Size structure, age-size dynamics and life history variation

Mikko Heino, David S. Boukal, Tone Falkenhaug, Uwe Piatkowski, Filipe M. Porteiro and Tracey T. Sutton

Here we present a new technique to study life history variation when only length distributions of populations are known. Shape of length distribution in a population is to a significant extent determined by the degree to which an average individual approaches its asymptotic maximum size. Statistically, the shape of a length can be characterised by its skewness, measuring the degree of symmetry in the distribution. Positive skew (long right tail) in a length distribution suggests that relative few individuals survive long enough to approach asymptotic size in a population, whereas the opposite is true for negative skew (long left tail). With a simple model of age-size dynamics in a population showing indeterminate growth, we show that skewness is strongly correlated with the ratio between mortality rate and the growth parameter k in the von Bertalanffy growth model; this ratio is a dimensionless number that is one of Beverton's 'life history statics'. We demonstrate the new technique with data from deep-pelagic fishes collected during the 2004 Mar-Eco expedition along the northern Mid-Atlantic Ridge.

Keywords: Dimensionless numbers, growth trajectory, life-history invariants, mortality

M. Heino (corresponding author): Department of Biology, University of Bergen, Box 7800, N-5020 Bergen, Norway, and Institute of Marine Research, Bergen, Norway, and International Institute for Applied Systems Analysis, Laxenburg, Austria. Tel.: +47 55584544, fax: +47 55584450, e-mail: mikko.heino@bio.uib.no.

D. Boukal: Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, and Department of Biology, University of Bergen, Box 7800, N-5020 Bergen, Norway.

T. Falkenhaug: Institute of Marine Research, Flødevigen Marine Research Station, N-4817, His, Norway.

U. Piatkowski: Leibniz Institute of Marine Sciences, IFM-GEOMAR, Düsternbrooker Weg 20, D-24105 Kiel, Germany.

F. Porteiro: Department of Oceanography and Fisheries, University of the Azores, PT-9901-862 Horta, Portugal.

T Sutton: Virginia Institute of Marine Science (VIMS), P.O. Box 1346, Gloucester Point, VA 23062, USA.

Introduction

Size is the most readily measured quantitative individual characteristic. For understanding population dynamics, or describing life history patterns, measurements on age, sex, maturity status etc. would obviously be very valuable but require more labour and expertise, and consequently are often not available. What then can be achieved with size data alone? In fisheries science, there is a long tradition for using length-based methods to study population dynamics and parameters (e.g., Beverton and Holt 1956, Pauly and Morgan 1987, Gulland and Rosenberg 1992). We continue this venerable tradition by showing a new, complementary method to estimate growth and mortality parameters from length frequency data.

Theory

Size distribution of a population results from three processes (e.g., Ebert 1981): recruitment that determines the input (numbers at size at birth), growth that determines how fast a newborn individual can reach a certain size, and survival that determines the probability of reaching that size. Generally the latter two processes depend on size although often in opposite

ways: growth rate is usually decreasing with size whereas the opposite is typically true for survival. Furthermore, size distribution as an observable depends on size-dependent catchability of individuals, or in more general terms, size-dependent observability.

We assume that recruitment is continuous and constant and can thereby be ignored in this general treatment. Furthermore, we assume that individual growth curves are monotonically increasing, that is, there is some growth throughout life (growth models that asymptotically approach a maximum size are thus allowed). This assumption guarantees that there is one to one correspondence between age (a) and size (l) of individual fish, which makes the following analysis simpler.

Let us first restrict ourselves to a hypothetical scenario when no mortality occurs. Age distribution is then uniform, and a population's size distribution is determined solely by the growth curve, denoted as $l(a)$. Proportion of individuals within a certain size class is proportional to time spent in that size class, which is inversely proportional to growth rate (= the derivative of growth curve, $dl(a)/da$) for individuals in that size class. As we are interested in the length distribution, it is convenient to directly operate with the inverse function of the growth curve[1], $a(l) = l^{-1}(a)$ – this gives age as a function of size. Density of individuals with a certain size is then proportional to the derivative of this function, $da(l)/dl$.

However, mortality is inevitable and must be accounted for. Because of mortality, density at certain length must be weighted by survival probability to that length. Focusing on survival from birth to length l, survival is

$$P(l) = \exp(-\int_0^{a(l)} m(l(a'))\,da')\,,$$

where $m(l)$ is instantaneous mortality rate as function of size and the integration is done from birth to the age when the length in question is attained. Thus, length distribution is now proportional to

$$d_{real}(l) \sim P(l)\,da(l)/dl\,.$$

In real life, individuals are not equally likely to be observed; sampling typically targets large or adult sizes, and the smallest individuals remain unobserved. Assuming a sigmoid shape for observability, the probability of observing an individual of size l relative to the maximum observability at some large size is

$$o(l) = 1/(1 + e^{-(l-l_{50})/l_w})\,,$$

where l_{50} is the length at which the relative probability of observing is 50% and parameter l_w describes how steeply the observability increases with length around l_{50}. Putting all these elements together, we find that the observed length distribution is proportional to

$$d_{obs}(l) \sim o(l)\,P(l)\,da(l)/dl\,.$$

Examples

We now proceed by making some concrete choices for the functions describing growth, survival and observability. At a population level, growth in fish is often well described by the

---

[1] For monotonically increasing growth curves assumed here, the inverse function always exists and is defined in the interval between the minimum and maximum size.

von Bertalanffy growth model, $l(a) = l_\infty (1 - e^{-ka})$, where l_∞ is asymptotic maximum size and k is a parameter related to how fast the asymptotic maximum size is approached, often somewhat misleadingly referred to as the growth constant. The inverse function of the von Bertalanffy function is $a(l) = -\ln(1 - l/l_\infty)/k$. The derivative of this function is $da(l)/dl = (k(l_\infty - l))^{-1}$. For the simple case of constant mortality ($m(l) = m$) and uniform observability we obtain $d_{obs}(l) \sim e^{-ma(l)}/(k(l_\infty - l))$. Rescaling such that we obtain probability density distribution yields

$$p_{obs}(l) \sim m/k\,(l_\infty - l)^{m/k-1}/l_\infty^{m/k}.$$

This equation has been previously presented at least by Wetherall et al. (1987, p. 54). Yet, its full implications have been overlooked.

The first thing to note is that parameters m and k always occur together as a dimensionless ratio m/k. Second, the only parameter that is measured in length units is l_∞. Thus, the shape of the length distribution is determined by the ratio m/k alone, whereas l_∞ is only influencing its horizontal spread. Moreover, the length distribution is monotonically decreasing if $m > k$ and monotonically increasing in the opposite case. This is illustrated in Figure 1.
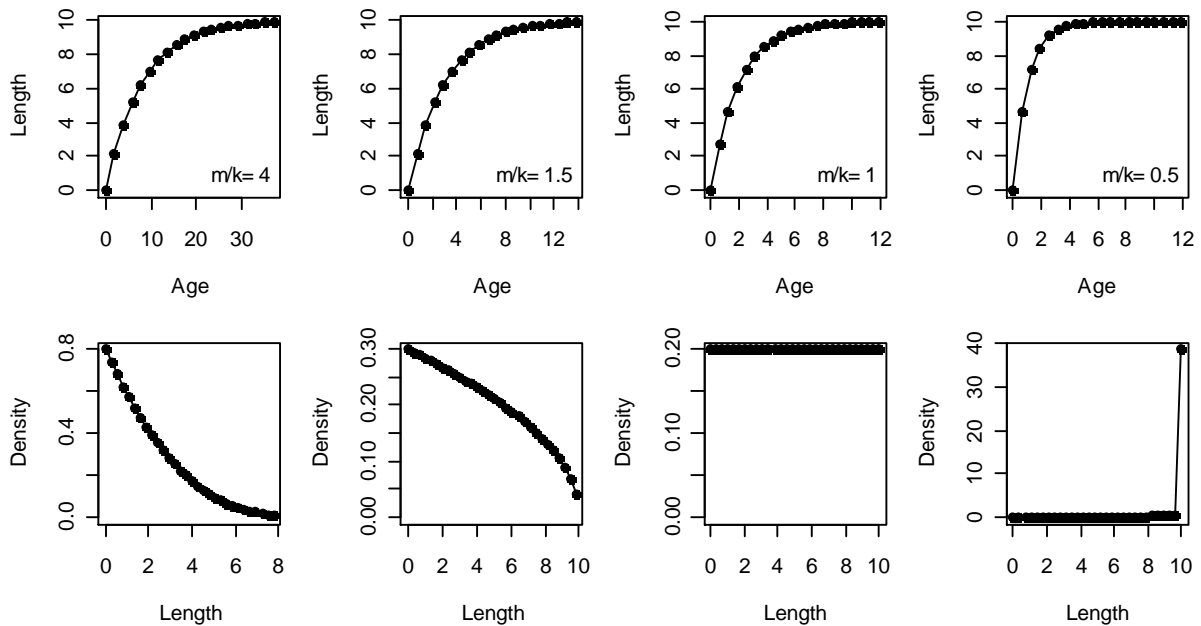

Figure 1. Growth curves and length distributions (not normalized here) for increasing k (0.125 yr^{-1}, 0.333 yr^{-1}, 0.5 yr^{-1} and 1.0 yr^{-1}), $m = 0.5$yr^{-1} and $l_\infty = 10$. Length distributions change from monotonically decreasing to monotonically increasing when the ratio m/k exceeds the critical value at $m/k = 1$.

The length distributions in Fig. 1 do not appear very realistic, particularly because they are either monotonically increasing or decreasing. There are at least two reasons why observed length distributions are humped instead. First, smallest individuals are not observable. Smoothly increasing observability will make monotonically decreasing length distributions roughly bell-shaped. This is accounted for by including include the size-dependent observability function introduced above. This does not, however, influence monotonicity when

increasing length distributions are considered ($m < k$). However, if asymptotic size is not constant but varies between individuals, then we expect the length distribution to portray a humped shape, with the hump reflecting variation in asymptotic size. We implemented this by assuming that l_∞ is normally distributed with mean equal to l_∞ and standard deviation σ. A sequence of length distributions generated for different values of k is illustrated in Fig. 2. For m/k larger than 1, these distributions look 'normal' whereas for m/k less than 1, the distributions looks somewhat unusual but not implausible.

When m/k is close to 1, the shape becomes sensitive to the actual value of the ratio. In particular, the skewness changes from negative to positive when the ratio m/k passes value one from below. Fig. 3 illustrates this relationship for the same example that is used in Fig. 2. Using the moment-based definition of skewness, we see that the skewness indeed changes its sign very close to the critical value of the ratio m/k. When m/k is close to unity the relationship between this ratio and skewness is approximately linear. .

Second, we can allow for size-dependent mortality. For example, the following equation gives ample flexibility to depict size-dependent mortality:

$$m(l) = m_i + m_d \exp(-l/l_0),$$

where m_i is size-independent component of total mortality, m_d is maximum size-dependent component, and the parameter l_0 characterizes at which length the size-dependent component of mortality drops to $1/e = 36.8\%$ relative to its value at size $l = 0$ (e.g., Taborsky *et al.* 2003).

Varying strength of size-dependent mortality can change the observed length distributions in an opposite way to the observability effect; strong size-dependent mortality makes large individuals even more rare in comparison to small individuals (results not shown).

Concluding remarks

Ratio m/k is one of the Beverton and Holt (1959) life history 'invariants' or 'statics' that are sometimes assumed to be relatively constant within taxonomic groups (Charnov 1993). For fish, m/k of about 1.5 has been proposed as the canonical value (Charnov 1993), based on the data reported by Pauly (1980) and supported by a simple life history model (Jensen 1996). Our model-generated length distribution for $m/k = 1.5$ indeed looks quite realistic, although a much higher ratio looks perhaps even more realistic.

Our preliminary results suggest that the skewness coefficient can be used to estimate the ratio m/k. Skewness appears to be not very sensitive to the threshold in the observability function or to modest size dependence of mortality. However, more work is needed to confirm this preliminary postulation. Another open question is whether using skewness coefficient has advantages over other ways of estimating the ratio m/k from length distributions (e.g., Beverton and Holt 1956).

Fig. 4 illustrates length distributions for two deep pelagic fish species from northern Atlantic. The length distribution of *Scopelogadus beanii* is clearly left-skewed, whereas that of the glacier lanternfish *Benthosema glaciale* is right-skewed. This suggests $m < k$ for *Scopelogadus*, whereas *Benthosema* has $m > k$ in the study area. This result is in accordance with the published estimates of m and k for *Benthosema glaciale*, yielding $m/k \approx 4.9$ and $m/k \approx 1.5$ for two different populations (Gjøsæter 1973, as cited by Pauly 1980). No estimates of m and k are available for *Scopelogadus beanii*. Nevertheless, its length distribution suggests that this species has low mortality relative to its growth, something which is unusual if we believe that fish typically have m/k ratio larger than one.

Figure 2. Length distributions for different values of growth parameter k when asymptotic size follows a normal distribution and observation probability increases sigmoidally with size. Values for k: 0.005, 0.02, 0.03, 0.04 and 0.08; the ratio m/k takes values 6, 1.5, 1.0, 0.75 and 0.375. Mortality is size-independent in these examples. Parameter values: m=0.03, l_{50}=8, l_w=1, l_∞=25, σ=2.
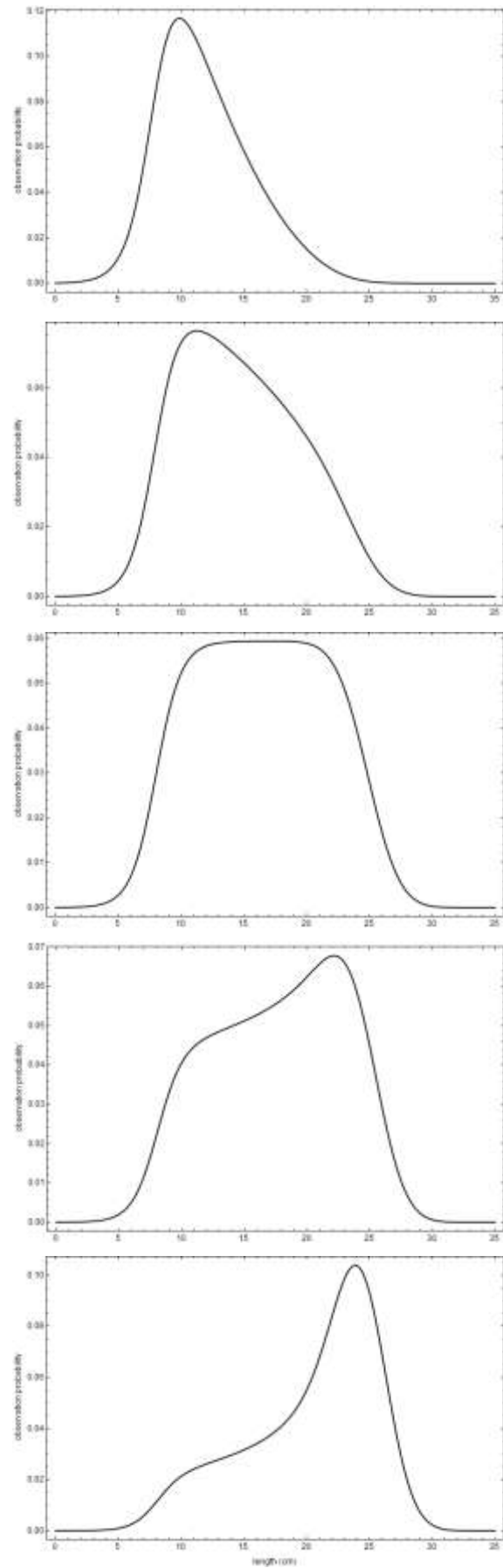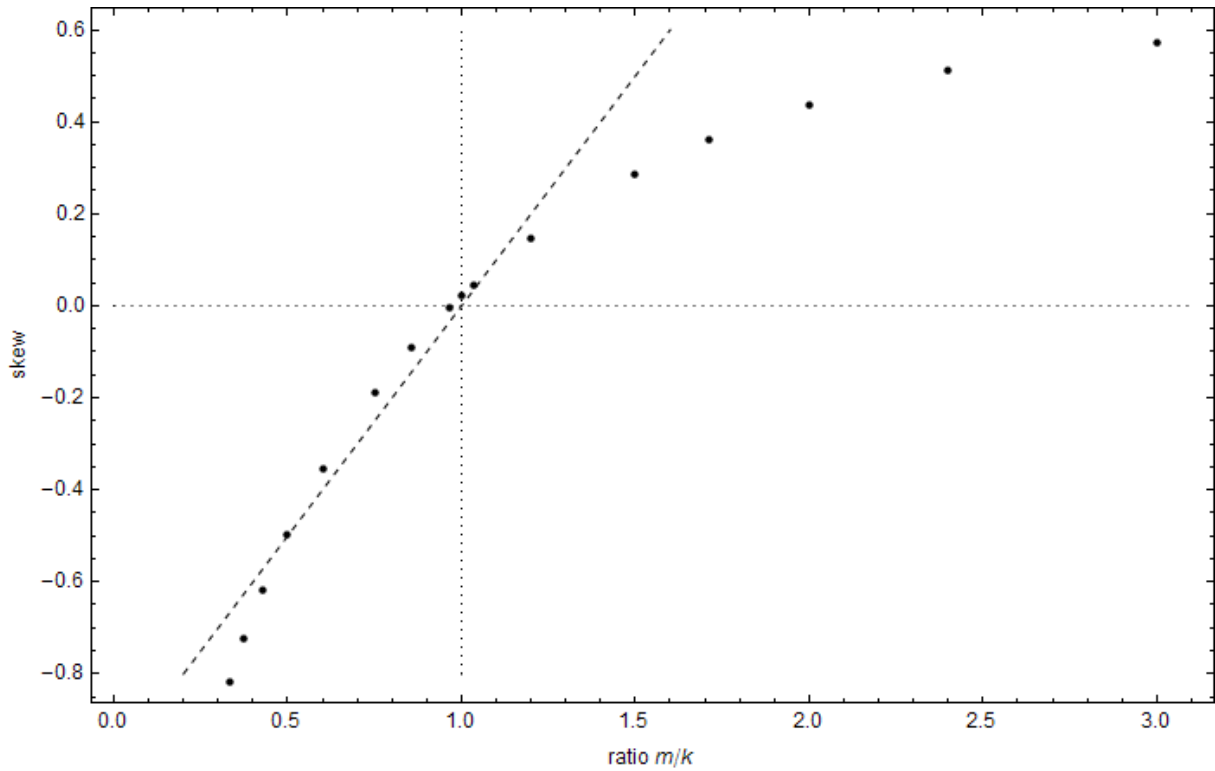
Figure 3. The relationship between skewness of the length distribution and the ratio m/k. The skewness changes its sign very close to the critical value of the ratio m/k. When m/k is close to unity the relationship is approximately linear.
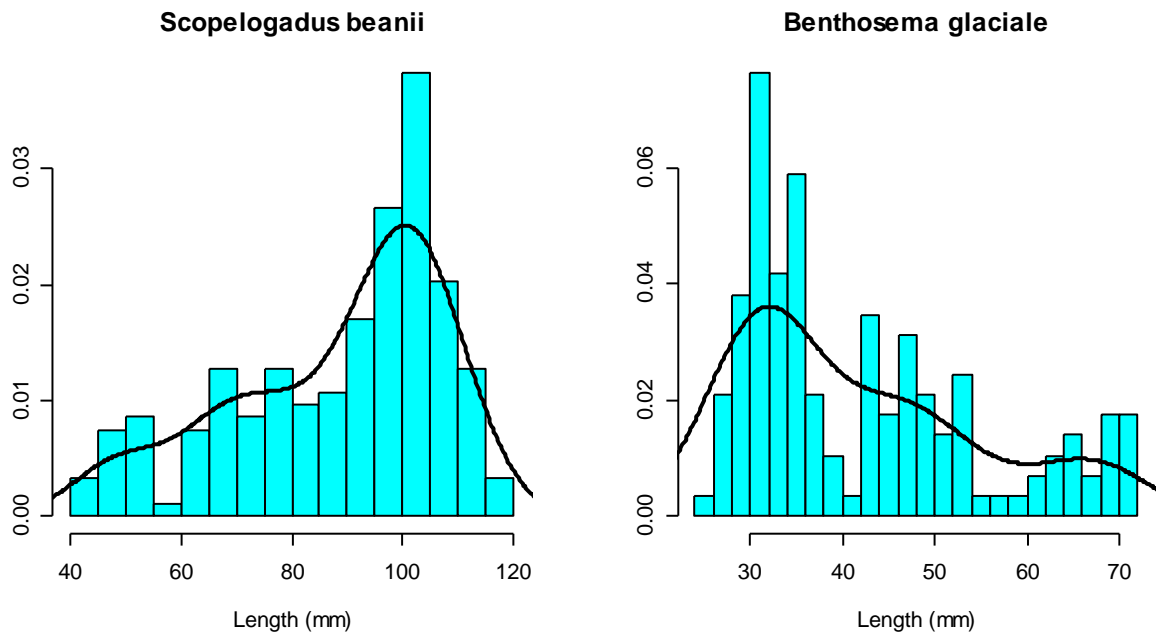

Figure 4. Empirical length distributions for two species of deep pelagic fish, bigscale fish *Scopelogadus beanii* (Melamphaidae) and the glacier lanternfish *Benthosema glaciale* (Myctophidae). Data from the northern Mid-Atlantic Ridge collected during the G. O. Sars expedition in June 2004 (see Wenneck *et al.* 2008 for details).

References

Beverton, R.J.H. & Holt, S.J. (1956). A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer 140, 67-83.

Beverton, R.J.H. & Holt, S.J. (1959). A review of the lifespans and mortality rates of fish in nature and their relation to growth and other physiological characteristics. CIBA Foundation Colloquia on Ageing 5, 142–177.

Charnov, E. (1993). Life history invariants. Oxford University Press, New York.

Ebert, T.A. (1981). Estimating mortality from growth parameters and a size distribution when recruitment is periodic. Limnology and Oceanography 26, 764-769.

Gjøsæter, J. (1973). Age, growth, and mortality of the myctophid fish *Benthosema glaciale* (Reinhardt) from western Norway. Sarsia 52, 1-4.

Gulland, J.A. & Rosenberg, A.A. (1992). A review of length-based approaches to assessing fish stocks. FAO Fisheries Technical Paper. No. 323. Rome, FAO. 100p.

Jensen, A.L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53, 820-822.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'Exploration de la Mer 39, 175-192.

Pauly D. & G.R. Morgan, eds. (1987). Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.

Taborsky, B., Dieckmann, U., & Heino, M. (2003). Unexpected discontinuities in life-history evolution under size-dependent mortality. Proceedings of the Royal Society London Series B, Biological Sciences 270, 713-721.

Wenneck, T. de L., Falkenhaug, T. & Bergstad, O.A. 2008. Strategies, methods, and technologies adopted on the R.V. G.O. Sars MAR-ECO expedition to the Mid-Atlantic Ridge in 2004. Deep-Sea Research II, 55: 6–28.

Wetherall, J.A., J.J. Polovina & S. Ralston (1987). Estimating growth and mortality in steady-state fish stocks from length-frequency data. In Pauly D. and G.R. Morgan (eds.). Length-based methods in fisheries research. ICLARM Conf. Proc., 13:53–74.