



**Abstract**—Fisheries for Caribbean sponge species began in the mid-1800s and landings peaked around the early 1900s before crashing because of a combination of overexploitation, disease, and hurricanes as well as, later, the introduction of artificial sponges. Still, artisanal sponge fisheries remain in Florida and areas of the Caribbean like The Bahamas, but none of those fisheries or the sponges upon which they depend are well studied. On the basis of data and information published by J. Storr in 1964 as well as of our own data, von Bertalanffy growth parameters were estimated for the most commercially valuable Caribbean sponge, the sheepswool sponge or wool sponge (*Hippospongia lachne*), along with related statistics, notably longevity. Also, morphological dimensional constraints that are likely to limit the supply of oxygen deep within this and other near-spherical sponge species are presented, along with the sponges' evolutionary and ontogenic responses to these constraints. These considerations are also illustrated with data from species other than the wool sponge and are consistent with a general theory of growth for water-breathing ectotherms, the gill-oxygen limitation theory. The information provided herein should be useful for quantifying the ecosystem effect of sponge fisheries in Florida, The Bahamas, and elsewhere and for improving the management of sponge fisheries and mariculture worldwide.

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## Growth and related traits of the sheepswool sponge (*Hippospongia lachne*): practical and theoretical considerations

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This contribution addresses issues related to the growth, longevity, reproduction, and respiration of sponges, with emphasis on the sheepswool sponge (*Hippospongia lachne*), also known as and henceforth referred to as the *wool sponge*, and to the roles of sponges in fisheries, ecosystems, and ecosystem models. Emphasis is given to the relationship between growth and respiration in the wool sponge and other sponges because this issue is often overlooked in studies of water-breathing ectotherms (WBE), in which an appropriate supply of oxygen is as important for survival and growth as an appropriate amount of food (Pauly, 2021a).

Our emphasis on respiration is incorporated in the use of a growth curve, the von Bertalanffy growth function (VBGF) that is widely used in fisheries research and can be derived from the “dimensional tension” (Pauly and Cheung, 2017) between oxygen supply and demand in growing WBE.

Sponges are important if underappreciated components of marine ecosystems, including coral reefs where

sponge diversity reaches its zenith (Diaz and Rützler, 2001, 2011). Many ecological functions and services, including benthic-pelagic coupling through filtration and nutrient cycling (Valentine and Butler, 2019; Pawlik and McMurray, 2020), enhancement of habitat complexity (Herrnkind et al., 1997), alterations in sediment structure (Neuweiler and Burdige, 2005), contribution to underwater soundscapes (Butler et al., 2016), provisioning of food for spongivorous species (Loh and Pawlik, 2014), and support of fisheries (Butler et al., 2017), are attributable to sponges and their associated microbiomes (Bell, 2008; Bell et al., 2017). With respect to support of fisheries, some shallow-water species are, or have been, commercially exploited, notably the wool sponge, which is also farmed (Storr, 1964; Osinga et al., 1999; McClenachan, 2008) and grown for use in habitat restoration (Butler et al., 2021).

Despite there being over 1000 genera of marine sponges (de Voogd et al., 2021; Palomares and Pauly, 2021), in the past, only 2 genera were fished

commercially, *Hippospongia* and *Spongia* (McClenachan, 2008). Because of their soft and absorbent skeletons, species of these 2 genera had, and still have, a variety of uses (McClenachan, 2008). Before the appearance of synthetic sponges, natural sponges were used for personal hygiene, house and car cleaning, medical surgery, glazing pottery, cleaning industrial machinery and railroad equipment, tile and brick laying, and dressing leather and were used as gun swabs in the army and navy and in the manufacture of hats, soldiers' helmets, and jewelry, among other things (Corfield, 1938; Stuart, 1948; Storr, 1964; McClenachan, 2008). Recently, the demand for commercially harvested sponges has extended beyond these 2 genera and has been driven primarily by the cosmetic, biomedical, and aquarium trades (Belarbi et al., 2003; Oronti et al., 2012; Mehbub et al., 2014).

The work described in this contribution is the first attempt to fit to a sponge the standard version of the VBGF, an equation commonly used in marine biology and fishery research. There are several practical reasons to fit the VBGF to a sponge. First, since the publication of the classic text of Beverton and Holt (1957), the VBGF has been and remains part of the basic toolkit of fisheries science, mainly because of its versatility and realism. As such, its parameters are components of numerous models used to understand and manage the exploitation of fish and invertebrate populations. Second, a standard growth curve should be useful for sponge mariculture, for example, to assess and compare the performance of individual sponges raised under different environmental conditions. The growth rates (in summer and winter) of 4 species of commercial sponges, the wool sponge, yellow sponge (*Spongia barbara*), glove sponge (*S. cheiris*), and grass sponge (*S. graminea*), from the Caribbean have been measured in the field, but those estimates do not include the full range of sponge sizes and ages (Butler et al., 2017).

The third reason for fitting the VBGF to sponges is theoretical. The VBGF was derived from first-order physiological principles involving the interplay of surfaces and volumes leading to asymptotic growth (see von Bertalanffy, 1938, 1951; Pauly, 2019a, 2021a). It should therefore be enlightening to test if these principles, first derived for fish, also apply to sponges, the oldest multicellular animal taxon. Also, this contribution might assist ecosystem modelers, who so far have usually neglected sponges (but see Opitz, 1996; Tudman, 2001; Butler, 2003; Pinkerton et al., 2008; Butler and Dolan, 2017).

This contribution does not address the growth of encrusting or tubular sponges that, because of their laminar bodies, may not suffer from the respiratory

constraints that are emphasized later herein. Rather, this study dealt with nearly sphere-shaped species, such as the wool sponge (Fig. 1). Our use of the wool sponge as an example is also pertinent because it is one of the most valuable and abundant commercially exploited species and therefore has been better studied than many other sponge species (Stevely et al., 1978; Witzell, 1998; Butler et al., 2017, 2018; Butler et al., 2021).

## Materials and methods

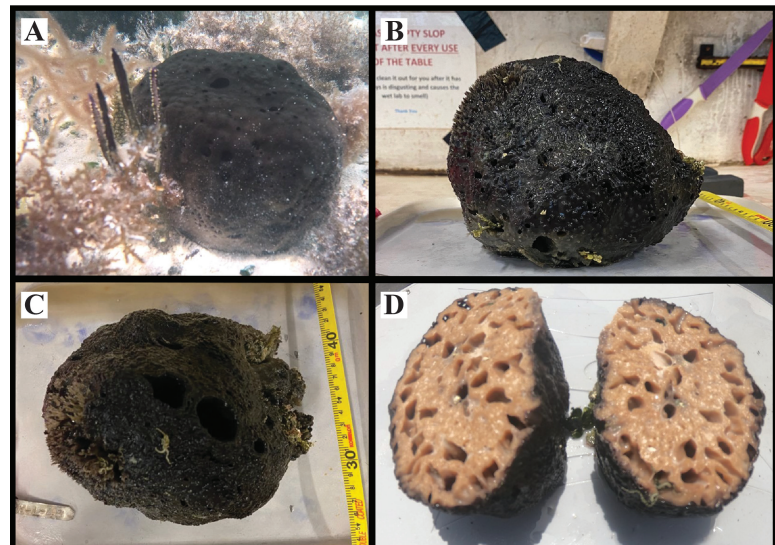
### Growth

We fitted the VBGF to the empirical growth curve published by Storr (1964), which is based on wool sponges tagged in the upper Gulf of Mexico. Storr (1964) described the way he obtained growth data (mainly from sponges in grounds at Piney Point in Florida) as follows:

“When the annual rates of increase between units of diameter were plotted, it was found that for growth beyond a diameter of 3-1/2 inches the growth factor could be expressed by the standard formula:

$$y = Ae^{Bx}, \quad (1)$$

where  $y$  = annual rate of increase—the growth factor; [and]  $x$  = radius of the sponge in inches at beginning of a year and  $A$  and  $B$  are constants, while  $e$  is the base of the Napierian logarithms.



**Figure 1**

Images of a sheepswool sponge or wool sponge (*Hippospongia lachne*) that was 18 cm in diameter and was collected in Florida by M. Butler on 18 September 2021 and photographed by J. Butler: (A) shown in the wild in the Florida Keys; (B) side view, taken in the laboratory; (C) top view, taken in the laboratory; and (D) inside of the specimen, after horizontal sectioning in the laboratory.

This is assuming a regular spherical shape for the sponge.

For the particular values obtained on the growth rate [of sponges] off the Piney Point area the formula, modified for ease in working, became [as follows]:

$$y = 1 + 11.2e^{-(1.07x)} \quad (2)$$

Since the data gathered were for diameters from 2 to 7 inches, the use of this formula for extrapolation of the curve beyond 7 inches was particularly useful. . . . The formula indicates that growth will almost completely stop when the sponge reaches a 12-inch diameter.”

The caveat that must be mentioned here is that it is risky to extrapolate beyond the range of one’s supporting data. Storr (1964) included only data for wool sponges with diameters up to 7 in (18 cm). Therefore, his estimated asymptotic size of a diameter of 12 in (~30.5 cm) for wool sponges is tentative. Indeed, larger wool sponges exist, although from 12 inches on, they usually take a more cylindrical shape, a theme to which we return later.

Storr (1964) writes further, “The rate of growth in diameter indicated by [Equation 2] appears to be valid for the first 5 or 6 years. Beyond this point the growth rate must be assumed to be somewhat less than indicated by the formula, the increase in diameter gradually approaching a uniform rate as the sponge assumes the doughnut shape.”

Using the software WebPlotDigitizer (vers. 4.5; Rohatgi, 2021), we read the size (diameter in inches) and volume (in cubic inches) from figure 7b of Storr (1964) and transposed them (Table 1). We used these data to estimate the

value of the parameter  $a$  of a diameter-to-volume relationship of the following form:

$$V = aD^3, \quad (3)$$

where  $V$  = the volume;

$D$  = the diameter; and

$a$  = the mean value estimated by solving  $a=V/D^3$  and averaging the resulting estimates of  $a$ .

The diameter-age pairs in Table 1 were then used to estimate the parameters of the VBGF (von Bertalanffy, 1938), as presented by Beverton and Holt (1957):

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right), \quad (4)$$

where  $L_t$  = the mean size (here: diameter) at age  $t$  of the animals in question;

$L_\infty$  = their asymptotic size (i.e., the mean size attained after an infinitely long time);

$K$  = a growth coefficient (here: year<sup>-1</sup>); and

$t_0$  = the (usually negative) age they would have had at a size of zero if they had always grown in the manner predicted by the equation (which, in fish species, they usually have not; see, e.g., Pauly, 1998).

Combining Equations 3 and 4 leads to a version of the VBGF that can express growth in volume:

$$V_t = V_\infty \left(1 - e^{-K(t-t_0)}\right)^3, \quad (5)$$

where  $V_t$  = the predicted volume of wool sponge at age  $t$ ; and

$V_\infty$  = the mean volume attained after an infinitely long time.

The different forms of the VBGF are derived by integrating the differential equation posited by Pütter (1920):

$$dw/dt = HW^d - kW, \quad (6)$$

where  $dw/dt$  = the growth rate in weight (here: volume), conceived as the difference between a process adding weight and a process reducing it;

$H$  = the rate of anabolism or the synthesis of new protein and other molecules (a process adding weight);

$W$  = weight, representing mass and volume;

$d$  = an exponent power <1; and

$k$  = the rate of catabolism or molecule denaturation (a process reducing weight).

The parameter  $d$  takes a value of 2/3 when Equation 4 is integrated to produce the VBGF, and whose parameter  $K$  is  $k/3$ . Also note that stressful environmental factors, especially high temperatures, tend to increase  $k$  (and  $K$ ) and therefore to reduce asymptotic sizes and longevity (Pauly, 2021a).

Pauly (1981, 2019a, 2021a), based on von Bertalanffy (1951), interpreted Pütter’s (1920) equation such that—because oxygen is required for anabolism—the positive

**Table 1**

The diameter, volume, and age of sheepswool sponges (*Hippospongia lachne*), also known as wool sponges, tagged off Florida in the Gulf of Mexico, as read off the graph in figure 7b in Storr (1964). Ages in parentheses were extrapolated by using the equation  $V=aD^3$  (Equation 3), where  $V$  is volume,  $D$  is diameter, and  $a$  is estimated by solving  $a=V/D^3$ . Volumes in parentheses were derived through Equation 2.

Age (years)	Diameter (in)	Volume (in <sup>3</sup> )
1	2.6	8.6
2	4.3	44.2
3	5.5	88.8
4	6.6	181.9
5	7.5	269.4
6	8.2	333.3
7	8.9	388.7
(8)	9.5	434.8
(9)	10.0	480.8
(10)	10.7	(609.8)
(11)	11.3	(716.3)



term in Equation 6 corresponds to the oxygen supply to a growing fish or invertebrate, and the catabolic term corresponds to its maintenance oxygen requirements or demand, because of the fact that denatured proteins and other molecules need to be replaced for an animal's body to maintain itself. Therefore, when the anabolism exceeds the catabolism, growth occurs (given that food is also available). However, as the anabolic term grows with a power of weight  $d < 1$  (here:  $d=2/3$ ), the catabolic term, which generates an oxygen demand proportional to weight, will eventually catch up—and growth will become zero, at the asymptotic volume  $V_\infty$  or the corresponding asymptotic weight  $W_\infty$ .

There are various debates about this interpretation, with some arguing that the respiratory surface providing the oxygen required for anabolism is capable of growing proportionately to weight (i.e.,  $d=1$ ) and hence that oxygen supply cannot be limiting to the growth of fish species and other WBE. This notion was refuted by Pauly and Cheung (2017) on the basis of numerous meta-analyses of gill surface areas in fish and other WBE (e.g., Hughes and Morgan, 1973; de Jager and Dekkers, 1974), which consistently have estimated  $d$  as  $< 1$ , and by (Pauly, 2021a), who grouped the detractors' arguments in detailed tables depending on their nature (e.g., not appreciating the 2-D nature of gills, mistaking causes and effects, and making unfalsifiable claims) and refuted them point by point with references to the aforementioned meta-analyses and other reliable peer-reviewed sources.

Surface-to-volume issues also apply to sponges, because the cumulative cross section of the pores through which water enters their bodies is a surface. This (2-D) surface, at least in compact sponges such as the wool sponge, cannot keep up with the growth of (3-D) bodies. Therefore, as a compact sponge grows, its interior will become increasingly hypoxic (Hoffmann et al., 2005; Lavy et al., 2016), and tissue maintenance will be increasingly compromised.

Sponges have therefore evolved a complex symbiotic relationship with microbes to deal with the geometric constraints imposed on sponge physiology. The sponge canal system operates as subdivided units among which pumping rates (i.e., oxygen acquisition) vary, creating spatiotemporally variable zones of hypoxia and anoxia that serve to support the respiratory activity of anaerobic symbionts (Lavy et al., 2016). Nevertheless, in some sponge species, the development of internal hypoxic zones apparently leads to tissue necrosis, as suggested by Storr (1964), who, however, attributed central tissue "death" in large wool sponges to lack of food, rather than to lack of oxygen. In comparison, in fish tissues subject to increased hypoxia, the reduced availability of oxygen leads to an increase of the role of glycolytic enzymes, which, as individual fish grow, gradually replace oxidative enzymes (Somero and Childress, 1980; Burness et al., 1999; Norton et al., 2000; Davies and Moyes, 2007).

Storr (1964), with regard to 12 in being the maximum diameter attained by spherical wool sponges, wrote the following: "This is confirmed in the observed growth of wool sponges by the death of the central portion of the sponge when this diameter is reached. The form of the sponge from

then on becomes more and more doughnut in shape. Continued growth beyond a 12-inch diameter suggests that one other growth factor operates as the sponge approaches the limit of growth indicated by the formula. Since the sponge is uniform in structure and the intake of water carrying the food is through the sides, the greatest amount of food uptake is in the periphery of the sponge. This area, therefore, continues to grow vigorously, but the rate of food intake is not sufficient nor the rate of food transfer through the sponge efficient enough to support active metabolism in the central portion of the sponge when the diameter of the sponge is 12 inches or over. The growth formula obtained would probably be directly applicable to the rate of sponge growth except for this phenomenon of sponge physiology."

Therefore, the growth phase documented herein pertains to spherical wool sponges; beyond this phase, wool sponges change shape, a shift that leads to different ratios between respiratory surfaces and the mass of oxygen-consuming tissues. This transition could be modeled by using a biphasic version of the VBGF (Soriano et al., 1992), but we did not attempt such modeling, mainly because the second-phase growth of this sponge species is not well documented and is of little interest to the sponge fishing and farming industries.

### Longevity

Storr (1964) wrote, "Little is known of the life span of wool sponges although the records have indicated that they can live at least 25 years. Presumably, the limiting factor to continued growth is the capability of the sponge to draw in sufficient food for self-maintenance. Any lack of food intake is counteracted in part by the dying of the central portion of the sponge so that after a certain point in growth in diameter, the volume of the sponge remains a constant in relation to the surface area."

In fish, it is commonly observed that the longest-lived individuals of a population reach about 95% of their  $L_\infty$  (Taylor, 1958); therefore, longevity is approximately equal to the time required to reach  $0.95L_\infty$ . Therefore, given Equation 4, we also have the following equation:

$$\text{longevity} \approx 3/K, \quad (7)$$

which assumes that the parameter  $t_0$  can be neglected. A rough estimate of the uncertainty inherent in Equation 7 is provided by assuming that the longest-lived individual reaches at least 90% or at most 99% of their asymptotic length (i.e.,  $2.3/K$  and  $4.6/K$ ).

Another useful model, from Hoenig (1983), links longevity with the instantaneous rate of total mortality ( $Z$ , year<sup>-1</sup>) in fish, mollusks, and other marine animals (134 populations in 79 species) and which has the following form:

$$\ln(Z) = 1.44 - 0.982\ln(t_{\max}), \quad (8)$$

where  $t_{\max}$  = the age (in years) of the oldest individuals in a population; and

$Z$  = the annual mortality experienced by a population ( $N$ ) between time  $t_1$  and  $t_2$  or

$$N_2/N_1 = e^{Z(t_2 - t_1)}. \quad (9)$$

Note that  $Z$ , in fisheries science, is commonly thought to consist of fishing mortality ( $F$ ) and natural mortality ( $M$ ), in the form of  $Z=F+M$ .

Equation 8 was derived to estimate  $Z$  from  $t_{\max}$  but can also be inverted (i.e., used to obtain rough estimates of longevity, given estimates of  $Z$ ). Such estimates are available from ecosystem models, in which the ratio of production to biomass ( $p/b$ ) of sponges was computed under the assumptions that the VBGF described individual growth and that population numbers decayed exponentially. Given these 2 assumptions,  $p/b=Z$  (Allen, 1971), an equation that makes it easier to estimate ratios of production to biomass than the complicated approach proposed by Winberg (1971).

## Reproduction

The predictability and relative fixity of the ratio between  $L_{\infty}$  and mean length at first maturity ( $L_m$ ) of different groups of fish (Beverton and Holt, 1959) has led to the concept of “a reproductive load” (Cushing, 1981), whose values tend to range from 0.4–0.5 in large fish species, such as tuna, to 0.6–0.7 in smaller fish species, such as sardines (Beverton and Holt, 1959; Beverton, 1963; Mitani, 1970; Froese and Binohlan, 2000). This concept embodies the notion that fish and other WBE stop growing because their “energy,” once  $L_m$  is reached, is channeled into reproduction rather than somatic growth (van Oosten, 1923; Hubbs, 1926; Jones, 1976; Lagler et al., 1977; Charnov, 2008; Quince et al., 2008). However, this notion is contradicted by the following facts: 1) in the majority of fish species, the females grow faster than males, even though they devote more energy to reproduction (Pauly, 2019b); 2) in long-lived fish (Liang, 2021) and other long-lived WBE, maturity is reached while growth in weight is still accelerating (Pauly, 2021b); and 3) a number of WBE continue to grow and reproduce throughout their lifetimes without suffering from senescence (Nussey et al., 2013; Gnanalingam and Butler, 2018). Still, it remains the case that  $L_m$  and  $L_{\infty}$  are correlated within different populations of the same species and even between species (see Pauly, 1984, 2019a).

## Respiration

Sponges are considered textbook examples of animals that use current-induced flow (e.g., Vogel, 1996), but Ludeman et al. (2017) have demonstrated that at least 5 demosponge species respond to increased current velocity by reducing their filtration. The results of their study also indicate that pumping rates (mean volumetric flow rate: liters per hours per grams of dry weight), although variable, are positively correlated ( $y=1.7559+x^{0.9416}$ ; coefficient of determination [ $r^2$ ]=0.66) with oxygen consumed by the sponge (mean oxygen removal: micromoles per hours per grams of dry weight). Estimates of the energetic cost of pumping in demosponges varies widely from <1% for temperate sponges (Riisgård et al., 1993) to 25% or more for tropical demosponges (Hadas et al., 2008;

Leys et al., 2011; Ludeman et al., 2017), such as the wool sponge.

Recall that the volume of a sphere is calculated as  $V=(4/3)\pi r^3$ . Therefore, the volume in a layer of a sphere can be obtained by using this equation:

$$r = (\frac{3}{4} \times V/\pi)^{1/3}, \quad (10)$$

where  $r$  = the radius of a spherical sponge.

Measurements of oxygen levels in the interior of a roughly spherical sponge, the Barrett’s horny sponge (*Geodia barretti*), performed by Hoffmann et al. (2005) were read off their figure 2, re-expressed as fractions of ambient oxygen levels, and fitted with a logistic curve with the following form:

$$\text{Fraction of ambient oxygen level} = 1 / \left( 1 + e^{-S(I-r)} \right), \quad (11)$$

where  $r$  = the radius, measured as the depth within the sponge;

$S$  = the slope; and

$I$  = the inflection point at which oxygen is 50% of the ambient level.

The confidence interval (CI) of the slope  $S$  at the inflexion point  $I$  is estimated through bootstrapping (Fieberg et al., 2020).

## Sponges in fisheries, ecosystems, and ecosystem models

Pending a more detailed “reconstruction” of the catches of wool sponges and other commercial sponges in the world, to match the reconstruction of the catches of exploited fish and invertebrates (Pauly and Zeller, 2016a, 2016b; see also Pauly et al.<sup>1</sup>), we extracted the main features of the sponge harvest data in the global fisheries catch statistics submitted by member countries to, and harmonized and disseminated by, the FAO.

In shallow-water tropical ecosystems, sponges compete for substrate with corals and algae, and they alter plankton communities in the water column and water chemistry (Peterson et al., 2006; Valentine and Butler, 2019). They also provide food and structure for animals (Herrnkind et al., 1997; Duffy, 2007; Butler et al., 2016), among other services. As such, they are frequently included in food-web models for ecosystems. However, they are usually included as a group (e.g., as a group called *sponges* in Opitz, 1996) or as part of larger groups (e.g., as *epibenthos* in Okey et al., 2004), not as distinct species, even in cases in which one species was clearly dominant.

The growth parameters presented herein, complemented by generic estimates of food consumption and turnover ratio for sponges (Table 2), may lead to better food-web models, at least for the areas of Florida and the Caribbean where sponge biomass is substantial in shallow coastal waters and on coral reefs. In the Florida Keys, a hectare of hard-bottom habitat in shallow waters harbors

<sup>1</sup> Pauly, D., D. Zeller, and M. L. D. Palomares (eds.). 2020. Sea Around Us concepts, design and data. [Available from [website](#).]

**Table 2**

Estimates of food consumption ( $q$ ) and production ( $p$ ) per unit biomass ( $b$ ) and trophic levels from sources by the authors of 3 Ecopath food-web models in which a *sponge* group is explicitly included. These authors sampled sponges from 3 marine ecosystems: the Virgin Islands (Opitz, 1996), the central Great Barrier Reef in Australia (Tudman, 2001), and the Te Tapuwae o Rongokako Marine Reserve (TTMR) off the North Island of New Zealand (Pinkerton et al., 2008). See tables 3 and 5 and text in Pinkerton et al. (2008) for issues with the TTMR estimate, which appears to be the most credible of the 3 estimates of  $p/b$  in this table.

Location	Trophic level	$q/b$ (year <sup>-1</sup> )	$p/b$ (year <sup>-1</sup> )	Source
Virgin Islands, Caribbean	2.0	4.2	1.7	Opitz (1996)
Central Great Barrier Reef	2.0	3.0	0.9	Tudman (2001)
TTMR, North Island, N.Z.	2.3	0.8	0.2	Pinkerton et al. (2008)

an estimated 47,000 individual sponges of all types with a volume of approximately 17 m<sup>3</sup>/ha. On average, 10% of those sponges have diameters that exceed 25 cm, and wool sponges make up about 1% of the total sponge biomass (Butler et al., 2021). On coral reefs in the Caribbean, over 500 species of sponges have been identified and their average percent cover of 16% (range: 2–75%) exceeds that of corals (Miloslavich et al., 2010; Loh and Pawlik, 2014). Clearly, sponges are a major component of many tropical marine ecosystems as are their ecological ramifications, and this importance is reflected in sponges being part of published ecosystem models. We examined this issue through the coverage of sponges in successive implementations of the commonly used Ecopath food-web modeling software (Christensen and Pauly, 1992; Colléter et al., 2015).

## Results

### Growth

The parameters of the VBGF (Equation 4) from the diameter-at-age data in Table 1 led to the following equation:

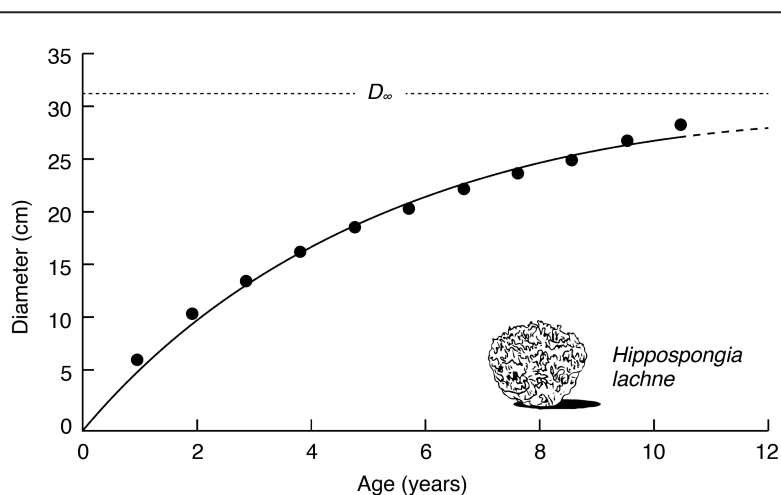
$$D_t = 31.5(1 - e^{-(0.191t)}), \quad (12)$$

where  $D_t$  = the predicted diameter at age  $t$  in centimeters.

The parameter  $t_0$  (see Equation 4) is not included in this equation because it was set at zero, forcing the growth curve to start at the origin of the age scale in Figure 2. As for the value of 0.191 year<sup>-1</sup> for the parameter  $K$ , its 95% CI, estimated by bootstrapping the data in Table 1, is 0.185–0.199 year<sup>-1</sup>. This interval is likely to be an underestimate

because the age-at-length data in Table 1 are means and therefore do not include variability in individual growth. However, even when available, data on individual growth variability are still difficult to consider when estimating VBGF parameters (Sainsbury, 1980; Wang and Thomas, 1995). The estimate of asymptotic size is close to the maximum size reported by Storr (1964), 12 in (or ~30.5 cm) up to the size at which the sponge's spherical shape is maintained.

Using Equation 3 to compute the relationship of diameter to volume indicated by the data in Table 1 leads to a mean value of parameter  $a$  of 0.55 for mediating between diameter in inches and volume in cubic inches. For the

**Figure 2**

Growth of the sheepswool sponge (*Hippospongia lachne*), also known as the wool sponge, in the upper Gulf of Mexico as indicated by a von Bertalanffy growth curve fitted to diameter-at-age data from Storr (1964) (see Table 1). The estimates of asymptotic length (i.e., diameter) and growth coefficient are 31.5 cm and 0.191 year<sup>-1</sup>, respectively. The horizontal dashed line indicates the asymptotic diameter ( $D_\infty$ ).

diameter in centimeters and the volume in cubic centimeters, the expression of the diameter-to-volume relationship in the wool sponge becomes

$$V = 0.055 \times D^3. \tag{13}$$

Therefore, the equation for the relationship between the age in years and the volume in cubic centimeters becomes

$$V_t = 1046 \left(1 - e^{-(0.191t)}\right)^3. \tag{14}$$

Opitz (1996), for her detailed food-web model of Caribbean reefs, used a ratio of dry weight to wet weight of 333:100 and considered 22.5% of wet mass to be “inorganic skeletal material,” on the basis of a personal communication from a scientist working mainly on deepwater or cold-water sponges.

Our own determination of the percentage of wet weight to dry weight for wool sponges collected in the Florida Keys (number of samples [n]=15) is 3.9% of wet mass. A larger percentage (11%) was estimated for another commercial sponge species that we collected in the same area (n=20): the grass sponge (*Spongia graminea*), which is the second-most valuable commercial sponge in Florida.

**Longevity**

The estimated longevity of the wool sponge, that is of its first, spherical phase, is as follows, given Equation 7:  $3/0.191 \approx 16$  years, with uncertainty ranging from 12 to 24 years. On the other hand, the values of production per unit biomass (which can be considered equal to Z) in Table 2, used with the inverse of Equation 8, lead to estimates of longevity of 2.5 years (for Z of 1.7 year<sup>-1</sup>), 4.8 year (for Z of 3.9 year<sup>-1</sup>), and 22.3 years (for Z of 0.2 year<sup>-1</sup>). Only the last of these estimates appears realistic, whereas the first estimate of 16 years is compatible with that of Storr (1964, p. 18–19), whose longevity estimate includes the life history phase during which wool sponges change shape (which was not considered in our study). In the meantime, however, experiments have been conducted, and their results indicate that the longevity of wool sponges is strongly influenced by environmental stress (e.g., stress caused by high temperatures, extreme levels of salinity, and phytoplankton blooms) (Butler et al., 2018).

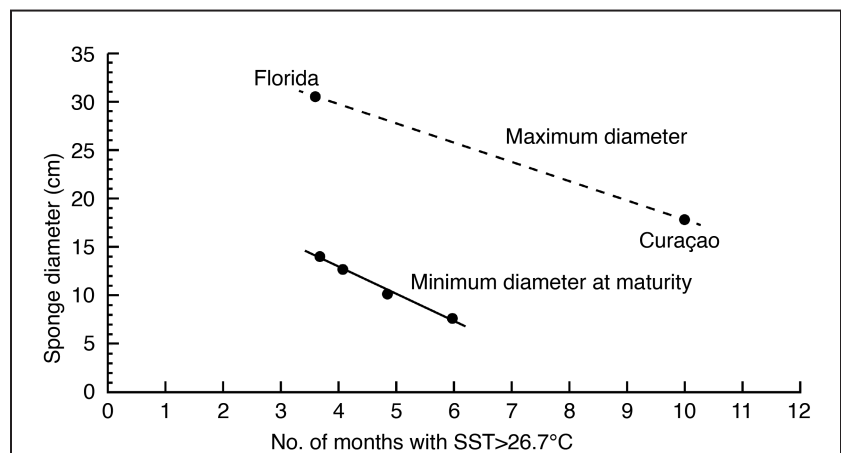
Also note that the value of Z that was based on estimates of production per unit biomass in Table 2 and was used to produce, through Equation 8, the only reasonable estimate of  $t_{max}$  also leads to the following ratio for sponges:  $Z/K=0.2/0.191 \approx 1.1$ . In the absence of fishing (as was the case in the model developed with data from work in the

Te Tapuwae o Rongokako Marine Reserve in New Zealand; Pinkerton et al., 2008) (Table 2),  $Z/K$  is also  $M/K$  and  $M/K \approx 1.1$ , which is a very plausible value for low-activity or sessile animals. Therefore, for example, although  $M/K$  is 1.5 for many populations of bony fishes (Taylor, 1958; Froese et al., 2016), the mean  $M/K$  is 0.76 for 16 populations and 13 species of bivalves (from Vakily, 1992, appendix 4) and is 1.1 for 11 species of sea urchins (see Longhurst and Pauly, 1987, figure 10.2, based on Ebert, 1975), with both groups represented by both warmwater and cold-water species.

**Reproduction**

Butler et al. (2017) established that the number of gametocytes in tissue samples from 3 species of commercial sponges from the Florida Keys were positively and significantly related to sponge size, whether measured as sponge volume ( $F=4.762$ ;  $df=1, 15$ ;  $P=0.047$ ;  $r^2=0.254$ ) or as diameter ( $F=9.270$ ;  $df=1, 15$ ;  $P=0.009$ ;  $r^2=0.398$ ); the relationships explained ~40% of the variance in gametocyte number.

van Soest (1978) concluded that wool sponges reach a size up to 18 cm in diameter in the waters of Curaçao, where the waters are warmer than those of the upper Gulf of Mexico and where wool sponges reach diameters of over 30 cm (Storr, 1964). These numbers lead to Figure 3, which shows that maximum sizes reached by wool sponges decline with temperature (as indicated by the definition of the parameters of Equation 6) and which also illustrates the inverse relationship between minimum length at first maturity and water temperature, as has been reported for other WBE (Pauly, 2021a). This finding is supported by measurements of the growth of wool sponges in the Florida Keys, where average growth rates varied 5-fold seasonally (Butler et al., 2017).



**Figure 3**

Apparent temperature dependence of size at first maturity (solid line) and maximum size (dashed line) for the sheepswool sponge or wool sponge (*Hippospongia lachne*) off Florida in the Gulf of Mexico (based on data from Storr, 1964) and in the waters of Curaçao in the Caribbean Sea (based on data from van Soest, 1978). SST=sea-surface temperature.



However, the mean of 0.4 for the ratio of  $L_m$  to  $L_\infty$ , shown in Figure 3, cannot be used for the wool sponge to test the hypothesis in Pauly (1984) (see also Pauly, 2021a), which predicts values for this ratio in WBE. The reason is that the data in Storr (1964) do not pertain to the *mean* size at which wool sponges mature (i.e., the length at which 50% of a cohort reaches maturity) but do indicate the *minimum* size at which some of them do.

### Respiration

The respiratory area of the wool sponge is not known. Measurements of the respiratory area for the European coastal sponge *Suberites massa*, taken decades ago, have been used to estimate the area at 100 cm<sup>2</sup>/g (Pütter, 1914; von Ledeber, 1939). Gatti et al. (2002) used oxygen microprobes to measure oxygen concentrations within the tissue of the Mediterranean bacteriosponge *Suberites domuncula* and detected oxygen concentrations of approximately 50% of the surrounding ambient seawater. Weisz (2006) used oxygen microprobes and tetrazolium salts to examine oxygen concentrations and the occurrence of anoxic zones in 4 species of low-microbial-abundance and high-microbial-abundance sponges. Oxygen concentrations within the ectoderm and endoderm of low-microbial-abundance sponges were similar to ambient seawater concentrations, whereas endoderm tissues in high-microbial-abundance sponges were all hypoxic or anoxic.

The decline of the oxygen content in the interior of the near-spherical sponge Barrett's horny sponge studied by Hoffmann et al. (2005) can be re-expressed as follows:

$$\text{Fraction of ambient oxygen level} = \frac{1}{1 + e^{-0.675(2.76 - r)}}, \quad (15)$$

where  $r$  = the depth (in centimeters) within the sponge.

The decline of oxygen level is most rapid at the inflexion point of 2.76 cm (95% CI: 2.52–2.98), and the slope at the inflexion point ( $S = -0.675$ ) has a 95% CI of  $-0.998$  to  $-0.548$  (Fig. 4). The generality of the numbers estimated with Equation 15 and illustrated in Figure 3 cannot currently be assessed, given that they were derived from an experiment on one species at one (low) temperature (6–15°C) (Hoffmann et al., 2003). However, the shape of this relationship is likely realistic and could be adapted to different species by increasing or decreasing the 2 parameters of Equation 15 (or Equation 10). The provided equations allow computing the oxygen level in near-spherical sponges by adding the dissolved oxygen in successive

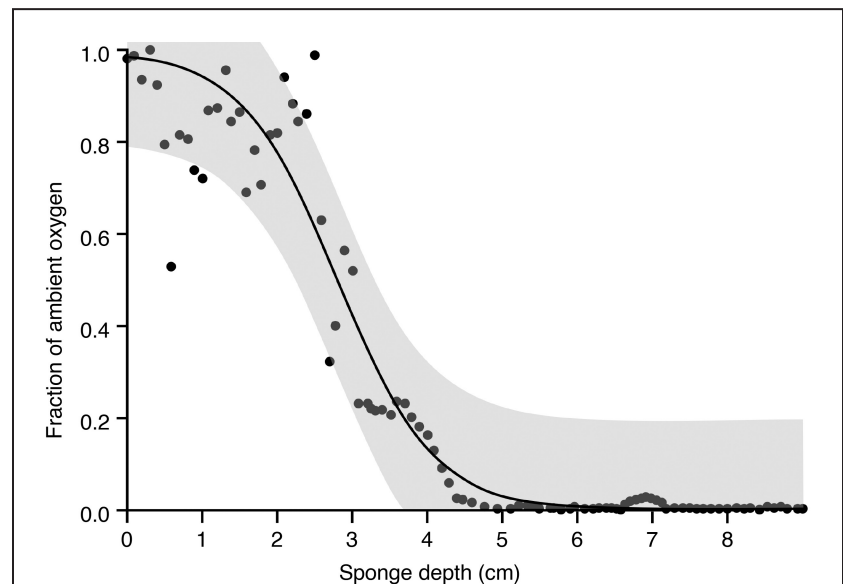
depth layers, and the oxygen level of each depth layer is the mean of the oxygen level at its outer and inner limits.

### Sponges in fisheries, ecosystems and ecosystem models

Official estimates of fisheries catch of sponges are available from the FAO (available from [website](#)), originating from 25–30 countries and territories and adding up to nearly 40,000 metric tons (processed dry weight) from 1950 to 2019. However, both the number of countries exploiting sponge populations and the level of their catches are likely underestimates, requiring correction as has been recently performed through catch reconstruction for the catch of the world's marine fisheries (Pauly and Zeller, 2016a, 2016b), even if done with the exclusion of sponges.

Empirical estimates of effects of commercial fisheries on sponge communities are virtually unavailable, although in south Florida, management limitation of harvest based on the use of artisanal techniques appears to have resulted in a sustainable fishery (Butler et al., 2017). More devastating to sponges in many areas are mass die offs of sponges due to disease, cyanobacteria blooms, and poor water quality that can extend over hundreds of square kilometers with strong effects on ecosystems (Butler et al., 1995; Herrnkind et al., 1997; Webster, 2007; Gochfeld et al., 2012; Wall et al., 2012; Butler et al., 2018).

In EcoBase, a database of Ecopath food-web models (Colléter et al., 2015; available from [website](#)) that included



**Figure 4**

The decline of oxygen content inside an approximately spherical sponge, the Barrett's horny sponge (*Geodia barretti*), based on specimens sampled at depths between 100 and 200 m on the hard-bottom slope of Korsfjord near Bergen, Norway. The values were read off figure 2 in Hoffmann et al. (2005) and re-expressed as a fraction of ambient oxygen levels. The relationship between oxygen content and sponge depth is fitted with a logistic curve, and the gray shaded area represents the 95% confidence interval.



459 models as of December 2019, 84% of the models described marine ecosystems, but only 12 models included sponges. Moreover, in only 3 of those models were sponges a group of their own, not combined with corals or other benthic animals.

Table 2 presents the food consumption and production per unit biomass estimated for sponges from a variety of sources by the authors of the 3 models in which sponges were not grouped with other organisms. Other stage-based or individual-based models depicting sponge population or community stability under fishing or environmental pressure also exist (Cropper and DiResta, 1999; Butler and Dolan, 2017), but they do not explicitly incorporate food consumption or respiration in relation to production.

## Discussion

We hope that the relationships given in the “Results” section will be useful to colleagues involved in the comparative study of sponges, the assessment of the status of fisheries for the wool sponge and similar sponges, the modeling of the ecosystems in which such fisheries are embedded, and the potential mariculture of sponges. There is, however, another interesting aspect to the growth and related traits of wool sponges pertaining to the first author’s attempt to formulate, test, and illustrate a comprehensive theory of growth for WBE, the gill-oxygen limitation theory (Pauly and Cheung, 2017; Pauly, 2019a, 2021a).

Sponges originated approximately 800 million years ago in the Pre-Cambrian (Reitner and Wörheide, 2002; Turner, 2021); therefore, they had ample time to evolve sophisticated defenses in the form of spicules embedded in a tough matrix, which partly protects them against spongivores (Wulff, 2006; to generate a list of spongivorous fishes, select *sponges* in the drop-down list of the food item search tool on FishBase, available from [website](#)), a strategy resembling that of thorny land plants. Also, similar to plants, sponges cannot evade predators and as a result have evolved an ability to synthesize a dazzling array of complex organic molecules to protect themselves against potential consumers and pathogens (Pawlik, 2011; Loh and Pawlik, 2014; Rohde et al., 2015), and that array is the reason they are sought after as a source of potentially useful medical compounds (Blunt et al., 2003).

On the other hand, sponges did not evolve the many differentiated cells, tissues, organs, and appendages that are characteristic of other phyla, such as mollusks, arthropods, and chordates. Therefore, we can more easily detect in sponges the constraints that have shaped the transition to multicellularity in the first animals and the emergence of the first body plans. In particular, we agree with Ward (2006), who believes that “*respiration was perhaps the most important driver of animal body plans.*” Indeed, the appearance of sponges on earth, predating oxygen-producing multicellular plants by 300 million years (Brocks et al., 2017), occurred during a period when dissolved oxygen was at a premium. At that time, a day on earth was 21 h long and atmospheric oxygen levels were only about 50% of what they

are today (Klatt et al., 2021). Although global oxygen stores later increased rapidly with the evolution of multicellular plants, for 500 million years sponges evolved in a world depauperate in oxygen. In the absence of tissues or organs specialized for oxygen acquisition, sponge morphology was likely strongly constrained by physiological oxygen demand.

The notion that oxygen constrains sponge energetics and morphology is contrary to the suggestion in Storr (1964) that the supply of nutrients (i.e., food) is the limiting factor to the survival and multiplication of the cells in the interior of a cell mass. In their review of food competition and limitation for coral-reef-dwelling sponges, Pawlik et al. (2015) found no evidence for food limitation of sponge growth. However, the reef sponge community is dominated by low-microbial-abundance sponges with high filtration rates and large canal volumes, and they dwell in an oxygen-enriched environment. The opposite is true for shallow-water-dwelling coastal sponges for which growth appears to be limited at high densities of sponges because of limitation of either food or oxygen (Valentine, 2019). Herein we show that oxygen supply could indeed be a primary constraint on sponge growth, at least for spherical high-microbial-abundance sponges.

The effects of a limited capacity to deliver oxygen to tissues is evidenced across many animal phyla (Heim et al., 2020). For *Homo sapiens*, effects are manifested in heart insufficiencies and attacks (Weber and Janicki, 1979) and in ischemic strokes (Janardhan and Qureshi, 2004). This phenomenon also applies to cancerous tumors whose cells shift to glycolytic metabolism when their interior is deprived of oxygen or when a temperature increase drives their oxygen demand beyond the capacity of the blood supply that they have commandeered (Warburg, 1930; Al Tameemi et al., 2019).

The fundamental reason for a limiting role of oxygen is that, because of its toxicity, molecular oxygen cannot be stored in living animal tissue (Lane, 2002); the oxygen that is stored in the mesoglea of jellyfish (Thuesen et al., 2005) is no exception because the mesoglea is not living tissue. The only way oxygen can be stored is through chemical bonding as in blood (Lenfant et al., 1970; Noren et al., 2002), and oxygen storage requires an internal circulatory system that is absent in many phyla (Heim et al., 2020), including the Porifera.

As a result, the growth of poriferans, and especially those with a spherical shape, is constrained by the aforementioned dimensional tension (Pauly and Cheung, 2017) inherent in having to supply a growing (3-D) body with oxygen in water whose flow is determined by the cumulative (2-D) cross section of the inhalant ostia (inhalant pores). This constraint remains even if a sponge’s pumping rate increases with body size.

If they are limited by oxygen, we can predict that sponges, especially sphere-shaped demosponges when fully grown, will experience hypoxia and even anoxia in the central part of their bodies, as is commonly observed. Yet, this oxygen limitation also permits the presence of anaerobic bacteria and archaea within the commensal community dwelling inside sponges, not too dissimilar to

the microbiome in the human gut (Cénit et al., 2014). The microbiome of sponges can be equivalent to 40% of sponge wet body weight (Lavy et al., 2016), and high densities of microbes confer multiple beneficial functions, including access to microbially mediated metabolic pathways (Hentschel et al., 2006; Weisz, 2006; Schläppy et al., 2010; Webster and Taylor, 2012; Poppell et al., 2014).

The gill-oxygen limitation theory, which building on Equations 3–6, is structured around the constraints resulting from a 2-D oxygen system having to supply the 3-D bodies of water-breathing animals (Pauly and Cheung, 2017; Pauly, 2019a, 2021a), may also apply to sponges—at least to high-microbial-abundance sponges with approximately spherical shapes.

But not all sponges are spherical. Indeed, among their various morphologies are tube-shaped sponges, vase-shaped sponges, encrusting sponges, and irregularly shaped globular sponges. Their internal structure is equally variable. The internal tissues of some are dense, whereas the extensive canal system of others makes them full of voids. There are also striking differences in the skeletal structure and makeup of spicules that define in large part sponge families. All of these characteristics play a role in water flow through sponges and influence oxygen availability.

In addition to an illustration of the gill-oxygen limitation theory, we can now consider sponges more completely in the context of ecosystem functioning. Prior to this contribution, it was difficult to accurately convert the dry weight of wool sponges into wet weight. Without these conversions, one cannot fully understand the ecological consequences of the historical collapse of the sponge fishery throughout the Americas in the early part of the 20th century, a fishery that to this day has never fully recovered (Stuart, 1948; McClenachan, 2008; Oronti et al., 2012).

The commercial export of sponges in the Americas began in The Bahamas in 1841 with the shipwreck in The Bahamas of a French merchant who later carried 500–600 specimens to Paris, where he sold them (Corfield, 1938; Stuart, 1948). Note, however, that prior to this shipment, the merchant observed “*a great number of sponges in use among the natives*” in The Bahamas, suggesting that a market for sponges might have already existed there locally before the first exports to Europe (Corfield, 1938). Additionally, Moore (1910) notes that in the Florida Keys “[*it is known that long before these [i.e., sponges] became an article of commerce they [i.e., sponges] were in limited domestic use among the inhabitants.*” It is unclear when exactly sponges were first harvested in the Americas. However, it is well documented that following the first commercial export of sponges from The Bahamas in the mid-1800s, the large-scale export of sponges quickly spread throughout the Western Atlantic region, with Tarpon Springs in Florida and Batabano in Cuba becoming areas of major importance (Moore, 1910; Corfield, 1938; Bethell, 2017).

The rise and collapse of the sponge fishery in The Bahamas in many ways mirrors the events that occurred throughout the Western Atlantic region (Stuart, 1948; McClenachan, 2008; Oronti et al., 2012). At its peak in 1917, the industry employed one-third of the Bahamian workforce and included

the harvesting, processing, and trading of sponges (Oronti et al., 2012; Bethell, 2017). However, by the late 1930s, a combination of disease, hurricanes, and overexploitation led to orders of magnitude decline in catches, so that by 1947, sponge exports had plummeted to 14.8 metric tons (Oronti et al., 2012). Of note is a fungal blight in the late 1930s that killed 70–95% of the already drastically reduced populations of sponges in The Bahamas before spreading to adjacent countries (Galtsoff et al., 1939). Beginning in the early 1990s, repeated phytoplankton blooms similarly destroyed up to 95% of the sponge communities over large swaths of the Florida Keys, where commercial sponge fishing continues to this day (Butler et al., 1995; Wall et al., 2012). The conversion from dry weight to wet weight that we present for the wool sponge, which was (and still is) a regionally abundant species and a commercially valuable species in the global trade (Moore, 1910; Corfield, 1938; Stuart, 1948; McClenachan, 2008), allows the quantification of the effect of the collapse of the sponge fishery in the Western Atlantic Ocean on patterns of past ecosystem biomass-dependent functions.

## Conclusions

The contention, herein illustrated with the wool sponge, that the growth of large, near-spherical sponges may be limited by the oxygen supply to their interior allows a number of inferences on their likely response to ocean warming and deoxygenation, and these inferences should be important to sponge fisheries and aquaculture and to the study of sponges in their ecosystem context.

Moreover, we demonstrate that the gill-oxygen limitation theory, developed mainly with data for vertebrate, molluscan, and arthropod WBE, also applies to compact, near-spherical sponges. This demonstration provides a new avenue for their study, as it should allow the formulation of various hypotheses about their biology, notably on their shape-shifting past certain sizes, that should be straightforward to test.

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