Eusiridae s.s., which are present down to hadal depths (Thurston, 2001). The 25 species in this group have a mean length of 17.4 mm and constitute one of the largest sized families. The majority of Eusirid species occur at high latitudes. It is also worth noting that a number of large Southern Ocean *Eusirus* (which includes *Eusirus perdentatus* (Chevreux, 1912), 87 mm, the largest species in this data set) were omitted from the analysis due to some taxonomic uncertainties. All these elements establish the Eusiroidea as a large sized and predominantly polar taxon. They strongly support our second hypothesis.

13. In this analysis, the Iphimedioidea constitutes the group most oriented towards large size. They are not only the taxon with the greatest mean size and slope, but also rank first by a large margin in the proportion of species present in the 10% largest species. This superfamily is dominated by two families, the Iphimediidae and Epimeriidae. Both clades experienced their maximal radiation around the Antarctic continent (Watling & Thurston, 1989 ; De Broyer & Klages, 1991), and contain considerable numbers of « giants ». In the Iphimediidae (64 species in our data set), nearly all the low latitude species are bathyal (Thurston, 2001) and the continental shelves are poorly colonized, with the exception of the speciose genus *Iphimedia*, which represents half of the non giant species. With the exception of this genus, most of the others have a primarily or exclusive Southern Ocean distribution, with a mean size of 21 mm. The Epimeriidae shows a similar predominance in the shallow waters around the Antarctic with a secondary worldwide bathyal distribution. Their size is even greater than the Iphimediidae, with a mean length of 28 mm for the family, and 30 mm for the genus *Epimeria*. Considered as a whole, the superfamily outclasses the Eusiroidea in supporting our hypothesis.

To sum up, both the latitudinal gradient in size for superfamilies, families and genera and their respective size spectra revealed similar trends in size distribution from the superfamily level down to genera. This extension of the phenomenon already described at the suborder level does not contradict the hypothesis of oxygen availability as the main causal factor. In this context, it should be noted that oxygen is not a driving force towards big size, but is better considered as a ceiling, which fixes the amplitude of the evolutionary space available for the suborder and its superfamilies, families and genera. The fact that these lower taxonomic ranks make use of this space constitutes the main cause of polar gigantism.

However, our data have shown that the widening of the spectrum and the higher mean size in cold waters is also due to a disappearance or reduction of tropical small sized taxa coupled to an appearance or increase of polar large sized taxa. Causal factors for this progressive shift remain to be explained.

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Table 1 : The 14 areas used in the analysis. N gives the number of species for which the maximum size relates to the longest mature animal recorded. O_2 gives the mean surface oxygen content (absolute concentration) in µmolO_2.kg^{-1} of water. Oxygen solubility in water varies with temperature and salinity, described by the relationship: $\ln k_{o,s} = 3.718 + 5596.17/T - 1049668/T^2 + S(0.0225 - 13.608/T + 2565.68/T^2)$, with T = temperature in °C, and S = salinity (Benson & Krause, 1984). Areas are ranked along an increasing oxygen content gradient.

Area	*O_2*	*N*
Red Sea	198	136
Oceania	199	142
Madagascar	206	314
Mediterranean Sea	225	347
South Africa	228	185
British Isles	271	249
Black Sea	276	92
Subantarctic islands	279	145
Magellanic region	280	160
Caspian Sea	296	69
Barents Sea	322	134
South Georgia	337	147
West Antarctica	344	275
East Antarctica	352	186

Table 2 : Mean size versus oxygen availability within superfamilies : R^2 refers to the linear regression between mean amphipod size and oxygen concentration at any area ; P refers to the slope estimation, as does the standard error ; « areas » gives the number of areas with at least 6 species belonging to this superfamily ; « n spp » is the total number of observations (and not of species since some species are found in several areas); « spp/areas » is the mean number of species per area.

Superfamily	R2	P (Fischer)		slope	st error	areas	n spp	spp/area
Amphilochoidea	0,57	0,138	NS	0,020	0,010	5	46	9,2
Corophioidea	0,70	0,0002	HS	0,039	0,007	14	539	38,5
Eusiroidea	0,77	0,0018	HS	0,072	0,015	9	192	21,3
Hadzioidea	0,73	0,0073	HS	0,136	0,034	8	195	24,4
Haustorioidea	0,87	0,0008	HS	0,037	0,006	8	115	14,4
Iphimedioidea	0,97	< 0,0001	HS	0,146	0,011	8	136	17,0
Lysianassoidea	0,88	< 0,0001	HS	0,067	0,008	11	344	31,3
Oedicerotoidea	0,82	0,0018	HS	0,069	0,013	8	89	11,1
Talitroidea	0,93	0,0017	HS	0,094	0,012	6	55	9,2
All species	0,93	0,0001	HS	0,078	0,006	15	2805	187

Table 3 : Mean size versus oxygen availability within families : headings as in Table 1, except for the additionnal first column, giving the superfamily to which each family belongs. By alphabetical order, CORO = Corophioidea, EUSO = Eusiroidea, HADZ = Hadzioidea, HAUS = Haustorioidea; IPHO = Iphimedioidea; LYSO = Lysianassoidea, OEDO = Oedicerotoidea.

SF	Family	R2	P (Fischer)		slope	st error	areas	n spp	spp/area
	Ampeliscidae	0,92	0,0002	HS	0,100	0,012	8	102	12,8
CORO	Aoridae	0,76	0,0023	HS	0,064	0,014	9	121	13,4
EUSO	Calliopidae	0,39	0,136	NS	0,050	0,028	7	71	10,1
HADZ	"Ceradocus group"	0,89	0,0154	S	0,167	0,033	5	128	25,6
	Dexaminidae	0,84	0,0291	S	0,059	0,015	5	45	9,0
IPHO	Iphimedidae	0,92	0,0105	S	0,140	0,244	5	72	14,4
CORO	Isaeidae	0,78	0,0007	HS	0,046	0,009	10	123	12,3
CORO	Ischyroceridae	0,82	0,0008	HS	0,048	0,009	9	89	9,9
LYSO	Lysianassidae s.s.	0,93	< 0,0001	HS	0,072	0,007	11	267	24,3
OEDO	Oedicerotidae	0,99	< 0,0001	HS	0,071	0,004	6	69	11,5
HAUS	Phoxocephalidae	0,74	0,0286	S	0,044	0,013	6	62	10,3
EUSO	Pontopogeneidae	0,43	0,227	NS	0,053	0,035	5	62	12,4
	Stenothoidae	0,38	0,102	NS	0,012	0,006	8	119	14,9

Table 4 : Mean size versus oxygen availability within genera : headings as in Table 1, except for « areas », which gives the number of areas with at least 3 species belonging to this genus. By alphabetical order, CORO = Corophioidea, HADZ = Hadzioidea, LYSO = Lysianassoidea, TALO = Talitroidea.

Family (SF)	Genus	R2	P (Fischer)		slope	st error	sites	spp	spp/site
Ampeliscidae	*Ampelisca*	0,85	< 0,0001	HS	0,101	0,014	11	86	7,8
Ampithoidae (CORO)	*Ampithoe*	0,81	0,0152	S	0,094	0,023	6	29	4,8
Corophidae (CORO)	*Corophium s.l.*	0,72	0,0674	NS	0,036	0,013	5	43	8,6
Isaeidae (CORO)	*Gammaropsis*	0,82	0,0003	HS	0,038	0,006	10	77	7,7
Hyalidae (TALO)	*Hyale*	0,56	0,0327	S	0,072	0,026	8	40	5,0
Aoridae (CORO)	*Lembos s.l.*	0,88	0,0173	S	0,095	0,020	5	21	4,2
Leucothoidae	*Leucothoe*	0,45	0,148	NS	0,085	0,047	6	47	7,8
Liljeborgidae	*Liljeborgia*	0,75	0,012	S	0,069	0,018	7	33	4,7
Lysianassidae s.s. (LYSO)	*Lysianassa*	0,75	0,0561	NS	0,064	0,021	5	21	4,2
"Ceradocus group" (HADZ)	*Maera*	0,96	0,0005	HS	0,246	0,024	6	55	9,2
Melitidae (HADZ)	*Melita*	0,95	0,0053	HS	0,119	0,016	5	24	4,8
Podoceridae (CORO)	*Podocerus*	0,75	0,0565	NS	0,036	0,012	5	20	4,0
Lysianassidae s.s. (LYSO)	*Tryphosella*	0,75	0,0251	S	0,091	0,026	6	28	4,7

Table 5 : Giant species in families and superfamilies : taxa are ranked according to 3 parameters. Taxa abbreviations refer to the same groups as fig. 5 ; families and superfamilies in bold and normal characters are predominant at high and low latitudes respectively. By alphabetical order, AMPE = Ampeliscidae, AMPO = Amphilochoidea, CORO = Corophioidea, DEXA = Dexaminidae, EUSO = Eusiroidea, HADZ = Hadzioidea, HAUS = Haustorioidea; IPHO = Iphimedioidea; LEUC = Leucothoidae; LYSO = Lysianassoidea, OEDO = Oedicerotoidea, STEN = Stenothoidae, TALO = Talitroidea.

The three parameters : TS90/10 gives for each taxon its percentage of species with a length higher than the overall TS90/10 value for all gammaridean amphipods. Mean size is given in mm. The slope comes from the regression lines as given in Table 2 and 3. Bold figures are for the slopes of non significant regression lines.

TS90/10		mean size		slope	
29.7	**IPHO**	17.3	**IPHO**	146	**IPHO**
13.8	*AMPE*	13.6	**EUSO**	136	HADZ
12.5	**EUSO**	13.0	*AMPE*	100	*AMPE*
9.6	HADZ	11.4	HADZ	94	TALO
8.6	**OEDO**	10.2	**LYSO**	**83**	LEUC
5.8	**LYSO**	9.9	**OEDO**	72	**EUSO**
5.4	DEXA	7.4	TALO	69	**OEDO**
2.2	TALO	7.2	DEXA	67	**LYSO**
1.9	CORO	6.7	CORO	59	DEXA
0	AMPO	6.0	*HAUS*	39	CORO
0	LEUC	5.9	LEUC	37	*HAUS*
0	**STEN**	4.7	**STEN**	**20**	AMPO
0	*HAUS*	3.4	AMPO	**12**	**STEN**

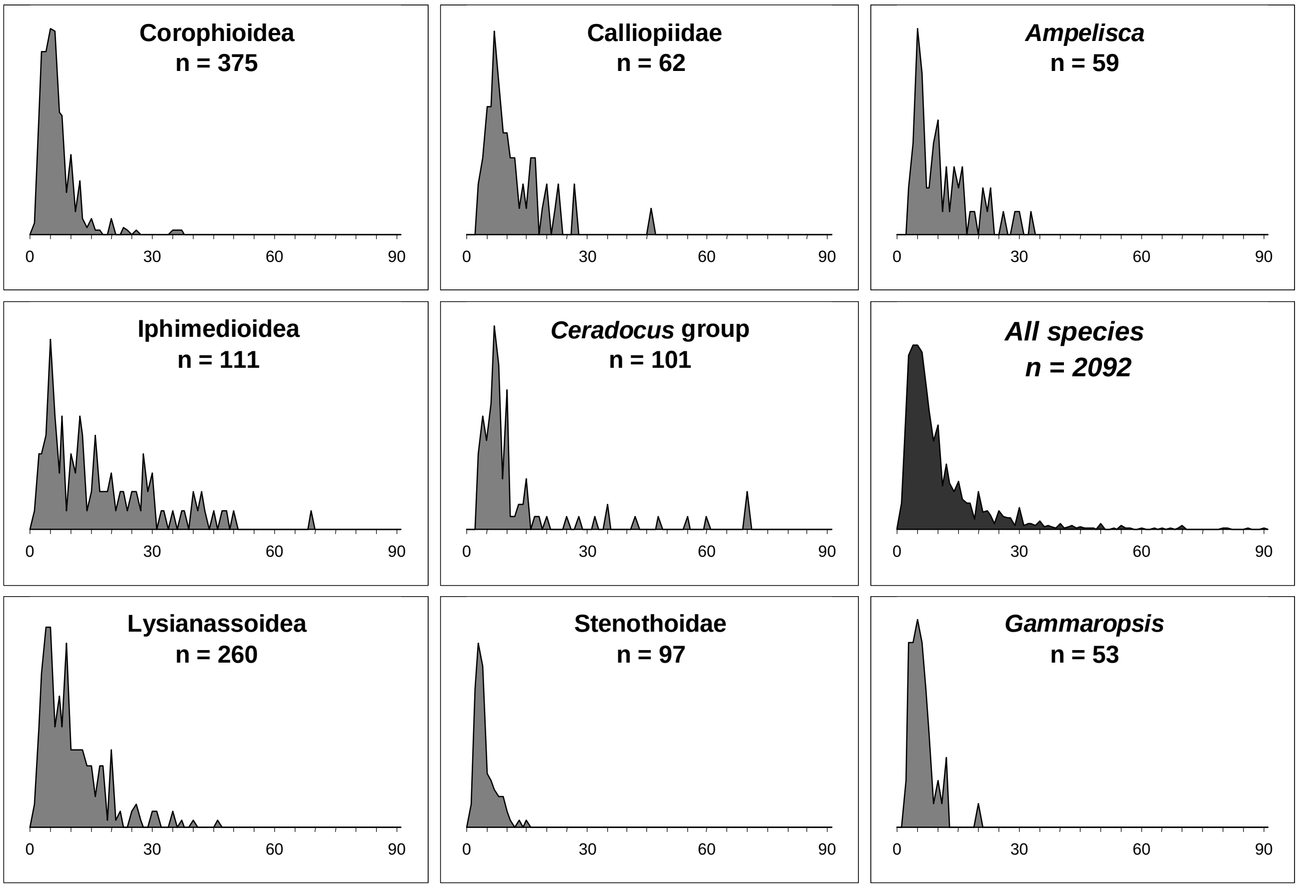

Fig. 1 - Size spectra of various superfamilies, families and genera : for each taxon, all species from the 14 sites are included. X- axis gives size in mm. Y-axis gives the number of species. The 8 histograms were selected to illustrate the differences in size range between taxa. From the 24 established spectra, examples are given for 3 superfamilies (first column), 3 families (second column; the *Ceradocus* group includes several genera) and 2 genera (third column). The all species size spectrum is provided for comparison.

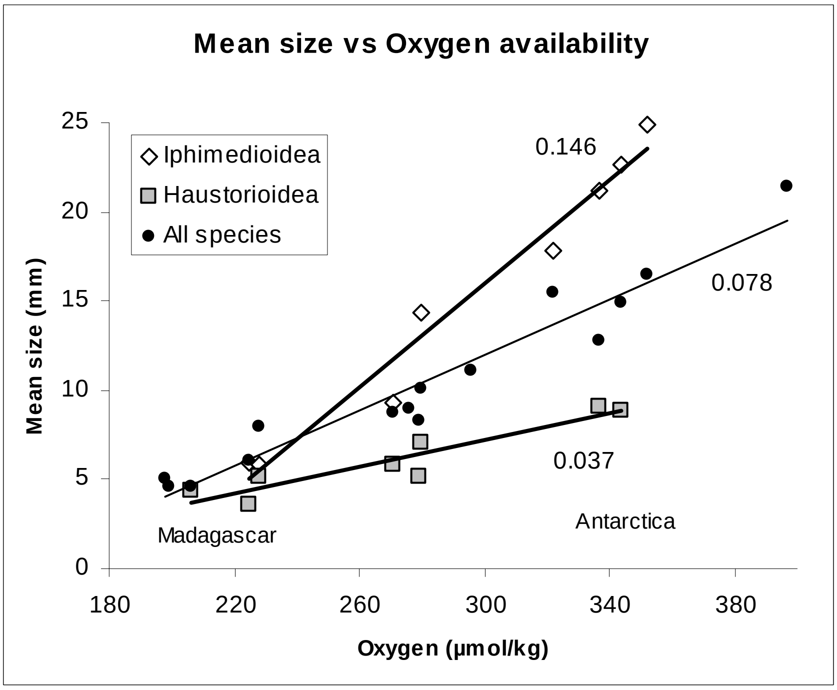

Fig. 2 - Mean size versus oxygen availability within superfamilies : Significant regression lines for the groups with the highest and lowest slopes are shown. Slope values are on the graph. The thin regression line in the middle is for all gammaridean amphipod species pooled together. The X-axis gives water oxygen content, from tropical to polar areas. The Y-axis gives the mean size of each taxon.

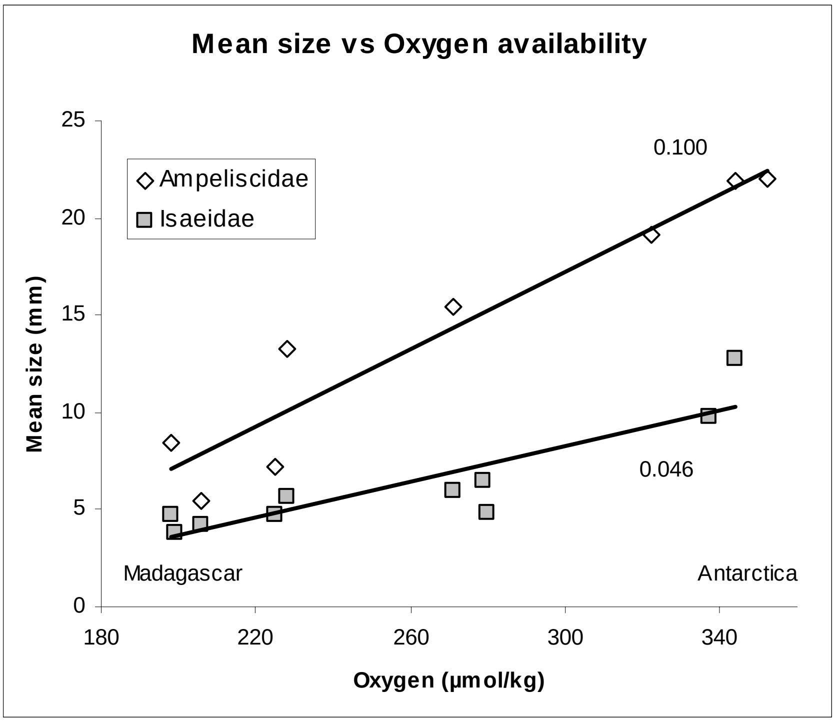

Fig. 3 - Mean size versus oxygen availability within families *:* Significant regression lines for the groups with the highest and lowest slopes are shown. Axes as Fig. 2.

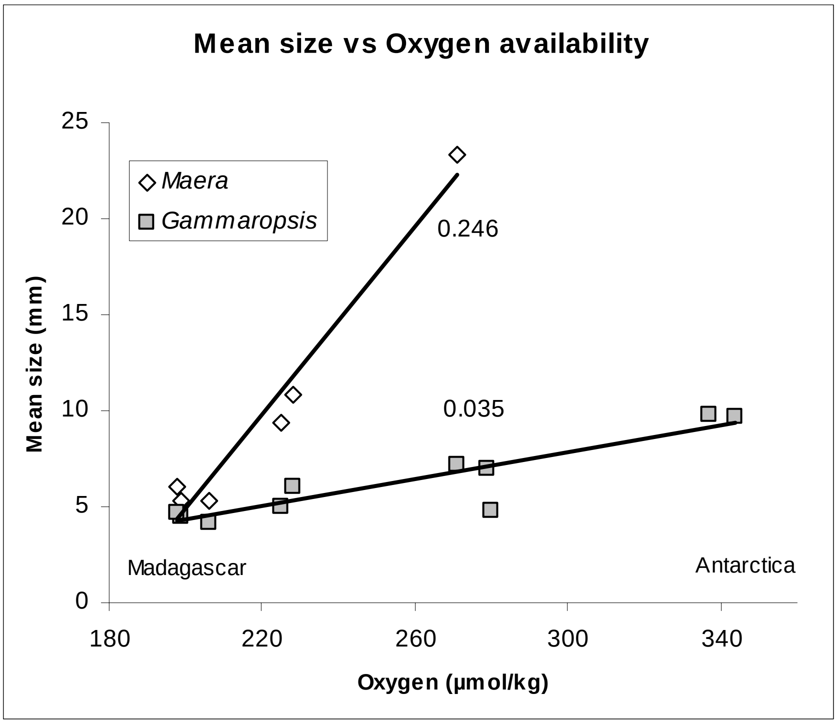

Fig. 4 - Mean size versus oxygen availability within genera : Significant regression lines for the groups with the highest and lowest slopes are shown.
Axes as Fig. 2.

Fig. 5 (see next page) – Relative occurrence of superfamilies and families versus latitude : All superfamilies and families representing 5% or more of the total species number present in at least one area have been selected. The X-axis shows the latitudinal gradient, from East Antarctica to the left, to the Barents Sea to the right. Notice that the middle does not exactly coincide with the equator. Y-axis gives the percentage of each taxon dominating the low latitudes (A), dominating the high latitudes (B), or with no latitudinal trends (C). By alphabetical order, AMPE = Ampeliscidae, AMPO = Amphilochoidea, CORO = Corophioidea, DEXA = Dexaminidae, EUSO = Eusiroidea, HADZ = Hadzioidea, HAUS = Haustorioidea; IPHO = Iphimedioidea; LEUC = Leucothoidae; LYSO = Lysianassoidea, OEDO = Oedicerotoidea, STEN = Stenothoidae, TALO = Talitroidea.

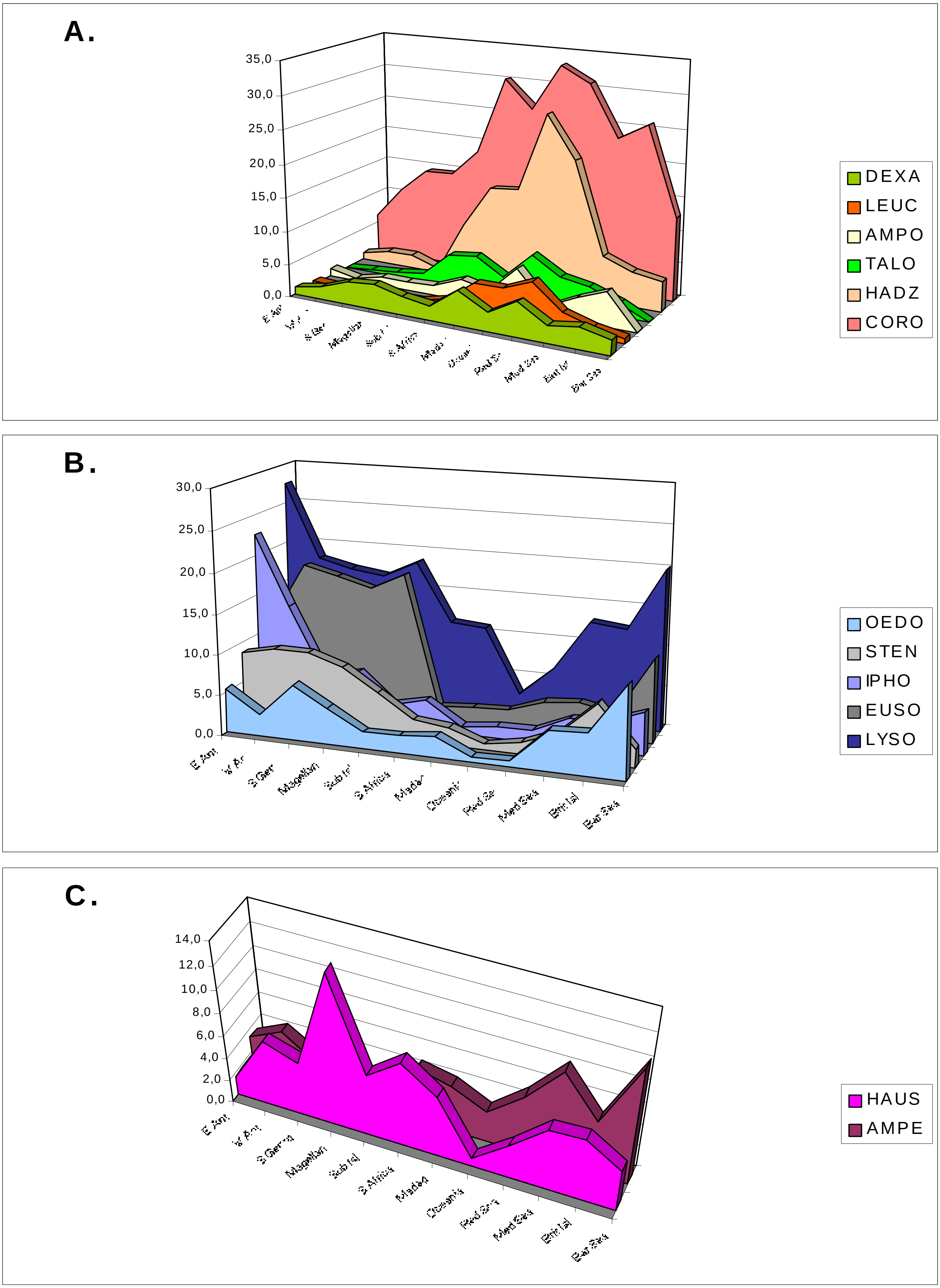
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Fig. 5

Chapter 5: Effect of oxygen within species

Contents

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CHAPELLE G, PECK L & GODDEERIS B., in prep. Relationship between size and oxygen availability in amphipod crustaceans within species.

Publication V

Relationship between size and oxygen availability in amphipod crustaceans within species

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in prep.

Abstract

Maximum potential size in benthic gammaridean amphipods has been shown to be limited by oxygen availability from the suborder to the generic level. The present paper investigates the effect of oxygen on size at the species level. Amphipod maximum length of 11 areas worldwide were compiled from the literature, and species present in more than one area were compared. On average, the body size increases significantly by 0.03 mm per µmol $O_2.kg^{-1}$ water, and species displaying the largest size in the most oxygenated area were 1.7 times more numerous than species displaying the inverse trend. Adjustment of body size to oxygen within species is constant from small to large species when the size variation is expressed in length percentage, but differs from one family (or superfamily) to the other. Families with the strongest reaction to oxygen at the intraspecific level dominate the high latitude faunas in terms of total diversity and richness in large species.

Introduction

Although reports of bigger specimens at higher latitudes for a known amphipod species are rather frequent in the literature (for example Sars, 1895 ; Stephensen, 1925; Barnard, 1962 ; Steele & Steele, 1970 ; 1973), this phenomenon has never been investigated in a specific study. Recently, we have established the existence of polar gigantism for gammaridean amphipods at the suborder level and linked it to oxygen availability (Chapelle & Peck, 1999 ; Peck & Chapelle, 1999 ; Chapelle & Peck, submitted ; Chapelle & Peck, in prep). Furthermore, the relationship between maximum potential size and oxygen concentration has also been shown at the superfamily, family and genus levels (Chapelle et al., in prep). The following step was to test the phenomenon at the species level with enough data to validate or disprove the existing anecdotal accounts. The data set we used in previous papers to investigate polar gigantism allowed this type of analysis because of the large number of species recorded and measured in more than one area.

Material and methods

Maximum length of benthic gammaridean amphipods, measured from the tip of the rostrum to the tip of the telson, was compiled from the literature for 11 brackish and marine areas worldwide (Table 1). For each of these areas, we also calculated a mean dissolved oxygen content at saturation based on the mean annual temperature and salinity at surface. Although not every habitat in the considered locations will experience permanent high oxygen saturation, this 100% value represents the optimal conditions for species to attain large size.

To allow the detection of an intraspecific effect of oxygen on size, species present in more than one area were selected from the data set, that is to say 349 from a total of 1543 (Table 2).

To each of these data was ascribed the oxygen concentration (in µmol $O_2.kg^{-1}$ water) corresponding to the area where it was recorded. Each of these pairs of data (size, oxygen concentration) was centered to the average size and oxygen content calculated within each species. A F-test on the slope of a linear regression was then performed on the data.

A similar analysis has been applied to the 13 superfamilies and families studied in Chapelle et al. (in prep.) to investigate possible differences in the capacity for increasing size with oxygen.

Regarding taxonomy, attribution to superfamilies and families follows the index compiled by De Broyer et al. (2000), itself based on the last synthesis on the subject (Barnard & Barnard, 1983 ; Bousfield, 1983 ; Barnard & Karaman, 1991 ; Bousfield & Shih, 1994 ; Lowry, unpublished).

Results and Discussion

The most significant contribution of our study on polar gigantism has been to show that oxygen availability was a key factor in determining gammaridean amphipod size (Chapelle & Peck, 1999), as opposed to the widely proposed temperature (Gunter, 1957; Barnard, 1962; De Broyer, 1977; Sainte-Marie, 1991; Atkinson & Sibly, 1997). Using fresh (Lake Baikal) and brackish water areas (Black & Caspian Sea) data allowed a first decoupling of the covariation of oxygen content and temperature when salinity is constant (Chapelle & Peck, 1999). It showed that if the correlation between temperature and maximum potential size existed, it only did so for marine areas, thus pointing to temperature more as a proxy of oxygen concentration than the active factor itself. This was later confirmed by the analysis of amphipods from Lake Titicaca (Chapelle & Peck, submitted), which due to its high altitude, has a lower oxygen content making it similar to an hypersaline lake.

These considerations clearly indicated oxygen availability as the variable to correlate with intraspecific size variability, although the decoupling between oxygen and temperature was considerably reduced in this data set. Indeed, very few species have a distribution encompassing fresh, brackish and marine waters. Thus no amphipods from Lake Baikal, the only freshwater ecosystem of the data set, were present in another area. As for the brackish areas, namely the Black and Caspian Seas, which provided only a small part of the data, their salinity is indeed lower than marine waters. However, this is only true when averaged for the whole seas, whereas in both cases, a rather steep latitudinal salinity gradient exists within the area. This variability could have been analyzed in the intraspecific comparisons only with salinity and temperature data for each species, which were not available.

Therefore with, on one hand, no data allowing us to distinguish between oxygen and temperature, and on the other hand, the assumption that what was found from the gammaridean suborder down to genera might be extended to the species level, the correlations discussed further will always be considered as linking size and oxygen content of the water.

In our first analysis of gammaridean amphipod size spectra established for 12 areas (Chapelle & Peck, 1999), we showed that the biggest species are not the only ones to react to oxygen content variations. Mean, and more importantly, modal size also increased significantly with oxygen concentration, even if it was at a smaller rate. This link between oxygen and modal size was thus an indication of a possible widespread body size optimization with oxygen availability.

However, many other factors can also act on size, in various directions. To give just a few examples, a bigger size potentially allows a greater brood size (Van Dolah & Bird, 1980 ; Sainte-Marie, 1991), a wider foraging range or a wider prey size spectrum (Peters, 1983; Gage & Tyler, 1991). On the other hand, a bigger size may reduce the ability to hide from predators (Strong, 1972; Wellborn, 1994 ; Blumenshine et al., 2000), or to maintain a balanced relationship with its host for a commensal species. It also demands a higher energy input per specimen. Therefore, although an increase in oxygen might offer a potentially wider size range for any given species, the combination of selective pressures will probably not drive them all to the upper part of that range.

So if a body size optimization was to exist, for any given area, we might expect to find a general trend towards bigger size with increasing oxygen level. Although usually attributed to colder temperature, this trend was indeed often mentioned in the literature, in various families and superfamilies. It was established for some species of the Ampeliscidae by Stephensen (1925), Mills (1967), Kaim-Malka (1969) and Dauvin (1988a, 1988b, 1989), for at least one Corophioidea by Barnard (1954), for at least one Eusiroidea by Steele & Steele (1973), for some Gammaroidea by Dahl (1915), Steele & Steele (1969, 1970), Sheader (1983) and Takhteev & Mekhanikova (1996), for some Haustorioidea by Sameoto (1969b), for some Lysianassoidea by Sars (1895), Stephensen (1923) and Steele & Brunel (1968), and finally for at least one Oedicerotoidea by Sainte-Marie & Brunel (1983).

It should be noted that other species could still show an inverse or no trend at all when this body size optimization would generate adverse effects more costly in terms of fitness than the benefits obtained for oxygen acquisition.

A first examination of the general results confirms these expectations. Indeed, there are about X1.7 more size data proportional to oxygen than the ones inversely proportional (Table 3). Furthermore, the linear regression has a highly significant slope ($F = 7.18$, $P<0.0001$) of 0.029 ± 0.004 mm/µmol $O_2.kg^{-1}$ water (Fig. 1).

In most ecosystems including aquatic ones, the range size of any species is related to its body size (Reaka & Manning, 1987; Gaston & Blackburn, 1996). It is therefore not surprising that the 1194 species distributed in only one area (mean size: 8.7 mm) are smaller than the 349 others, present in at least two areas (mean size: 14.1 mm), and on which this paper is based.

As at the suborder level, the maximum size increased faster than the mean, and the mean faster than the modal size with increasing oxygen concentration, it was interesting to see whether a similar trend existed at the species level. Therefore we have divided the 349 species ordered by size in five groups of 70 species each, following a 20% increment; thus the first from the smallest species to percentile 20, the next from percentile 20 to percentile 40, etc... to the last one, from percentile 80 to the biggest species. A covariance analysis was performed in which each group was attributed a slope. F-test were applied to test the equality of slopes among groups. For each group, a linear regression was fitted and their associated slopes were calculated (Table 4). The five slopes showed a steady increase with increasing size class and differed significantly from each other ($F_{4,\ 819}$ = 11.62, P < 0.0001). However, if the size data were expressed as relative size (%) instead of absolute (mm), the new slopes could not be distinguished any more from each other ($F_{4,\ 819}$ = 2.31, P < 0.056). This shows that at the intraspecific level, the increase in size due to a higher oxygen content is proportional to the body size of the amphipods.

In a previous study (Chapelle et al., in prep), it was shown that the increase in size with oxygen across species was not the same between the 13 different families and superfamilies tested. For example, the mean size of the Iphimedioidea grew with oxygen at a rate twice higher than the one followed by the Oedicerotoidea. It was decided to investigate if these differences between families and superfamilies regarding size reactivity to oxygen between species also existed within species. The tests already used on the slopes of the five 20% increment groups, using first absolute values, and then relative values, were applied to the same 13 families and superfamilies.

Unsurprisingly, the first one not only revealed that 9 of the 13 slopes were significantly different from 0, but also that their ranking followed the one established for the mean size of each family or superfamily by Chapelle et al. (in prep). So the families with the biggest mean sizes were the ones displaying the highest rate of absolute (in mm) size increase with oxygen within species (Table 5). This was consistent with the previously noted increase in size proportional to the body size of the amphipod but did not suggest any phylogenetic effect.

However, the second test, using differences in size expressed as percentages instead of mm, produced 11 significant slopes from 13, with the steepest x3 bigger than the smallest (Table 5). Differences between these slopes indicate the existence of a phylogenetic effect. This is further supported by the new ranking. Indeed, the families and superfamilies mainly found in polar regions, the highest oxygen environments, displayed steeper slopes for species size variation with oxygen than the taxa predominant in tropical waters. This suggests that, when oxygen content of the polar regions rose with the cooling of its waters, the taxonomic groups with the greatest capacity for increasing size with oxygen were able to reach the highest part of the size spectrum and create new niches faster than the other families and superfamilies.

Thus it seems clear that within amphipod species, there is a trend for populations living in more oxygenated areas to display bigger size than their counterparts exposed to lower oxygen environments. However, this is not more than a trend and therefore, in many cases, other selective pressures keep amphipod size constant or even make them smaller.

It should be noted that intraspecific variations also occur within a much shorter evolutionary timescale. Indeed, numerous authors reported that many bivoltine crustacean species from temperate regions mature at smaller size in summer than in spring or winter. This life history trait seems widespread and has been encountered amongst other groups in Copepoda (e.g. Riccardi & Mariotto, 2000), Tanaidacea (e.g. Salvat, 1967) or Isopoda (e.g. Naylor, 1955), as well as in many amphipod species (see for example Fish & Mills, 1969; Lim & Williams, 1971; Sheader, 1983;

Hiwatari & Kajihara, 1984). In a number of cases, this difference in size has been attributed to the effect of temperature on growth and development. As the latter is more sensitive to high temperature, maturation occurs sooner and thus at smaller size in summer. The fact that growth goes on later in the warm season brings further support to this temperature hypothesis (Dauvin, 1988 a, b, c; Powell & Moore, 1991).

However, there is a number of cases reported in the literature for which the role of temperature is not as clear and could be mixed with the oxygen effect described in this paper. Indeed the female size of several species reproducing year round and with a life span from 8 to 15 months are inversely proportional to temperature, and consequently maybe to oxygen (Hynes, 1955; Sameoto, 1969a,b; Fenwick, 1984). Also, the summer migrations of the adults of *Hyalella azteca* (Saussure, 1858) towards deeper cold habitats were cited to be not only temperature-induced, but also "bioenergetically advantageous", despite a probable increase in predation risk (Panov & McQueen, 1998). If no firm evidence of such an effect exists at this time, we hope that in similar future life cycle studies, oxygen measures (in parallel with temperature and salinity) could be made to clarify this question.

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Table 1 : The 11 areas. N gives the number of species per area for which the known maximum size relates to a mature animal. O_2 gives the surface mean oxygen content (absolute concentration) in µmol of O_2 per kg of water. Oxygen solubility in water varies with temperature and salinity, described by the relationship: $\ln k_{o,s} = 3.718 + 5596.17/T - 1049668/T^2 + S(0.0225 - 13.608/T + 2565.68/T^2)$, with S for salinity and T for temperature in °C (Benson & Krause, 1984).

Areas	*O_2*	*N*
Madagascar	206	314
Mediterranean Sea	225	347
British Isles	271	249
Black Sea	276	92
Subantarctic islands	279	145
Magellanic region	280	160
Caspian Sea	296	69
Barents Sea	322	134
South Georgia	337	147
West Antarctica	344	275
East Antarctica	352	186

Table 2: Number of areas with size data per species. N gives the number of species. Note that a number of species were recorded from other areas, but without adult size data.

N(areas)/species	N
1	1194
2	**245**
3	**84**
4	**17**
5	**3**
Subtotal	**349**
Total	1543

Table 3 : Trend within species between size and oxygen content. The table refers to data plotted on figure 1. N gives the number of data (not species) per category.

Size to O_2 relationship	N
size proportional to O_2	444
size constant	123
size inversely proportional to O_2	258
Total	825

Table 4: Increase in size with oxygen versus species size The second and third columns give the estimated slope of the regression of each size class between absolute (mm) and relative (%) size respectively. The last row gives the significance of the covariance analysis on the slopes. *** indicates significant relationship at P < 0.0001

Groups by perc.	Slope intrasp abs	Slope intrasp %
0-20%	0.010 NS	0.260***
20-40%	0.015 NS	0.245***
40-60%	0.017 NS	0.189***
60-80%	0.035***	0.285***
80-100%	0.090***	0.464***
F-Test	***	NS

Table 5: Increase in size with oxygen according to superfamily or family: superfamilies and families selected represented more than 5% of the species present in at least one area (cf. Chapelle et al., in prep). Mean size (mm) of each family or superfamily was calculated using the maximum size of the involved species. AMPE = Ampeliscidae, AMPO = Amphilochoidea, CORO = Corophioidea, DEXA = Dexaminidae, EUSO = Eusiroidea, HADZ = Hadzioidea, HAUS = Haustorioidea; IPHO = Iphimedioidea; LEUC = Leucothoidae; LYSO = Lysianassoidea, OEDO = Oedicerotoidea, STEN = Stenothoidae, TALO = Talitroidea. Families and superfamilies in bold and normal characters are predominant at high and low latitudes respectively.

Slope intrasp abs		Mean size		Slope intrasp %	
IPHO	0.094**	**IPHO**	18.7	**EUSO**	0.588***
EUSO	0.09***	**EUSO**	13.9	**IPHO**	0.502**
AMPE	0.058**	HADZ	13.6	*AMPE*	0.429**
HADZ	0.05 NS	AMPE	13.3	AMPO	0.418*
LEUC	0.044*	**LYSO**	10.5	**OEDO**	0.409***
LYSO	0.025*	**OEDO**	10.1	LEUC	0.337*
OEDO	0.025**	DEXA	8.0	**STEN**	0.313*
STEN	0.017*	TALO	7.8	HADZ	0.294*
AMPO	0.016*	CORO	7.1	**LYSO**	0.239**
CORO	0.016*	*HAUS*	6.1	CORO	0.218**
DEXA	0.011 NS	LEUC	5.9	*HAUS*	0.187*
HAUS	0.01 NS	**STEN**	4.7	DEXA	0.121 NS
TALO	0.005 NS	AMPO	3.7	TALO	0.095 NS

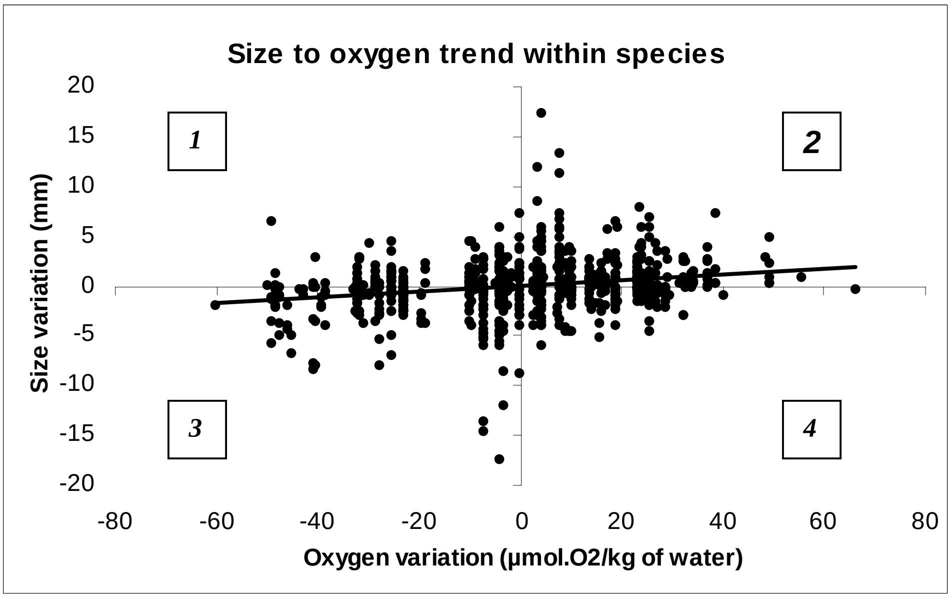

Fig. 1 - Size to oxygen trend within 349 species. Each data point, combining the length (mm) and the oxygen concentration (µmol.O_2/kg of water) was centered to the average size and oxygen content calculated within each species. The upper right (2) and lower left (3) quadrants are responsible for the positive slopes (size proportional to oxygen in Table 3); the upper left (1) and lower right (4) quadrants for the negative slopes (size inversely proportional to oxygen in Table 3); the remaining dots are packed at the intersection of the axis (constant size throughout all areas in Table 3).

Chapter 6: New insights in the relationship between size and oxygen

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Publication VI

Amphipod crustacean size spectra: new insights in the relationship between size and oxygen

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in prep.

Abstract

Oxygen availability has been shown to limit the maximum potential size in benthic gammaridean amphipods from the suborder to the generic level, while also influencing size within species. This paper investigates the effect of oxygen on 15 size spectra worldwide, established by compiling maximum length data of more than 2000 amphipod species. TS95/5 was defined as the Threshold Size between the 95% smallest and the 5% biggest species of a given site. The data show that beside TS95/5, minimum, mean and modal sizes, as well as all 10% increment threshold sizes (from TS10/90 to TS90/10) are also significantly linked to oxygen concentration. Size distributions are very similar in shape from one area to another, whatever the width of the spectrum, hence more small species should coexist at low than at high latitudes. This consequence is obscured by the insufficient taxonomic coverage for small species in all areas. No amphipod species were found in water with an oxygen content lower than the minimum requirement predicted. These results show that minimum amphipod size is probably limited by the minimum possible egg size, whereas maximum size is set by the physico-chemical ceiling of oxygen availability.

Introduction

In a recent review about Antarctic benthic biodiversity in a latitudinal context, Gray (2001) expressed the need for worldwide size spectra to elucidate the still contested size gradient hypothesis (Thorson, 1957; Barnard, 1962; Brey & Clarke, 1993; Clarke, 1996; Brey & Gerdes, 1997). However, following the first systematic study on that topic (De Broyer, 1977), it is precisely by establishing such size spectra that we confirmed the existence of larger amphipod species in polar regions and in Lake Baikal (Chapelle & Peck, 1999; Peck & Chapelle, 1999; Chapelle & Peck, submitted).

A crucial finding was that this trend followed in fact the variations in oxygen content of the water rather than the temperature. This was best illustrated by the Caspian Sea and Lake Baikal size spectra, as both were wider than marine areas with similar mean temperature, but less oxygen because of the higher salinity.

These spectra also allowed us to elucidate the importance of Baikalian and Antarctic gigantism. The curves clearly showed that if an outstanding size was indeed attained in these regions, it was only for a very limited number of species, while the adult length for the vast majority was situated in the lower half of the size range. Thus at first sight, oxygen availability appeared mainly to set an upper limit to maximum adult size more than acting as a selection pressure towards big size.

Since these papers were published, size spectra have been produced for three new areas, and more importantly, an effect of oxygen on size was shown to exist both at the family and genus level, and intraspecifically (Chapelle et al., in prep,a,b). These additional facts justify the more thorough study of amphipod size spectra in the present paper.

Material and methods

Maximum sizes for benthic gammaridean amphipods were compiled from the literature. The length of the animal is usually measured from the tip of the rostrum to the tip of the telson following the dorsal line (e.g. Stebbing, 1914; Barnard, 1932; Thurston, 1972; see Chapelle, 1995 for details). For the few authors using a straight line instead of the curved dorsal line, or excluding the telson, the data were kept as such, although these were known underestimates (Chevreux, 1905; 1906a, b, c, d; 1911; 1912; Nicholls, 1938; Barnard, 1967; Breggazzi, 1972) except when they could be recalculated from *habitus* (Chevreux, 1913; Coleman, 1998).

The data set of this study is an extension of the one used in our first papers about polar gigantism in amphipods (Chapelle & Peck, 1999; Peck & Chapelle, 1999). Data of three supplementary areas have been added, namely the Red Sea, Oceania and the South African coasts and continental shelf, and some have been updated with more recent data (British Islands, Magellanic region, West & East Antarctica). Each of the 15 areas was attributed a mean oxygen content at saturation, based on the mean annual temperature and salinity at surface (Table 1). Although such a saturation does not occur in every habitat, its existence in some of them would offer the optimal conditions for evolution towards big size.

Furthermore, the analysis was limited to the species of the continental shelf, hence to 250 m depth, with the exception of East and West Antarctica which included species down to 500 m, as the south polar shelf is depressed by the Antarctic icecap.

These 2805 data, covering 2092 species, were converted to size spectra for each area. In our previous work (Peck & Chapelle, 1999; Chapelle & Peck, 1999; submitted), which addressed gigantism, we had selected a parameter allowing quantification of the upper part of each spectrum. TS95/5 was defined as the Threshold Size between the 95% smallest and the 5% largest species of a given site. For this study, this method was extended to the whole distribution with steps of 10%, e.g. the steps of 20/80%, 50/50% and 95/5%, Fig. 1). This proved to be an efficient way to describe the shape of these spectra, allowing comparisons to be made.

Results and discussion

All 15 size spectra are skewed to the right (Fig. 2), a pattern commonly reported for animal communities (e.g. May, 1986; Blackburn & Gaston, 1994). They also follow an oxygen gradient, as already mentioned, with the largest species to be found in the areas with the maximum oxygen availability.

The mechanism proposed to explain the link between oxygen and maximum potential size relied on a relatively small ability to deliver oxygen via the hemocyanin pigments present in the amphipod haemolymph, leading to oxygen transport mainly in the dissolved form. Therefore, although the difference in partial pressure between the external water and the hemolymph remained constant between areas, more oxygen in mass units could enter through the respiratory surfaces in the low temperature and salinity areas, because of variations in solubility. This greater mass could be circulated on a longer path length before exhaustion, thus allowing a larger size (Chapelle & Peck, 1999; Peck & Chapelle, 1999).

However, in the light of additional data, a number of previous conclusions established in our early papers (Chapelle & Peck, 1999; Peck & Chapelle, 1999) needed reevaluation. The first was connected to the minimum size, which in our first study, could not be linked to the oxygen water content (Chapelle & Peck, 1999). On the contrary, modal size did increase significantly with oxygen availability and this suggested a possible effect of oxygen on size within species, with populations living in more oxygen-rich environments attaining greater lengths. Using size data from species present in several areas of our data set, we recently demonstrated this phenomenon. Overall, for the gammaridean amphipods, the maximum adult size of a given species increased of 0.28 % for every additional µmol of oxygen added per kg of water (Chapelle et al., in prep,b).

This result indicated the need for reconsideration of the variation of the minimum size from area to area. Including three more sites in the data produces a significant correlation between minimum size and area ($F=7.63$, $P<0.016$, Table 2). Together with the intraspecific trend, this observation suggests the existence of a spontaneous adjustment of maximum adult size to the concentration of oxygen at the population level. The selective pressure for this optimization presumably exists for all species irrespective of their position in the local size spectrum. However, this is not an overriding selective force, as shown by the numerous species displaying no size increase in more oxygenated sites (Chapelle & Peck, in prep,b).

At the interspecific level, we had used the threshold size separating the smallest 95% of species from the largest 5% to quantify gigantism. Extending this method to the other 10% increments revealed consistent fits between the 15 spectra (Table 2, figure 3). Beside the already discussed linear relationship for the minimum size (TS0/100) and oxygen availability, all slopes for other TS values were highly significant ($P<0.0001$). This points to an important role for oxygen along the whole spectrum, and not only for the largest size as identified in our first paper (Chapelle & Peck, 1999).

In the same paper, we also inferred from the intercept value of the TS95/5 regression line a minimum oxygen content requirement for gammaridean amphipods. The additional data provided in the present study put this threshold close to 175 µmol $O_2.kg^{-1}$ of water. This is slightly lower than the value produced by Chapelle & Peck (1999), but still predicts the conditions which amphipods would not be capable of inhabiting. Such conditions exist in a variety of hot and/or highly saline environments dominated by copepods, ostracods and brine shrimps. A thorough search in the literature has confirmed that no amphipods have been reported in such waters.

A seeming problem for this limit would be that a number of Gammaridea have been described from various oceanic hot vents (Barnard & Ingram, 1990). However, the extreme temperatures are restricted to a very small bottom area around the chimneys, and to this date, no data exist suggesting a perfectly sedentary mode of life for amphipods in these hot waters. Similarly, some populations of *Hyalella azteca* (Saussure, 1858) are known to inhabit freshwater warm springs (40°C) at high altitude, impoverished in oxygen (Strong, 1972). No oxygen content data were available to certify that our theoretical threshold was crossed. However, Strong insists there is high spatial thermal variability at this site, and states that the amphipods mainly congregate in the 20 to 25°C patches, but not in warmer waters.

Populations of the same species, but living in a colder environment, have been shown to cease reproduction above 20°C. In the mean time, the summer migrations of the adults towards deeper cold habitats appear to be bioenergetically advantageous, despite a probable increase in predation risk (Panov & McQueen, 1998).

Another interesting but unsolved case regarding this oxygen lower limit is provided by *Austrochiltonia subtenuis* (Sayce, 1902), a widespread inhabitant of the saline australian lakes. Although it is usually restricted to a salinity below 29 (Lim & Williams, 1971), an exceptional population of this amphipod was reported in two lakes of a salinity of 70 (Halse, 1981). Unfortunately, neither oxygen or temperature were recorded. However, because of a dramatic decline of both populations with no evidence of reproduction, while neighboring populations of weakly saline lakes were actively breeding, Halse concluded that the species could not sustain the immigrating populations at these high salinities.

Thus within each spectrum, according to our general hypothesis, the largest species were selected to possess the most efficient trade-off between various biological functions (such as nutrition, growth, competition or predation pressure) and oxygen acquisition to the benefit of size. At the opposite end of the spectrum, it is the adoption of a small size which has increased the fitness of the concerned species, through another trade-off combination. Between these two extremes, still other complex combinations, differing from one species to the other, has allowed to create the existing niches along the whole size spectrum.

The fact that these niches are more packed in the lower part of the spectrum is shared by many other taxonomic groups or communities such as mammals (Maurer et al., 1992), birds (Blackburn & Gaston, 1996), fish (Brown et al., 1993; Vidondo et al., 1997) butterflies (Barlow, 1994), grassland insects (Siemann et al., 1996) or benthic organisms (Warwick & Clarke, 1996). This characteristic distribution has been interpreted as the consequence of, among others, an energetic mechanism, or the fractal nature of the environment (for further discussion, see Blackburn & Gaston, 1994; Loder et al., 1997). Our result suggest that oxygen might be another key factor to be taken into consideration.

In this regard, it should be noted that the slopes between Threshold Size and oxygen content from the TS10/90 to the maximum size (TS100/0) increase exponentially (Fig 4, Table 2).

A consequence of the consistency of all regression lines between TS10/90 and the maximum size is the striking similarity from site to site in the shape of the size distributions across species. This is best demonstrated by the regression lines established between each of them and the one from the Mediterranean Sea, chosen as the reference for its maximum number of species (n = 347). All of them are highly significant ($P<0.0001$) and with r^2 comprised between 0.90 and 0.998 (Fig. 5, Table 3).

Another inference from this similarity in shapes between all size distributions is that relatively to the large, more small species, for example with a length comprised between 2 and 5 mm, should coexist in warm waters with less oxygen than in cold and well-oxygenated waters. It is difficult however to be definitive on this question. As for any taxonomic group, big amphipod species were the first to be described, especially in polar waters, where "temperate" scientists marveled at their spectacular size compared to the usual gammarideans of lower latitudes. Description of smaller species then increased gradually, as illustrated for the Southern Ocean on Fig. 6.

In this area, recent surveys have revealed a flurry of small to very small new species. Six additional species belonging to the Stenothoidae, the most speciose family for dwarf species in the Southern Ocean, were described for the Antarctic by Rauschert and Andres in four years (Andres & Rauschert, 1992; Andres, 1993; Rauschert & Andres, 1993; 1994; Rauschert, 1995). More recently, a single expedition to the canals of Patagonia yielded as many as 15 new species of this family (De Broyer & Rauschert, 1999). This sudden expansion of a family thanks to the efforts of just two taxonomists suggests a similar increase will be likely in future for other small-sized taxa. The relative scarcity in the Southern Ocean of some taxa usually considered as inhabiting mainly warm waters, like Corophioidea, could be linked to a parallel scarcity of specialists working on them (Myers, comm. pers.).

These considerations point to a possible bias away from small species especially in the areas where big species are present. This potentially exacerbates the contrast between polar and tropical realms. However, the uncertainty around the percentage of undescribed species is not limited to polar regions. In a recent study, extrapolating from endemism rates of coral reef Isopoda, and from the five to one ratio in diversity between amphipods and isopods respectively, Kensley (1998) estimated that up to 46,000 amphipod species could live in the various coral reef habitats (to be compared with the roughly 8,000 described species for the world fauna). According to our curves, at least half of these species should have lengths below 5 mm. The questions around the relative diversity of small species across oxygen gradients remain wide opened.

We insisted earlier on the low number of species attaining the largest sizes allowed by the oxygen concentration at all sites, a situation also encountered at the superfamily, family or generic level (Chapelle et al., in prep,a). This suggests that only a limited number of strategies allow large size, and become increasingly narrow when approaching the highest part of the spectrum. The size spectrum encompassing all gammaridean species clearly demonstrates the predominance of small-sized species, with 45% represented between 3 and 8 mm. Similarly, the slope of the regression line linking modal size to oxygen content across areas is intermediate between that of TS20/80 and TS30/70 respectively, suggesting a close proximity between what can be proposed as an optimal size and the minimum size.

This proximity is a very different situation compared to the upper part of the spectra, and suggests minimum size may be limited by a biological "wall" as opposed to the "ceiling" set by oxygen availability on maximum size.

The underlying factor setting this wall has been suggested to be egg size by various authors (e.g. Mills, 1967). This hypothesis is supported by the latest review of reproductive bionomics of aquatic gammaridean amphipods (Sainte-Marie, 1991). From the 214 species listed, the only species laying just one egg was also the smallest of all, with a mature size of 0.9 mm for the female. Furthermore, the size of the unique egg of *Seborgia minima* (Bousfield, 1970), although representing one quarter the length of the female, was also the second smallest from the data set (0.25 mm of diameter; Sainte-Marie, 1991). It should be noted that the size of the mature males, which cannot be constrained by the egg dimensions, reached a record of 0.7 mm, which was 0.2 mm less than the females, for a species where dwarfness clearly was a successful strategy (Bousfield, 1970). The fact that the smallest amphipods in the world are male supports the hypothesis that egg size is a limiting factor.

Other minute gammaridean species not included in Sainte-Marie's review (1991) are *Raumahara dertoo* (Barnard, 1972), with a mature size of 1.5 mm and three eggs (Barnard, 1974; cited in Krapp-Schickel, 2000), and *Gitana bilobata* (Myers, 1985), 0.9 mm and a single egg (Myers, 1985). Similarly, the 1.6 mm female of *Caprella lilliput* (Krapp-Schickel & Ruffo, 1986), one of the smallest caprellidean amphipod, lays only one or two large eggs (Krapp-Schickel & Ruffo, 1986). Although a systematic study is needed before a definite answer can be given, these various examples seem to indicate that minimum size's threshold is fixed by the *bauplan*. This limit would thus be an intrinsic biological factor, as opposed to the physico-chemical ceiling represented by oxygen availability for the maximum size.

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Table 1: The 15 areas investigated. N gives the number of species for which the maximum size relates to the longest mature animal recorded. T° is the mean surface annual temperature in °C. S is the mean annual surface salinity. Temperature and salinity data are from Freegard (1983). O_2 gives the mean surface oxygen content (absolute concentration) in $\mu molO_2.kg^{-1}$ of water. Oxygen solubility in water varies with temperature and salinity, described by the relationship: $\ln k_{o,s} = 3.718 + 5596.17/T - 1049668/T^2 + S(0.0225 - 13.608/T + 2565.68/T^2)$, with T = temperature in °C, and S = salinity (Benson & Krause,1984). Areas are ranked along an increasing oxygen content gradient

Area	O_2	T°	S	N
Red Sea	198	26.0	39.0	136
Oceania	199	27.5	34.5	142
Madagascar	206	25.0	35.2	314
Mediterranean Sea	225	19.0	38.0	347
South Africa	228	19.5	35.0	185
British Isles	271	11.0	34.5	249
Black Sea	276	16.5	17.0	92
Subantarctic Islands	279	9.5	34.5	145
Magellanic region	280	9.7	33.2	160
Caspian Sea	296	15.0	13.0	69
Barents Sea	322	4.0	32.2	134
South Georgia	337	1.5	34.2	147
West Antarctica	344	0.7	34.0	275
East Antarctica	352	0.0	33.5	186
Lake Baikal	397	6.0	0.0	226

Table 2: Regression lines between threshold sizes (TS) and oxygen: the first and second columns give the slope, in mm per µmol $O_2.kg^{-1}$ of water, and its standard error; the third, fourth and fifth give the F value, the associated probability and the correlation coefficient respectively; the last one gives the intercept.

TS	slope	Std Error	F	P<	r^2	Int
100/0	0.3675	0.0449	67.04	0.0001	0.84	-63.49***
95/5	0.2113	0.0185	129.98	0.0001	0.91	-35.26***
90/10	0.1627	0.0147	122.17	0.0001	0.90	-26.11***
80/20	0.1159	0.0100	136.82	0.0001	0.91	-17.40***
70/30	0.0928	0.0082	127.75	0.0001	0.91	-13.56***
60/40	0.0717	0.0060	144.82	0.0001	0.92	-9.61***
50/50	0.0569	0.0041	196.38	0.0001	0.94	-7.08***
40/60	0.0450	0.0035	163.68	0.0001	0.93	-5.16***
30/70	0.0359	0.0026	191.14	0.0001	0.94	-3.87***
20/80	0.0278	0.0029	90.11	0.0001	0.87	-2.72***
10/90	0.0166	0.0029	32.95	0.0001	0.72	-0.82 NS
0/100	0.0072	0.0026	7.63	0.0161	0.37	-0.062 NS
mean	*0.0777*	*0.0057*	*186.93*	*0.0001*	*0.93*	*-11.36****
mode	*0.0336*	*0.0022*	*226.85*	*0.0001*	*0.95*	*-2.48****

Table 3: Similarity of amphipod size distributions throughout areas: for each area, r^2 gives the correlation coefficient of the regression line between the TS values of that site and the Mediterranean Sea values as shown on Fig 5.

Areas	r^2
Red Sea	0.99
Oceania	0.99
Madagascar	0.96
South Africa	0.98
British Isles	0.99
Black Sea	0.90
Subantarctic islands	0.996
Magellanic region	0.99
Caspian Sea	0.99
Barents Sea	0.96
South Georgia	0.998
West Antarctica	0.99
East Antarctica	0.99
Lake Baikal	0.995

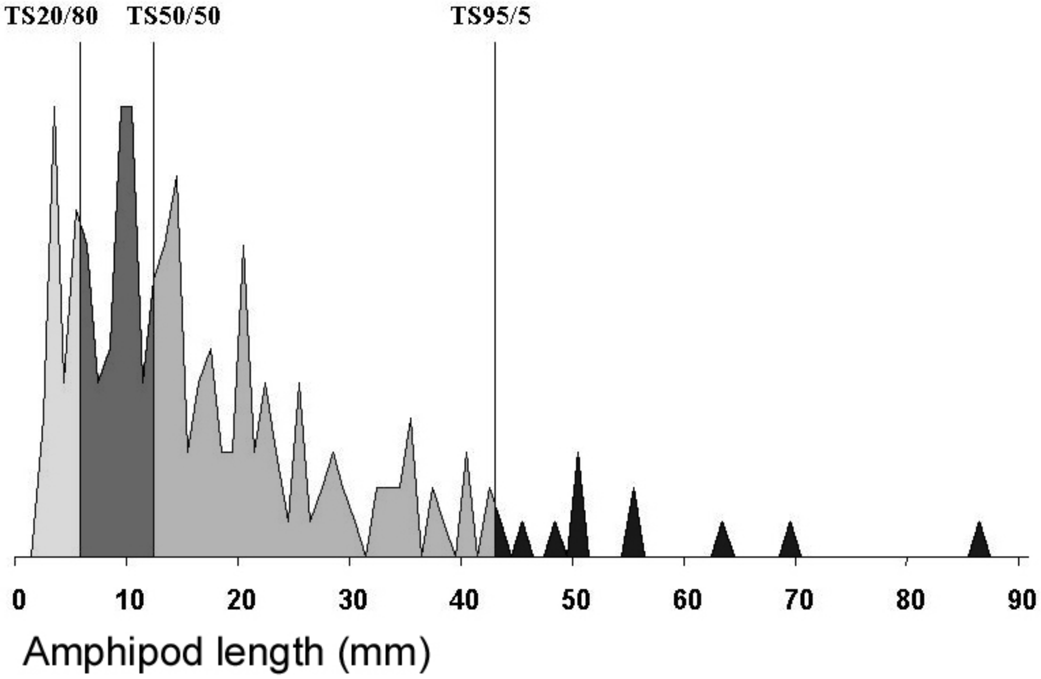


Fig. 1 - Use of threshold sizes to evaluate the size spectra: the X-axis is for the maximum size of each species in mm; Y-axis is the number of species. The three vertical lines cut the distribution at percentile 20 (TS20/80), 50 (TS50/50) and 95 (TS95/5) respectively. The size spectrum is the one for East Antarctica.

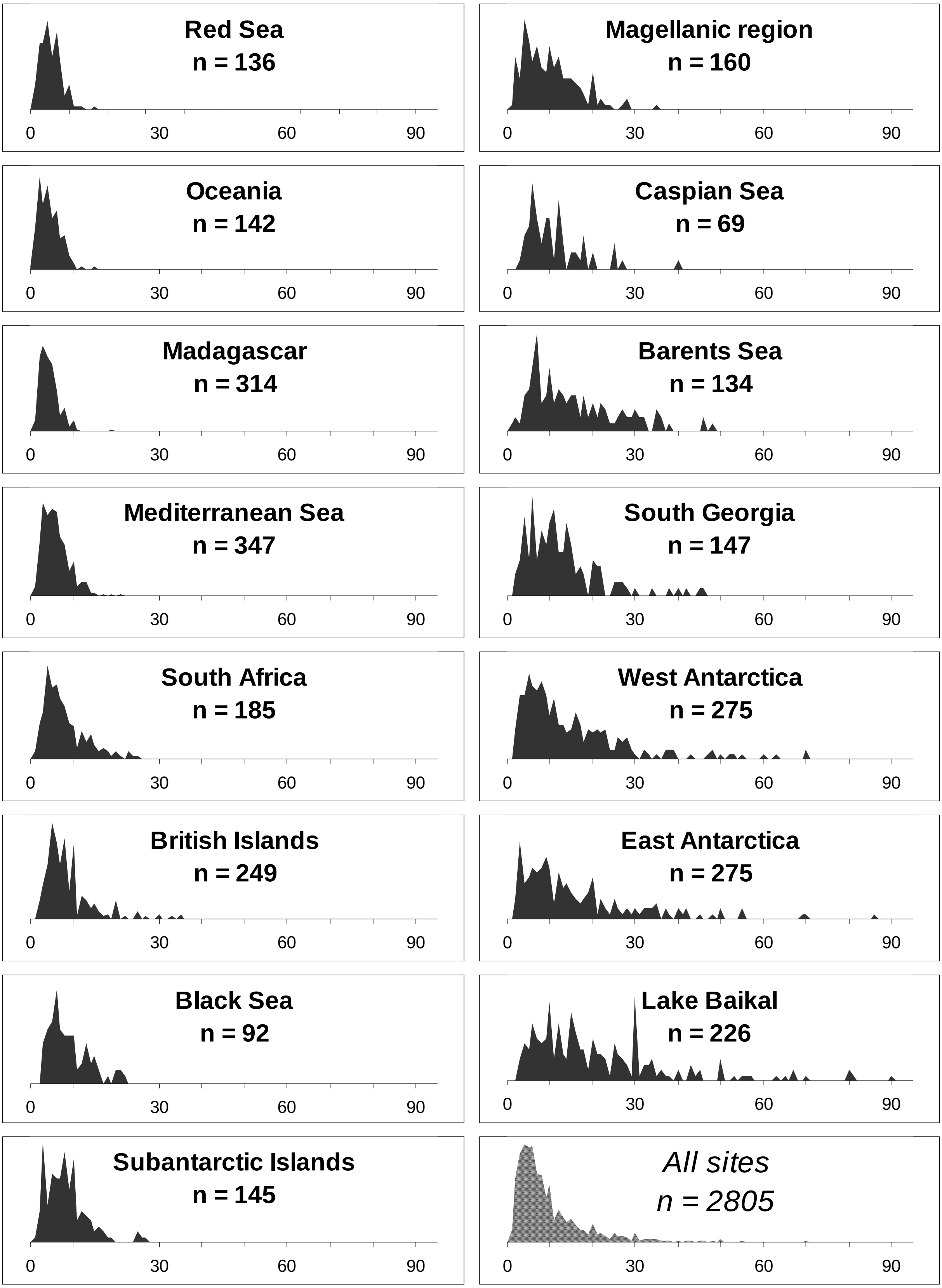


Fig. 2 - Gammaridean amphipod size spectra: areas are ordered in relation to water oxygen content (cf. values in Table 1) from top left to bottom right. Axes as in Fig. 1. The number of species (n) is indicated for each area. The last graphic pools all the data together.

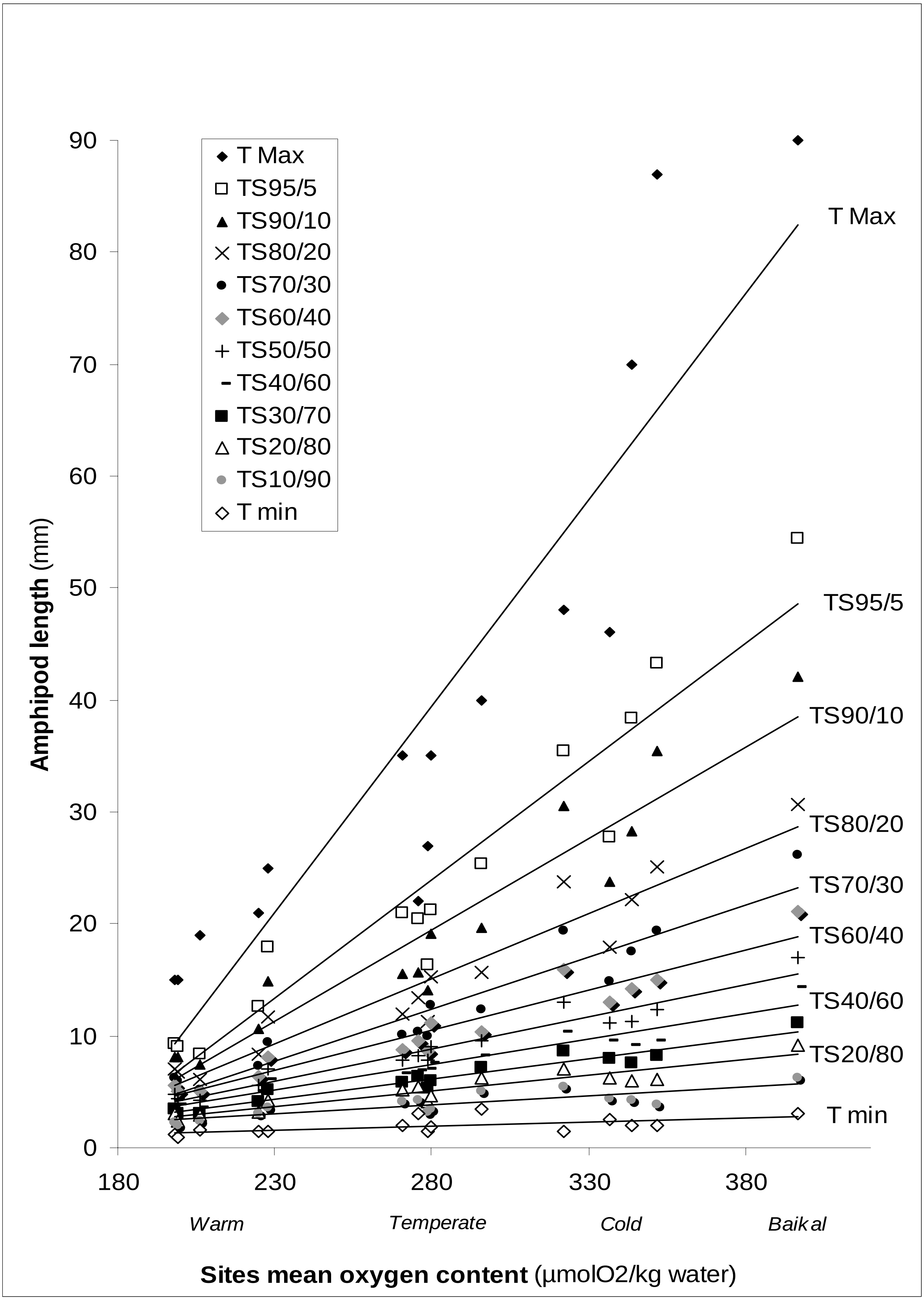


Fig. 3 - Regression lines between Threshold Sizes and oxygen: The X-axis gives the mean annual oxygen content of each area for which the Threshold Sizes were calculated. From the left to the right, mean temperature and salinity decrease. The Y-axis gives the Threshold Sizes in mm. Values are plotted for every 10% increment from the minimum (TS0/100) to TS90/10, and then for TS95/5 and the maximum size (TS100/0). (see next page)

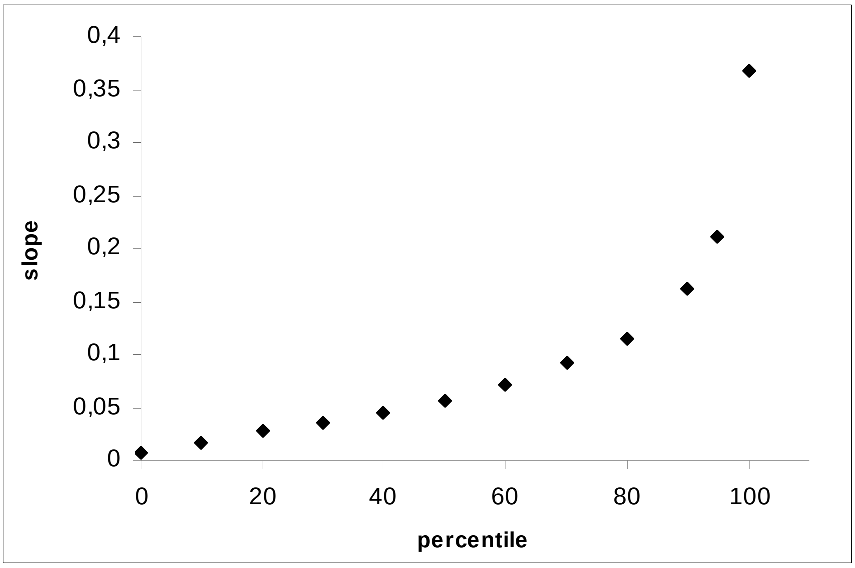


Fig. 4 - Variation of the slopes between Threshold Size and oxygen content: The X-axis follows the 10% increment percentiles from 10 to 100, including the additional value at 95%. The Y-axis gives the slope values from Table 2.

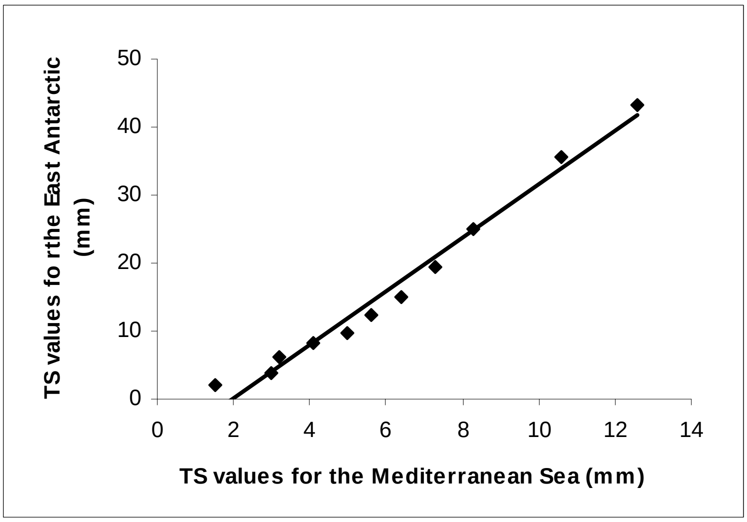


Fig. 5 - Comparison of Mediterranean and East Antarctic amphipods size distributions according to threshold size values: The successive dots give TS0/100 to TS100/0 for every 10% increment, with the Mediterranean values on the X-axis and the East Antarctic on the Y-axis.

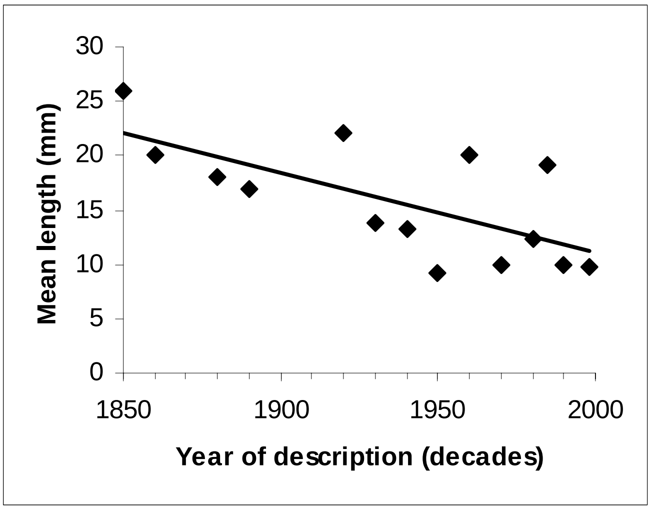
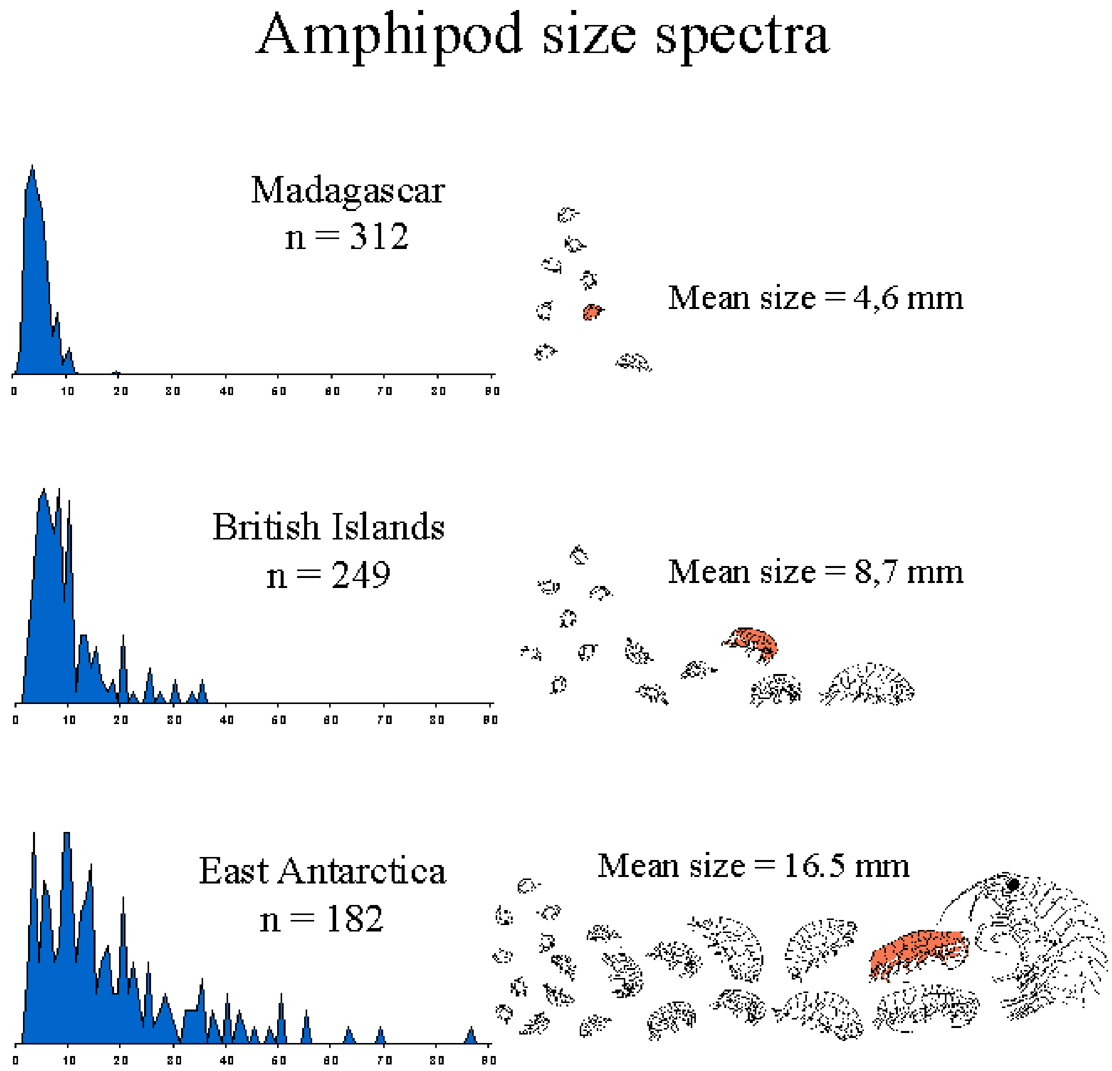


Figure 6: The size bias in gammaridean amphipod description for the Southern Ocean: the X-axis gives the time scale, the Y-axis is for the mean size in mm of the species described during each decade.


Amphipod size spectra
Madagascar
n = 312
Mean size = 4,6 mm
British Islands
n = 249
Mean size = 8,7 mm
East Antarctica
n = 182
Mean size = 16.5 mm
0
10
20
30
40
50
60
70
80
90

General conclusions & prospects

Firstly, in this section, we will present an overview of the main results obtained in the six papers and give a broad picture of the links between oxygen content in the water and benthic gammaridean amphipod size.

Secondly, a brief discussion of the other major factors acting on size, and where appropriate, their possible interaction with oxygen, will be given.

Finally, a number of future research themes and the role of oxygen effect on size will be extended to other groups.

1. Overview of results

Oxygen availability and maximum size in amphipods

In our first paper (Chapelle & Peck, 1999), the amphipod size spectra showed a pattern of gradual widening towards large size from low to high latitudes, while the increase in modal size was more limited. This initial finding was crucial, as from that stage onwards, efforts were directed towards looking for a factor **allowing large size** rather than an **overall selective pressure towards large size**.

We defined TS95/5, the parameter used as a proxy for the largest size of any spectrum, in the same paper. Its use confirmed the correlation existing between the maximum size and the mean temperature at any given marine site.

However, because of the data from the freshwater Lake Baikal, and to a lesser extent, the brackish Black and Caspian seas, an even better correlation of the maximum size could be established with the mean water oxygen content at saturation, measured in mass (µmol $O_2.kg^{-1}$ of water).

The mechanism explaining this correlation was proposed in the paper and was further discussed in Peck & Chapelle (1999). Underpinned by the lack of efficient respiratory pigments in amphipods, our hypothesis stated that size was limited by the decreasing ratio between surface needed for oxygen acquisition, and volume, using it for metabolic requirements.

In the same paper, we insisted on the importance of only using data from areas with many species in order to detect such a link between size and oxygen. Indeed, our hypothesis proposed that oxygen concentration sets a Maximum Potential Size as a ceiling attained by very few species of each fauna, but not as a driving factor with a major effect on all species.

Lake Titicaca, due to its high altitude, offered another factor, namely atmospheric pressure, which affected oxygen concentration in excess of salinity and temperature. In a third paper (Chapelle & Peck,submitted), Titicaca's remarkable amphipod fauna provided further evidence of a major role played by oxygen, with temperature best considered as a subsidiary factor.

Oxygen availability and size at the superfamily, family and genus level

In the fourth paper, the existence of right-skewed size distributions were confirmed for worldwide species data pooled together at the superfamily, family and genus levels (Chapelle et al., in prep,a).

After having established the close correlation between mean and maximum species size for each area investigated at the amphipod suborder level, we have shown that this mean size was linked linearly to oxygen concentration for the vast majority of the lower taxonomic units considered.

Furthermore, the wide range of values found for the slopes of these regression lines (Tables 2, 3 and 4) indicated a variation in the capacity to respond to oxygen availability at the superfamily, family or genus level in their size response to oxygen. In other words, these groups are not equal in the face of oxygen change. This is important, since we also showed that in general, superfamilies and families dominating the higher latitudes in term of diversity and rich in large species were also the ones with the highest slope values.

Thus, the skewedness of any local marine amphipod size spectrum originated in the conjunction of two distinct factors: when oxygen content of the water rose from one area to another, there was an increase in maximum size with oxygen within each lower taxonomic group; and at the same time, a gradual predominance of families with a greater capacity to response to this oxygen concentration occurred. The latter factor is best illustrated by the diversity of large species belonging to the family Eusiridae, Iphimediidae and Epimeridae, or the genus *Paraceradocus*, in Antarctica.

Effect of oxygen availability within species

In a fifth paper (Chapelle et al., in prep,b), oxygen concentration was shown to have an intraspecific effect. However, species displaying larger size in more oxygenated areas were only 1.7 times more numerous than species displaying the reverse trend. This phenomenon was interpreted as "body size optimization" to the oxygen level, but which could also be affected by other selective pressures acting on size, such as increased predation on large specimens, or excessive energy demands per specimen.

This adjustment of body size within species is constant from small to large species when size variation is expressed proportionally as length percentage. However, this is not the case from one family (or superfamily) to another. Furthermore, the families (or superfamilies) with the strongest response to oxygen at the intraspecific level are also the ones which occupy the extreme right end of the species size distribution in the most oxygenated areas and hence have the highest mean size. Thus, for example, the Eusiroidea, Iphimedioidea and Ampeliscidae, the families with the steepest intraspecific slope, were also ranked n°2, 1 and 4 respectively according to species mean size.

Towards a synthesis of the effect of oxygen on size in amphipods

Evaluating the results obtained in the fourth and fifth paper in relation to the initial size spectra (and three new ones) allowed additional conclusions to be drawn in our sixth paper (Chapelle & Peck, in prep). One is that in accordance with expectations from the observed intraspecific effect of oxygen content on body size (Chapelle et al., in prep,b), minimum size, and similarly, all 10% increment threshold sizes (e.g. TS10/90, TS30/70, TS60/40,...) are significantly linked to oxygen concentration.

In the first paper, we had inferred from the intercept value of the TS95/5 vs water oxygen content regression line a minimum oxygen requirement for the gammaridean amphipods. The prediction that amphipods could not inhabit waters with an oxygen content lower than 175 µmol $O_2.kg^{-1}$ of water was confirmed by a thorough literature search; the very few species exceptionally found in such hot and/or hypersaline environments only occur temporarily and without any indications of successful reproduction.

Another significant finding is the remarkable similarity in the shape of the size distributions from one area to another, irrespective of the width of the spectrum. As a consequence, more small species should coexist in low than in high latitudes. However, this hypothesis is difficult to confirm, as both tropical and polar regions are still yielding significant numbers of unknown species.

Finally, we also proposed that minimum size was not affected by oxygen, but instead by egg size. Indeed, the smallest known amphipods usually lay either very few or one large egg compared to their own body size.

2. Oxygen and other factors acting on size

Oxygen does not explain "everything"...

In this work, oxygen content was shown to be an important factor explaining size in benthic gammaridean amphipods. In particular, because it sets the upper limit of the size spectrum in any given area, the oxygen availability in mass can be seen as the key factor answering the fundamental question of this study: **Why do giant amphipods exist mainly in the Antarctic and Lake Baikal ?** The reason is that these sizes could not be attained without the high oxygen concentration found in both areas.

This is not to say, however, that oxygen is the only factor responsible for polar and Baikalian gigantism. As already stated throughout this work, **we consider oxygen availability as a ceiling**, opening or not a range of "size niches", but **not acting as a selective pressure *per se*** driving species into these niches. If this were the case, the translation to the right of the lower part of the spectrum, while moving from tropical to polar waters, would be much greater than the 2 mm observed in our data set.

Thus other factors are needed as selective pressures pushing species to occupy the entire range of available size niches. It is these various selection pressures and their possible link with oxygen that will now be discussed. Unlike the “oxygen ceiling” which is the same for all species in a given area, many of these pressures vary between species, if not from one population to another. This creates in each instance a unique combination of factors, which is best evaluated using careful case studies.

For the sake of clarity, we considered the various factors one by one. However, it is again essential to bear in mind that the adult size of any given species or population is the result of complex interactions between all of them, which means that a dominant factor in a particular situation can be easily counteracted by another in the next one.

Size and reproduction

The existence of a minimum egg size was mentioned earlier as being probably linked to the amphipod *bauplan* (Chapelle & Peck, in prep). It is remarkable that *Seborgia minima* (Bousfield, 1970), the smallest amphipod recorded by Sainte-Marie (1991), lays a single egg of this minimum diameter (0.25 mm). In this case and for unknown reasons, there is a selection pressure clearly favoring small size, as this reproductive strategy lies as close to **the "reproductive wall"** as possible. This example on the minimum size side of the question is a good reminder that for any given species, selective forces exert an important pressure on size at maturity without which, obviously, reproduction would not be possible.

Like most oviparous animals, larger amphipods on average lay more and/or larger eggs, both within and across species (e.g. Van Dolah & Bird, 1980 ; Sainte-Marie, 1991). This relationship is in itself a powerful selective pressure towards large size, especially in semelparous species. It is possibly no coincidence that amongst the few studied Antarctic species, the two largest both adopted this life cycle strategy (Thurston, 1970; Klages, 1993). Similarly, the largest amphipod of our data set, the 90 mm Baikalian *Acanthogammarus grewingkii* (Dybowsky, 1874), is also presumed to be an semelparous species with a maximum brood size of 1878 eggs, the world record for gammaridean amphipods (Bazikalova, 1954a; Sainte-Marie, 1991).

However, the relationship between egg and/or brood size and female body size can be circumvented by other strategies. For instance, juveniles from commensal or infaunal amphipod species are supposedly less subject to predation than their epifaunal counterparts (Van Dolah & Bird, 1980; Nelson, 1980; challenged by Fenwick, 1984), allowing smaller broods of larger eggs.

Size and temperature

Although oxygen appears to be the main element underlying Antarctic and Baikalian gigantisms, temperature is of course another key factor in the determination of size. Like oxygen availability, and unlike the biological factors to be discussed, temperature is a uniform factor that most amphipod species from a given area will experience. Its influence is manifested through various biological processes.

Within species, growth rate and molting frequency generally increase seasonally with temperature, and are often associated with shorter life span and smaller size at maturity, which has been explained by an even faster increase in development rate (e.g. Nair & Anger, 1979a,b; Hiwatari & Kajihara, 1984). This is best known from species experiencing large temperature variations throughout the year, typically intertidal or shallow subtidal temperate species.

Several studies also demonstrated for temperate amphipods a threshold temperature under which no reproduction will occur (e.g. Hynes, 1955; Sameoto, 1969), with a potential effect on life cycle strategies. Therefore a number of species typically experience univoltine life cycles in their colder locations, but become bivoltine in the middle of their range, and even sometimes reproduce year-round in warmer localities (e.g. Salvat, 1967; Kaim-Malka, 1969). This trend between populations is also paralleled by a decrease in size at maturity, which could be the result of the higher oxygen content in cold waters, more than the effect of temperature *per se* (Chapelle et al., in prep,b).

Finally, at the interspecific level, amphipod lifespan is usually much longer at high latitudes between species of similar size (Sainte-Marie, 1991). Furthermore, the very few Antarctic and Baikalian large species for which such data exist show even longer intervals between molting events. These intervals reach six months for both the Antarctic 54 mm long *Bovallia gigantea* (Pfeffer, 1888) (Thurston,1970) and the Baikalian 50 mm long *Pallasea cancellus* (Pallas, 1776) (Chapelle,unpublished), and up to one year for the Antarctic 35 mm long *Waldeckia obesa* (Chevreux, 1905) (Chapelle,unpublished). However, the slow growth and development usually observed for Antarctic benthos is possibly limited by ecological constraints rather than low temperature (Clarke, 1979; 1983). Cold temperature would thus be relevant only for the low basal metabolic rate it allows.

Size and resource availability

The overall smaller size of deep sea meio- and macrobenthos has often been attributed to the low amount of food reaching the bottom (e.g. Madsen, 1961; Gage, 1978; Starobogatov & Sitnikova, 1992), and Takhteev (1997; 2000) has described two species previously considered as juveniles of other larger taxa from the most oligotrophic abyssal part of Lake Baikal. However, this causal link remains disputed, as this average small size seems to be balanced out between individual food demand, increasing with size, and the mass specific metabolic rate (Thiel, 1975; Gage & Tyler, 1991). Furthermore, and as already pointed out for the abyssal giant amphipods *Alicella gigantea* (Chevreux, 1899) and *Eurythenes gryllus* (Lichtenstein, 1822), increasing size also enables the establishing of a wider foraging range to locate widely dispersed food falls (Dayton & Hessler, 1972; Thiel, 1975).

At the intraspecific level, evidence of such a correlation between size and resource availability has been demonstrated in various groups such as reptiles (Wikelski et al., 1997), insects (Sweeney & Vannote, 1986; Ernstig et al., 1993) and isopod crustaceans (Panov, 1988a). Similar evidence was also provided for for the freshwater gammaridean amphipods *Gammarus lacustris* (Sars, 1863) and *Hyalella azteca* (Saussure, 1858) (Panov,1988b; Panov & McQueen,1998). Finally, a difference in food quality has been shown to decrease the growth rate but without influencing size at maturity in *Gammarus fasciatus* (Say, 1818) (Delong et al.,1993).

Size and trophic type

As a general rule, large size is more important to predators than herbivores or suspension-feeders, as their prey range is extended (Cammen, 1980; Peters, 1983). This has also been highlighted for amphipods where many, but not all herbivores and detritivores are small (Bazikalova, 1949). Similarly, in the special case of the the two abyssal giants *Alicella gigantea* (Chevreux, 1899) and *Eurythenes gryllus* (Lichtenstein, 1822), their quasi exclusive necrophagous diet coupled to their impressive swimming abilities in an impoverished environment probably represented a significant selective pressure towards very large size (Smith & Baldwin, 1984; Gage & Tyler, 1991).

However, a number of behavioral or trophic specializations allow the existence of large herbivores, detritivores or micropredatory grazers, as well as small predators or scavengers, and thus reduce the effect of trophic type on size determination. This is demonstrated by several giant Iphimedidae which graze on bryozoans, sponges or cnidarians around Antarctica (Dauby et al., 2001), or by the wide size spectrum displayed by scavengers in many marine locations (e.g. Thurston, 1979; Sainte-Marie, 1986; De Broyer et al., 1997).

Size and predation

Predation affects amphipod size in various directions. Small species are usually more difficult to detect than large ones, and within species, the absence of predators allow larger maximum size (Fish & Preece, 1970; Strong, 1972; Wellborn, 1994). On the other hand, large size may afford a refuge from small predators (Hynes, 1955) or increase the efficiency of defensive strategies such as spines. The latter has been neatly demonstrated intraspecifically in the armored Baikalian genus *Acanthogammarus* (Bazikalova,1954b). Similarly, the same *Acanthogammarus* species display very large densities in shallow waters heavily predated by fish, whereas large and smooth species are much rarer and reach their highest densities much deeper (Bazikalova, 1949).

Although some authors have suggested predation is responsible for the overall small size of tropical amphipods (Nelson, 1979; Steele, 1983), conflicting data from species to species indicate that a global effect on an entire fauna is unlikely. This also illustrates the complexity of size determination and confirms the need for careful case studies, encompassing the whole array of factors which might influence body size.

3. Future research themes

After having stressed the role of a range of factors in determining amphipod body size, we will now return to oxygen and briefly suggest a number of directions for future research.

There is a general lack of data on several aspects of morphological and physiological adaptations to large size in gammaridean amphipods (Peck & Chapelle, 1999). A first area of uncertainty surrounds the gas exchange sites responsible for oxygen acquisition, as there is no firm evidence that oxygen uptake should be restricted to the gills (Graf & Magniez, 1969). Data are also needed to describe any possible relationship of changing relative gill surface area with amphipod size, within or between species. Folding of the gill surface, for instance, might constitute an efficient way to attain larger size by increasing the surface to volume ratio. Such increases have been reported in the largest of two sister species of *Ampelisca* in the North East Atlantic (Mills, 1967), and more remarkably, in the giant abyssal *Eurythenes gryllus* (Lichtenstein, 1822) (Bowmann & Manning,1972).

There is a similar lack of data regarding both concentration of amphipod hemocyanin and its exact role in oxygen transport and respiration. This means that the partition between bound and dissolved oxygen in the circulating haemolymph remains largely unknown for most amphipods (Peck & Chapelle, 1999). Thus the possible differences between large and small species from the same genus, or from various sites of a wide range of ambient oxygen availability are unknown.

Another logical step would be to test experimentally the "oxygen ceiling" hypothesis on captive amphipods. Controlling oxygen availability and selecting large sized specimens could yield significant information, for instance on the smallest morphs of large Baikalian species sampled in the shallowest locations (Takhteev & Mekhanikova, 1996). However, rearing amphipods is a time consuming and sometimes difficult task, especially for Antarctic and Baikalian species because of their slow growth rate and deferred maturity. Such experiments have been recently initiated on insects, and the preliminary results seem to support our hypothesis (Peck & Maddrell, unpublished).

This extension of oxygen limitation of maximum size to other groups also requires investigations. Such a latitudinal cline in maximum size has been described for caridean shrimps and brachyuran crabs, with no firm conclusions regarding its origin (Steele, 1988). We have also mentioned pycnogonids and nemerteans as possible targets for such size spectrum studies (Chapelle & Peck, 1999). Isopods, pelagic copepods, freshwater mites, flat worms or nematodes appear to be other good candidates, while a recent study on deep sea gastropods has yielded results showing a similar trend (McClain & Rex, 2001).

It is an intriguing coincidence that Pörtner and his colleagues demonstrated the upper lethal temperature of Antarctic bivalves to be oxygen dependent (Peck et al., submitted) precisely at the time we were building our own hypothesis, and it might show that oxygen effects has sometimes been overlooked by physiologists, in favor of most tangible parameters such as temperature, salinity or food supply.

One billion years ago, oxygen was excreted as a toxic waste by the first blue-green algae. Its concentration began to increase in the atmosphere and it was poisonous to life (Margulis & Sagan, 1986). Because of the evolution of new biochemical pathways, some hundreds of million years later, it became necessary for most living organisms, and its gradual increase has been proposed as the possible trigger of the Cambrian Explosion (Thomas, 1997). The highest levels, around 35%, were attained during the Carboniferous period, and this was correlated with giant size in insects such as dragonflies (Graham et al., 1995).

On the contrary, marine organisms like foraminiferans or mollusks that survived mass extinctions are often of minute size (Gould, 1996). Such cataclysmic events were usually followed by episodes of very low oxygen content in the world's oceans (e.g. Hsu, 1972; Harries, 1999), whether caused by asteroids or volcanism. In this context, our "oxygen ceiling" hypothesis might be of use to paleontologists working on the subsequent radiations, as it might explain some of the faunal relations seen either side of mass extinction events.

Finally, this study has also some environmental implications, as a reduction in oxygen, due to an organic pollution in Lake Baikal, or to a global increase in temperature in Antarctica, would be expected to affect primarily the largest species. These demanding needs for oxygen could be considered as a form of specialization, and could be an important factor making the giant species more prone to extinctions.

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Annex A : Consulted publications for size data

In this section, we give the comprehensive list of the240 publications consulted to establish the maximum size of the 2092 amphipod species used in this work. These publications have been divided per geographical area. The "Southern Ocean" list pools together references for the Subantarctic islands, the Magellanic region, South Georgia, West and East Antarctica.

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Lake Baikal

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Annex B: Baikalian amphipods publications.

Throughout these years, and thanks to our Russian colleagues from Irkutsk (mainly Irina Mekhanikova, Vadim Takhteev and Ravil Kamaltynov), a significant percentage of the papers devoted to Baikalian amphipods were collected and most of them were partly or entirely translated by Veronique Arkosi (IRSNB). This led to the establishment of one of the most extensive collections outside from Russia, and could facilitate the access to this literature for other English-speaking scientists.

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