

# The growth of jellyfishes

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**Abstract** To date, a disparate array of concepts and methods have been used to study the growth of jellyfish, with the result that few generalities have emerged which could help, e.g., in predicting growth patterns in unstudied species. It is shown that this situation can be overcome by length-frequency analysis (LFA), applied to jellyfish bell diameter (i.e., “length”) frequency data. A selection of LFA methods (ELEFAN, Wetherall plots and length-converted catch curves, all implemented in the FiSAT software) is applied here to 34 sets of bell diameter frequency data of jellyfish. This led to the estimates of parameters of the von Bertalanffy growth function (VBGF), which, especially in its seasonal form, was found to fit the available size-frequency data reasonably well. We also obtained numerous estimates of mortality, useful for modeling the life history of jellyfish. Finally, by scaling their asymptotic weight ( $W_{\infty}$ , a parameter of the VBGF) to the weight they would have if they had the same water content as fish, we show that most jellyfish grow at the same rate as

small fishes (guppies and anchovies). As in fish, the VBGF parameters  $K$  and  $W_{\infty}$ , when plotted in a double logarithmic (“auximetric”) plot, tend to cluster into ellipsoid shapes, which increase in area when shifting from species to genera, families, etc. If validated by subsequent studies, auximetric plots for jellyfish would provide a powerful tool for testing comparative hypotheses on jellyfish life history.

**Keywords** Von Bertalanffy growth function · Length-frequency analysis · ELEFAN · FiSAT · Natural mortality · Water content

## Introduction

Much more attention is recently being devoted to jellyfish than previously, possibly because of some spectacular outbreaks, such as for example in the Benguela ecosystem (Lyman et al., 2006). Also, targeted fisheries catches of jellyfish are increasing (Kingsford et al., 2000). As a result, it can be expected that studies of the life history and ecology of jellyfish are likely to be intensified. Most of these studies require estimates of individual growth (i.e., the relationship between size and age), which then allows mortality rates to be inferred.

Jellyfishes differ from most other aquatic metazoans, notably fishes, in having very high water content. This feature (which they share with salps), along with their externalized anatomy, render direct comparisons

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of growth rates with other groups, e.g., fishes, difficult. This has led to situations where the authors of papers on jellyfish growth and related topics have not attempted to apply the methods and concepts used successfully in other branches of marine biology, i.e., in studies of the growth of fish. Rather, we find in papers on life history of jellyfishes, a confusing mix of methods, with a preference for percent and/or instantaneous growth rates (“this jellyfish grew 2% per day, while that grew 5%”), which cannot be used for comparisons within species and even less for comparisons between species.

This is a situation similar to that prevailing in the 1970s with tropical fish, and with squids and shrimps, about which little was known and a number of contradictory inferences were made (see Longhurst & Pauly, 1987, Chap. 9). The growth of all three of these groups was tackled, as suggested in Kingsford et al. (2000), using length-frequency analyses (LFA; see Longhurst & Pauly, 1987; and contributions in Pauly & Morgan, 1987). In the process, an understanding of their growth emerged, and their life history is now understood, and their mortality rates readily inferred, as required, e.g., for their incorporation in ecosystem models (Pauly et al., 2008).

We propose to do this for jellyfish in three steps. First, we show that frequency distributions of bell diameters, habitually collected by jellyfish scientists, provide an appropriate basis for standard LFA. Second, we show that the von Bertalanffy Growth Function (VBGF; von Bertalanffy, 1957), commonly used in fisheries research, can describe the growth of jellyfishes, especially when seasonal growth oscillations are explicitly taken into account. Finally, we show that the asymptotic weight ( $W_\infty$ ) of jellyfishes, when scaled to the same water content as in fishes, leads to growth curves that resemble those of small fishes, e.g., guppies and anchovies. This becomes particularly visible on auximetric plots (plots of  $\log K$  vs.  $\log W_\infty$ ), which allow for growth comparisons between widely disparate groups.

## Materials and methods

### Growth parameter estimation

Bell diameter frequency distributions of 34 jellyfish populations were assembled from the published

literature, or kindly made available to the authors. This consisted mainly of graphs representing a sequence of samples from which the length-frequencies were read-off, or spreadsheets were made available to us by colleagues (Table 1).

These were arranged sequentially in time, and fitted with the VBGF using a non-parametric, robust approach known as ELEFAN (Pauly, 1987, 1998a), implemented in the FiSAT software package (Gayaniilo et al., 1995, available at [www.fao.org/fi/statist/fisoft/fisat](http://www.fao.org/fi/statist/fisoft/fisat)).

The bell-diameter frequency measurements were analyzed using the ELEFAN routine of FiSAT, i.e., a routine for fitting the von Bertalanffy growth function (VBGF) to length-frequency data (Gayaniilo et al., 1995). This routine, although non-parametric, was preferred over more sophisticated approaches (e.g., MULTIFAN; Fournier et al., 1998), because it makes less demand on the underlying data, and especially because it can accommodate any unknown number of cohorts originating of the same year (Pauly, 1987), a feature common in jellyfish (Kingsford et al., 2000).

The standard version of the VBGF has the form:

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

where  $L_t$  is the length at age  $t$ ,  $L_\infty$  is the asymptotic length, i.e., the mean length the animal would reach if they were to grow indefinitely (and similar to the size of the largest specimens),  $K$  is a coefficient of dimension  $t^{-1}$ , and  $t_0$  is a parameter setting the origin of the curve on the  $X$ -axis.

As it is obvious that the growth of jellyfish, like that of any poikilothermic organism, tends to fluctuate seasonally (Longhurst & Pauly, 1987; Pauly, 1998b), a form of the VBGF (Somers, 1988) was also used that accounts for seasonality, i.e.,

$$L_t = L_\infty \cdot \left(1 - e^{-[K \cdot (t-t_0) + S_{ts} - S_{t0}]}\right) \quad (2)$$

where  $S_{ts} = CK/2\pi \cdot (\sin 2\pi \cdot (t - t_s))$ ,  $S_{t0} = (CK/2\pi \sin 2\pi \cdot (t_0 - t_s))$ , and  $L_t$ ,  $L_\infty$ ,  $K$ ,  $t$ , and  $t_0$  are as defined in Eq. 1.

In Eq. 2,  $C$  is the intensity of the (sinusoid) growth oscillations of the growth curve and  $t_s$  is the onset of the first oscillation relative to  $t = 0$ . A “winter point” (WP), can also be defined (from  $WP = t_s + 0.5$  year) as the period of the year when growth is slowest. This is usually during the coldest month of the year, i.e., in February in the northern, and July in the southern

**Table 1** Summary of jellyfish (Scyphozoa and Hydrozoa) and comb jelly (Tentaculata: Ctenophora) stocks with size-frequency distributions obtained from various published and unpublished sources

Species (class)	Locality (number of stocks)	b	a	N (r)	Water content (%)	Source
<i>Aequorea aequorea</i> (Forskål, 1775) (Hydrozoa)	Namibian shelf (1)	2.017	1.10*	2475 (0.770)	(96)	Brierley et al. (2001) and Buecher et al. (2001)
<i>Aurelia aurita</i> (Scyphozoa)	Kertinge Nor, Fyn Island, Denmark (1); Tokyo Bay, Japan (3); Black Sea (2); Kiel Bight, Germany (1); Urazoko Bay, Japan (1); Kagoshima Bay, Japan (1); Wadden Sea, Netherlands (1); Vagsbøpollen, Norway (1), Topeng Bay, Taiwan (1); Tomales Bay, USA (1); Big Jelly Lake, Koror, Palau (1)	2.79; 2.32	0.0556; 0.290	52 (0.990); n.a.	97.6	Chen (2002), Dawson & Martin (2001), Hamner & Janssen (1974), Ishii & Båmstedt (1998), Ishii & Tanaka (2001), Miyake et al. (1997), Mutlu (2001), Möller (1980), Olesen et al. (1994), Omori et al. (1995), van der Veer & Oorhuysen (1985), Weisse & Gomoju (2000), and Yasuda (1971)
<i>Catostylus mosaicus</i> (Scyphozoa)	Australia (4)				(96)	Pitt & Kingsford (2000) and Pitt & Kingsford (2003)
<i>Chiropsalmus</i> sp. (Scyphozoa)	Australia (1)				(96)	Gordon et al. (2004)
<i>Chrysaora hysoscella</i> (Linnaeus, 1766) (Scyphozoa)	Namibian shelf (3)	2.706; 2.896	0.100*; 0.060*	40 (0.970); 635 (0.970)	(96)	Brierley et al. (2001); Buecher et al. (2001)
<i>Chrysaora melanaster</i> Brandt, 1838 (Scyphozoa)	USA (1)				(96)	Brodeur et al. (2002)
<i>Cotylorhiza tuberculata</i> (Maeri, 1778) (Scyphozoa)	Vlyho Bay, Ionian Island, Greece (1)	3.100	0.080	11 (0.935)	95.8	Kikinger (1992)
<i>Cyanea</i> sp. (Scyphozoa)	Niantic River Estuary, USA (1)	3.340	0.0306*	n.a.; (0.982)	(96)	Brewer (1989)
<i>Halecticum petrosium</i> Stechow, 1919 (Hydrozoa)	Tossa de Mar, Spain (1)				(96)	Coma et al. (1992)
<i>Halecticum pusillum</i> Sars, 1856 (Hydrozoa)	Tossa de Mar, Spain (1)				(96)	Coma et al. (1992)
<i>Mastigias</i> cf. <i>papua</i> <i>etipisoni</i> Dawson 2005 (Scyphozoa)	Ongemim'l Tketau, Mecherchar Island, Koror, Palau (1)				(96)	Unpublished data from Lori J. Bell (Coral Reef Research Foundation), Michael N Dawson (Coral Reef Research Foundation and University of California, Merced), Laura E. Martin (Coral Reef Research Foundation and University of California, Merced) and Sharon Patris (Coral Reef Research Foundation).

Table 1 continued

Species (class)	Locality (number of stocks)	b	a	$N(r)$	Water content (%)	Source
<i>Mnemiopsis leidyi</i> A. Agassiz, 1865 (Tentaculata)	Narragansett Bay, USA (1)	2.636	0.0303*	n.a.; (0.96)0	96.6	Deason (1982)
<i>Periphylla periphylla</i> (Péron & Lesueur, 1810) (Scyphozoa)	Lurefjorden, Norway (1)	2.870	0.148	n.a.; (0.950)	96.0	Fosså (1992)
<i>Physalorhiza punctata</i> (Scyphozoa)	Paraná State, Brazil; Laguna Joyuda, Puerto Rico (4)	2.689; 2.625	0.152; 84.7*	22 (0.995); 31; (0.966)	(96)	García & Durbin (1993), García (1990), and Haddad & Noqueira (2006)

Here, a and b refer to the  $\gamma$ -intercept and the slope of log transformed length weight relationship of the form  $W = aL^b$ , respectively, while  $N$  refers to the number of individuals considered in the regression analyses, and  $r$  is the square of the regression's coefficient of determination. Values of the length-weight relationship coefficient a with \* were adjusted to weight in grams and bell diameter in cm. Water content values in brackets refer to the mean water content of 96% reported by Larson (1986)

hemisphere, corresponding to  $WP = 0.1$ , and  $WP = 0.7$ , respectively (Pauly, 1987, 1998a).

Although the  $C$ -parameter, which defines the amplitude of growth oscillations up to  $C = 1$ , when a complete halt of growth is induced (at  $WP$ ), can be estimated from detailed, well-sampled length frequency data (as can  $WP$ , see Pauly, 1987, 1998a), Eq. 2 was fitted to the available length-frequency data with fixed values of  $C = 0.25, 0.5$ , and  $0.75$  for populations sampled from sub-tropical, temperate and boreal localities, respectively. This is justified by the observation that  $C$  in fishes and aquatic invertebrates correlates strongly with the summer-winter difference in temperature in various environments ( $\Delta T$ ), and usually takes a value of 1 when  $\Delta T = 10^\circ\text{C}$ , i.e., in temperate, and boreal waters (Pauly, 1987, 1998a). Tropical samples were treated without seasonality using Eq. 1. This fixed the temperature-induced oscillations at predictable levels, and reduced the number of free parameters to one (i.e.,  $K$ , with  $L_\infty$  fixed see below) or two ( $K$  and  $L_\infty$ ).

In some cases, when the available length-frequency samples were too sparse to use ELEFAN, another LFA method was used, the Wetherall Plot (Wetherall, 1986; Gayanilo et al., 1995). This method requires a single sample representative of a population, which is generally approximated by adding up a number of samples collected at different times.

The version of the Wetherall plot used here consists of successive mean lengths ( $L_{\text{mean}}$ ) computed from successive cut-off lengths ( $L_i$ ), minus the  $L_i$  (i.e.,  $L_{\text{mean}} - L_i$ ) being plotted against  $L_i$ . This results in a series of points trending downward, which can be fitted with a linear regression of the form  $Y = a + b \cdot X$ , with  $L_\infty = a/(-b)$  and  $Z/K = (1 + b)/(-b)$ , where  $Z$  is the instantaneous rate of total mortality (Gayanilo et al., 1995; Pauly, 1998a). The cases where we used Wetherall plots for LFA can be identified in Table 2 as they provide only estimates of asymptotic size and  $Z/K$ , which is equivalent to  $M/K$  in unexploited populations (see below).

In a few more cases, length at (presumed) age or growth increment data were available in the literature. These were fitted with a non-seasonal version of the VBGF (Eq. 1) through direct non-linear fitting. Such cases can be identified in Table 2 as they provide only estimates of asymptotic size and  $K$ .

ELEFAN, the Wetherall plot, and the direct non-linear fitting of the VBGF all assume that shrinkage

**Table 2** Summary of von Bertalanffy growth parameters estimated for 34 populations of jellyfishes (Scyphozoa and Hydrozoa) and comb jellyfishes (Ctenophora) from analyses of length-frequency distributions, growth increment, and age-at-length data

Species	Locality (temp in °C)	Sample size ( $L_{min} - L_{max}$ , cm)	$L_{\infty}$ (cm)	$W_{\infty}$ (WW, g)	$W_{\infty}$ (norm)	$K$ (year <sup>-1</sup> )	$C$	WP	$M$ (M/K)	Data source(s)
<i>Aequorea aequorea</i>	Namibian shelf, Namibia	3396 (4–10)	11.1	141	22.6	0.87	0.50	0.7	2.09	Buecher et al. (2001); Brierley et al. (2001)
<i>Aurelia aurita</i>	NW Black Sea (17.0)	1909 (1.5–10.5)	11.6	69	6.6	0.62	0.25	0.1	2.03	Weisse & Gomoju (2000)
<i>Aurelia aurita</i>	Kertinge Nor, Denmark	300 (0–6)	11.5	67	6.4	1.80	–	–	–	Olesen et al. (1994)
<i>Aurelia aurita</i>	Kiel Bight, Germany	n.a. (1–19.7)	25.2	482	46.3	3.11	–	–	–	Möller (1980)
<i>Aurelia aurita</i>	Urazoko Bay, Japan (17.5)	3631 (1–32)	34.5	1079	103.6	0.45	0.50	0.1	1.35	Yasuda (1971)
<i>Aurelia aurita</i>	Tokyo Bay, Japan (19.4)	2915 (5–29)	31.4	848	81.4	1.50	0.50	0.1	5.38	Ishii & Tanaka (2001)
<i>Aurelia aurita</i>	Tokyo Bay, Japan (17.5)	3101 (1–31)	35.5	1161	111.4	0.86	0.50	0.1	2.95	Omori et al. (1995)
<i>Aurelia aurita</i>	Tokyo Bay, Japan	272 (0–30)	31	821	78.8	0.54	0.50	0.1	1.03	Kinoshita et al. (2006)
<i>Aurelia aurita</i>	Kagoshima Bay, Japan	n.a. (0–23)	27.0	575	55.2	3.83	–	–	–	Miyake et al. (1997)
<i>Aurelia aurita</i>	Dutch Wadden Sea	1094 (2–30)	37.4	1326	127.3	2.90	0.50	0.1	10.3	van der Veer & Oorthuysen (1985)
<i>Aurelia aurita</i>	Vagsbøpollen, Norway (11.9)	1228 (0.5–11.5)	12.0	75	7.2	3.70	0.50	0.1	6.61	Ishii & Bamstedt (1998)
<i>Aurelia aurita</i>	Topeng Bay, Taiwan	2051 (1–30)	33.4	993	95.3	0.74	0.25	0.1	1.74	Chen (2002)
<i>Aurelia aurita</i>	Black Sea, Turkey (17)	973 (1.5–31.5)	35	1119	107.4	0.68	0.25	0.1	2.33	Mutlu (2001)
<i>Aurelia aurita</i>	Tomales Bay, USA	31 (0–17)	19.4	250	24.0	2.93	–	–	–	Hamner & Jenssen (1974)
<i>Aurelia</i> sp.	Big Jellyfish Lake, Koror, Palau (30.0)	2474 (2–38)	33.2	978	93.9	0.98	0.25	0.1	1.74	Dawson & Martin (2001)
<i>Catostylus mosaicus</i>	Botany Bay, Australia	n.a. (15–25)	31.2	1867	298.7	2.28	–	–	–	Pitt & Kingsford (2000)
<i>Catostylus mosaicus</i>	Botany Bay, Australia	n.a. (15–25)	28.2	1376	220.1	2.14	–	–	–	Pitt & Kingsford (2000)
<i>Catostylus mosaicus</i>	Botany Bay, Australia	3409 (1.5–28)	37.0	3083	493.2	0.60	0.50	0.7	4.25	Pitt & Kingsford (2003)
<i>Catostylus mosaicus</i>	Lake Illawarra, Australia	5710 (1–31)	35.5	2727	436.3	1.50	0.50	0.7	4.46	Pitt & Kingsford (2003)
<i>Chiropsalmus</i> sp.	Four Mile Beach, Australia (28.6)	1627 (0.5–12.5)	14.8	210	33.6	1.50	–	–	5.99	Gordon et al. (2004)
<i>Chrysaora hyosocella</i>	Namibian shelf	1954 (7.5–62.5)	68.8	10993	1758.8	1.10	0.25	0.1	(3.12)	Buecher et al. (2001)
<i>Chrysaora hyosocella</i>	Namibian shelf	283 (10.5–55.5)	60.8	7777	1244.3	–	–	–	(2.26)	Brierley et al. (2001)
<i>Chrysaora hyosocella</i>	Namibian shelf	2240 (7.5–62.5)	68.2	10725	1716.0	4.30	0.25	0.7	4.83	Buecher et al. (2001); Brierley et al. (2001)
<i>Chrysaora melanaster</i>	SE Bering Sea, USA	304 (1.5–55)	56.3	6252	1000.4	–	–	–	(3.04)	Brodeur et al. (2002)
<i>Cotylorhiza tuberculata</i>	Vlyho Bay, Ionian Sea, Greece (21.5)	3500 (2–35)	39.0	6845	1150.0	0.73	–	–	–	Kikinger (1992)
<i>Cyanea</i> sp.	Niantic River Estuary, USA	704 (1.5–13.5)	14.2	214	34.2	2.30	0.50	0.1	5.97	Brewer (1989)
<i>Halectium petrosium</i>	Mediterranean Sea, Spain	2918 (1–19)	19.2	427	68.3	0.85	0.25	0.1	1.17	Coma et al. (1992)
<i>Halectium pusillum</i>	Mediterranean Sea, Spain	695 (1–27)	28.1	920	147.2	1.20	0.25	0.1	1.73	Coma et al. (1992)

**Table 2** continued

Species	Locality (temp in °C)	Sample size ( $L_{min} - L_{max}$ , cm)	$L_{\infty}$ (cm)	$W_{\infty}$ (WW, g)	$W_{\infty}$ (norm)	$K$ (year <sup>-1</sup> )	$C$	WP	$M$ ( $M/K$ )	Data source(s)
<i>Mastigias cf. papua epipisoni</i>	Mecherchar Island, Palau	160343 (0–21)	23.7	2115	338.4	–	–	–	(11.7)	Unpublished data (see Table 1)
<i>Mnemiopsis leidyi</i>	Narragansett Bay, RI, USA	501 (0–4)	4.3	1	0.2	–	–	–	(1.14)	Deason (1982)
<i>Periphylla periphylla</i>	Lurefjorden, Norway (7.0)	438 (5.5–13.5)	13.5	262	41.9	–	–	–	(1.19)	Fosså (1992)
<i>Phyllorhiza punctata</i>	Laguna Joyuda, Puerto Rico (28.0)	191 (1–50)	57.5	7960	1273.6	2.30	0.25	0.1	4.69	García (1990, Fig. 4)
<i>Phyllorhiza punctata</i>	Laguna Joyuda, Puerto Rico (28.0)	3667 (2.5–38.5)	40.2	3048	487.7	3.00	–	–	–	García (1990, Table 1)
<i>Phyllorhiza punctata</i>	Laguna Joyuda, Puerto Rico (28.0)	n.a. (3–24)	38.3	2681	428.9	4.69	–	–	–	García & Durbin (1993)

Here,  $L_{\infty}$  and  $W_{\infty}$  are the asymptotic bell diameter (in cm) and weight (in grams), respectively, while  $K$  is the growth coefficient of the von Bertalanffy growth equation. The unitless parameter  $C$  refers to the amplitude and WP is the winter point, i.e., the coldest point of the year when growth is assumed to stop for a seasonal von Bertalanffy growth curve. Finally,  $M$  is the natural mortality expressed in year<sup>-1</sup>. Note that in cases where length-frequency distributions cover only a few samples, and/or are not adapted to the VBGF, the Wetherall method was used, and thus only providing an estimate of  $L_{\infty}$  and  $M/K$

does not occur. We believe that this is a second-order effect (but see below).

**Mortality estimation**

In fishery biology, mortality rates are usually expressed as instantaneous rates, defined by  $Z$  in:

$$N_{i+1} = N_i \cdot e^{-Z \cdot (t_{i+1} - t_i)} \tag{3}$$

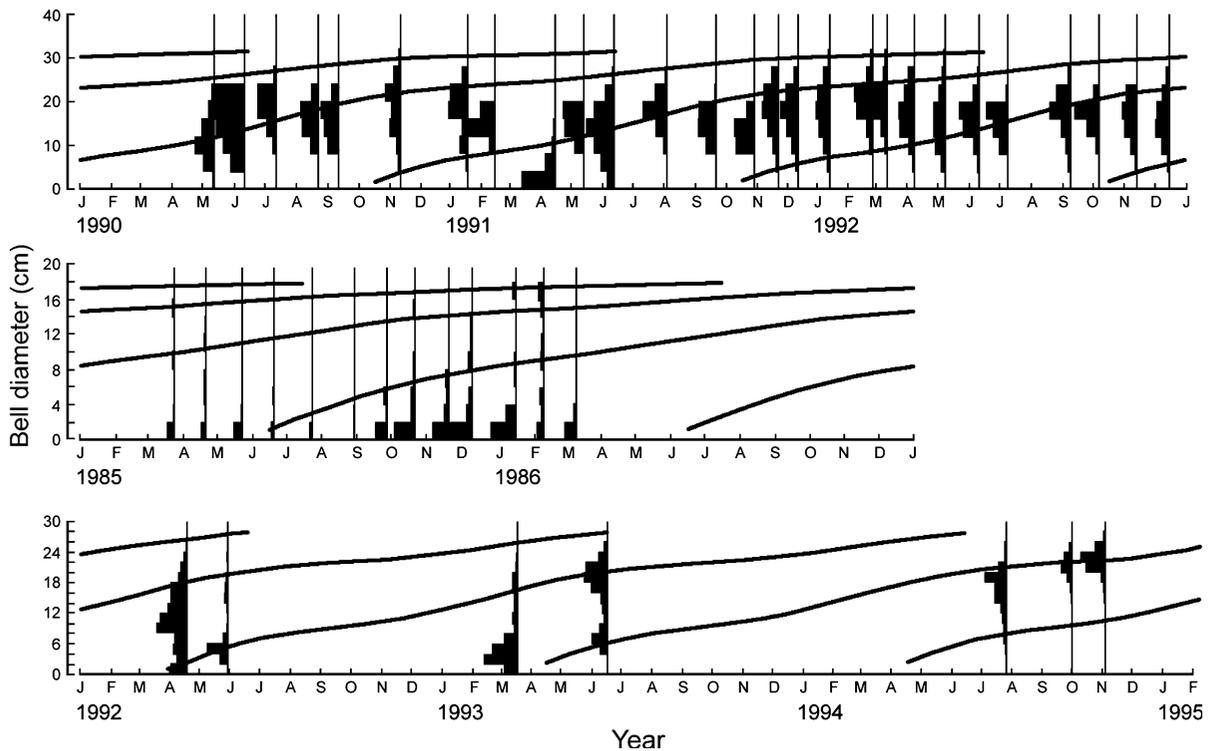
where  $N_{i+1}$  is the population size at time  $t_{i+1}$ ,  $N_i$  is the starting population size, and  $Z$  is the total mortality rate, which is the sum of natural mortality,  $M$ , and fishing mortality,  $F$ . As the jellyfish populations reported here are not exposed to fishing mortality, we have  $Z = M$  throughout.

Length-frequency data can be used to infer mortality rates if certain assumptions are met pertaining to the quality of the data, notably, that the samples should be representative of the population in the juvenile and adult phases (Wetherall, 1986; Wetherall et al., 1987). With the Wetherall plot, mortality itself cannot be estimated, but the ratio  $M/K$  can.

Another method for estimation of mortality from length-frequency samples are length-converted catch curves (Gayanilo et al., 1995; Pauly 1987, 1998a), which require growth parameters, but which, contrary to the Wetherall plot, explicitly accounts for seasonal growth (Gayanilo et al., 1995; Pauly, 1998a). We abstain here from describing this method in detail. Suffice to say that it results in a plot of the logs of numbers (corrected for the effect of non-linear growth) reflecting population abundances by age, and whose descending slope is an estimate of  $Z$  (Pauly, 1998a).

**Scaling jellyfish weight for water content**

The length–weight relationships in Table 1 (i.e.,  $W = aL^b$ ), as obtained from pairs of live wet weights ( $W$ ) in g and bell diameters in cm ( $L$ ), were used to convert our estimates of  $L_{\infty}$  into estimates of  $W_{\infty}$ . In cases where length–weight relationships were not available for a given species, length–weight relationships of other species in the same genus or higher taxa were used. In cases where several length–weight relationships were available, the average of  $W_{\infty}$  was calculated for each length–weight relationship that was used. The parameters of length–weight



**Fig. 1** Jellyfish growth curve fitting with ELEFAN. Top panel: *Aurelia aurita* from Tokyo Bay, Japan in 1990–1992 (Omori et al., 1995), with  $L_{\infty} = 35.5$  and  $K = 0.86 \text{ year}^{-1}$  for fixed values of  $C = 0.5$  and  $WP = 0.1$ . Central panel: *Halecium petrosum* from the Mediterranean Sea, Spain, sampled from 1985 to 1986 (Coma et al., 1992) with  $L_{\infty} = 19.2$  and  $K = 0.85 \text{ year}^{-1}$  for fixed values of

$C = 0.25$  and  $WP = 0.1$ . Bottom panel: First 3 of the 6-year samples of *Catostylus mosaicus* from Botany Bay, Australia between March 1990 and February 1998 (Pitt and Kingsford, 2003) with  $L_{\infty} = 37.0$  and  $K = 0.60 \text{ year}^{-1}$  for fixed values of  $C = 0.5$  and  $WP = 0.7$ . These three growth curves were selected from thousands of alternatives using a search algorithm in FiSAT (see Fig. 5 and text)

relationships are usually estimated with great precision, and the uncertainty in the  $W_{\infty}$  values discussed here is mainly due to the water content of various species of jellyfish not being known with precision.

The reported water content of jellyfish species (see Table 1) was obtained from available reports in the scientific literature. In cases where no water content estimate was available, the average water content of jellyfish (96%) estimated by Larson (1986) was used. Fish water content were obtained from data in FishBase ([www.fishbase.org](http://www.fishbase.org)), based mainly on Bykov (1983), which yielded for 530 fish species, a mean water content, mainly for muscle tissue, of  $75 \pm 5.13\%$ .

The re-scaled  $W_{\infty}$  values of jellyfish were then calculated, i.e., the asymptotic weight they would have if they had the same water content as fish. This was achieved by multiplying the original value of

$W_{\infty}$  by the ratio of the % dry weights, i.e., in most cases  $25/4 = 6.25$  (see Table 1).

Comparing the growth of jellyfish with fish and invertebrates

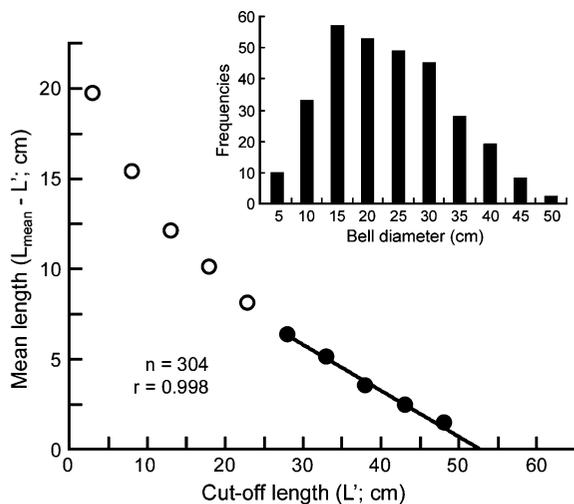
The parameter  $K$  of the VBGF tends to vary inversely with the parameter  $W_{\infty}$ . Thus, if an organism is small, it will have a high value of  $K$ , and vice versa. This makes it difficult to compare “growth” in different organisms using a single number. On the other hand, a bivariate “auximetric plot” can be used to compare the parameters  $K$  and  $W_{\infty}$  in different populations of the same species or between species. Such plots thus allow various inferences on the likely range of growth parameters of organisms, which are related to organisms whose positions on such auximetric plot is known and thus for which the value of

$K$  can be inferred from the  $W_{\infty}$  value (which itself can be inferred from the maximum reported weight in a population).

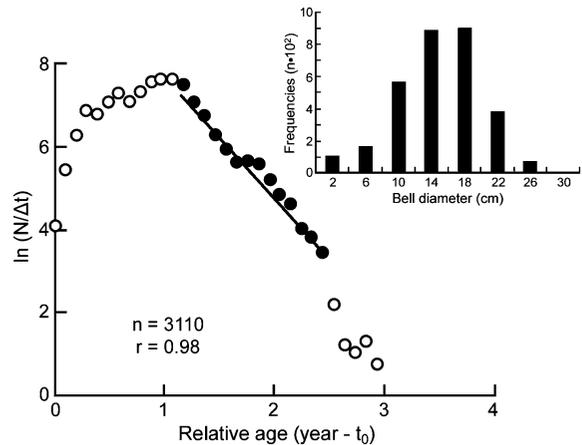
## Results

Table 2 presents the key results of growth and mortality studies we performed on the 34 populations of jellyfishes in Table 1. The available size-frequency data were sufficient for the use of ELEFAN in 30 of these (as illustrated in Fig. 1), though Wetherall plots were used in all cases to provide estimates of asymptotic length (see Fig. 2 for an example). Mortality was then obtained from a catch curve (see Fig. 3 for an example).

Table 3 presents the values  $L_m/L_{\infty}$  that we were able to assemble,  $L_m$  being the mean length at first maturity in a given population. The mean value of  $L_m/L_{\infty}$ , is 0.43 (Table 3), which is lower than the mean value reported from fishes, i.e., around 0.6–0.7 (Froese & Binohlan, 2000). Figure 4 presents an



**Fig. 2** Example of a Wetherall Plot (see methods section) applied to a cumulative sample of bell diameters of *Chrysaora melanaster* from the Bering Sea, USA (inset; from Brodeur et al., 2002, Fig. 8) obtained in September of 1996, 1997, and 1999. Only the lengths assumed to be fully retained by the gear (straight section of graph; bell diameters >25 cm) are used for the regression, which yields  $L_{\infty} = 56.3$  cm and  $M/K = 2.86$ . Note that the points are weighted by cumulative sample size, which give a crucial importance to the selection of the 1st point (see text)



**Fig. 3** Example of a catch curve analysis (see methods section) applied to a cumulative sample of bell diameters of *Aurelia aurita* in Tokyo Bay, Japan (inset; from Omori et al., 1995; Fig. 4) obtained between May 1990 and December 1992. Using the von Bertalanffy growth parameters  $L_{\infty} = 35.5$  and  $K = 0.86$  year<sup>-1</sup> for fixed values of  $C = 0.5$  and  $WP = 0.1$  (see Fig. 1, top panel) yields an estimate of  $Z = 2.95$  year<sup>-1</sup>, which may correspond to an estimate of  $P/B$  (see text and Table 2)

auximetric plot with the growth parameters in Table 2.

## Discussion

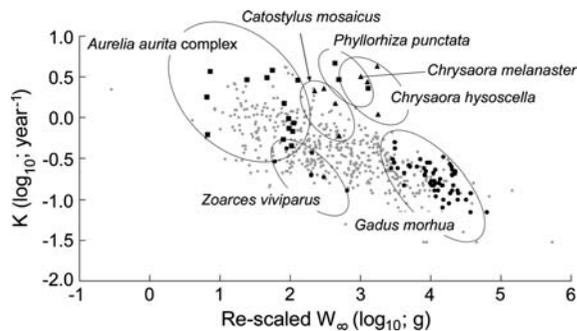
This paper adapted various concepts from length-based fish population dynamics to jellyfish, and the literature cited above discusses the various assumptions and pitfalls.

Here, we will mention only an important feature of the Wetherall plot, i.e., that on statistical grounds, it should be estimated from a regression where each point is weighted by the number of animals in the sample (Wetherall et al., 1987). This results in the first point included in the regression (representing the smallest length fully retained by the sampling gear) having a strong impact on the estimation of results ( $L_{\infty}$  and  $Z/K$ ). Moreover, the points are not strictly independent, thus violating an assumption of regression analysis. Thus, the Wetherall method should be considered mainly as a useful heuristic.

Our conclusion regarding growth is that many papers on jellyfish biology present size frequency data, which can be fitted with the VBGF (see Table 2 for a subset of that literature). We suspect, moreover,

**Table 3** Summary of available length at first maturity ( $L_m$ ) data for five species of scyphozoan jellyfishes with computed  $L_m/L_\infty$  ratio ( $L_\infty$  values, i.e., asymptotic bell diameter, from Table 2)

Species	Locality	$L_m$	$L_m/L_\infty$	Remarks (source)
<i>Aurelia aurita</i>	Tokyo Bay, Japan	8.75	0.246	Seasonal (Omori et al., 1995)
<i>Aurelia aurita</i>	Vagsbøpollen, Norway	9.40	0.783	Only summer months (Ishii & Båmstedt, 1998)
<i>Catostylus mosaicus</i>	Botany Bay, Australia	13.0	0.351	Seasonal (Pitt & Kingsford 2000)
<i>Chiropsalmus</i> sp.	Four Mile Beach, Australia	5.50	0.371	M from 5 samples winter to spring (Gordon et al., 2004)
<i>Cyanea</i> sp.	Niantic River Estuary, USA	8.15	0.574	Seasonal (Brewer, 1989)
<i>Phyllorhiza punctata</i>	Laguna Joyuda, Puerto Rico	15.0	0.261	Seasonality due to rainfall (García, 1990)
Means	–	–	0.431	This study

**Fig. 4** Auximetric plot of ( $\log_{10}$ )  $K$  against re-scaled values of ( $\log_{10}$ )  $W_\infty$  for the major groups of jellyfishes, on a background of grey dots representing fishes (in addition to two highlighted species, *Zoarces viviparus* and *Gadus morhua*). As might be seen, the *Aurelia aurita* complex and *Catostylus mosaicus* resemble small fishes in their growth pattern, but *Chrysaora* spp. and *Phyllorhiza punctata* (and other species in Table 2) may grow faster (higher  $K$  for a given  $W_\infty$ ) than fishes. This result might need to be validated using more growth parameter sets. Also, it is very sensitive to the assumed ratio between the water contents of jellyfish and fish (see text)

that the VBGF is not only a convenient mathematical function for describing the growth of jellyfish, but also that it does so because their respiratory physiology makes this growth function, derived from physiological considerations, the model of choice (von Bertalanffy, 1957; Longhurst & Pauly, 1987; Pauly, 1998b).

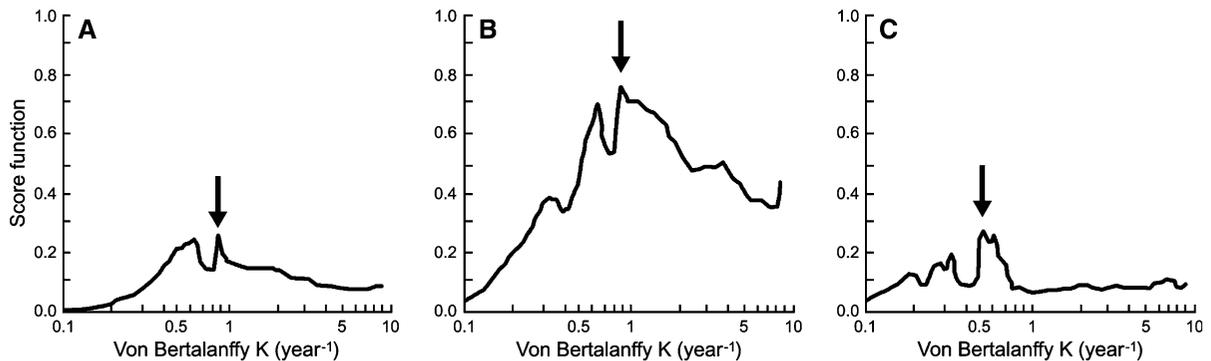
The crucial step in estimating the parameters of the VBGF does not consist of the estimation of asymptotic size, for which the maximum size in a field sample usually provides a good approximation, nor with the parameter from seasonal growth, which can be approximated from first principles. Rather, the crucial parameter is  $K$ . How well this parameter is estimated can be assessed by plots such as that shown

in Fig. 5, which are a standard feature of the ELEFAN procedure.

Our estimate of the mean value of  $M/K$  in jellyfish is 3.03, about two times higher than the values reported for fishes, which usually range between 1 and 2 (Beverton & Holt, 1956; Pauly, 1998a). This high value of  $M/K$  may be due to, at least in some cases, shrinkages of the bells of jellyfish (Hamner & Jenssen, 1974), which could have biased the (fixed) interrelationships of number, size, and age, which are assumed in LFA. Note that when  $K$  is underestimated by ELEFAN or other LFA,  $M$  is also underestimated (and conversely for overestimation), for which reason our estimates of  $M/K$  should be robust.

The auximetric plot in Fig. 4, finally, suggests that some jellyfish, once account is taken of their high water contents, have growth patterns similar to small and very small fishes, such as guppies and anchovies (*Aurelia aurita* (Linnaeus, 1758) complex, *Catostylus mosaicus* (Quoy & Gaimard, 1824)). Others (*Phyllorhiza punctata* (von Lendenfeld, 1884), *Chrysaora* spp.) may grow faster than fishes (i.e., have higher values of  $K$  for their value of  $W_\infty$ ). However, the accuracy of the position of an organism on an auximetric plot depends on the accuracy of the growth parameters, and in the case of jellyfish, on correct conversion to standard water content. Because of this, we consider the results of this study to be preliminary.

We are, however, encouraged by the observation that, as in fish (here exemplified by *Gadus morhua* Linnaeus, 1758 and *Zoarces viviparus* (Linnaeus, 1758), the different populations in a given species appear to form ellipsoid clusters on an auximetric plot (see [www.fishbase.org](http://www.fishbase.org) for more). Genera and higher taxa can be expected, as well, to form such



**Fig. 5** Examples of response surface of the goodness-of-fit estimator of ELEFAN, as used to estimate  $K$  (and to assess the uncertainty associated with the point estimate) when the other parameters of the seasonally oscillating VBGF ( $L_\infty$ ,  $C$  and  $WP$ ) are known or assumed (see arrows). Here, the panel A pertains to the top of Fig. 1, i.e., to *Aurelia aurita* from Tokyo Bay, and the best fitted  $K$  value is not very distinct from adjacent values;

clusters, albeit larger ones. This suggests that the large cluster we drew for the *Aurelia aurita* complex would, indeed, include more than one species.

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