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Mediterranean Marine Science

Vol 20, No 4 (2019)

special issue

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doi: 10.12681/mms.19285

To cite this article:

PAULY, D. (2019). A précis of Gill-Oxygen Limitation Theory (GOLT), with some Emphasis on the Eastern Mediterranean. *Mediterranean Marine Science*, *20*(4), 660–668. https://doi.org/10.12681/mms.19285

https://epublishing.ekt.gr | **e-Publisher:** EKT | **Downloaded at:** 01/09/2025 20:30:19

Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.19285

This paper was presented at *"12th Panhellenic Symposium of Oceanography & Fisheries"*,
which was held at the Ionian University, Corfu, from 30th May to 3rd June 2018

A précis of Gill-Oxygen Limitation Theory (GOLT), with some Emphasis on the Eastern Mediterranean

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Handling Editor: Christos ARVANITIDIS

Received: 7 December 2018; Accepted: 10 June 2019; Published on line: 7 October 2019

Abstract

A summary of the Gill-Oxygen Limitation Theory (GOLT) is presented, i.e., of a theory seeking to explain a variety of life processes in fish and aquatic invertebrates by the fact that the surface of their gills (and hence their oxygen supply) cannot, as in 2-dimensional objects, keep up with the growth of their 3-dimensional bodies, and thus with their oxygen requirements. Various processes and attributes of fish and aquatic invertebrates are presented which had to date no mechanistic explanation, but which fit within the GOLT, offered here as a tool to interpret phenomena that until now were perceived as unrelated. However, the GOLT should also help to address practical problems, such as arise for fish farming when water temperature increases because of global warming.

Keywords: Fish growth; Temperature; Mariculture.

Introduction

When studying the various adaptations and behaviors of fish and aquatic invertebrates (here 'fish'), ichthyologists and other scientists also study the biology of water-breathing organisms which live a medium containing little oxygen and from which it is difficult to extract (Table 1).

However, there has always been a temptation for humans – an air breathing, warm-blooded mammalian species – to project our preoccupations with food, the fuel needed to maintain our high temperature, onto fish, animals that do not need as much food, their main problem being how to extract the oxygen they need from the oxygen-poor medium that surrounds them.

This neglect of how oxygen constrains water-breathers has led to profound misunderstandings of their biology, with each of their life processes being explained by a distinct *ad hoc* hypothesis, endlessly repeated until it acquires the status of an obvious fact, even when demonstrably wrong.

Thus, many authors have stated that, in fish, growth slows down upon reaching first maturity because "*energy is redirected toward reproduction*" (Hubbs, 1926; van

Table 1. Comparison of water and air as media for respiration

Property	Comment[a]
O_2 content	20-30 times less in water than in air.
Viscosity	Water is 55-95 times more viscous than air.
Permeability	Diffusion through membranes is 300,000-350,000 times faster in air than in water.
Density	Water is 840-1085 times denser than air.

a) based on Schumann and Piiper (1966) and De Ricqlès (1999); the wide ranges of the properties' ratios are due to different conditions of temperature, pressure and salinity.

Oosten, 1929; Jones, 1976; Lagler *et al.,* 1977; Charnov, 2008; Quince, *et al.* 2008; Marshall & White, 2018). But this is not so: if reproduction were the reason why somatic growth slows down in fish, then the growth of non-reproducing fish (e.g., a lone goldfish in a house aquarium) would outgrow all aquaria. Most importantly, given that the female sex, by definition, invests more into reproduction than the male sex, female fish should, as adults, always be smaller than males. However, in over 80% of the 825 fish species that have growth parameters by sex in FishBase (www.fishbase.org; accessed Nov. 8, 2018), it is the females that get larger (Fig. 1).

The Gill-Oxygen Limitation Theory (GOLT) is an attempt to replace the various *ad hoc* hypotheses that populate ichthyology, limnology and marine biology by a single, unifying theory that explains the growth and related phenomena of marine and freshwater fishes and aquatic invertebrates without recourse to just-so hypotheses, based only upon first principles and their corollaries (Table 2).

In the following sections, a précis of the GOLT (as elaborated in more detail in Pauly 2010 and restated in Pauly & Cheung, 2017) is given, with each of the twelve items in Table 2 elaborated upon in one or a few paragraphs.

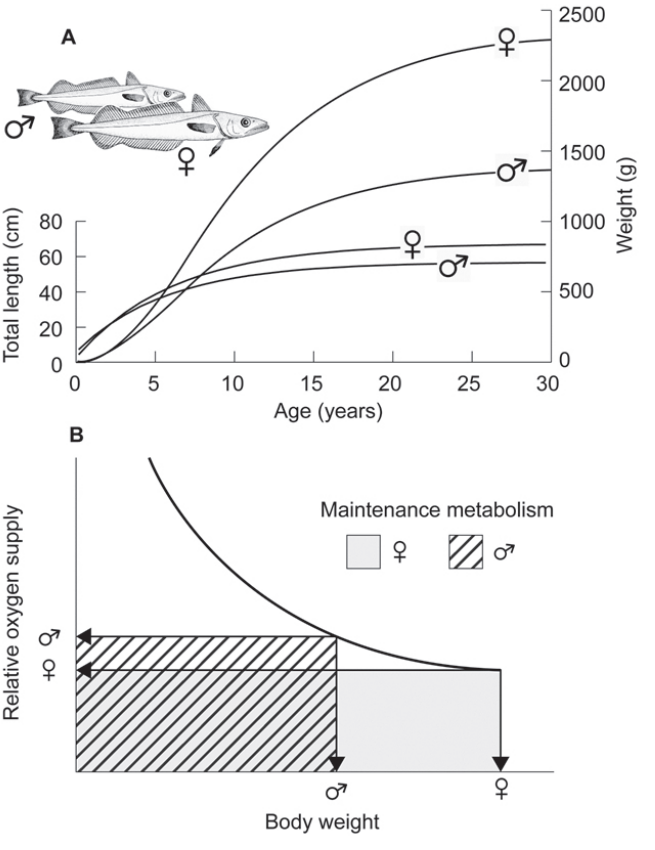

Fig. 1: Most female fish grow bigger than the males. **A:** The example of female and male European hake (*Merluccius merluccius*) from the coast of Croatia in terms of length (Dulcic *et al.* 2005) and weight (via a length-weight relationship from Mandic and Regner 2009). **B:** The better growth of the females is explained by their lower maintenance metabolism, due to a lower rate level of activity (see text).

Item 1. Fish growth is asymptotic

Growth (dw/dt) in fish can be represented as the difference between two processes with opposite tendencies, i.e.

$$dw/dt = Hw^d - kw^m \qquad \ldots 1)$$

where Hw^d is the rate of synthesis of body protein (and other substances) and kw^m is the rate at which proteins denatures (or otherwise reaches a state at which they need to be replaced).

Both terms on the right side of Equation (1) grow as body mass or weight (*w*) increases, but eventually kw^m always catches up with Hw^d because protein synthesis requires oxygen, and gills, as a surface, cannot grow as fast as a volume (i.e., fish weight). This is due to the value of parameter *d*, which usually ranges between 0.6 (in small fishes such as gobies and guppies; von Bertalanffy, 1951; Pauly, 1982) and 0.9 (in large fishes such as tuna; Muir & Hughes, 1969; Pauly, 1981), and in various invertebrates (Pauly, 2010). On the other hand, *m* in Equation (1) is equal to 1 (and hence can be omitted) because protein denaturation (Somero & Doyle, 1973) occurs all over the body. Thus, whatever the value of *H,* the second term of the right side of Equation (1) will always grow faster than its first term, and a size reached where

$$Hw^d - kw = 0 \qquad \ldots 2)$$

This size is the asymptotic length in the integral form of Equation (1), i.e.

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

where L_t is the predicted length at age t, L_∞ is the asymptotic length, or the mean length the fish would reach if they grew indefinitely, K is the rate at which L_∞ is approached (of dimension 1/time) and t_0 is the (usually negative) age at which *L* would have been zero if the fish had always grown as predicted by the equation. The corresponding equation for growth in weight is

$$W_t = W_\infty \left(1 - e^{-K(t - t_0)}\right)^b \qquad \ldots 4)$$

where *K* and t_0 are as in Equation (3), W_t and W_∞ are the weight corresponding to L_t and L_∞, where b is the exponent of length-weight relationship of the form $L=a{\cdot}L^b$, and where a value of $d = 2/3$ is implied (Fig. 1A). Versions of Equation (3) and (4), i.e., the von Bertalanffy growth function (VBGF) exists in which $d \neq 2/3$ (Pauly, 1981), but they are not relevant to the arguments presented here.

For the interpretation the VBGF in terms of the GOLT to be correct, all that is needed is for the two terms of the right side of Equation (1) to have different exponents ($d < m = 1$), and for the denaturation of proteins to be a spontaneous process, requiring neither ATP nor other forms of 'energy,', which is the case (Rechcigl, 1971; Goldberg & St. John, 1976; Cox & Nelson, 2008).

Table 2. Non-anatomical features in the biology of fishes and/or aquatic invertebrates that are explained by the Gill-Oxygen Limitation Theory (GOLT)

Item	A: Features or observation	B: Explanation provided by the GOLT
1	Asymptotic growth, i.e., the continuous growth of individual, with asymptotic length or weight (L_∞, W_∞) never reached, but usually near the maximum size of old individuals (L_{max}; W_{max}).	A consequence of O_2 *supply* through the gills not being able to keep up with the growth of the body generating the O_2 *demand*. Asymptotic size is reached when O_2 supply equals the demand of maintenance metabolism.
2	Food conversion efficiency (i.e., K_1 = weight gain/food consumed) declines with size.	A consequence of gills delivering, in large/old fish, less oxygen per unit body weight than in small/young ones, with K_1 = 0 at W_∞.
3	Mean size at first reproduction in a population is a predicable fraction of the mean maximum size in that population.	Declining relative O_2 supply as weight increases triggers maturation when metabolic rate drops below 1.3 times the level at which somatic growth ceases (i.e., at L_∞ or W_∞).
4	Young adults, upon reaching maturity, occasionally generate gonadal tissues, but then resorb them (‘abortive maturation’).	Young adults entering a spawning season often fail to complete spawning because their metabolic rate is not clearly below 1.3 times the level at which somatic growth ceases.
5	Big/old fish of a given species tend to occur at the higher latitude/colder end of their distribution range, and in deeper water.	Lower temperatures – as also occur at greater depths - imply lower O_2 demand, and thus higher sizes at which O_2 supply from the gills equals the demand for maintenance metabolism.
6	Growth and food conversion efficiency are reduced when the O_2 content of water declines, e.g., at night in fish farming ponds.	More water must pass through the gills for an equal amount of O_2 to be extracted by a breathing fish. The work required for this results in more O_2 not being available for growth.
7	Fish often perform large-scale migrations. Their amplitude is highest in the larger/older individuals of a population.	Sensitivity to temperature changes forces most fish to migrate seasonally, to stay at similar temperatures; this is stronger in larger/older fish, which are more sensitive to temperature.
8	Since the 1970s, the center of the distribution ranges of fish species has been moving poleward and/or toward deeper waters.	Sensitivity to temperature extremes forces the poleward migration of fish, and/or increases in the depth in which they occur.
9	The pH in the muscles of fish ‘played’ by anglers increases and gradually immobilizes the fish. Extreme cases are ‘burnt tuna.’	The gills cannot replace fast enough the O_2 used by fish to fight against a line, and the lactic acid they then produce causes immobilizing pain, then induces tissue autolysis which kills them.
10	Daily ‘rings’ (and also ‘stress rings’) are formed on the hard parts of organisms, i.e., the otoliths of fish and the statoliths of invertebrates.	Oscillating pH levels cause the rings (marked in larvae and juveniles, but not in adults), due to alternating periods of activity (low pH) and rest (high pH), Also, storms cause stress rings.
11	The otoliths of big/old fish contain less organic matter than those of small/young fish. Also, the muscle tissues of big/old fish are rich in glycolytic enzymes, while those of small/young fish are rich in oxidative enzymes.	Big/old fish experience near constant oxygen stress, thus their bodies and the lymph around their otoliths have a low pH, which results in less organic matter being incorporated in their otoliths. This due to the fact that big/old fish get relatively less oxygen than small/young fish, and thus rely more on glycolytic enzymes.
12	On coral and other reefs, fish of different size and species give – most of the time - the (false) impression of coexisting peacefully.	Fish cannot easily risk depletion of the O_2 store in their muscles and blood, and they hence attack prey only when it can be done quickly, without the predator risking a dangerous O_2 depletion.

Figure 1B links these considerations to the GOLT; also, it explains why, as mentioned above, the female fish generally grow larger than males: they are calmer (Koch & Wieser, 1983; Bozynski & Pauly, 2017), and thus their routine metabolism (of which the overwhelming fraction is usually devoted to various activities, with only a small fraction toward somatic growth) is less elevated than that of males.

Item 2. Food conversion efficiency declines with size

As every fish farmer or experimentalist knows, fish convert less of their food into growth as they become larger (see e.g., Jones, 1976; Kinne, 1960; Menzel, 1960). While this is well known to practitioners, only a few authors, notably Gerking (1952, 1971), have attempted to explain this phenomenon.

The GOLT follows up on this author, who suggested that a "*change in metabolism*" (Gerking 1952) was responsible for the decline of fish growth efficiency (K_1 = growth increment / food ingested). As fish grow, their gill area (and hence oxygen delivery to their tissues) per unit of body weight must therefore decrease. Thus, with less O_2 to oxidize the food offered to them, fish either avoid consuming it, or it is ingested and "*is excreted by the gills and kidney as incompletely oxidized nitrogenous compound*" (Webb, 1978). Theoretically, the decline of K_1 should proceed until W_∞ is reached or, in practical terms, until maximum size (W_{max}) is reached, at which point the fish has an oxygen supply that is just sufficient to process the food that maintains its weight, but net growth is zero (Silvert & Pauly, 1987).

Item 3. Size at first reproduction and maximum size correlate

Numerous authors have noted that fish of similar taxa reach their size at first maturity (L_m) at a more or less constant fraction of the maximum size they can reach (Beverton, 1963; Froese & Binohlan, 2000). Figure 2A shows that the size at first maturity of fish corresponds to a metabolic rate (Q_{m1}) that is necessarily higher than the metabolic rate corresponding to their W_∞ ($Q_{\infty 1}$). When, for example, temperature is increased, oxygen requirement necessarily increases (notably because spontaneous protein denaturation increases with temperature) and hence fish stay smaller (Figure 2B), and thus $Q_{\infty 2}$ will increase.

Consequently, Q_{m2} must also increase. As shown in Pauly (1984, 2010), these changes maintain the same Q_m/Q_∞ ratio as occurred in Figure 2A, i.e., 1.356 : 1, with a 95% confidence interval of 1.218 – 1.534 subsequently estimated by the method of Fieller (1940) as implemented on www.graphpad.com/quickcalcs/ErrorProp1.cfm

This ratio appears to apply to all fishes, from guppies to tuna, and thus provides a mechanism for triggering first maturity at a size compatible with the environmental conditions to which a fish population is exposed: when conditions are favorable for growth and reaching a large size, the size at first maturity is high, and conversely when conditions are inimical to growth; see, e.g., Kolding *et al*. (2008) for an experimental test of this proposition and Cottingham *et al.* (2014) for a field example. All that fish need is a sensor that monitors their metabolism, and which triggers, when respiration becomes stressful, i.e., when Q_m drops to about 1.3-1.4, the onset of the hormonal cascade that induces maturation.

Item 4. Some young adult fish skip spawning

When fish get heavier and thus their oxygen supply per unit weight declines, the stress this induces causes them to initiate spawning and to elaborate gonads, as mentioned above. However, maturation-inducing stress can decline before spawning has occurred (e.g., because it was temporarily increased by temperature-induced respiratory stress, with the temperature then declining). In such cases, the gonad material that has been synthesized but not extruded can be resorbed and thus spawning be 'skipped.'

When skipping occurs, actual spawning takes place during the next reproductive season, when the size-induced respiratory stress becomes overwhelming. More details on this mechanism are provided in Pauly (2010). This appears to be the only mechanism proposed so far that works at the level of *individual* fish. Simulations, such as that by Jørgensen *et al*. (2006) showing that skipped spawning can be a component of the evolutionary stable strategy (ESS) of a *population* are not sufficient here, because an ESS does not provide cues to *individuals*.

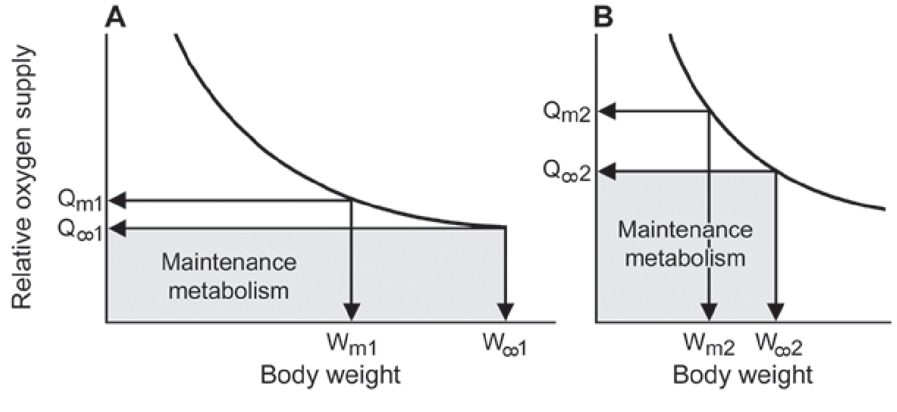

Fig. 2: The GOLT explains the apparent constancy of L_m/L_∞ ratios in fishes as follows: **A**: If a declining oxygen supply ultimately limits the size at $W_{\infty 1}$ (and hence $Q_{\infty 1}$ is the minimum rate of oxygen supply that is tolerated), then, given $L_m < L_\infty$, oxygen supply at maturity (Q_{m1}) must be higher than when growth ceases (i.e., $Q_m > Q_\infty$, and $W_m < W_\infty$). **B**: When an external factor (e.g., high temperature) increases oxygen demand, $Q_{\infty 2}$ will be higher and $W_{\infty 2}$ smaller. However, the ratio Q_m/Q_∞ will be maintained, and the fish will mature and spawn at Q_m2 and W_{m2}. Thus, the constancy of the Q_m/Q_∞ ratio will be imperfectly mirrored in L_m/L_∞ ratios (adapted from Pauly 1984).

Table 3. Response to aeration of some farmed fish (√: increase explicitly noted; - : item not mentioned).

Species & country	Increase of:					Source
	Con.[a]	**Growth**	**Survival**	**Harvest**	**Profits**	
Common carp (*Cyprinus carpio*), Hungary	-	-	-	√	√	Abdul Amir (1988)
Japanese eel (*Anguilla japonica*), Taiwan	√	√	-	-	√	Anon. (1988a)
Tilapia spp. (Family Cichlidae), Singapore	-	√	√	-	√	Anon. (1988b)
Channel catfish (*Ictalurus punctatus*), USA	√	√	√	√	√	Hollerman & Boyd (1980)
Atlantic cod (*Gadus morhua*)	√	√	-	-	-	Thorarensen *et al.* (2017

a. Food consumption and/or conversion efficiency.

Item 5. The biggest fish of a population occur in colder water

The phenomenon is well-known wherein the largest/heaviest fish of a population occur at the coldest end of their range (Randall *et al.*, 1973; Smith-Vanitz *et al.*,1999). This is easily explained in terms of the GOLT: as shown in Figure 2, low temperatures result in low oxygen demand; combined with the higher dissolved oxygen concentration in colder water, this results in fish that can get larger. This is also the reason why fish move to deeper and colder water as they grow (Heincke, 1913; Macpherson & Duarte, 1991).

Items 6. Low oxygen is bad for fish farmers

Fish farmers know, often from hard-won experience that, if the oxygen in their pond drops below a certain level, as can occur late in the night, they risk losing all the fish therein to asphyxiation. However, they also know that the sub-lethal effects of low oxygen can affect their bottom line, via fish feed that is not converted into growth (see e.g., Yi & Lin, 2001). Table 3 summarizes the reasons why, therefore, many fish farmers invest in the relatively costly aeration of their ponds. This is an issue where aquaculture practitioners are way ahead of theoreticians, who continue to focus almost exclusively on food as the driver of fish growth; sufficient food is, however, only a necessary condition for growth; oxygen is the sufficient condition.

Items 7. Fish undertake temperature-mediated seasonal migrations

The major textbook on fish migration (Harden-Jones, 1968) does not list temperature in its subject index. This reflects the fact that most accounts of fish migrations refer to ‘feeding grounds’, ‘overwintering areas’ and the like as if fish were mammals. But they are not; they are poikilotherms that are exquisitely sensitive to the temperature of their habitat.

This translates into fish generally attempting to remain throughout the year in the water temperature to which they are adapted, i.e., moving along temperature gradients. This is partly obscured in most representations of fish migration, but clearly visible when explicitly addressed, e.g., Nikolioudakis *et al.* (2018) vs. Nøttestad *et al.* (1999), or Pauly & Keskin (2017) vs. Galtsoff (1924) in the case of Atlantic mackerel *Scomber scombrus*.

Item 8. Ocean warming induces poleward migrations

Given the above comments on the seasonal migration of fish, it is also clear that with ocean warming, they will have to shift their distribution poleward. In the Eastern Mediterranean, this amounts not only to an increase of Lessepsian migrants that can be counted one at a time (Por, 1978), but to the entire Red Sea fauna invading a new habitat.

This process, given that fish can change their species-specific temperature preferences only over evolutionary time, means that the increased presence of fish with a high temperature preference will increase the “temperature of the catch” recorded from the waters of countries previously peopled by fish with cold-water affinities (Cheung *et al*., 2013).

This phenomenon is well documented in the Eastern Mediterranean (Tsikliras & Stergiou, 2014), where it has also been used to demonstrate the structuring effect of temperature on fish (Tsikliras *et al.,* 2015; Keskin & Pauly, 2014) and ichthyoplankton communities (Keskin & Pauly*,* 2019). Here, the GOLT, which stresses the structuring role of temperature (and hence fish respiration), contributes to studies that elucidate the community changes brought about by ocean warming.

Item 9. Internal pH drops in stressed fish

Anglers know that if they can 'play' the fish they have hooked only for a while, the hooked fish will cease fighting and go limp. This is brought about by the fish's blood and muscles running out of oxygen, and lactic acid accumulating in their muscles. We know what lactic acid in our muscles means – pain – and this will be the same in fish. Indeed, pain is the first phase of a process, which, if continued to its bitter end, leads to the pH in the fish tissue dropping to the extent that the membranes around cell organelles are dissolved and enzymes are released that induce apoptosis, i.e., cell death.

This is what occurs in 'burnt tuna', i.e., tuna that have fought so long before dying that their flesh becomes unsuitable for sushi (Cramer *et al.,* 1981; Konno & Konno, 2014). This is also what makes catch and release programs suspect as to their vaulted sustainability because many of the released fish to not survive their ordeal.

Item 10. Daily rings in the otoliths of fish and the statoliths of invertebrates

Fish larvae and juveniles have had clear 'rings' on their otoliths which are deposited daily, as do small/young invertebrates on their statoliths (Pauly, 1998, 2010). There are no good explanations for these rings, except that they are the result of a sequence of periods with a high level of activity (= low pH, see above) and low activity (= high pH), as occur in animals that are active at day and rest at night, or vice-versa. The low pH period - including in the lymph surrounding the otoliths (Mugiya *et al.,* 1981) or statoliths (Lipinski, 1993) - corresponds to a period during which the matrix of the otoliths or statoliths is 'etched' by the low pH of the lymph surrounding them, while the high-pH periods corresponds to a period where new otolith/statolith matrix is deposited (Lutz & Rhoads, 1974; Mugiya & Ichimura, 1989).

In bigger/older individuals, whose size implies a low gill area (and hence O_2 supply) per body weight, the oxygen stress that is experienced is between day and night is similar, and hence daily rings will be blurred or not occur (Ralston, 1985).

Here, the GOLT explains a widespread phenomenon without the need for *ad hoc* assumptions and hypotheses.

Item 11. The physiology of fish radically changes as they grow

Growing, for a fish, implies a radical change in its internal 'milieu'. Thus, while teleost larvae (and presumably the larvae of various aquatic invertebrates) do not suffer from oxygen undersupply (their value of $d \geq 1$; Bochdansky & Leggett, 2001), fish, as they become older and heavier see their oxygen supply per unit weight decline (because their $d < 1$). Thus, they shift from a metabolism based on oxidative enzymes (in younger/smaller fish) to one based on glycolytic enzymes (in larger/older fish), which are more efficient under anaerobic conditions (Burness *et al.,* 1999; Davies & Moyes, 2007; Norton *et al.,* 2000; Somero & Childress, 1980).

Item 12. Bakun knows it's not really peaceful...

We have all been mesmerized by the ethereal beauty and peacefulness of coral reefs, whether we dive in them, or watch an underwater movie. Indeed, such scenes appear to contradict biologists' view of a Darwinian world in which every predator, e.g., shark or barracuda, is always hunting, and every potential prey, e.g., sardine or anchovy must always fear for its life.

Bakun (2011) explains this paradox with the GOLT: because of their size differences, small fish can more easily recover from a bout of oxygen-consuming activity than larger fish. Thus, if predators were constantly chasing after prey, they would run out of oxygen faster than most of their prey and then themselves become easy prey to their predators.

Hence, the peacefulness that we think we see is only apparent: at the smallest disturbance likely to give a predator an easy way to overwhelm potential prey, it will attempt to do so, but all the while remaining careful not to use up its small aerobic store.

There is more to Bakun's resolution of the paradox of peacefulness, but here is not the place to reproduce his entire argument. Suffice it to say that he thinks he can explain, using the GOLT, why marine ecosystems maintain their prey populations despite all their predators seeming to be individually capable of overwhelming all prey fish. Or, in other words, the GOLT explains why ecosystems do not collapse onto themselves in an instantaneous and all-engulfing predatory frenzy.

Discussion

This account of the GOLT is only a brief summary – indeed, it is a caricature. Not only are there more phenomena than the twelve items above that can be explained parsimoniously by the GOLT, but the explanations given above are not nuanced. For example, they do not address the evolution and the anatomy of gills and their implications for other organ systems, nor do they address the objections that may be – or have been – raised to each of my claims (Box 1). I therefore urge the reader to read the book (Pauly, 2010) in which the GOLT is presented in detail, and of which a second edition will soon appear.

Despite its full name, which includes the word 'theory', the GOLT has numerous practical implications. For example, it predicts that fish farming operations such as those performed in Greek waters with gilthead sea bream (*Sparus aurata*) and European sea bass (*Dicentrarchus labrax*) will suffer from increasing temperatures. Thus, for example, what may appear to be unsuitable feed in summertime will be due simply to the oxygen demand of the fish in question becoming excessive due to high summer temperatures, leading to their feed neither being ingested nor, or excreted without being assimilated, and thus wasted.

Box 1. An application of the GOLT to the ocean sunfish *Mola mola*

Lefevre *et al.* (2017), who criticized the GOLT (Pauly & Cheung, 2017), claimed that the ocean sunfish *Mola mola,* which is reported to reach up to 2.3 t, would not occur in the tropics if the GOLT were correct, as it implies that large sizes, in fish, are incompatible with high temperatures.

Here is why this critique missed key adaptations of the fish chosen as a counterexample. Contrary to earlier accounts, juvenile sunfish are extremely active (Davenport *et al.,* 2018), which requires them to have relatively a large gill surface area. The adults are generally calmer, even though their peak swimming speed is "*comparable with cruising speeds of fish with axial musculature such as salmon and marlin*" (Davenport *et al.,* 2018). However, they do spend much time drifting passively on the sea surface, the reason why they were earlier assumed to be 'planktonic.' Moreover, large *M. mola* are hulled in a gelatinous 'capsule' contributing well over half of their weight. Thus, according to Watanabe & Sato (2008), *"the proportion of the mass of the gelatinous tissue to body mass significantly increased with body size ($P<0.0001$, $n=21$), from an average of 26=+/-6 % for 2-kg individuals ($n=4$) to 44% for a 247-kg individual.*" Watanabe-san kindly provided the author with the raw weights and gelatinous tissues (GT) percentages that were used for the above inference. From these, one can derive $GT\% = 23.8 \cdot W^{0.129}$. Based on this relationship, a 2300 kg sunfish would consist of about 64 % gelatinous tissue, consisting of 90% water, and which is thus, for all practical purposes, metabolically inert. Thus, the metabolically effective weight of an ocean sunfish of 2.3 t would be around 830 kg. This, along with their feeding on jellyfish and other easy prey (Syväranta *et al.,* 2012), and the fact that they perform frequent 'cooling dives' lead one to think that adult *Mola mola* have a low oxygen consumption per unit weight, and thus that they can live in tropical waters, as they do.

The main forte of the GOLT is, however, that it offers a coherent interpretation of key features and processes in the biology (i.e., anatomy, physiology, ecology, behavior, etc.) of fish and aquatic invertebrates such as crustaceans, mollusk and other aquatic taxa, and thus should facilitate research and teaching about water-breathing animals in general.

Acknowledgements

The author thanks Sandra Wade Pauly for her assistance in assembling the elements of this contribution, which is based on my keynote presentation, at the 12th Panhellenic Symposium on May 31, 2018, at the Ionian University, in Corfu, Greece. Also thanks Dr. Christos Arvanitidis for his invitation to participate at this event.

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