



The growth, respiration, and reproduction of crustaceans: a synthesis through the Gill-Oxygen Limitation Theory (GOLT)

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ABSTRACT

Gill surface area (S) and respiration (R) in juvenile and adult crustaceans scale with their body weight (W) such that $S \propto R \propto W^d$, with d ranging mostly between 0.6 and 0.9, but always <1 , as in other water-breathing ectotherms (WBE). The growth of adult crustaceans therefore approaches an asymptote, whether or not seasonal growth oscillations are explicitly considered in the model used to describe that growth (e.g., von Bertalanffy growth function). On the other hand, the variation in asymptotic size (L_{∞} or W_{∞}) among crustaceans is primarily determined by water temperature, which impacts on the oxygen requirements of WBE. Through multiple examples, this and related aspects of the Gill-Oxygen Limitation Theory (GOLT), first developed for fishes and later extended to other WBE, are shown to also apply to the growth of a wide range of crustacean taxa. The GOLT also explains certain aspects of crustacean reproduction, such as the relationship between size at first maturity and maximum size, and, possibly, the feature that female crustaceans hold their eggs outside of their bodies instead of internally.

KEY WORDS: asymptotic size, Bertalanffy growth function, oxygen consumption in water-breathing ectotherms, reproductive biology, seasonal growth oscillation, size at first maturity, temperature-size relationships

INTRODUCTION

Major scientific advances occur when the hypothesis or theory providing the explanation for a class of phenomena also can be used, without substantial modifications, to explain another class of phenomena (Keas, 2018). The Gill-Oxygen Limitation Theory (GOLT) was developed mainly to explain regularities in the growth, respiration, and reproduction of bony fishes (Pauly, 1979) and precisely predicts these patterns in a variety of fishes, from fast-swimming tuna to gliding seadragons (Pauly, 2021a; Pauly *et al.*, 2022a). Here we examine the efficacy of the GOLT in predicting the patterns of growth and reproduction in crustaceans. Crustaceans are often perceived as different enough from fishes, principally because of their moulting, to require different models to describe their growth and other life-history patterns (Breen, 1994; Foo, 2019, 2020;

Zeng & Wan, 2000). As shown below, however, this may not be necessary in most cases.

Key features of each of the phenomena examined herein (growth, respiration, and reproduction) are best interpreted within the context of the GOLT, as opposed to taxonomic specificity. The generality of the GOLT applied to crustaceans is demonstrated by a few examples from various groups of crustaceans. We refer to water-breathing ectotherms (WBE) when there is no need to specify taxa; all scientific names mentioned herein were verified against the World Register of Marine Species (WoRMS) (<https://www.marinespecies.org/>). Table 1 presents and briefly defines the parameters of the few equations presented below.

Table 1. Definitions of the parameters (and their units), symbols, and acronyms used in this article

Item (unit)	Definition
α	Proportional to...
α	Multiplicative term in relationship linking gill surface and weight, i.e., $S = \alpha \cdot W^d$
a	Multiplicative term of a length-weight relationship, i.e., $W = a \cdot L^b$
b	Exponent of a length-weight relationship, i.e., $W = a \cdot L^b$
C	A fraction (≤ 1) quantifying the amplitude of seasonal growth oscillations
C.I.	Confidence interval (here 95%)
d	Exponent in a relationship linking respiratory surface and weight, i.e., $S = \alpha \cdot W^d$
D or D'	$D = b \cdot (1-d)$ or $D' = 3 \cdot (1-d)$, used to simplify some equations
dW/dt	Growth rate, in weight (or mass)
F	Here: dummy variable, with $F = 0$ for fresh and $F=1$ for frozen stalked barnacles
H	Coefficient of anabolism, i.e., of protein synthesis
k (year ⁻¹)	Coefficient of catabolism; here: of protein denaturation. Note: $k = 3K$
K (year ⁻¹)	In the VBGF, the rate at which asymptotic size is approached
L (cm)	Any measure of length (e.g., cephalothorax), with L_t the length at age t
L_∞ (cm)	Asymptotic length in the VBGF, as reached after an infinitely long time
L_m (cm)	Mean length at first maturity in a given population
L_{max} (cm)	Maximum length in a given population; generally close to L_∞
LWR	Length-weight relationship, of the form $W = a \cdot L^b$
NGT	A period of zero growth (in length) occurring seasonally
Q_m	Weight-specific oxygen consumption at first maturity
Q_{maint}	Weight-specific oxygen consumption at maximum or asymptotic weight
s	A variable in the seasonally oscillating growth curve (Equation 4)
S (cm ²)	A surface, here respiratory surface, i.e., gill surface area, as in $S = \alpha \cdot W^d$
t (year)	Absolute age; relative age = $t - t_0$
t_0 (year)	The usually negative 'age' at $L = 0$ predicted by the VBGF
t_s	A fraction of the year (≤ 1) when seasonal growth is most rapid
W (g)	Weight (or mass); W_t is weight at age t ; here fresh, or wet weight
W_∞ (g)	Asymptotic weight in the VBGF, as reached after an infinitely long time
W_m (g)	Mean weight at first maturity, weight corresponding to L_m
W_{max} (g)	Maximum weight in a given population, generally close to W_∞
WBE	Water-breathing ectotherms (fishes, crustaceans, and other invertebrates that breathe water)
WP	Winter Point, i.e., the fraction of the year (≤ 1) when seasonal growth is slowest

THE GOLT: GROWTH AND RESPIRATION OF WBE, WITH AN EMPHASIS ON CRUSTACEANS

Pütter (1920) appears to have been the first to conceive the growth (dW/dt) of WBE as being the net result of two processes with opposite tendencies, i.e.,

$$\text{Corrected: } dW/dt = HW^d - kW \quad (1)$$

where HW^d is conventionally referred to as 'anabolism' and kW as 'catabolism.' Based on von Bertalanffy (1951) and Pauly (2019, 2021a), H is defined herein as the rate of synthesis of body proteins while k is defined as the net rate of (spontaneous) denaturation of proteins.

One major difference between these two processes is that the HW^d term requires free oxygen, typically supplied by the gills of a WBE, whereas the kW term, which only encompasses the loss of the quaternary structure of proteins, does not require an oxygen supply (Nelson & Cox, 2017). Another major difference is that anabolism is limited by the respiratory surface (S) of the WBE in question, which scales with body weight (W) according to $S \propto$

W^d with $d < 1$, whereas protein denaturation scales in direct proportion to body weight. Note that the d parameter (also defined in Table 1) can be estimated either via studies of gill surface area or through respiratory studies because the amount of oxygen diffusing through gills is, among other things, proportional to respiratory surface area (Fick, 1855).

As WBE grow and their weight (W) increases, the anabolic term of equation (1), because of its exponent $d < 1$, cannot keep up with the catabolic term, and growth ends at the asymptotic weight (W_∞), i.e., when

$$\text{Corrected: } HW^d kW = 0 \quad HW^d - kW = 0 \quad (2)$$

Asymptotic growth, resulting from $d < 1$, is therefore a necessary condition for the GOLT to apply to crustaceans, though it is not a sufficient one.

In fishes, d ranges from about 0.60 to 0.90 (Muir & Hughes, 1969; De Jager & Dekkers, 1975; Pauly & Cheung, 2017). There is a strong tendency for fish species that remain small (e.g., gobies and guppies) to have gills with $d \approx 0.60$ (Bertalanffy, 1951; Pauly, 1982), whereas species capable of reaching large

sizes have higher values (i.e., $d \approx 0.85\text{--}0.90$). This is similar to crustaceans, where the tiny brine shrimp *Artemia salina* (Linnaeus, 1758) has gills growing approximately according to the 'surface rule,' i.e., $S \propto W^{2/3}$ (Fig. 1), whereas larger crustaceans (but not their larvae, where $d \geq 1$) can be shown to have values of d similar to those of fishes of the same size (Fig. 2). The relationship between oxygen consumption on body weight is well documented for many crustaceans, e.g., Bridges & Brand (1980) for decapod crustaceans.

Given the preceding considerations, the claim can be made, even if their moulting has the effect of growth proceeding in steps, that crustaceans grow asymptotically in general, with their maximum (L_{\max} and W_{\max}) or asymptotic size (L_{∞} and W_{∞}) often corresponding to a terminal moult when such occurs (Vogt, 2012).

Asymptotic growth is best represented by the von Bertalanffy Growth Function (VBGF), which, for $d = 2/3$, has the form:

$$L_t = L_{\infty} \left(1 - e^{-K(t-t_0)} \right) \quad (3)$$

where L_t is the length at age t , L_{∞} is the asymptotic length, i.e., the mean length the individuals of a given population would reach if they were to survive and grow indefinitely, K is the rate (year⁻¹ herein) at which L_{∞} is approached, and t_0 is the age at which $L = 0$. For illustration, Figure 3 documents asymptotic growth in populations of four crustaceans widely differing in size and

habitat, i.e., a common water flea (Fig. 3A), Antarctic krill (Fig. 3B), Southern rock lobster (Fig. 3C), and red king crab (Fig. 3D).

The growth of WBE in general, and of crustaceans in particular, tends to oscillate seasonally, usually as a result of temperature fluctuations. Seasonal growth can be readily described by a seasonally oscillating version of the VBGF (Somers 1988; García-Berthou et al., 2012), i.e.,

$$L_t = L_{\infty} \left\{ 1 - \exp - [K(t - t_0) + s(t) - s(t_0)] \right\} \quad (4)$$

where $s(t) = (CK/2\pi) \cdot \sin(2\pi(t - t_s))$, $s(t_0) = (CK/2\pi) \cdot \sin(2\pi(t_0 - t_s))$, and L_{∞} , K and t_0 are defined as above.

Equation 4 requires two parameters more than the standard VBGF: C and t_s . Of these, the former expresses the amplitude of growth oscillations; when $C = 0$, Equation 4 turns back into Equation 3; when $C = 0.5$, the seasonal growth oscillations increase growth by 50% at the height of summer, and reduce it by 50% in the depth of winter. When $C = 1$, growth rates increase by 100%, doubling at the height of summer, and becoming zero for a day in the depth of winter. The other new parameter, t_s , expresses the time between $t = 0$ and the start of a growth oscillation. However, we define $t_s + 0.5 = \text{WP}$ ('winter point'), expressed as a fraction of the year, and represents the period when growth is slowest. WP is usually near 0.1 (= early February) in the Northern Hemisphere and 0.6 (early August) in the Southern Hemisphere.

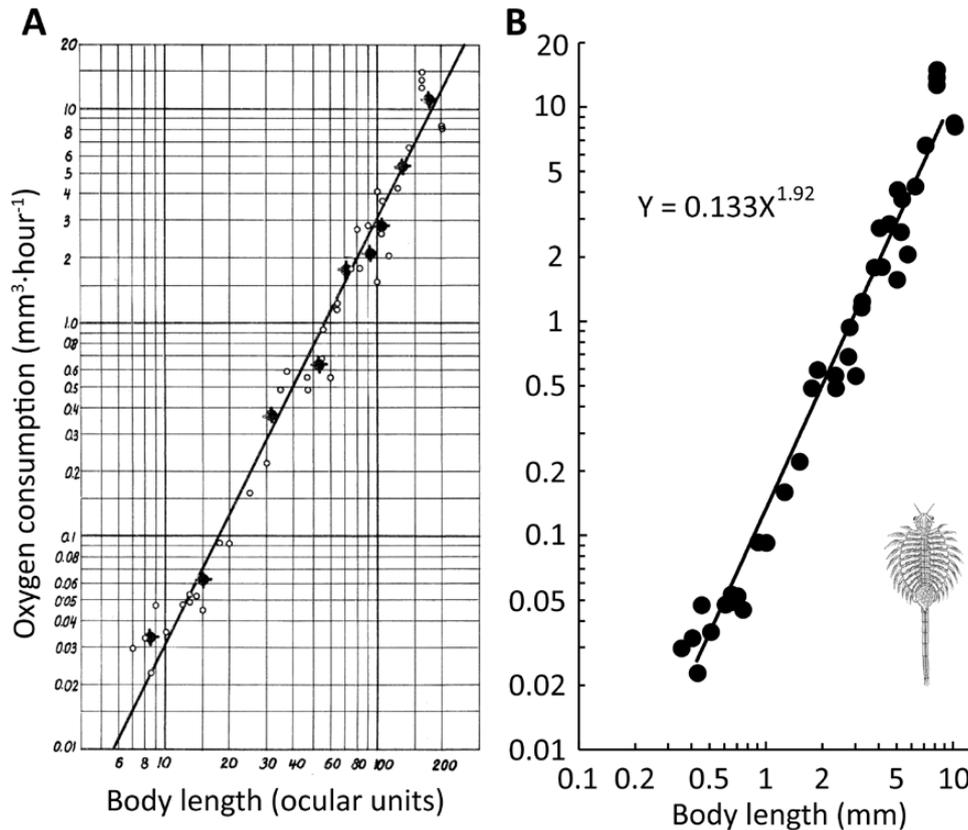


Figure 1. Oxygen consumption of the brine shrimp *Artemia salina* as a function of their length. Reproduction of the graph published by von Bertalanffy & Krywienczyk (1953), showing how they 'guesstimated' from the black dots (i.e., the means of the white circles) a slope of 2 for the $\log(\text{O}_2 \text{ consumption})$ vs. $\log(\text{length})$ relationship (A). Plots of the actual data in A (the small white circles, large black dots herein), showing that the slope was 1.92, corresponding to $d = 0.64$ (B).

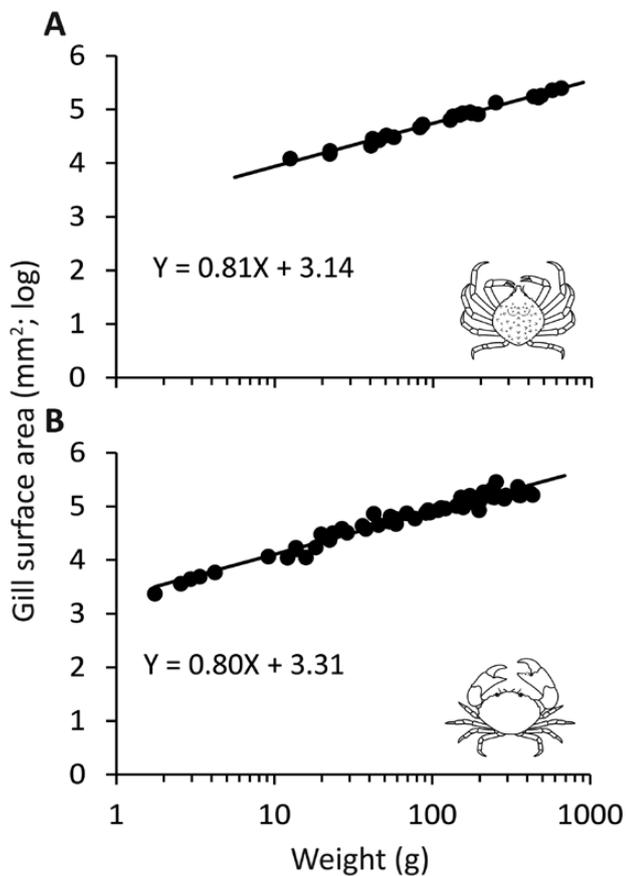


Figure 2. Relationship between the gill surface area of crabs and their live (or wet) weight depicted on a log scale; adapted from Gray (1957). Portly spider crab (*Libinia emarginata* Leach, 1815) (A); stone crab, *Menippe mercenaria* (Say, 1818) (A).

Equation (4) can be used where the WBE maintains a positive growth rate (in length) throughout the year, as illustrated in Fig. 4A, with Figs. 4B, C illustrating the role of the amplitude parameter. When growth in length ceases entirely for an extended period, the no-growth time (NGT) can be estimated by a modification of Equation 4, developed by Pauly *et al.* (1992), and which is now implemented in the R-software (Ogle, 2017; see Fig. 5). Note, however, that an estimate of no-growth time is not an estimate of the an intermoult period, although NGTs and intermoult periods may accidentally overlap.

Another temperature effect on the growth of WBE, including crustaceans, i.e., the fact that adults are smaller at higher temperatures, can be straightforwardly predicted from Equation 1, whose anabolic term is less sensitive to temperatures than the catabolic term. Thus Darwin (1854: 264) noted, with regards to the cretate barnacle (*Balanus crenatus* Brugière, 1789), that [t]he arctic specimens, and those from the northern United States, are larger than the British. This is because above 5 °C, higher temperatures increase the spontaneous denaturation of proteins and force WBE to resynthesize new ('native') proteins. Given scarce respiratory oxygen, this has the effect that the WBE approach faster a weight at which $HW^d = kW$.

Adult (and maximum) size in crustaceans thus declines with temperature as illustrated in Figure 6A for the west Australian

rock lobster (*Panulirus cygnus* George, 1962), and as predicted by various temperature-size relationships.

In terms of the VBGF's parameters, this results in asymptotic length (L_{∞}) being reduced and K increasing, and the VBGF parameters for the various populations of the same or closely related species forming ellipsoid clusters on 'auximetric' plots (Pauly, 1998a, 2019; see Fig. 7). Such plots can be extended to cover disparate taxa and used, for example, to compare their growth and/or identify outliers. The growth of WBE with widely different shapes (e.g., copepods vs. lobsters), however, cannot be compared reliably in terms of length and should be performed using weights, as in the insert of Figure 7, featuring penaeid shrimps.

The length-weight relationships (LWR) in fishes are used for this purpose, among other things. They usually have the form $W = a \cdot L^b$, where b , past the larval stage, usually ranges between 2.5 and 3.5 (Froese, 2006), although there are noteworthy exceptions (Pauly *et al.*, 2022a). This is also the case in crustaceans (Fig. 8A), and the exceptions here are also of interest. Thus, for the stalked barnacle, or *percebes* (*Pollicipes pollicipes* (Gmelin, 1791)), an LWR relationship of the form

$$\log(W) = 1.81 + 0.1195 \cdot F + 1.484 \cdot \log(L) \quad (5)$$

was estimated, where W is the wet weight in g, L is the total length (2.4–8.4 cm), based on 57 fresh specimens caught in Baiona (northwest Spain; 42°7.64' N and 8°52.04' W) in January 2022, for which the dummy variable $F = 0$, with $F = 1$ for 40 specimens caught and frozen earlier (Supplementary material Table S1 and Fig. S5). This allowed for all available L – W data pairs to be used, and at the same time, for a significant effect of freezing on the weight of stalked barnacles to be identified (Supplementary material Table S2) and for two LWRs to be estimated, one for fresh specimens ($W = 0.015 \cdot L^{1.484}$), and the other for frozen specimens ($W = 0.020 \cdot L^{1.484}$), both of which relate weight to length via an exponent $\ll 3$ (Fig. 8B).

The GOLT and crustacean reproduction

Reproduction in crustaceans is a complicated affair that no single review can cover exhaustively. Although we reflect on possible links between the GOLT and various aspects of crustacean reproduction below, our emphasis is on one issue: the concordance between the GOLT and the fact that, at least in lobsters and other long-lived crustaceans, reproduction usually occurs when an individual is several years old. One fundamental question arises: what initiates spawning in the year that spawning occurs?

Barring exceptional circumstances, any year and spawning season is like the others and the trigger for spawning must be found in the individual lobster in question. It is likely not its absolute age (though computer models of lobster populations frequently use 'age' as the trigger), and it also cannot be a critical size because size is temperature-dependent (see above), and spawning should be possible at all tolerated temperatures. Research on teleost fishes summarized in Pauly (2021b) suggests that the triggering mechanism for maturation and spawning must precede the environmental stimuli that are conventionally stated to trigger maturation and spawning, and that this trigger is, for an individual WBE, the ratio between its current oxygen

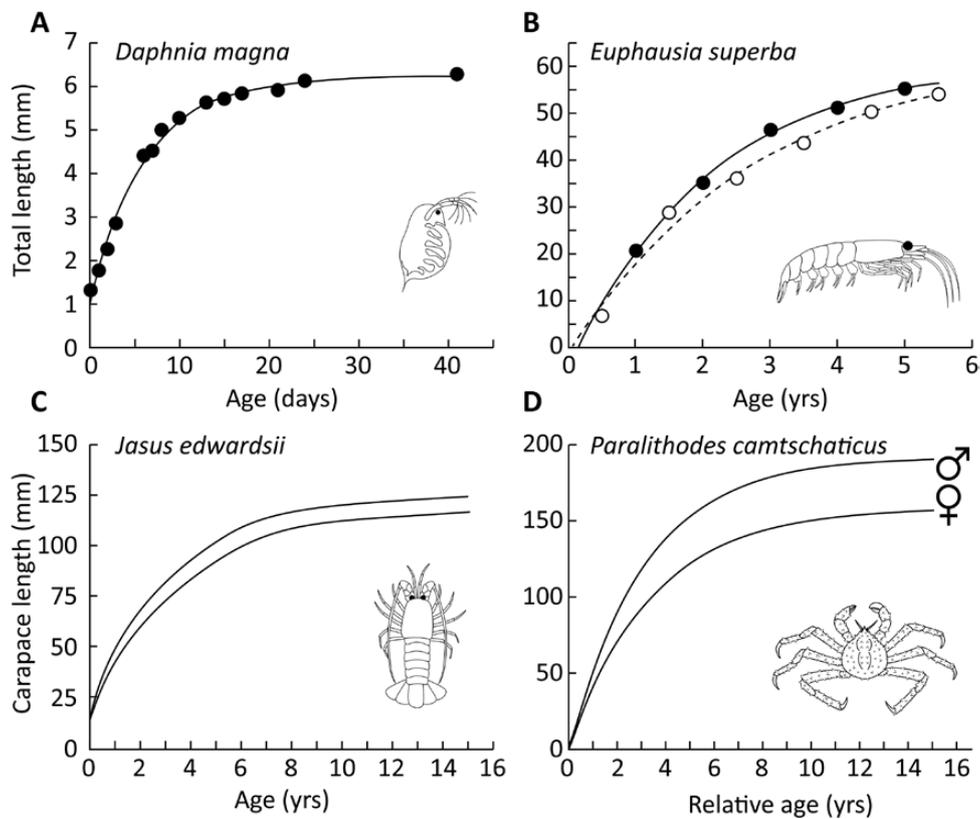


Figure 3. Asymptotic growth in four crustaceans, the cladoceran (*Daphnia magna* Straus, 1820) at 20 °C (modified from Martínez-Jerónimo, 2012) (A); Antarctic krill (*Euphausia superba* Dana, 1850) sampled in 1977 (black dots) and 1981 (circles), modified from Siegel (1987) (B); the red rock lobster *Jasus edwardsii* Hutton, 1875) at two localities in New Zealand, adapted from McKoy & Esterman (1981) (C); and red king crab *Paralithodes camtschaticus* (Tilesius, 1815), adapted from Windsland *et al.* (2013) (D).

supply (Q_m) and the oxygen supply corresponding to its maintenance metabolism (Q_{maint}) (Fig. 9A).

We hypothesize that the same mechanism applies to crustaceans. Thus, as lobsters grow according to Equation 1, their Q_m/Q_{maint} ratio declines (because $d < 1$) and they experience more frequent periods of internal hypoxia, especially after a strenuous activity. This ratio drops so low at some point as to be equal to unity, and there will be no surplus oxygen to produce eggs and sperm. Maturation and spawning must therefore be triggered at a size corresponding to an oxygen consumption $Q_m > Q_{\text{maint}}$, with the weight at which Q_m occurs declining when Q_{maint} increases, such as occurs at higher temperatures (Fig. 9B; see also Fig. 6A).

In bony fishes, this trigger is ensured by a fixed Q_m/Q_{maint} ratio ~ 1.35 with a 95% confidence interval of 1.23–1.53 (Pauly, 1984, 2021b; Amarasinghe & Pauly, 2021; Chen *et al.*, 2021; Meyer & Schill, 2021). The Q_m/Q_{maint} ratio can be shown to be mathematically equivalent to $(L_{\text{max}}/L_m)^D$, where $D = b \cdot (1-d)$, b being the exponent of the LWR, and d the species-specific scaling factor between the respiratory area and weight (Table 1). To apply this to decapods, we sought values of L_m , L_{max} , b , and d from palinurid lobsters and crabs (Fig. 9C, D based on the data in Supplementary material Tables S3, S4, respectively). Those data suggest a mean Q_m/Q_{maint} ratio of 1.46 and 1.42, respectively, which is within the confidence interval of this ratio as estimated for bony fishes.

These results suggest not only that the heuristic (*sensu* Budaev *et al.*, 2019) providing the trigger for maturation and spawning

in crustaceans may be the same as for fishes, but that the threshold Q_m/Q_{maint} ratio is roughly similar to that observed in fishes. Studies on other groups of crustaceans should provide additional tests of the generality of these results. But for now, the data for decapods suggest that the life-history constraints on (large) crustaceans are similar enough to those of fish to have led to the emergence of the same heuristics that initiate maturation and spawning (Morbey & Pauly, 2022).

Seasonal changes in size-specific crustacean reproductive phenology driven by temperature may also be tied to the GOLT. In temperate seas, most crustaceans extrude their eggs (i.e., spawn) in the spring as water temperatures rise and therefore the metabolic cost of internal egg provisioning of oxygen increases. Similarly, in deep-sea isopods (suborder Asellota) significantly more females (25%) brood eggs during the winter months compared to the summer (5%) (Harrison, 1988). It is also common for the largest females to spawn first within the spawning season (Minagawa *et al.*, 2000; Butler *et al.*, 2015; Marciano *et al.*, 2021), which is consistent with predictions of the GOLT as rising seawater temperatures challenge larger individuals more than smaller conspecifics. Other crustaceans, particularly in warm-temperate or tropical areas, spawn throughout the year and in some cases repeatedly during a spawning season (Restrepo & Watson, 1991). Repeated in-season spawning in contrast to one spawning season per year also occur in fishes and are consistent with predictions of the GOLT (see Pauly, 2019; Pauly & Liang, 2022) and those arguments can potentially be extended to crustaceans.

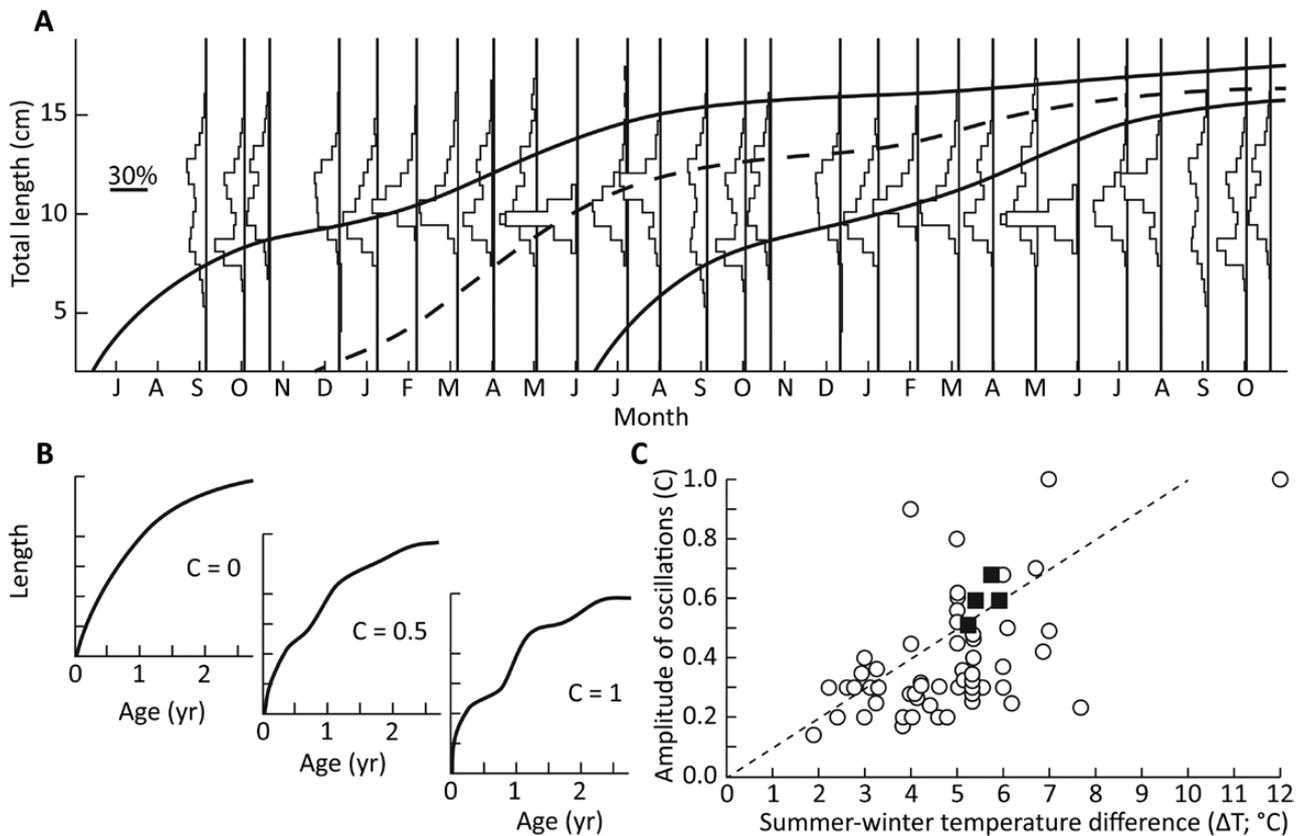


Figure 4. Seasonal growth in crustaceans. Seasonal growth of male pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) (= *Penaeus duorarum*), from the Dry Tortugas, Florida, 1957/58, with $L_{\infty} = 17.6$ cm, $K \approx 1.3$ year $^{-1}$, and $C = 0.6$ (from Pauly et al., 1984, based on length-frequency data in Iversen et al., 1960) (A). Effect of different values of C on growth curves (B). Relationship between the summer-winter temperature differences (in $^{\circ}\text{C}$) and estimates in fishes and invertebrates, including four species of penaeid shrimps (black squares; from Pauly et al., 1984 and Pauly, 2019) (C).

Limitations imposed by the GOLT may also explain the remarkable feature that female crustaceans, ranging from the smallest copepods to the largest lobsters, carry fertilized eggs outside their bodies. Thus, their eggs are supplied with oxygen from the water surrounding them, rather than through the flow of hemolymph inside their bodies, that in turn is supplied with oxygen through gills. Similar behavior occurs only in a few bony fishes, members of Syngnathidae (i.e., seadragons, seahorses, and pipefishes) that have small, inefficient gills (Pauly et al., 2022a), and in five species of ‘pelvic brooders’ in the family Adrianichthyidae (Gani et al., 2022). For large, cold-water decapods (e.g., clawed lobsters, king crabs) the developmental period for eggs is nearly a year and therefore would represent a huge oxygen demand on the female if eggs developed internally.

Crustaceans like some copepods, euphausiids, and dendrobranchiates do not brood eggs and instead are broadcast spawners, which nevertheless serves the same function of relieving the female from the additional oxygen demand posed by carrying developing eggs internally but without the advantages of material investment. These broadcast spawners are largely limited to smaller, effectively planktonic taxa, which suggests a striking evolutionary divergence from the benthic crustacean norm. External egg development in most crustaceans and arthropods, whether expressed as external egg brooding, broadcast spawning, or demersal egg deposi-

tion, has generally been perceived as an evolutionary solution to limits on the storage space for eggs contained within a rigid exoskeleton (Hines, 1992). But if necessary for successful reproduction, what is to have prevented the evolution of larger carapaces or of different shapes to provide more internal space for egg development? Alternatively, there often is unused internal space inside the crustacean carapace that is filled by water when crustaceans lose weight. So, it remains that most crustaceans are not broadcast spawners, nor do they bury or ‘abandon’ their eggs as do many terrestrial arthropods: they brood them externally, which is peculiar and bears some explanation as we have attempted within the context of the GOLT. The notion that the GOLT may explain that the fertilized eggs of most crustaceans develop outside of their bodies is a hypothesis that requires further scrutiny.

The GOLT and crustacean behavior

Recognizing the constraints posed by the GOLT on crustaceans may also help interpret observed patterns in their behavior and activity. For example, approached by a predator, large crustaceans are typically less apt to flee than smaller individuals (Lang et al., 1977; Bouwma, 2006), which can be explained by size-dependent differences in defensive capabilities or perhaps constraints on their ability to flee. If large crustaceans do flee, they cannot match the endurance of small individuals.

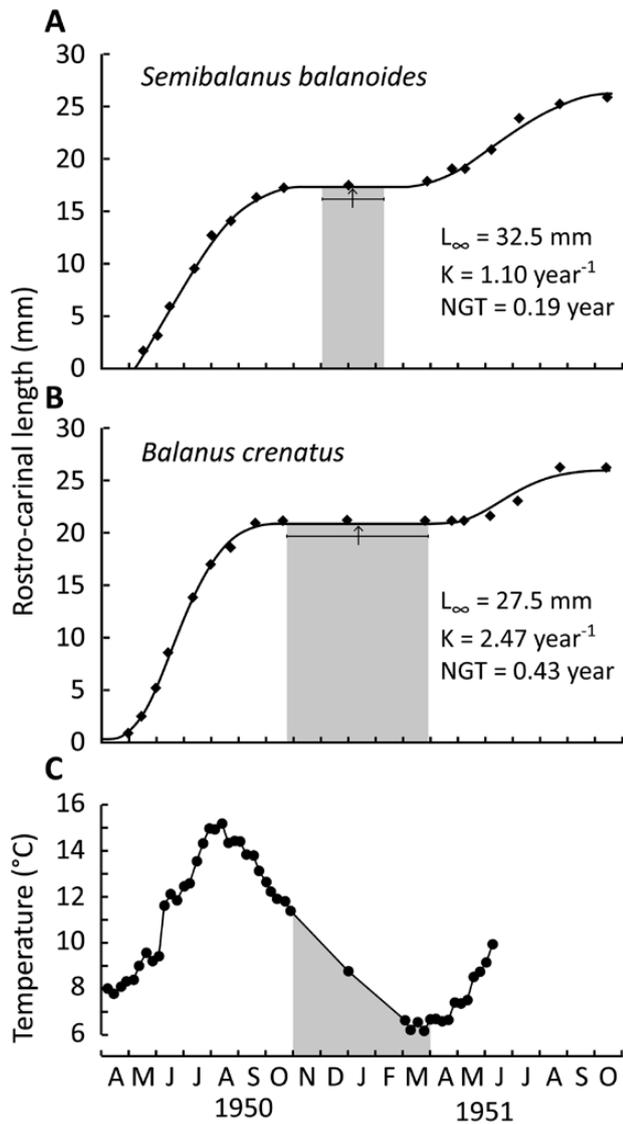


Figure 5. Seasonal growth barnacles. Northern rock barnacle *Semibalanus balanoides* (Linnaeus, 1767), confirming the life span suggested in Darwin (1854) (A); crenate barnacle (*Balanus crenatus* Bruguière, 1789 [Bruguière, 1789–1792] (B). A and B were based on growth curves in Figure 1 in Barnes & Powell (1953), fitted with the software of Ogle (2017) allowing for no-growth periods in winter (NGT; in grey) when temperatures (same source as the growth data) are dropping (in grey in C).

Laboratory studies of tail-flip escape response of the brown shrimp *Crangon crangon* (Linnaeus, 1758) investigated across a range of body lengths using high-speed video analysis revealed a decrease in the efficiency of tail-flips as shrimps increase in size (Arnott *et al.*, 1998). Physiological studies also demonstrate that the aerobic scope for activity decreases significantly with weight and that activity such as tail flipping to avoid predators has the largest influence on oxygen consumption (Crear & Forreath, 2000; Jimenez *et al.*, 2008; Kemp *et al.*, 2009). Indeed, large decapod crustaceans typically take around 8 h to return to pre-exercise levels of oxygen consumption after a period of exercise (McMahon *et al.*, 1979; Field *et al.*, 1991). This size-specific difference in escape behavior and limits to aerobic endurance is consistent with the GOLT.

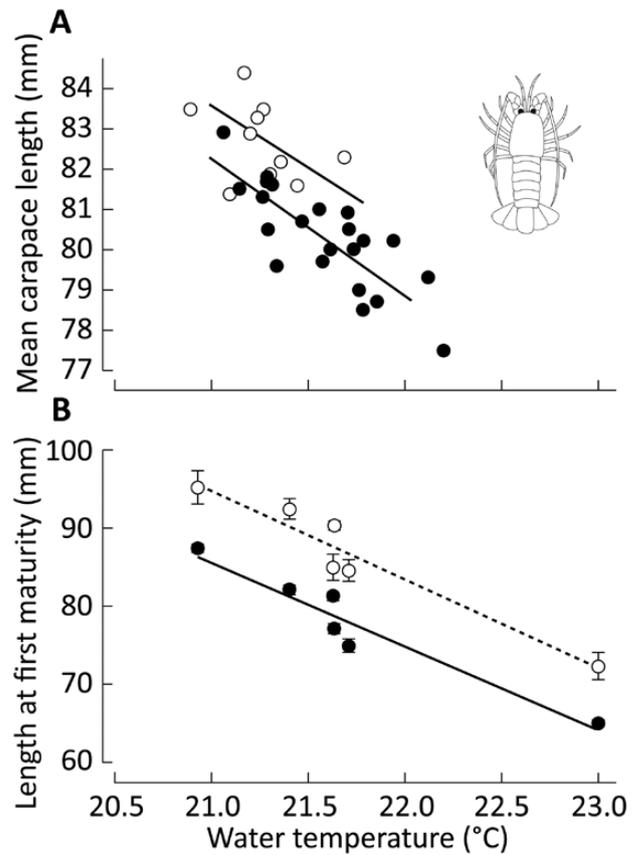


Figure 6. Effect of temperature on growth and reproduction of West Australian rock lobster (*Palinurus cygnus*). Decline of the standardized carapace length of migrating adults vs. the mean water temperature four years earlier (modified from Caputi *et al.*, 2010) (A); length at which 50% of rock lobster reach first maturity vs. mean temperature (modified from Melville-Smith & De Lestang, 2006) (B).

Activity levels of WBE after feeding is also influenced by oxygen availability because an increase in oxygen consumption is associated with the extra energy required for transportation of food in the alimentary tract, its digestion, absorption, and post-absorptive metabolic processes collectively referred to as specific dynamic action or SDA (Jobling, 1981). This is also true of large crustaceans whose aerobic scope for activity is reduced, often for hours, after feeding (Crear & Forreath, 2001). Looking into the future, Simões *et al.* (2021) have hypothesized that both shallow-water and deep-sea crustaceans will shift their distribution ranges poleward because of rising sea temperatures and the associated strain of oxygen-limitations on crustacean physiology and activity.

DISCUSSION

As air-breathing animals, it is perhaps difficult for us to conceive that oxygen availability could have such profound effects on WBE growth, reproduction, and behavior because, for terrestrial animals, oxygen limitation is rarely experienced except at high altitudes. The conditions are different for aquatic animals. Although oxygen concentration in our current atmosphere is ~ 21%, it is only 0.75% in the sea. Moreover, the availability of oxygen on Earth has varied

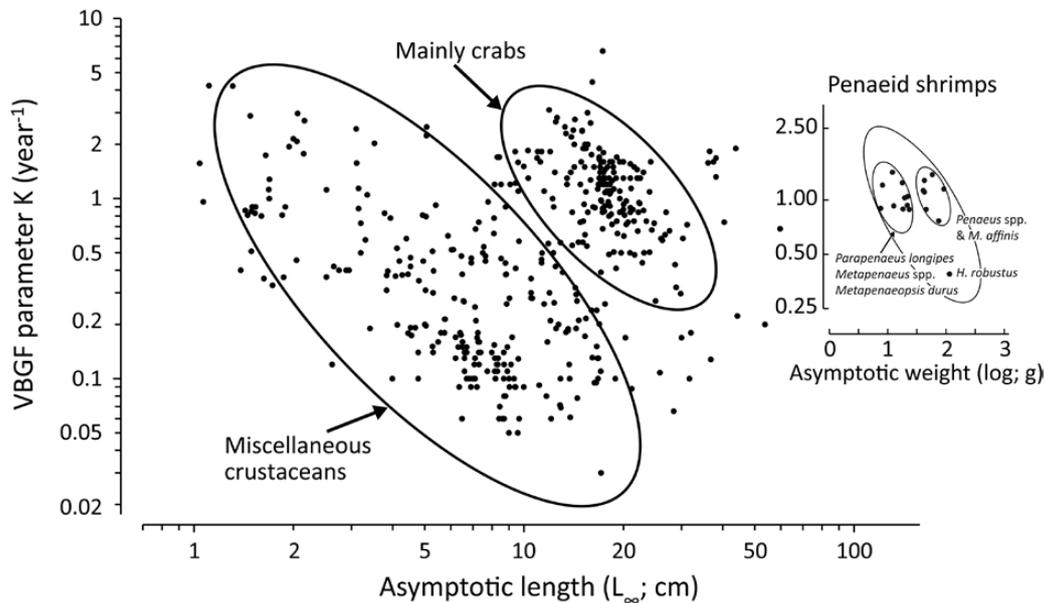


Figure 7. Auximetric plots for crustaceans, double-logarithmic plots of the von Bertalanffy parameter K vs. the corresponding asymptotic length in the larger plot, with each dot (i.e., K - L_{∞} pair) describing a growth curve documented in www.sealifebase.org. The insert (adapted from Pauly *et al.*, 1984) documents the tighter fit obtained when W_{∞} values are used instead of L_{∞} values.

dramatically in geologic time. Crustaceans first appeared during the Cambrian species explosion (~ 450 mya) after oxygen concentrations rose from ~5% to ~15% (Krause *et al.*, 2018), but large decapod crustaceans only emerged later during the Devonian once atmospheric oxygen concentrations reached near present levels (Ward, 2006; Wolfe *et al.*, 2019).

Patterns in the growth, respiration, and reproduction of various crustaceans presented above suggest that key features of the life-history of crustaceans can be explained by the effect of the 'dimensional tension' (Pauly & Cheung, 2017) between the growth of their gills and that of their bodies as articulated by the Gill-Oxygen Limitation Theory (GOLT). The simplicity and generality of the fact that physical constraints limit oxygen availability for WBE, hence their biology, suggests that the implications of the GOLT emerged very early in the evolution of metazoans and is conserved in various taxa, including crustaceans. This aligns with recent demonstrations of the applicability of the GOLT from sponges, the earliest metazoans (Pauly *et al.*, 2022b), which first appeared 890 mya (Turner, 2021). The growth of large, near-spherical sponges is asymptotic and appears to be limited by oxygen supply to their interior as predicted by the GOLT (Pauly *et al.*, 2022b). Pauly & Holmes (2022) also showed that the growth of at least one species of trilobite that roamed the seafloor 450 mya conformed to the VBGF. A Q_m/Q_{maint} ratio of 1.34 (for $d = 2/3$) can also be computed from the length at first maturity and the maximum lengths of trilobites in McNamara (1978: fig. 6), pertaining to five species of *Olenellus* from the Early Cambrian.

The GOLT was initially developed to explain features of the growth of fishes (Pauly, 1979), but has since been extended to water-breathers in general (Table 2) and appears robust enough to suggest a unified hypothesis: 'A theory that

exhibits simplicity explains the same facts as rival theories, but with less theoretical content. A unified theory, however, is one that explains more kinds of facts than rival theories with the same amount of theoretical content' (Keas, 2018: 2275, citing Thagard, 1978).

Even as a unified theory, the GOLT does not explain everything crustaceans do; however, it limits what they can do under constraints such as hypoxia and/or elevated temperatures. The applicability of the GOLT suggests that fishes, crustaceans, and other WBE are subjected to the same constraints: scarce oxygen in the medium they inhabit and a scarce oxygen supply via their gills relative to the demands of their body tissues and their (potential) activity levels. Physics dictates that the surface area of gills needed for the acquisition of oxygen can never 'catch up' to the biological oxygen demand of a three-dimensional organism. Gill surface area therefore sets the maximum rate of oxygen procurement that, in reality, may not be realized. There is a price to evolving gills with a large surface area. For example, large gills themselves require energy, are more easily clogged by suspended particulate matter, and are a favored site for the attachment of various parasites (Davies *et al.*, 2014; Jansen *et al.*, 1998). Crustaceans and other WBE therefore have the gill surface area that they need to grow rapidly to adulthood, but not more, which is the reason why the oxygen supply of WBE become limiting as they continue to grow.

Admittedly, much of the behavioral and reproductive evidence from crustaceans that can be marshalled to evaluate the relevance of the GOLT is based on studies performed with other purposes. So far, there have been no comprehensive reviews of data or direct experimental tests of the GOLT for crustaceans. What we hope to have established, however, is that many physiologically driven aspects of crustacean biology are consistent with the GOLT.

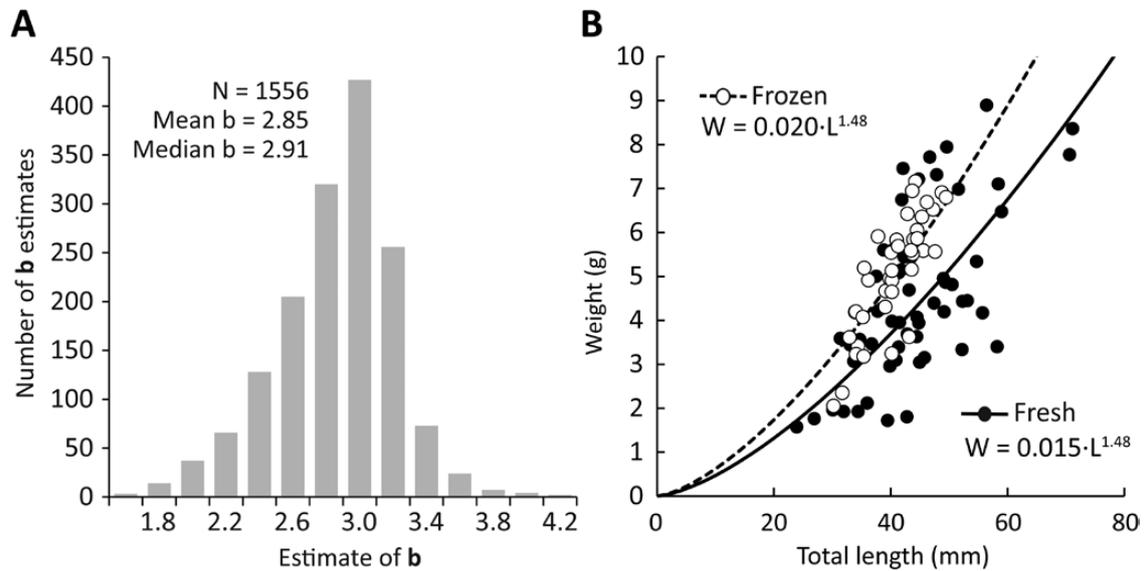


Figure 8. Length-weight relationships (LWR) in crustaceans. Frequency distribution of the parameter b of length-weight relationships of the form $W = a \cdot L^b$ in 1,566 populations of crustaceans (from www.sealifebase.org) in 370 species, 193 genera, 80 families, 8 orders, and 2 classes, ranging 1.52–4.13. Mean $b = 2.86$, median 2.91, and standard deviation 0.354. Note the tendency toward negative allometry (i.e., values of $b < 3$) (A). Two LWR for fresh (filled dots) and frozen (open dots) stalked barnacle (*Pollicipes pollicipes*) with very pronounced negative allometry (B).

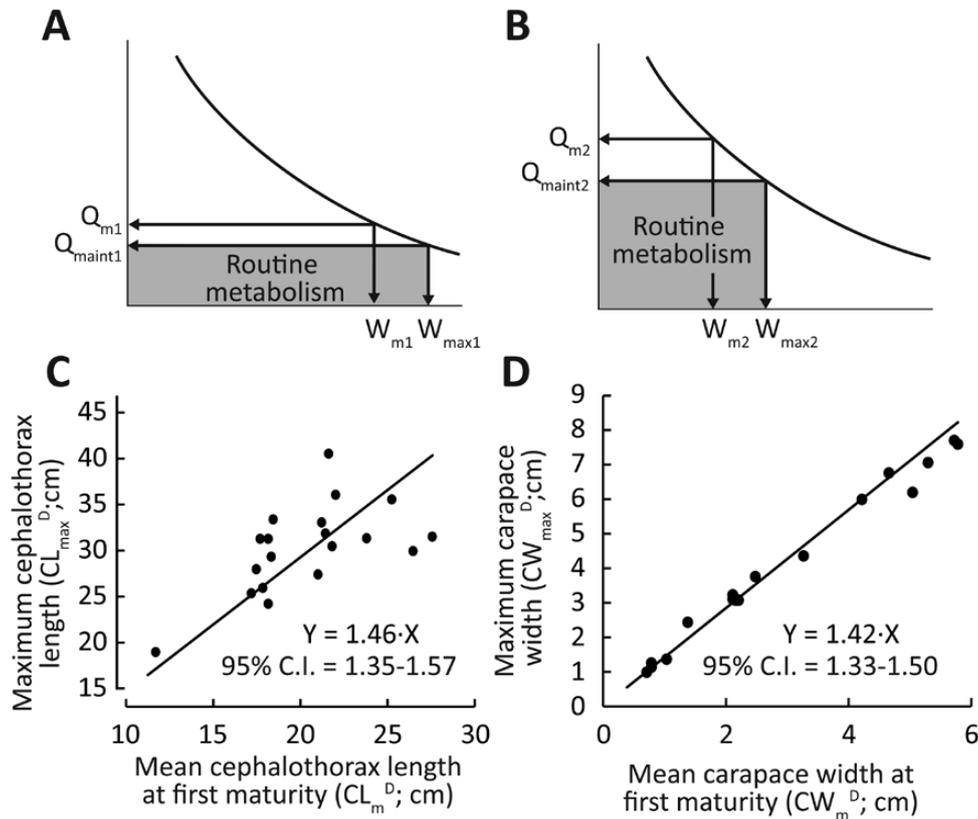


Figure 9. Relationships between size at first maturity and maximum size in WBE. Given that gill area per weight declines with weight, relative oxygen supply (Q) also declines, down to the minimum level possible at the maximum weight (W_{\max}), where all available oxygen is used for maintenance (Q_{maint}) (A). This implies that maturation and spawning must occur at $Q_m > Q_{\text{maint}}$. When temperature increases, Q_{maint} increases, and thus Q_m must also increase to remain $> Q_{\text{maint}}$ (B). This is ensured by a fixed Q_m/Q_{maint} ratio, which is similar in palinurid lobsters (C) and crabs (D), i.e., 1.46 (95 % C.I. = 1.35–1.57) and 1.42 (95 % C.I. = 1.33–1.50), respectively (see [Supplementary material Tables S3, S4](#) for species and data sources).

Table 2. Non-exclusive list of criteria that should be met for the Gill-Oxygen Limitation Theory (GOLT) to apply to a given taxon of water-breathing ectotherms (WBE). Note that criterion no. 1 is a necessary condition, whereas 2–8 are sufficient conditions (see text). ¹The singular is used when the reference in question dealt with only one species. ²Except for very cold environments where cold denaturation can also cause sizes to decline (Pauly, 1979; Lavin et al., 2022), and which also appears to occur in crustaceans (Burmeister & Sainte-Marie, 2010).

No.	Criterion for the GOLT to apply...	...to miscellaneous taxa ¹	including crustaceans
1	Growth rates decline asymptotically after metamorphosis. This also implies that food conversion efficiency must decline with size	Sponge (Pauly et al., 2022b); jellyfishes (Palomares & Pauly, 2009); trilobite (Pauly & Holmes, 2022); chaetognaths (Pauly et al., 2021); pteropod (Wang et al., 2017); gastropod (Pauly & Calumpo, 1984); cephalopods (Pauly, 1998b, 2019); cephalochordates (Pauly & Chu, 2021); fishes (Pauly, 1986, 2019, 2021a)	See Figures 3, 4; Dwiponggo et al. (1986); Wyban et al. (1995); Robertson & Butler (2003), Frisch (2007); Ehrhardt (2008); Crowley et al. (2019)
2	The oxygen consumption in adults must be proportional to W^d , with d ranging 0.5–0.9	Sponge (Pauly et al., 2022b); jellyfishes (Palomares & Pauly, 2009); planarian (Whitney, 1942); chaetognaths (Pauly et al., 2021); cephalochordates (Pauly & Chu, 2021); horseshoe crabs (Suzuki et al., 2008); fishes (Pauly, 2019, 2021a)	See Figures 1, 2; Hughes (1983); Diaz-Iglesias et al. (2011)
3	Growth is exponential in (well-fed) larvae, for which $d \geq 1$	Fishes (De Sylva, 1974; Overnell & Batty, 2000; Pauly, 2019)	Anger (1998); Miller (2008); Tunberg & Creswell (1991)
4	Within a tolerated range of temperature, increasing temperatures reduce adult size ²	Sponge (Pauly et al., 2022b); planarians (Whitney, 1942); polychaetes (Forbes & Lopez, 1990); trilobites (Gutiérrez-Marco et al., 2009); chaetognaths (John, 1933; Pauly et al., 2021); fishes (Pauly, 2019)	See Figure 6 for rock lobster in West Australia; Gardner et al. (2006)
5	Large individuals of a given taxon are more sensitive than small ones to hypoxia and/or high temperatures	Leech (Davies et al., 1992); polychaete (Forbes & Lopez, 1990); fishes (Fish, 1956; Robb & Abrahams, 2003; Lindmark et al., 2022)	Bridges & Brand (1980)
5	Seasonal temperature changes induce seasonal growth oscillations	Sponges (Butler et al., 2017); cephalopods and fishes (Pauly, 2019)	See Figure 4; Wolff & Soto (1992); Forcucci et al. (1994)
6	Feeding, growth, and maximum size are lower under (sub-lethal) hypoxia	Gastropod (Harris et al., 1999); amphipods (Chapelle & Peck, 2004); fishes (Pauly, 2019)	Das & Stickle (1993); Wu & Or (2005); Ocampo et al. (2000)
7	In environments where maximum sizes are small, sizes at first maturity are small, too	Sponges (Butler et al., 2017; Pauly et al., 2022b); fishes (Kolding et al., 2008; Pauly, 2019, 2021a)	See Figures 6, 9; Bouchard & Winkler (2018)
8	If a taxon includes water- and air-breathing species, the former are able to reach large sizes only at low temperatures	Air-breathing arapaima and Mekong giant catfish vs. similar-sized water-breathing teleosts (Pauly, 2019); salamanders with and without lungs (Rollinson & Rowe, 2018)	Compare red king crab with the tropical and huge coconut crab (Drew et al., 2010)

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Data for the establishment of length-weight relationships in *Pollicipes pollicipes*.

S2 Table. Parameters of Equation 5 based on the data in Table S1.

S3 Table. Lobsters (*Panulirus* spp.) with lengths at first maturity and maximum lengths.

S4 Table. Crabs with size at first maturity and maximum size.

S5 Figure. Length-weight relationships (LRW) in the stalked barnacle, *Pollicipes pollicipes*.

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