Theoretical analysis of the weight-length relationship in fish juveniles

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Abstract. The weight-length relationship in fish juveniles was investigated theoretically, to assess the significance of the allometric factor and the validity of the condition factor; these biological factors often remain undetermined, because most fishery studies have been conducted for commercial-sized and/or adult populations. The exponent b (allometric factor) seemed to be the main parameter, performing a key role in the equation $W = aL^b$, where W = weight, a is a constant and L = length. The parameters a (condition factor) and K (ponderal index; $K = 10^3 \, W/L^3$) were judged to be less important in comparative studies, since these parameters were closely correlated with b. It is recommended that the assumed theoretical value of $b = 3$ not be used in applied ichthyological surveys, since this value was rarely obtained in the studies, and since a much wider range is usually seen. These analyses led to a new working hypothesis – not yet verified – which opens a new approach to understanding the biological significance of the allometric factor. This approach involves the fractal theory (where b may be considered as a fractal dimension equivalent) linked to the theory of saltatory ontogeny [where b is a threshold characteristic in the (early) life history of fishes].

Introduction

In their early development, fish typically pass through several distinct stages, or "stanzas", of growth (Vanetsov 1953). During these stages, a rather abrupt change in structure or physiology occurs. Usually the stanzas are separated merely by the occurrence of morphological change (manifested in the weight-length relationship), or sometimes simply by a sudden change in growth rate. It has been found that, within any stanza in the life history

of fish, weight varies in relation to length. When a general weight-length relationship for a population is required, an effort should be made to obtain fish in a wide size range (Ricker 1980).

Almost all fishery surveys are focused on commercial species, and thus the growth parameters length and weight are described only for adult fish. When only older, commercial-sized fish are available, estimated parameters can deviate seriously from their actual values simply due to sampling variability. In previous nursery ecosystem studies I collected a large number of fish juveniles (Safran 1987a, b, 1990a, b, Safran and Omori 1990). Based on this material, the present work assesses the value of the allometric factor connecting weight to length and evaluates the validity of the condition factor, which has been applied in ichthyological studies. This study represents a theoretical analysis of the weight-length relationship in fish juveniles, with special attention to a possible linkage between the fractal theory (Mandelbrot 1984, Frontier 1987) and the theory of saltatory ontogeny (Balon 1984, 1986).

Materials and methods

Juveniles of various fish were caught during a nursery ecosystem survey along the French Opal Coast along the eastern English Channel (Safran 1987a, b, 1990a), and during an investigation of drifting seaweed communities which was carried out in the waters off Tohoku Coast, Japan (Safran 1990b, Safran and Omori 1990). Specimens were preserved in a 10% solution of buffered formalin, and stored for later sorting, identification and analyses. Standard lengths were measured to the nearest millimeter. The weight of preserved specimens of each species was determined to the nearest gram. Stomach content analyses were also performed.

Le Cren (1951) sought a formulation of the weight-length relationship more generally applicable to a wide range of species and body forms. He pointed out that, in fish, this relationship may be expressed generally by the following formula: $W = aL^b$, where W = weight, L = length, a is a constant (the condition factor, so called because it indicates the physiological condition of the studied species relative to a specific standard), and b is the allometric factor. This expression can also be written $\log W = \log a + b \log L$, in which case the weight-length data for fish with the same weight vs

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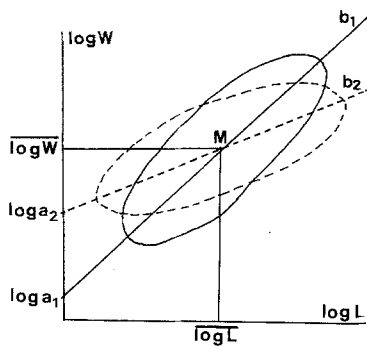
Fig. 1. Weight-length relationship. Relation between $\log W$ and $\log L$, with the value of b variable. W: weight; L: length; a: condition factor; b: allometric factor; M: mean point or center of the cloud of points

Fig. 2. The weight-length relationship, showing several instantaneous slopes b_i (with a mean value of $\bar{b} = \sum_{i=1}^{n} b_i/n$), and one general slope $\tilde{b}$

length relationship will fall approximately on a straight line if plotted on log-log paper (Weatherley 1972).

These expressions would apply best to an individual fish measured and weighed in successive years of its life. This, of course, is rarely possible. The value of b is usually determined by plotting the logarithm of weight against the logarithm of length for a large number of variously sized fish, the slope of the fitted line being an estimate of b (Ricker 1980). This line passes through the mean point M of a cloud of points, the coordinates of which are $\overline{\log W}$ and $\overline{\log L}$, the slope $b = \sigma \log W/\log L$, and the origin coordinate $\log a$. When the cloud of points is rectilinear (in log-log coordinates), parameters b and a are characteristic of the species within the studied interval. In juveniles, the interval always remained small and the mean point was fixed; the condition factor a became an indispensable parameter for fitting the allometric line, and $\log a$ was inversely proportional to allometric factor b (Fig. 1). For a given population, the instantaneous allometric factor b_i was deduced from a calculation of the slope of the fitted line obtained in each sample. To determine the typical allometric factor for a population, two methods were used. Firstly, from all these instantaneous b_i values, a mean value $\bar{b}$ was deduced $\left(\sum_{i=1}^{n} b_i/n \right)$, called the mean allometric factor. Secondly, all the graphic representations were superimposed and yielded approximately a straight line, the slope of which was $\tilde{b}$, the general allometric factor. Mean allometric factors $\bar{b}$ were due to instantaneous distributions, which explained the difference between their values and those of the general allometric factor $\tilde{b}$ (Fig. 2).

The functional regression value $b = 3$ describes isometric growth, which would characterize a fish of unchanging body form and unchanging specific gravity. Nevertheless, some variability – either individual or seasonal – remains, due to time, stomach contents, spawning conditions, etc. On the other hand, some species have b values characteristically greater or less than 3, a condition described as allometric growth. When $b < 3$, L^b increases faster than W (weight, and thus volume): the shape of the animal tends toward flatness or attenuation when length increases. When $b > 3$, the fish becomes more spherical as length increases.

To compare weight and length for a particular sample or individual, condition factors are used. One is the Fulton's condition factor, equal to W/L^3 (Fulton 1911). This is the parameter a in the allometric equation, with an assumed value of $b = 3$. The heavier a fish is for a given length, the greater the condition factor, and (by implication) the better the condition. From Fulton's factor, a condition factor $K = 100 \, W/L^3$ is derived, which seems to have been created for studies of Salmonidae (Frost and Brown 1967, Weatherley 1972). Nevertheless, it is difficult to apply, and Bauchot and Bauchot (1978) proposed a homogeneous formula: $K = 1000 \, W/L^3$. They called K the ponderal index, since it can be applied to a wide range of species and allows numerical comparison to be made more easily. Its value varies from 0.2 (Moringuidae) to 72 (Molidae); this index represents the somatic weight, in grams for a fish 10 cm in length, in kilograms for a fish 1 m in length, etc.
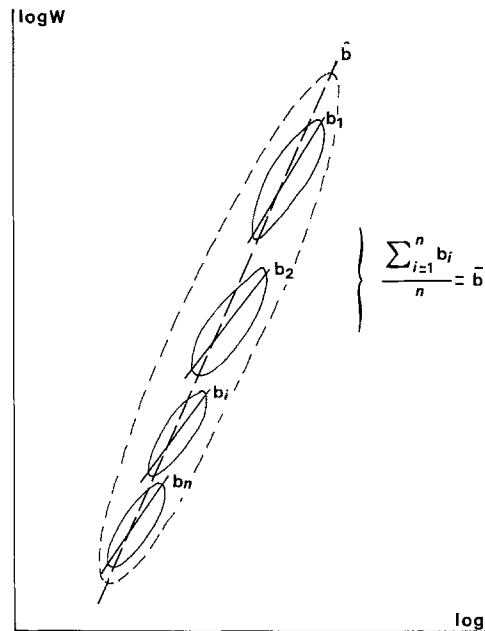
Some growth comparisons were made using the stomach contents index [SCI = (weight of total stomach contents) $\times 10^2$/(total fish weight); Hyslop 1980].

Results

The intraspecific relation was checked for pairs of W-L values in juvenile-stage Yellowtail, *Seriola quinqueradiata* Temminck et Schlegel, ranging in length from 19 to 157 mm. The correlation coefficient, $r = 0.995$, was greatest with the following equations, which fitted 223 pairs of values (with $x = \log L$ and $y = \log W$):

$$y = 3.089 \, x - 2.057;$$
$$y = 0.386 \, x^2 + 2.470 \, x - 1.814;$$
$$y = 0.658 \, x^3 - 1.225 \, x^2 + 3.765 \, x - 2.155.$$

The correlations of the quadratic fitting curve and the linear regression curve were almost equal. The cubic fitting curve, the correlation of which seemed better, was adjusted for irregularities in the small-sized juveniles. When the scale of observation was changed (and consequently the sampling) – as for example in Fig. 3, which represents this relation graphically in dual logarithmic coordinates fitted by 512 pairs of values – the following equation was obtained: $y = 3.039 \, x + 1.0223$, with $r = 0.996$. Fig. 4a illustrates clearly the different cases, where 146 pairs of values from all the samples collected yielded the general equation $y = 3.043 \, x - 1.927$ ($r = 0.992$), revealing two obvious groups: 23 pairs of values from one sample represented a group for which $y = 3.083 \, x - 1.917$ ($r = 0.989$); and 80 pairs of values from another sample represented a group for which $y = 2.788 \, x - 1.824$ ($r = 0.963$). In addition, using the same samples (Fig. 4b), a growth comparison was made
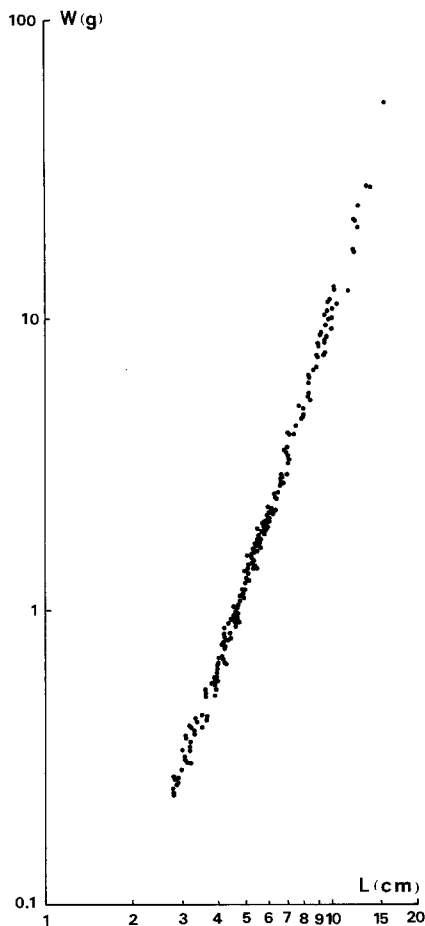
Fig. 3. *Seriola quinqueradiata.* Weight-length relationship in Yellowtail juveniles. The log-log diagram is fitted by 512 pairs of values ($W = 9.57 \times 10^{-3} L^{3.039}$; $r = 0.996$)

Table 1. *Seriola quinqueradiata.* Variability of instantaneous growth parameters in the weight-length relationship in juveniles. S: sample number; N: number of individuals in the sample; r: correlation coefficient; a: condition factor; b: allometric factor; L: mean length (cm); W: mean weight (g)

S	N	r	a ($\times 10^{-2}$)	b	L	SD	W	SD
1	78	0.992	1.29	2.837	4.86	1.25	1.145	1.905
2	44	0.994	0.92	3.108	5.81	1.44	2.131	3.105
3	10	0.997	1.05	2.985	5.42	1.27	1.635	2.067
4	37	0.997	0.97	3.009	4.43	1.32	0.856	2.305
5	190	0.995	1.42	2.813	3.91	1.33	0.656	2.257
6	232	0.993	0.93	3.039	6.18	1.22	2.358	1.835
7	258	0.901	1.91	2.578	3.59	1.18	0.516	1.594
8	291	0.982	1.34	2.872	4.76	1.11	1.184	1.354
9	223	0.926	1.05	2.998	6.04	1.29	2.312	2.296
10	512	0.996	0.96	3.039	5.97	1.41	2.180	2.858

2.17 (*Clupea harengus*) $\leq b_i \leq$ 5.38
(*Agonus cataphractus*)

2.64 (*Pleuronectes platessa*) $\leq \bar{b} \leq$ 3.66
(*Gaidropsarus vulgaris*)

2.64 (*Pomatoschistus minutus*) $\leq \bar{b} \leq$ 3.31
(*Gaidropsarus vulgaris*)

Values obtained for these allometric factors led to a mean value of $b = 3.06 \pm 0.38$.

Table 3 presents results on the weight-length relationship in fish juveniles associated with drifting seaweed in Tohoku waters off Japan (Northwest Pacific). The general allometric factor displayed the following range:

2.731 (*Pholis nebulosa*) $\leq \bar{b} \leq$ 5.013
(*Sebastes thompsoni*)

Values obtained led to a mean value of $\bar{b} = 3.07 \pm 0.41$. The correlation between a and b was examined [e.g. *Sebastes schlegeli*: $a = -0.0128b + 0.0507$ ($r = -0.969$); *Thamnaconus modestus*: $a = -0.0178b + 0.679$ ($r = -0.945$)].

Mean values obtained for the allometric factor b were approximately equal to 3, the theoretical value often used in applied ichthyology. The specific values, always different from 3, were associated with the scale of observation, and consequently with the particularity of the sampling. This variability in b reflects a difference in morphology among individuals and not allometric growth (the sample was instantaneous). The theoretical value $b = 3$ can be assumed to make calculation of the condition factor easier, although it is better to employ the specific value within specific species.

The ponderal index, calculated with the (assumed) value $b = 3$, is also given in Tables 2 and 3. The following ranges were found: 4.78 ± 2.43 (*Sprattus sprattus*) $\leq K \leq 28.11 \pm 16.33$ (*Limanda limanda*), with a mean value of $K = 9.47 \pm 5.61$; and 2.95 ± 0.07 (*Cololabis saira*) $\leq K \leq 62.4 \pm 10.32$ (*Histrio histrio*), with a mean value of $K = 16.47 \pm 15.06$.

The range of variation was wide and comparison of values, as well as determination of their biological significance, remained difficult and inappropriate.

using stomach-contents weight (SW) vs body weight (W), where 132 pairs of values led to the general equation $SW = 0.104 W - 0.0181$ ($r = 0.983$), revealing the same obvious groups: 22 pairs of values represented a group for which $SW = 0.0928 W + 0.176$ ($r = 0.935$), and 78 pairs of values represented a group for which $SW = 0.0707 W - 0.007$ ($r = 0.938$). The SCI revealed no obvious relation.

Analysis of instantaneous sample parameters (Table 1) yielded the following ranges: $0.901 \leq r \leq 0.997$, and $2.578 \leq b \leq 3.108$, with $\bar{b} = 2.93 \pm 0.148$, and $\hat{b} = 3.039$.

Parameters a and b were found to be closely related, with a correlation coefficient $r = -0.985$; a was dependent on b so that:

$a = -0.0191 b + 0.0678$

$a = 0.0118 b^2 - 0.0867 b + 0.164$

$a = 0.0404 b^3 - 0.333 b^2 + 0.890 b - 0.757$

It seemed that *Seriola quinqueradiata* kept its same general shape during growth, and that the allometric factor, which compares volume to length, was virtually isometric.

Table 2 presents results of similar analyses of fish juveniles from a coastal nursery along the Pas-de-Calais (eastern English Channel), with the following ranges:
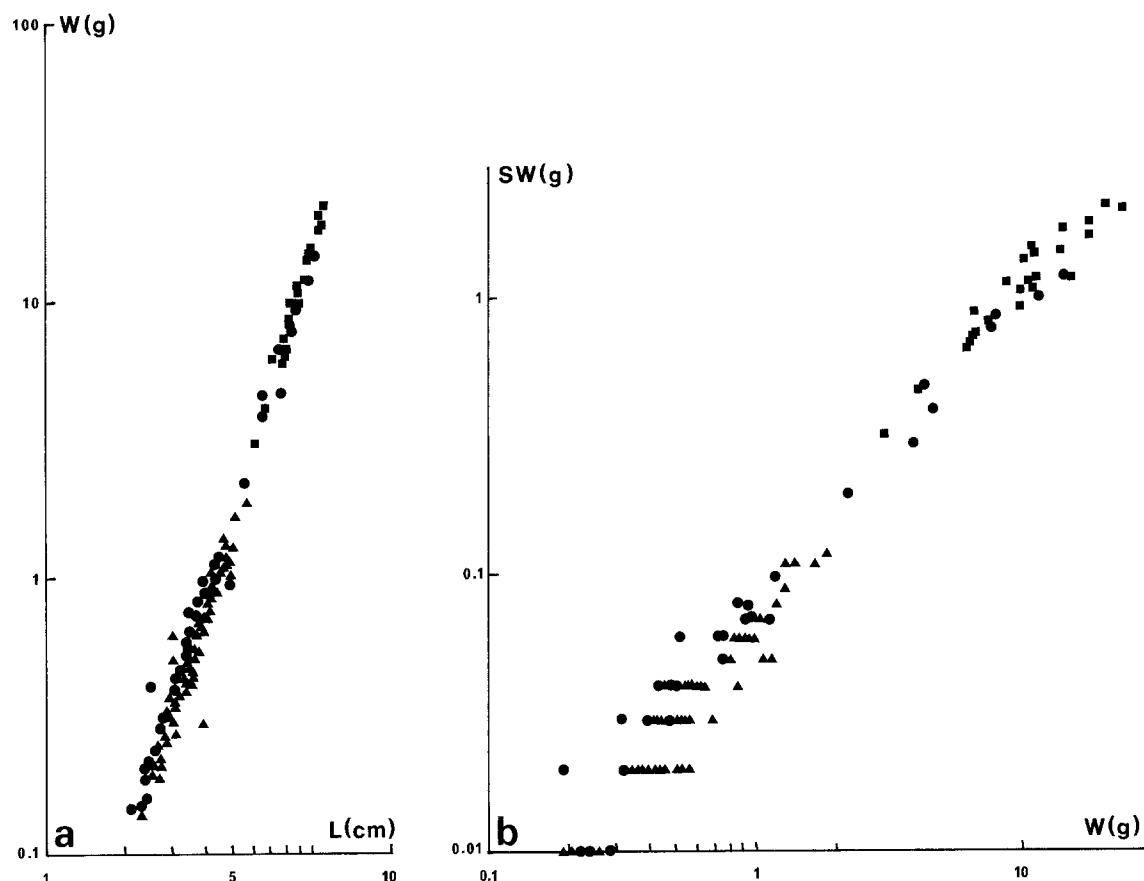
Fig. 4. *Seriola quinqueradiata*. (a) Weight-length (W-L) relationship plotted on a log-log diagram, fitted by 146 pairs of values (●: $W = 11.83 \times 10^{-3} \, L^{3.043}$, $r = 0.992$). ■: 23 pairs of values composing Group 1 ($W = 12.11 \times 10^{-3} \, L^{3.083}$, $r = 0.989$); ▲: 80 pairs of values composing Group 2 ($W = 14.99 \times 10^{-3} \, L^{2.788}$, $r = 0.963$).

(b) Stomach-content weight vs total fish weight (SW vs W) relationship plotted on a log-log diagram, fitted by 132 pairs of values (●: $SW = 0.959 \, W^{1.27}$, $r = 0.983$). ■: 22 pairs of values composing Group 1 ($SW = 1.499 \, W^{1.24}$, $r = 0.935$); ▲: 78 pairs of values composing Group 2 ($SW = 0.984 \, W^{1.18}$, $r = 0.938$)

Table 2. Inter- and intraspecific variability of growth parameters in juveniles of various fish species in a coastal nursery in the English Channel. b_i: instantaneous allometric factor; $\hat{b}$: general allometric factor; $\bar{b}$: mean allometric factor; K: mean ponderal index. Adapted from Safran (1987a, b)

Species	b_{i1}	b_{i2}	b_{i3}	b_{i4}	b_{i5}	b_{i6}	b_{i7}	$\hat{b}$	$\bar{b}$	SD	K	SD
Clupea harengus	2.86	2.17	2.64	3.46				3.09	2.78	0.46	7.62	0.18
Sprattus sprattus	2.63	2.98	3.72	3.47				3.37	3.21	0.42	4.78	2.43
Merlangius merlangus	3.07	3.14	3.11					2.85	3.11	0.03	7.33	0.39
Trisopterus minutus	2.67	3.52	3.13	3.42				3.56	3.31	0.33	11.04	1.12
Gaidropsarus vulgaris	3.12	3.50						3.66	3.31	0.19	6.41	1.14
Trachinus vipera	3.31	2.94	3.07	2.91	3.33	2.88		3.21	3.07	0.18	10.03	2.16
Pomatoschistus minutus	3.05	2.59	2.20	2.70				3.33	2.64	0.30	7.76	0.24
Callionymus lyra	3.01	2.91	2.86	3.01	2.82	3.25	3.06	3.15	2.99	0.13	6.32	0.97
Eutrigla gurnardus	3.01	2.79						2.78	2.90	0.11	8.81	0.02
Agonus cataphractus	5.38	2.99	2.66	2.73	2.97	2.87		2.95	3.27	0.95	7.99	0.70
Pleuronectes platessa	3.26	3.41	2.87	2.37	3.01	2.96	3.01	2.64	2.98	0.30	9.54	0.57
Limanda limanda	3.16	2.54	3.18	3.12	3.21	3.06	3.37	3.04	3.09	0.29	28.11	16.33
Solea vulgaris	3.14	2.87	2.96	2.89	3.11	3.15	3.01	3.50	3.02	0.11	7.40	0.19

Discussion

Variability in b and K

The mean values of b and K obtained in this study were $b = 3.13 \pm 0.396$ and $K = 12.83 \pm 11.73$, which accounted for 22.76% (minimal) and 77.24% (maximal) of the variability in b and for 16.92 and 83.38% of the variability in K. This variability might have been caused by the methods of measurement, and/or seasonal fluctuations (reflected in the change of weight over the course of a year), or variability in sampling. These results were compared with results adapted from Bauchot and Bauchot

Table 3. Interspecific variability of growth parameters in juveniles of fish associated with drifting seaweed in the Northwest Pacific. *r*: correlation coefficient; *a*: condition factor; *b*: general allometric factor; *K*: mean ponderal index. Adapted from Safran (1990b)

Species	*r*	*a* ($\times 10^{-2}$)	*b*	*K*	SD
Histrio histrio	0.995	3.53	3.219	62.40	10.32
Cololabis saira	0.969	0.41	2.779	2.95	0.07
Sebastes schlegeli	0.902	1.28	2.950	14.85	1.13
Sebastes inermis	0.980	1.39	2.939	16.81	0.37
Sebastes thompsoni	0.952	0.34	5.013	6.32	4.95
Hexamogrammus agrammus	0.994	0.38	3.545	11.34	2.84
Seriola quinqueradiata	0.996	0.96	3.039	14.21	0.38
Girella punctata	0.845	1.09	3.118	10.55	1.45
Oplegnathus punctatus	0.996	1.89	3.154	23.90	0.76
Pholis nebulosa	0.960	0.34	2.731	2.22	0.25
Hyperoglyphe japonica	0.995	2.85	2.751	16.33	3.83
Thamnaconus modestus	0.989	1.29	3.095	15.76	0.53

Table 4. Allometric factor (*b*) and mean ponderal index (*K*) of fish of various species and families. b_S and K_S: adapted from Safran (1987a, b); b_B and K_B: adapted from Bauchot and Bauchot (1978)

Species/Family	b_S	b_B	K_S	SD	K_B
Atherina presbyter	3.33	3.22	6.37		9.7
Callionymus lyra	3.15	3.02	6.32		12.4
Trisopterus luscus	2.66	3.21	9.44		15.6
Atherinidae			6.37	0.28	15.0
Callionymidae			6.32	0.97	12.4
Carangidae	2.93	3.28	14.21	0.38	18.9
Clupeidae			6.20	1.42	13.4
Gadidae	3.12	2.94	8.56	1.81	9.8
Gobiidae	2.75	2.79	7.76	0.24	20.7
Kyphosidae			10.55	1.45	31.7
Monacanthidae			15.76	0.53	29.9
Pholidae			2.22	0.25	3.2
Pleuronectidae			13.25	8.67	17.7
Scorpaenidae	3.36	2.81	12.66	4.55	34.7
Serranidae	5.78	3.00	9.46	1.87	21.7
Soleidae			8.46	1.06	17.3
Trachinidae			10.03	2.16	10.1
Triglidae			8.81	0.02	16.6

(1978), yielding the following mean values: $b = 3.13 \pm 0.18$; $K = 19.84 \pm 14.88$. The mean allometric factor deduced from the adapted data of Bauchot and Bauchot, which reflected a large number of fish, was within the range of variation for fish juveniles in the present study, whereas there was a significant difference between the two mean ponderal indices. The differences found in the ponderal index are shown in Table 4; the values for Trachinidae were quite similar, and the difference remained small for Gadidae and Pholidae, although in general the discrepancy was large. Nevertheless, the numerical values of *K* are not so important, since *K* is closely correlated with *b*. As a matter of fact, for applied ichthyological studies, only *b* seems to be important and to be a key parameter in the weight-length relationship.

The exponent *b* in the weight-length relationship of fish juveniles was generally different from 3, and a much wider range is usually observed, as shown by the results presented in this work. Therefore, assumptions concerning the values of *b* should be scrutinized when analysing growth of fish based on a model that involves this parameter. The strong correlation between *a* and *b* can be explained by colinearity, or "near colinearity", whereby – in the log *W* vs log *L* diagram – a slight variation in the estimated slope for the cloud of points leads to a strong variation closely correlated with the line origin coordinate (since the center of the cloud, *M*, remains generally fixed; Fig. 1). When necessary, as in this case, the equation should be rewritten with new, non-correlated parameters, obtained by principal component analysis performed on the two (or more) correlated parameters.

Moreover, according to Marr (1955), use of the stomach contents index reveals no obvious relation. This ratio plot did not yield any information which could not be obtained from the plot of original variates; the curvilinearity (when there is an intercept differing from zero) makes difficult, if not impossible, the computation of variance and comparison of lines; and, finally, a likely source of interpretive error is introduced. The use of original variates with appropriate transformation for regression analysis will not preclude the use of data involving allometric growth.

Is *b* a fractal dimension equivalent?

The importance of fractal geometry in the morphology of living beings has often been stressed, for scales of observation ranging from intracellular organelles to entire organisms or to vegetation physiognomies. The study of fractal geometry not only represents an attempt to search for order in the inextricable morphology of living beings, but seems to point out some properties that are essential for the functioning of life. The challenge of living matter is to manage a biomass, which is a volume, by means of fluxes through surfaces, at numerous, nested scales of activity. Such management does have dimensional constraints, because if growth is homothetic (without any change of form), surface areas increase less rapidly than volumes. In order for surfaces to grow at the same rate as a volume, a certain highly folded morphology has to develop, which is strongly reminiscent of fractal objects (Mandelbrot 1984, Frontier 1987). To date, fractal geometry has seldom been applied to this kind of biological problem. Nevertheless, it seems to offer significant perspectives. In the present circumstances, many more working hypotheses and questions can be proposed than results or solutions.

The formula $W = K L^3$ only describes the form of a fish and the ratio of its volume to the volume of a cube (where *L* is the length of the cube side and L^3 is the volume of the cube when the fish only occupies a part of this cube). This description is valid for each length *L* and for each individual, but *K* varies when the length varies, since the proportion of the cube occupied by the animal varies with the animal's age; thus, the allometry and the relation $W \propto L^b$ ($b \neq 3$) statistically describe the growth, without having a fractal geometry.

The fish's metabolism should be closely investigated. The metabolism necessary for the life of a fish with a

volume V is probably proportional to V (although this reasoning presumes the basal metabolism for an adult, whereas growth metabolism is higher relative to volume). This metabolism (flux of energy) should be proportional to the surfaces of exchange, both those between organism and milieu, and those between organs, tissues, etc. within the organism. This reasoning implies that it is necessary for living beings to generate a fractal geometry. If a living volume is multiplied by k^3, the "surfaces" (S) should be multiplied by this factor and not by k^2, because they should increase not like L^2 but like $(L^{3/2})^2$, as for example the fractal dimension of an "arborescence" (equal to 3/2; Mandelbrot 1984, Frontier 1987). Suppose that the fractal dimension of those "surfaces" is constant, for example 2.5 (power between 2 and 3, describing an "occupation degree in the three-dimensional space" by the "more than surface"). If the extent of this interface is really proportional to the volume, this volume should increase more slowly than L^3. As a matter of fact, if $V \propto L^D$, then V would be proportional to $S \propto L^D$; thus, for example:

$$\left. \begin{array}{c} \text{Fractal "exchange surface"} \\ S \propto L^{2.5} \end{array} \right\} \Leftrightarrow \left\{ \begin{array}{c} \text{Allometry} \\ V \propto 2.5 \end{array} \right.$$

Then b appears to be a "mean" fractal dimension or "global equivalent" of the "exchange surfaces" for the metabolism of an individual. This new working hypothesis seems to be supported by the theory of saltatory ontogeny (Balon 1984, 1986). As Claude Bernard says, "If an idea comes to us, we must not reject it only because it does not fit with the logical deductions of a reigning theory."

While perhaps not strictly pertinent to this discussion, any description and interpretation for relative growth data should take into account the following (Marr 1955): (1) the data may be representative of phenotypes rather than genotypes (Martin 1949, Tåning 1952); (2) length, which is commonly used as a measure of size, represents only one dimension and may, therefore, not be the best measure of size; (3) various life-history stages may involve different growth stanzas.

Balon (1986) states: "The phenotype is always recreated from an unspecialized single cell and must be more than a survival machine, being also an information gathering and transmitting system of equal importance to the genotype. A single cleaving cell cannot be in the same stabilized state as a differentiated multicellular embryo or reproducing adult. The entire ontogeny must consist of a sequence of stabilized states." During a stabilized state, cells and tissues differentiate, and structures (organs) grow at various rates, as if accumulated and formed in preparation for the next, more specialized state. The homeorhetic processes of the system resist destabilization as long as possible, enabling structures to be completed and functions to progress without interfering in stabilized life activities. When the system is ready for new or additional integrative actions, a shift is rapidly made – via a highly unstable interval – into the next stabilized state of ontogeny. Ontogeny is, therefore, a sequence of longer stabilized states and rapid changes in integrative actions (Alberch 1980, Adolph 1982, Balon 1984, 1986).

Balon (1984, 1986) developed the theory of saltatory ontogeny, which stipulates that development does not proceed as a continuous accumulation of inconspicuous, small changes but instead is a sequence of rapid changes in form and function alternating with prolonged intervals (steady states) of slower development, during which complex structures are prepared for the next rapid change. These times of rapid change from one steady state to the next are called thresholds and represent decisive events in an organism's life history.

A consequence of the theory of saltatory ontogeny is the hierarchical life-history model of embryo, larva, juvenile, adult and senescence periods, each separated by a decisive threshold; here it should be noted that in the fractal theory, organisms often display patchiness in space, which may be a fractal if patches are hierarchically nested (Frontier 1987). This model aids in recognition and interpretation of shifts in thresholds, which often result in new life-history patterns (Hall 1984). An organism passes through thresholds at much accelerated rates in order to achieve the relative security of the next stabilized state.

As a matter of fact, when the size range in individual samples is small and when the small size range is essentially the same for all samples that are to be compared, the allometric factor (b) can probably be used to determine the specificity of the threshold. For example, in Fig. 4, the two groups described might represent two different thresholds where changes (in morphology, physiology, etc.) were not obvious when using only the weight-length relationship (Fig. 4a) but could be identified when using stomach-content analysis (Fig. 4b). The dietary diversity of Group 1 (see Fig. 4) was greater, composed of algae debris, Copepoda, eggs of saury, fish larvae, Gammaridae, *Lucifer reynaudi* and Zoe larvae, while the diet of Group 2 was only made up of Copepoda (fishes associated with drifting seaweed were sampled in the same area and the same food items were found in the seaweeds; Group 1 was caught in July, while Group 2 was caught in May). The diet changed between the two thresholds as a consequence of growth (differentiation, development, and specialization of tissues, organs and functions etc.), thus resulting in the ontogenetic development observed.

It therefore follows that b may be a link between the fractal theory, as a fractal dimension equivalent, and the theory of saltatory ontogeny, as a threshold characteristic.

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