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Recruitment variability in exploited aquatic populations

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Abstract – While lognormal distributions have been proposed as useful descriptors of recruitment variability, the very nature of the recruitment distributions is still debated. To account quantitatively for recruitment distributions, I here propose a Weibull exponential model; it derives from a simple and natural hypothesis for uncorrelated recruitment processes of spawning, hatching, growth and survival through the early life stages to the point of vulnerability to the fishery. The quantification of Weibull exponentials is particularly important with regards to extrapolations to low recruits that have not yet been observed. To test the Weibull exponential null-hypothesis, I examine annual time-series of recruitment in major aquatic stocks. The Weibull exponential quite describes the bulk (95%) of the recruitment distributions of widely differing stocks, while the remaining 5% of the largest recruits are occurring with a much larger rate than predicted by the Weibull exponential. Further, I study the inter-event times between unusually high numbers in recruitment time-series data and find that intermittent pulses of strong recruitment follow non-Poisson statistics, which arises from year-to-year persistence of the magnitude of recruitment: large (or small) recruits are more likely to be followed by large (or small) recruits. This recruitment clustering effect is confirmed by the rescaled range analysis method. The empirical results imply that individual survivals on recruitment levels are independent of initial cohort sizes but year-to-year recruiting events exhibit long-term correlations.

Key words: Weibull exponential distribution / Lognormal / Stochastic survivorship / Early life history / Non-Poisson intermittency / Recruitment clustering

1 Introduction

Recruitment variability from year to year remains one of the most striking features of the dynamics of many marine populations. It is an inescapable consequence of the reproductive strategy of most marine fishes and invertebrates. Common to most aquatic species is the production of vast numbers of eggs. This kind of reproduction is favored in environments where the survival of the offspring depends on a number of ecological and environmental processes that cannot be precisely anticipated (Winemiller and Rose 1993). High mortality (predation and starvation) occurs in very early stages in the life history of extremely fecund aquatic fishes and invertebrates. Some variable proportion will, however, reach suitable environments (e.g. spatial and temporal patchiness of food), where larvae will grow and juveniles will survive to eventually join the fishable stock.

The very nature of the recruitment distributions is still debated (e.g. Daan and Fogarty 2000; Fogarty 2001). While the lognormal recruitment model has been widely applied as a description of the recruitment phenomena (Beddington and Cooke 1983; Caputi 1988; Fogarty 1993a,b; Hennemuth et al. 1980; Myers et al. 1995; Ripley and Caswell 2006), other alternative models have been proposed, e.g. symmetrical distributions (Shelton 1992) or a Weibull exponential distribution (Power 1996).

The conventional approach to the year-to-year variability in ecological time series effectively assumes that the form of distribution, chosen on the basis of a fit dominated by the majority of the observations in the center of the distribution, necessarily fits the lower and upper tails of the distribution satisfactorily as well, despite the disproportionate influence of extreme events on populations (Katz et al. 2005). Much of population ecology is concerned with the typical size of a distribution, yet extreme values may be of particular importance (Ariño and Pimm 1995). Unusually low recruits may doom a population to collapse and pose an economic threat. The precise characterization of the distribution of recruitment variations, especially in the low recruits régime (allowing us to analyze extreme variations), has important applications in assessing potential risk of stock collapse and/or delayed recovery.

Recruitment of offspring fluctuates under the action of many factors. Many physical, chemical and biological factors can potentially affect growth and survival rates during the early life stages. The number surviving to recruitment is a product of population fecundity (initial number in the cohort, i.e. total egg production) and randomly varying survival rates in the pre-recruit phases. These phases in some species can take years, and are not directly submitted to the fisheries exploitation. It appears reasonable to involve a multiplication of

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independent factors to account for the recruitment variability: a lognormal distribution is the center of the limit distribution for the product of a large number of independent, identically-distributed (iid) positive random variables.

Predicting the occurrences of such low numbers of recruiting fish that stock collapse is probable (or inevitable) is a central concern for those who manage heavily exploited populations. Extreme deviations in the régime, where the product of a finite number of iid positive random variables goes to zero, is not lognormally distributed, because central limit arguments are inapplicable. Here, I explore a Weibull exponential model and test possible universality in the recruitment distributions for low numbers, because the model is provided by the recent demonstration (Frisch and Sornette 1997) that it derives from a simple and generic mechanism in terms of multiplicative processes, i.e. the no-correlation hypothesis for survivorship events: a pre-recruit population declines in an exponential fashion with a finite survival rate for each life-history stage which is randomly fluctuating through sequential stages, e.g. egg, early larval, late larval, and juvenile (Mertz and Myers 1996; Rothschild 2000). The extreme deviations for products of a finite number of iid positive random variables (i.e. the tail of their distribution corresponding to the régime where the sum of logarithms goes to $-\infty$) generically follows a Weibull exponential, i.e. stretched or super-exponential law. The assumption that variates are identically distributed can be relaxed (Frisch and Sornette 1997): one can allow for different characteristic scales or standard deviations of different variates in applying the theory of extreme deviations. For low numbers of recruits, therefore, extreme deviations arguments are expected to apply as long as the density-independence assumption, that survival rates of young fish are uncorrelated with initial cohort size (or adult population), is a good approximation.

The Weibull exponential family has been proposed to account for a right-skewed (i.e. fat-tailed), an exponential, and a relatively symmetric distribution. In recent years, the Weibull exponential family has provided reasonable fits to many reported distributions in nature and economy (Laherrère and Sornette 1998; Johansen and Sornette 2001). In the fisheries sociometry literature, the Weibull exponential was found to describe the distribution of country population sizes employed in the fisheries sector (Niwa 2006). The extreme deviations régime may provide a very general and essentially model-independent mechanism.

Besides the recruitment distribution, I study the distribution of time intervals between unusually high numbers in recruitment time-series data. It has been generally observed that recruitment levels are low to moderate with occasional large year-classes (Fogarty 1993a, 1991). Some stocks exhibit low frequency pattern in recruitment variability, leading to boom-and-bust cycles over periods of decades (MacCall 1999). Inter-event statistics are a basis for understanding the way in which depleted populations recover.

2 Recruitment distributions

The number in the cohort surviving to recruitment is designated ξ. The cumulative distribution, i.e. number of times that recruits larger than or equal to ξ are observed in the recruitment records for each stock, is fitted to the cumulative Weibull exponential distribution defined by

$$P(\text{recruits} \geq \xi) = \mathfrak{N} \exp\left[-(\xi/\Xi)^{\gamma}\right], \tag{1}$$

where $\mathfrak{N}$ approximates to the total number N of year-classes in a historical data set (asymptotically $\mathfrak{N} = N$ for N large enough, i.e. $\lim_{N\to\infty} P\left(\text{recruits} \geq \xi_N\right)/N = 1$ for the smallest recruit $\xi_N \left(\equiv \min_{1\leq k\leq N} \xi_k\right)$ observed in a finite sample of N records; this is equivalent to a normalization of the corresponding probability distribution). When the Weibull exponent, i.e. shape parameter $\gamma < 1$ (or $\gamma > 1$), then $P(\text{recruits} \geq \xi)$ is a stretched exponential (or super-exponential). The special case $\gamma = 1$ corresponds to a pure exponential; in this case, the scale parameter Ξ is nothing but the standard deviation of recruitment variability. An exponent $\gamma < 1$ corresponds to a fatter tail than an exponential. The advantage of the Weibull exponentials is to be parsimonious with only two adjustable parameters with clear interpretation. The scale parameter Ξ and the Weibull exponent γ provide two useful measures of the recruitment and their rate of occurrence. The larger Ξ is, the larger are the recruits. The smaller γ is, the fatter is the tail of the distribution controlling large fluctuations: the distribution is more frequent for both small and large recruits and less frequent in intermediate recruits.

The adjustable parameter Ξ gives a characteristic (or reference) scale from which all moments can be determined (Laherrère and Sornette 1998), e.g. the mean of ξ is given by

$$\langle\xi\rangle = \Xi\gamma^{-1}\Gamma\left(\gamma^{-1}\right), \tag{2}$$

where $\Gamma(\cdot)$ is the gamma function. When γ is small, the mean recruits $\langle\xi\rangle$ will be much larger than Ξ. Another characteristic scale, corresponding to a 95% level confidence, is obtained: the 95 percentile (or 5 percentile) of the recruitment distribution, $\xi_{95\%}$ (or $\xi_{5\%}$), such that the probability to exceed (or fail in) this value is less than 5%,

$$\xi_{95\%} = 3^{1/\gamma}\,\Xi \quad \left(\text{or} \quad \xi_{5\%} = 0.05^{1/\gamma}\,\Xi\right). \tag{3}$$

These large (or small) recruits are expected to be recorded once in twenty years.

In the analysis, I use the rank-ordering technique (MacArthur 1960; Laherrère and Sornette 1998; MacCall 1999; Johansen and Sornette 2001; Halley and Inchausti 2002) that amounts to order the variables by descending values $\xi_1 > \xi_2 > \cdots > \xi_N$, and plot ξ_k as a function of the rank k $(= 1, 2, \ldots, N)$. Rank-ordering statistics and cumulative distribution plots are equivalent: the rank k is the number of events larger than or equal to ξ_k. Within the rank-ordering plot, the Weibull exponential distribution is qualified by a straight line when plotting $\ln k$, the natural logarithm of the cumulative number k, as a function of ξ_k^{γ}, the recruits ξ_k raised to the power γ. The values of the Weibull parameters, Ξ and γ, are evaluated by using the maximum likelihood method (Laherrère and Sornette 1998). The most probable determination of the parameters Ξ and γ is given as follows:

$$\gamma^{-1} = \frac{\sum_{k=1}^{N}\left(\xi_k^{\gamma}\ln\xi_k - \xi_N^{\gamma}\ln\xi_N\right)}{\sum_{k=1}^{N}\left(\xi_k^{\gamma} - \xi_N^{\gamma}\right)} - N^{-1}\sum_{k=1}^{N}\ln\xi_k \tag{4}$$

and

$$\Xi^{\gamma} = N^{-1}\sum_{k=1}^{N}\left(\xi_k^{\gamma} - \xi_N^{\gamma}\right). \qquad (5)$$

Equation (4) is implicit as γ appears on both sides of the equality. The expression Eq. (5) provides the most probable value for Ξ conditioned on the knowledge of the exponent γ. The estimate of the normalization is calculated from $\mathfrak{N} = \exp\left[\langle \ln k + (\xi_k/\Xi)^{\gamma}\rangle\right]$, over low numbers range, i.e. $\xi_k < \Xi$, with the maximum likelihood estimates Ξ and γ, where $\langle \ldots \rangle$ denotes the mean.

2.1 Multiple-age spawning stocks in the North Atlantic

Now, I analyze data on commercial fish stocks in the North Atlantic, extracted from the 2005 working group reports of the International Council for the Exploration of the Sea (ICES) prepared for advice on living resources and their harvesting provided by the ICES Advisory Committee on Fishery Management (ACFM), at ⟨http://www.ices.dk/advice/icesadvice.asp⟩. I select from the ICES-ACFM database those stocks for which the recruitment time series encompassed at least 30 years. There are examined all together 27 marine stocks of multiple-age spawning bony fishes (i.e. a spawning population consisting of two or more age-groups). For all studied stocks, I construct on the same graph the cumulative histogram of recruitment; Figure 1a groups the cumulative distributions of recruits of all these stocks. In order to construct this figure, I fit each distribution to the Weibull exponential distribution and obtain the corresponding parameters $\mathfrak{N}$, Ξ and γ, given in Table 1. I then plot the scaled quantities

$$y \equiv k/\mathfrak{N} \quad \text{versus} \quad x \equiv (\xi_k/\Xi)^{\gamma} \qquad (6)$$

using the triplet $\mathfrak{N}$, Ξ and γ which is specific to each distribution. If the Weibull exponential model held true for all the recruitments, all the "scaled" distributions should collapse exactly onto the "universal" function $y = e^{-x}$ (Johansen and Sornette 2001). We observe that this is the case for values of x up to about 3, i.e. up to the 95 percentile of the recruitment distribution, beyond which there is a clear upward departure. Figure 1b shows the differences (error plot) between the cumulative distributions of recruits and the fits with the Weibull exponential model, depicting errors fluctuate around 0 for the bulk of the distributions. The Weibull exponential model parameterizes an almost 95% of the ICES-ACFM data points in recruitment time series.

Figure 1c shows the type of dispersion of values in the plot of normalized recruits ξ/Ξ against Weibull exponent γ for the ICES-ACFM data, demonstrating that populations with small γ have high levels of recruitment variability.

2.2 Single-age spawning stocks

In addition to multiple-age spawning stocks, I analyze recruitment time-series data from Ricker (1997) for single-age spawning stocks (i.e. no mixing of ages in the spawning

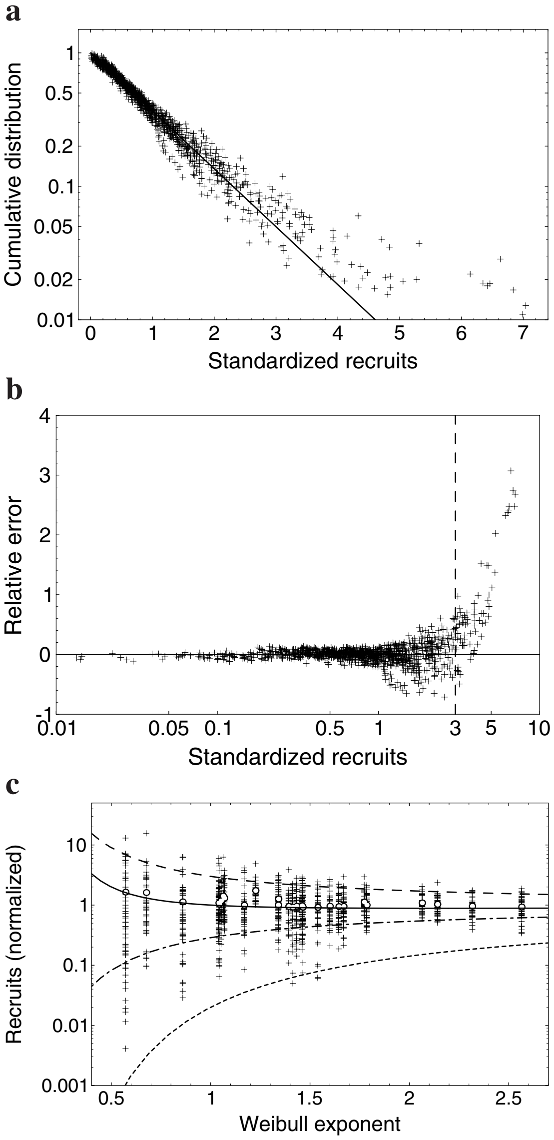

Fig. 1. Fish populations in the North Atlantic (27 stocks in ICES fishing areas). (a) Cumulative distributions of standardized recruitment (semilogarithmic scale plot). This figure plots each cumulative number k normalized by its corresponding factor $\mathfrak{N}$ as a function of the variable $x \equiv (\xi_k/\Xi)^{\gamma}$, where $\mathfrak{N}$, Ξ and γ are specific to each distribution (estimates are listed in Table 1). The solid line shows the universal curve $y = e^{-x}$. (b) Error plot. Log-differences between the cumulative distributions of recruitment and the fits with the Weibull exponential model, i.e. $\ln\left[k/\mathfrak{N}\exp\left(-(\xi_k/\Xi)^{\gamma}\right)\right]$, are plotted against standardized recruits $(\xi_k/\Xi)^{\gamma}$, on a logarithmically scaled abscissa. Errors fluctuate around 0 for $x < 3$, i.e. $\xi < \xi_{95\%}$, where $|\text{log-differences}| < \ln 2 \approx 0.7$. One observes a systematic deviation for recruits larger than $\xi_{95\%}$ (vertical dashed line). (c) Recruitment dispersion versus stock-specific Weibull exponent γ (plotted on semilogarithmic scale). The recruits of each stock are divided by the stock-specific characteristic scale Ξ. Open circles (○) indicate the empirical values of the mean recruitment. The solid line shows the normalized mean recruitment predicted by the Weibull exponential model, $\gamma^{-1}\Gamma(\gamma^{-1})$; the long-dashed line shows the 95 percentile of the survivorship distribution, $\xi_{95\%}/\Xi = 3^{1/\gamma}$; the dash-dotted line shows the first quartile $\xi_{25\%}/\Xi = (-\ln 0.75)^{1/\gamma}$; the short-dashed line shows the typical lowest recruits in $T = 50$ years, $\xi^{\dagger}/\Xi = T^{-1/\gamma}$.

Table 1. Statistical description of recruitment distributions for the North Atlantic stocks.

Fish populations [species & ICES areas]	Age at recruitment	N	$\mathfrak{N}$	Ξ [$\times 10^6$]	γ	R^2	Year-classes of recruits
Cod, *Gadus morhua*							
22–24	1	34	38.7	97.8	1.34	0.989	1970–2003
25–32	2	37	51.2	221.0	1.07	0.949	1966–2002
northeast Arctic	3	57	64.5	620.6	1.46	0.985	1946–2002
Faroe Plateau [Vb1]	2	43	47.2	17.8	1.60	0.979	1961–2003
Icelandic [Va]	3	48	51.5	195.7	2.57	0.983	1955–2002
VIIa	0	37	39.9	6.6	1.43	0.943	1968–2004
Kattegat	1	33	34.5	13.4	1.41	0.974	1971–2003
Greenland Halibut, *Reinhardtius hippoglossoides*							
I and II	5	36	59.8	18.9	1.77	0.814	1964–1999
Haddock, *Melanogrammus aeglefinus*							
IIIa and IV	0	43	55.6	24 812.7	0.68	0.979	1963–2005
Arctic [I and II]	3	53	57.2	163.0	0.86	0.948	1950–2002
Faroe [Vb]	2	43	48.1	28.2	1.04	0.975	1961–2003
Herring, *Clupea harengus*							
25–29 and 32 [*]	1	30	33.8	19 408.1	2.32	0.963	1974–2003
30	1	31	35.1	4562.8	1.39	0.915	1973–2003
IIIa, IV and VIId [†]	1	44	47.3	44 787.1	1.54	0.974	1960–2003
Norwegian [‡]	0	55	56.9	57 614.4	0.57	0.959	1950–2004
VIa	1	47	53.7	1596.1	1.04	0.952	1957–2003
Plaice, *Pleuronectes platessa*							
VIIa	1	41	53.1	14.6	2.14	0.956	1964–2004
IV	1	46	78.3	754.8	1.06	0.966	1957–2002
Saithe, *Pollachius virens*							
IIIa, IV and VI	3	36	58.2	123.2	1.34	0.976	1967–2002
Arctic [I and II]	3	41	47.9	188.5	1.79	0.953	1960–2000
Faroe [Vb]	3	41	45.4	30.1	1.67	0.982	1961–2001
Va	3	41	42.3	43.7	1.64	0.915	1962–2002
Sole, *Solea vulgaris*							
VIIf and g	1	33	91.0	2.9	1.23	0.937	1971–2003
VIIe	1	34	48.7	4.3	2.06	0.934	1969–2002
IV	1	46	49.9	129.8	1.17	0.884	1957–2002
Sprat, *Sprattus sprattus*							
22–32	1	30	36.8	66 733.7	1.05	0.892	1974–2003
Whiting, *Merlangius merlangus*							
IV and VIId	1	44	44.4	3279.2	1.46	0.963	1960–2003

Source of data: ICES Advice on fish stocks (ACFM Documents from May and October 2005), available at ⟨http://www.ices.dk/advice/icesadvice.asp⟩. For ICES fishing areas, see the ICES website ⟨http://www.ices.dk/aboutus/icesareas.asp⟩. N is the number of year-classes in a data set. The values of Ξ and γ are the maximum likelihood estimates over the full data range. The normalization $\mathfrak{N}$ is the expected value over the low recruits range ($\xi < \Xi$). The coefficient of determination R^2 is calculated for $\xi < \xi_{95\%}$. [*] Excluding Gulf of Riga, [†] autumn spawners, [‡] spring spawners.

stocks). Among Fraser River sockeye salmon (*Oncorhynchus nerka*) the principal age of maturity is four years, so that the most of the populations have been treated as though divided into four lines of descent. Lines are identified by the year in which each occurred at the start of the last century, i.e. 1901–1904; in some but not all sockeye populations there has been a persistently "dominant" line, a "subdominant" line about 10–20% as large, and two weak lines having less than 1% as many fish as the dominant one. As for abundance of the four lines at the Lower Adams River, the 1902 line has been dominant, the 1903 line subdominant, and the 1904 and 1901 lines have been quite scarce. Recruits count anadromous sockeye (catch plus escapees) produced by a given year-class; e.g. recruits from the 1922 year-class were the 3.0×10^5 spawners of 1926 plus 1.8×10^5 estimated caught by the Canadian fishery that year. I fit the cumulative distributions of adult recruits for each line in the Fraser River sockeye stock at the Lower Adams to the Weibull exponential model (estimates of parameters listed in Table 2), and find that the distributions are "self-similar", i.e. exhibit scaling (Fig. 2). The scaled data for the four lines collapse onto each other regardless of how low or high spawner abundance is, falling onto the Weibull exponential distribution.

Table 2. Estimates of the Weibull parameters for Fraser River sockeye salmon at the Lower Adams.

lines	N	$\mathfrak{N}$	Ξ [$\times 10^6$]	γ	R^2	year-classes (every 4 year)
1902 (dominant)	17	18.3	6.41	1.65	0.951	1922–1986
1903	10	14.4	1.18	0.89	0.649	1951–1987
1904	11	12.7	0.025	1.16	0.943	1948–1988
1901	10	11.2	0.026	0.91	0.906	1949–1985

Source of data: Ricker (1997). The values of Ξ and γ are the maximum likelihood estimates over the full data range. $\mathfrak{N}$ is the expected value over $\xi < \Xi$. R^2 is calculated for $\xi < \xi_{95\%}$.

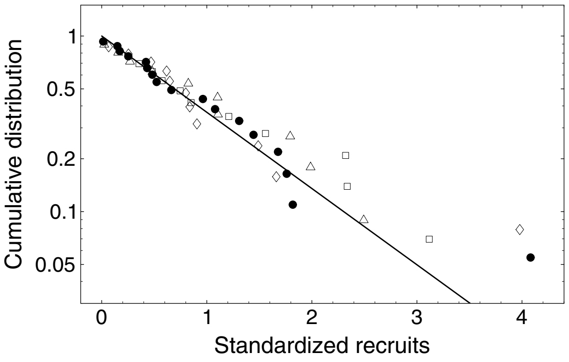

Fig. 2. Relative number of times a given level of standardized recruitment observed in the four lines of Fraser River sockeye salmon at the Lower Adams (Ricker 1997). This figure plots each cumulative number k normalized by its corresponding factor $\mathfrak{N}$ as a function of the variable $x \equiv (\xi_k/\Xi)^\gamma$, with a logarithmically scaled ordinate, where $\mathfrak{N}$, Ξ and γ are specific to each line. Estimates are listed in Table 2 for the lines 1902 (●), 1903 (□), 1904 (◇) and 1901 (△). The solid line shows the universal curve $y = e^{-x}$.

2.3 Invertebrate stocks

Moreover, I analyze data on exploited invertebrate stocks using recruitment time series for crustaceans and for a burrowing bivalve mollusk; data are extracted from the ICES-ACFM database (Advice from May and October 2005) at ⟨http://www.ices.dk/advice/icesadvice.asp⟩ and from Refs. (Gracia 1991; Hancock 1973; Penn and Caputi 1986; Shojima and Otaki 1982; Zheng et al. 1995). I fit the distributions of recruitment for each stock to the Weibull exponential model (estimates of parameters listed in Table 3). Though time series for invertebrates do not appear to be sufficiently long for statistical analysis, the scaled data fall onto the almost same straight line over the 95% range ($\xi < \xi_{95\%}$), as shown in Figure 3. Their recruitment variability is well-described by the Weibull exponential distribution as well as bony fishes.

2.4 Extreme variations

The quantification of Weibull exponentials is particularly important with regards to extrapolations to low number events that have not yet been observed. I now provide the distribution of extreme variations. Let us ask what is the probability $P_T\left(\xi_{\min} < \xi^\dagger\right)$ that the lowest value $\xi_{\min}$ among T realizations (i.e. in T years) is less than $\xi^\dagger$:

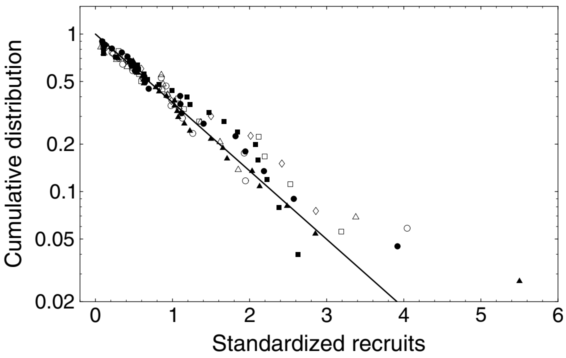

Fig. 3. Cumulative distributions of standardized recruitment for the 7 invertebrate stocks (semilogarithmic scale plot): *Nephrops* lobster in ICES VIIIa, b (□) and VIIIc (■) (ICES Advice, ACFM Documents 2005); *Penaeus* shrimp, *P. orientalis* in Po-hai Bay (▲) (Shojima and Otaki 1982), *P. esculentus* in Exmouth Gulf (○) (Penn and Caputi 1986), *P. setiferus* in the Gulf of Mexico (◇) (Gracia 1991); red king crab *Paralithodes camtschaticus* in Bristol Bay (●) (Zheng et al. 1995); Burry Inlet cockles *Cardium edule* (△) (Hancock 1973). This figure plots each cumulative number k normalized by its corresponding factor $\mathfrak{N}$ as a function of the variable $x \equiv (\xi_k/\Xi)^\gamma$, where $\mathfrak{N}$, Ξ and γ are specific to each distribution (estimates are listed in Table 3). The solid line shows the universal curve $y = e^{-x}$.

$$P_T\left(\xi_{\min} < \xi^\dagger\right) = 1 - \exp\left[-\left(\xi^\dagger/\Xi\right)^\gamma T\right]. \tag{7}$$

Denote p_T the chosen level of probability of tolerance for the lowest value $\xi_{\min}$, i.e. $P_T\left(\xi_{\min} < \xi^\dagger\right) = p_T$. Inverting Eq. (7) yields

$$\xi^\dagger = \left[-\ln(1 - p_T)\, T^{-1}\right]^{1/\gamma} \Xi. \tag{8}$$

The value $\xi^\dagger = \Xi T^{-1/\gamma}$ is the usual estimate of the typical lowest value, corresponding to a probability of 37% (i.e. $p_T = 1 - e^{-1} = 0.63$); the typical lowest value in $T = 50$ years is calculated (shown in Fig. 1c) to give $\xi^\dagger = 0.02\Xi$ for $\gamma = 1$. We thus realize that the precise characterization of the recruitment distribution is of great importance, because the statistical properties of recruitment fluctuations are the key input of the extreme variation analysis.

3 Testing of lognormality in time series

The recruitment variability raises challenging questions for anyone who has more than a passing interest in understanding population processes. It is thus important to ask whether

Table 3. Estimates of the Weibull parameters for invertebrate stocks.

stocks [species & area]	age	N	$\mathfrak{N}$	Ξ [$\times 10^6$]	γ	R^2	year-classes
Nephrops lobster in ICES areas[*]							
VIIIa, b	1	16	17.9	658.8	7.52	0.870	1987–2002
VIIIc	2	22	25.2	11.0	1.19	0.907	1982–2003
Penaeus shrimp							
P. orientalis, Po-hai Bay[†]	0	26	37.1	144.2	0.71	0.987	1952–1977
P. esculentus, Exmouth Gulf[‡]	0	14	17.1	(19.9)	2.20	0.948	1970–1983
P. setiferus, Gulf of Mexico[§]	0	11	13.3	144.7	5.07	0.868	1973–1983
red king crab *Paralithodes camtschaticus*							
Bristol Bay[¶]	7	20	22.2	27.6	0.85	0.961	1968–1987
cockles *Cardium edule* L.							
Burry Inlet[‖]	0	12	14.5	3028.2	0.97	0.947	1958–1969

Source of data: [*] ICES Advice (2005), [†] Shojima and Otaki (1982), [‡] Penn and Caputi (recruits ξ read index value; 1986), [§] Gracia (1991), [¶] Zheng et al. (1995), [‖] Hancock (1973). The values of Ξ and γ are the maximum likelihood estimates over the full data range. $\mathfrak{N}$ is the expected value over $\xi < \Xi$. R^2 is calculated for $\xi < \xi_{95\%}$.

real populations actually fit the lognormal on the same as the above-examined data, i.e. the typical fluctuations of logarithms around the (geometric) mean value are Gaussian.

3.1 Recruitment time series

By partitioning the pre-recruit phase into an arbitrarily number n of intervals, recruitment survival can be modeled by a multiplicative (rather than additive) process, such that offsprings survive (or decline) in an exponential fashion:

$$X_{i+1} = m_i X_i = m_i m_{i-1} \cdots m_0 X_0 \tag{9}$$

with survival rates m_i during the ith interval, where the positive factors m_i are all less than or equal to unity. X_i is cohort size; X_0 is the initial number in the cohort (total egg production). Taking the logarithm of both sides, one arrives at the expression:

$$\ln X_n = \ln X_0 + \sum_{i=0}^{n-1} \ln m_i, \tag{10}$$

where X_n is the number surviving to recruitment ($= \xi$). We now ignore the density dependence of survival rates on the adult population (or more specifically egg production). If $\ln m_i$ are iid variates with finite moments, then their summation in Eq. (10), and hence $\ln \xi$ will tend to be normally distributed, providing that X_0 is lognormally distributed (because the sum of two independent random variables, which have normal distribution, also has a normal distribution). This argument is essentially the central limit theorem working multiplicatively for X_i. It is the commonly held belief that population abundance S of spawners follows a lognormal distribution (Halley and Inchausti 2002); the initial cohort size X_0 is expected to be linearly dependent on S, and thus X_0 to be lognormally distributed. Lognormality in abundance distribution of spawners is argued in the next part. While the survival rates of young fish in different life history stages may not be identically distributed (Iles and Beverton 2000), the iid assumption need not hold exactly for the central limit theorem to be applicable. Rather, the variance of any separate distributions which exist must have variances which are not too dissimilar, so that no single variance dominates over all the others (Bouchaud and Potters 2000).

Figure 4a groups the cumulative distributions of standardized log-recruits $x \equiv \ln(\xi/\hat{\xi})/\sigma_{\ln \xi}$ of 27 fish stocks in the North Atlantic (same as Fig. 1a), where $\hat{\xi}$ and $\sigma_{\ln \xi}$ denote a geometric mean and geometric standard deviation of the distribution, respectively. The cumulative number k_+ of $\xi \geq \hat{\xi}$ (i.e. rank in descending order, $\hat{\xi} \leq \xi_{N_+} < \cdots < \xi_{k_+=2} < \xi_{k_+=1}$) and the complementary cumulative number k_- of $\xi < \hat{\xi}$ (i.e. rank in ascending order, $\xi_{k_-=1} < \xi_{k_-=2} < \cdots < \xi_{N_-} < \hat{\xi}$ with $N_+ + N_- = N$) are normalized by $\mathfrak{N}_\mathrm{G}$, the expected value for the normalization calculated from $\mathfrak{N}_\mathrm{G} = \exp\left[\left\langle \ln k_+ - \ln\left[1 - \mathrm{erf}\left(x_{k_+} / \sqrt{2}\right)\right]\right\rangle\right] + \exp\left[\left\langle \ln k_- - \ln\left[1 + \mathrm{erf}\left(x_{k_-} / \sqrt{2}\right)\right]\right\rangle\right]$, over data range such that $|\ln(\xi/\hat{\xi})| < \sigma_{\ln \xi}$, where $x_{k_\pm}$ (corresponding to $\xi \gtrless \hat{\xi}$) denotes the $k_\pm$th standardized log-recruit ranked in descending ($\xi \geq \hat{\xi}$) or ascending ($\xi < \hat{\xi}$) order. $\mathrm{erf}(\cdot)$ is the Gauss error function. I then plot

$$y_\pm \equiv k_\pm / \mathfrak{N}_\mathrm{G} \quad \text{versus} \quad x_\pm \equiv \ln(\xi_{k_\pm}/\hat{\xi})/\sigma_{\ln \xi} \tag{11}$$

in Figure 4a, showing the cumulative distributions of standardized log-recruits $x_+ \geq 0$ and the complementary cumulative distributions of $x_- < 0$. Figure 4b shows the differences (error plot) between the cumulative distributions of standardized log-recruits and the standard normal cumulative distribution functions. The central part (87%) of the distribution (i.e. $|\ln(\xi/\hat{\xi})| < 1.5\sigma_{\ln \xi}$) is tolerably well-fitted by the lognormal model (i.e. |log-differences| $< \ln 2 \approx 0.7$). The remaining of the ICES-ACFM data points in recruitment time series largely deviate from lognormality; both negative (low numbers) and positive (high numbers) tails (i.e. $|\ln(\xi/\hat{\xi})| > 2\sigma_{\ln \xi}$) are much heavier than expected (i.e. there are more data points). The lognormal model is not a better substitute for population dynamic and distributional information in the low recruits régime.

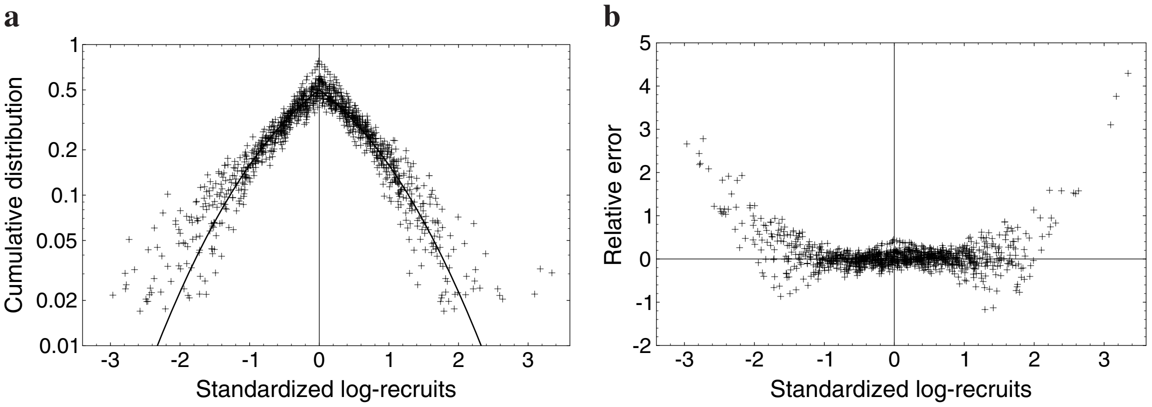

Fig. 4. Fitting ICES-ACFM time-series to a lognormal model (the same as the data in Fig. 1a). (a) Relative number of times a given level of recruits observed is plotted against standardized log-recruits $x \equiv \ln(\xi/\hat{\xi})/\sigma_{\ln\xi}$. Semilogarithmic scale plot. The positive and negative parts are the cumulative and complementary cumulative distributions. The solid lines show the standard normal cumulative distribution functions $\frac{1}{2}\left[1 \mp \mathrm{erf}(x/\sqrt{2})\right]$ for $x \gtrless 0$, where the Gauss error function is defined by $\mathrm{erf}(x) = (2/\sqrt{\pi})\int_0^x \exp\left(-u^2\right)\mathrm{d}u$. (b) Log-differences between the cumulative and complementary cumulative distributions of recruitment and the fits with the lognormal model, i.e. $\ln\left[k_\pm/0.5\mathfrak{N}_\mathrm{G}\left(1 \mp \mathrm{erf}\left(x_{k_\pm}/\sqrt{2}\right)\right)\right]$, are plotted against standardized log-recruits. $\ln\xi$ is Gaussian in the neighborhood of the peak of the distribution.

3.2 Abundance time series of spawners

Among ecologists, it is widely believed that population abundance S should be lognormally distributed (e.g. MacArthur 1960; Preston 1962; Sugihara 1980). The essence of the lognormal hypothesis is that the central limit theorem works multiplicatively for population processes: a population grows or declines in an exponential fashion with a finite replacement rate ϕ_t randomly fluctuating over times, $S_{t+1} = \phi_t S_t$. Let us now test the lognormal hypothesis for the abundance time series of spawning populations. Figure 5a groups the cumulative distributions of standardized log-abundances of 27 fish stocks in the North Atlantic, the same as the stocks listed in Table 1 (data from ICES-ACFM Documents, May and October 2005). Fits with the lognormal model are not so good as one believes in it.

These deviating from lognormality are compatible with an empirical characterization of the distribution of population abundance: Halley and Inchausti (2002) reported the poor fit of the lognormal to real data. To test the lognormal hypothesis, they analyzed 544 annual time-series of population abundance longer than 30 years, using the global population dynamics database (Inchausti and Halley 2001), and empirically found that the lognormal model fits about half of all the series tolerably well; the 544 datasets were divided into the following taxonomic groups: Mammalia, Insecta, Aves, Osteichthyes, Crustacea and Mollusca. For bony fishes, 42.6% of the series (40 of the 94 datasets) showed significant departures from lognormality.

Using the Weibull exponential model as a convenient and parsimonious tool, let us reanalyze the population process. We make the usual assumption of "knife-edged" recruitment at age α years ($\alpha \geq 1$) to the mature stock; after recruitment all fish are equally vulnerable to the fishery regardless of their ages. Fishing is assumed to take place in a pulse at the start of each year, and spawning to occur after fishing. By employing the delay-difference equation (Deriso 1980; Quinn and Deriso 1999) iteratively, the spawning stock biomass S_t, i.e. the escapement of catchable adults from the fishery in year t is written as

$$S_t = \frac{w_\alpha}{\ell} \sum_{i=0}^{\infty} \xi_{t-i} \frac{1-\rho^{i+1}}{1-\rho} \exp\left(-\sum_{j=0}^{i} \mu_{t-j}\right), \tag{12}$$

where w_α is the weight at recruitment of a fish (the pre-recruitment weight is assumed to be 0) and the annual weight increment decreases by the factor ρ with $0 < \rho < 1$; the natural survival fraction for catchable adults, ℓ, is constant; μ_j denotes the instantaneous mortality (i.e. the fishing and natural mortality rate) in year j. If fishing occurs throughout the year, then the spawning is assumed to occur at the end of the year, in which case Eq. (12) remains approximately valid as long as the natural mortality of adults remains constant and the total mortality of adults is not too large. The probability density function $\tilde{p}(S)$ to observe a stock of a given biomass S is expressed as a multiple convolution

$$\tilde{p}(S) = \prod_{n=0}^{\infty} \int_0^\infty \mathrm{d}\xi_n p(\xi_n) \times \delta\left(S - \frac{w_\alpha}{\ell} \sum_{i=0}^{\infty} \xi_i \frac{1-\rho^{i+1}}{1-\rho} \exp\left(-\sum_{j=0}^{i} \mu_{t-j}\right)\right) \tag{13}$$

for independent supply of recruits with a Weibull exponential probability density function

$$p(\xi) = \gamma \Xi^{-1} (\xi/\Xi)^{\gamma-1} \exp\left[-(\xi/\Xi)^\gamma\right]. \tag{14}$$

The Dirac delta function expresses the constraint on the sum, ensuring that all possible time series $\{\xi_0, \xi_1, \ldots\}$ yield a given S. Due to the exponential dumping factors, the spawning population consists of a finite group of different year-classes; S is the sum (rather than the product) of a finite number of independent random variables. The leading contribution comes

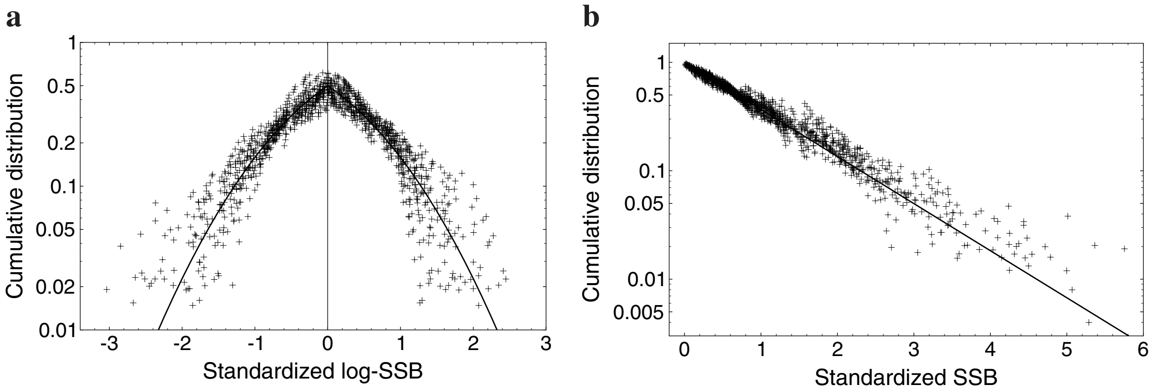

Fig. 5. Lognormal versus Weibull exponential distributions: spawning stock biomass S in the North Atlantic, the same as the stocks listed in Table 1 (data from ICES Advice, ACFM Documents 2005). Relative number of times a given level S of spawning stock biomass (SSB) observed in each stock is fitted to the standard lognormal (a) or standard Weibull exponential (b) distributions, where the values of the Weibull parameters are evaluated by using the maximum likelihood method. Remarkably, the scaled quantities, the same as the form in Eq. (6), fall onto the almost same straight line over the whole range of the distribution.

from individual terms in the sum which are localized across finite ν generations such that

$$-(1-\rho^{\nu})\rho + \sum_{j=1}^{\nu} \mu_{t-j} = 1. \qquad (15)$$

Cohorts in the population concentrate on the generation rank ν:

$$S_t \approx w_\alpha \ell^{-1} e^{-\mu_t} \sum_{i=0}^{\nu} \xi_{t-i}. \qquad (16)$$

By applying the theory of extreme deviations (Frisch and Sornette 1997) concerned with the régime of finite ν and large $\sum_{i=0}^{\nu} \xi_{t-i}$, when the recruitment distribution does not decay more slowly than an exponential, i.e. belongs to the class of (super-)exponential distributions, the tail of the distribution of the sum S is an exponential, while for stretched exponentials the tail behavior is asymptotically the same as the distribution of the individual recruits (Johansen and Sornette 2001).

This holds as long as the assumption, that successive recruitment variations are uncorrelated, is a good approximation. Figure 5b demonstrates that the Weibull exponential model accounts quantitatively for abundance distributions of spawning stocks in the North Atlantic: the distribution of scaled quantities is an almost perfect exponential. The results justify the choice of the Weibull exponential model for the recruitment distribution.

3.3 Historical spawning success

One may be inclined to investigate the statistics of recruits per spawner, because Eq. (10) suggests that a lognormal distribution is a descriptor of spawning success (referred to as survival denoted by λ). The quantity λ gives the ratio of the annual number of recruits to the spawning stock biomass (or egg production), which is the cumulative survival rate in the pre-recruit phase, λ $(\equiv \xi/S) = m_{n-1}m_{n-2}\cdots m_0$. Figure 6 compares lognormal versus Weibull exponential models for survivals of 27 fish stocks in the North Atlantic, the same as the stocks listed in Table 1 (data from ICES-ACFM Documents, May and October 2005). We see that the Weibull exponential is a superior universal descriptor of survival than the lognormal model when one is concerned with low numbers régime.

In the above analysis procedure, we ignore the density dependence of recruitment on spawner abundance. By employing the Ricker (1954) model, the cumulative survival rate is expressed as $\lambda^\star \equiv \exp[-\mu(1+X_0/K)]$, where μ is the cumulative mortality and K the carrying capacity. In Figure 7, the mean recruitment is plotted versus the decoupling between individual survival and reproduction, i.e.

$$y \equiv \langle \xi \rangle \quad \text{versus} \quad x \equiv \langle \lambda \rangle \langle S \rangle, \qquad (17)$$

of 27 fish stocks in the North Atlantic (same as Figs. 1a, 5b and 6b). The points in the decoupling plot do not show any substantial departures from the straight line "$y = x$", which represents their expected behavior under the Ricker model, $\langle \xi \rangle = \langle \lambda^\star \rangle \langle S \rangle + \sigma_{\lambda^\star X_0}$, because the covariance $\sigma_{\lambda^\star X_0}$ for density-dependent survival $\lambda^\star$ and spawner output X_0 (or adult population) will be nonzero, $\sigma_{\lambda^\star X_0} < 0$; $\lambda^\star$ tends to decrease as X_0 increases. The result (Fig. 7) provides empirical evidence against the density dependence: the covariance $\sigma_{\lambda X_0}$ for survival and initial cohort size is, approximately, zero.

In sum, the results shown in Figures 1a, 5b and 6b are consistent and clear evidence against important dependence in the successions both of surviving events (i.e. survival rates in the early life stages on an appropriate time scale) and of recruiting events from year to year. Although the successive events may not be strictly independent, i.e. uncorrelated (Fogarty 1993a; MacCall 1999), the actual amount of dependence may be so small as to be unimportant, because the Weibull exponentials quite describes low to moderate values of the distributions of widely differing stocks. Besides uncorrelated population processes, Figures 1a, 2, 3, and 7 show that the density-independence assumption is appropriate for the relationship between spawner abundance (or egg production) and individual survival on recruitment levels on an inter-annual. Considering the robustness of the results, we expect

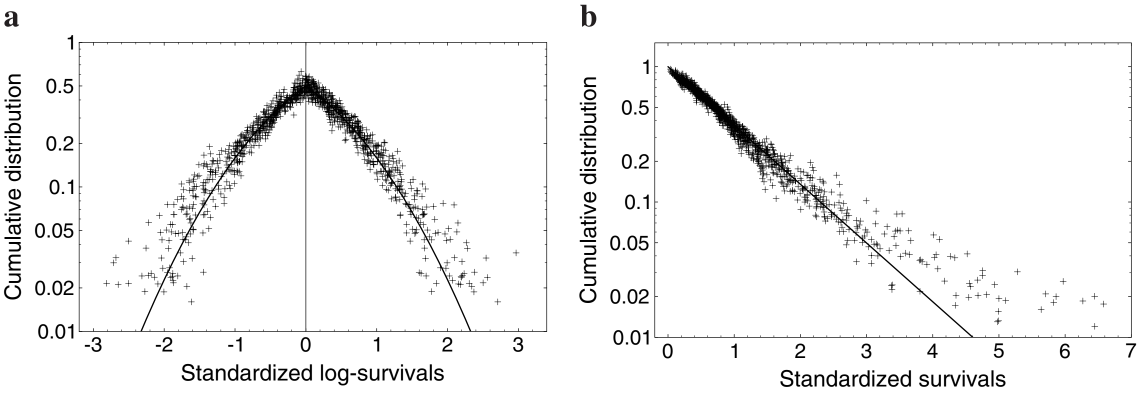

Fig. 6. Lognormal versus Weibull exponential distributions: survivals on recruitment levels, $\lambda \equiv \xi/S$, in the North Atlantic stocks, the same as the stocks listed in Table 1 (data from ICES Advice, ACFM Documents 2005). Relative number of times a given level λ of recruits per unit of spawning biomass observed in each stock is fitted to the cumulative standard lognormal (a) or standard Weibull exponential (b) distributions, where the values of the Weibull parameters are the maximum likelihood estimates.

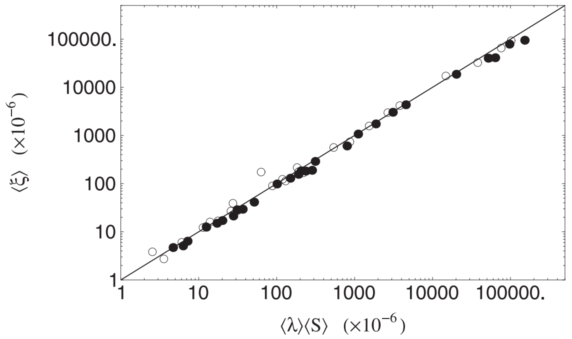

Fig. 7. Decoupling between individual survival and reproduction (data from ICES-ACFM Documents, May and October 2005). The averaged quantities $y \equiv \langle\xi\rangle$ versus $x \equiv \langle\lambda\rangle\langle S\rangle$ of 27 fish stocks in the North Atlantic (same as Figs. 1a, 5b and 6b) are plotted (●) on double logarithmic scale. The solid line shows $y = x$, exactly onto which all the points in the decoupling plot collapse. The open symbols depict the decoupling plot predicted by the Weibull exponential model, i.e. $\Xi\gamma^{-1}\Gamma\left(\gamma^{-1}\right)$ versus $\Lambda\gamma_\lambda^{-1}\Gamma\left(\gamma_\lambda^{-1}\right) \times \mathfrak{S}\gamma_S^{-1}\Gamma\left(\gamma_S^{-1}\right)$, using the maximum likelihood estimates of the Weibull parameters (Ξ, γ) of the recruitment distributions, $(\Lambda, \gamma_\lambda)$ of the survival distributions, and $(\mathfrak{S}, \gamma_S)$ of the abundance distributions of spawners, which are specific to each stock.

no-correlation and density-independence approximations to constitute first-order descriptions of population processes.

The Weibull exponential distributions, which are supposed theoretically to apply better for extreme deviations (i.e. very small recruits), seem to account for recruits near and above the center of the analyzed distributions. The stretched or super-exponentials have been found to provide a reasonable fit to the bulk (95%) of recruitment variations and have the advantage of a sound theoretical foundation, i.e. the theory of extreme deviations (Frisch and Sornette 1997) concerned with the régime of finite number n of independent random variables and events of low probability. On the other hand, when $n \to \infty$, the central limit theorem and the large deviations theory (Bouchaud and Potters 2000; Cramér 1938) apply in the center and the tail of the distribution, respectively.

We have however realized that the Weibull exponential model does not explain the distribution of the 5% largest recruits. For fish stocks in the North Atlantic, the empirical standardized distributions give about 2 to 20 times too many events larger than $\xi_{95\%}$, when comparing with the Weibull exponential model (Fig. 1b).

4 Non-Poisson intermittency

Finally in this section, I investigate the possibility that recruiting events (ξ_t's) from year to year exhibit long-range correlations (Fogarty 1993a; MacCall 1999).

Outstanding successful replenishments of marine populations are erratic and episodic (Doherty and Williams 1988; Dixon et al. 1999). A quantity that characterizes the occurrence of high-magnitude recruitment is the inter-event time of two consecutive extreme events, i.e. recruits above some large threshold. Because extreme events are rare, picking the recruitment above an intermediate threshold, i.e. ξ larger than the 86 percentile of the recruitment distribution, $\xi_{86\%}$ $(= 2^{1/\gamma}\,\Xi)$, for each separate stock, I study the distribution of time intervals between the 14% largest events (precisely, the 13.5335% $[= e^{-2}]$ largest events). By doing this, it is hoped to gain insight into the inter-event statistics of bursts in population processes. Figure 8a (solid symbols) shows the cumulative distribution of inter-event times across all the 27 fish stocks in the ICES-ACFM time-series data (listed in Table 1), which clearly differs from the simple exponential; the inter-event times follow a stretched exponential law, the same as the form in Eq. (1). The truncation of the stretched exponential behavior is due to finite-size effects: the period of time-series data for analyses is at most 57 years. For an uncorrelated recruitment trajectory, extreme events randomly distributed in time and following Poisson statistics, one expects that the inter-event times follow a pure exponential distribution. To test this expectation, I remove the long-term memory by shuffling the recruitment records for each stock, and I obtain a simple exponential (Fig. 8a, open symbols). The distinct difference between the distributions of the inter-event times in the real data

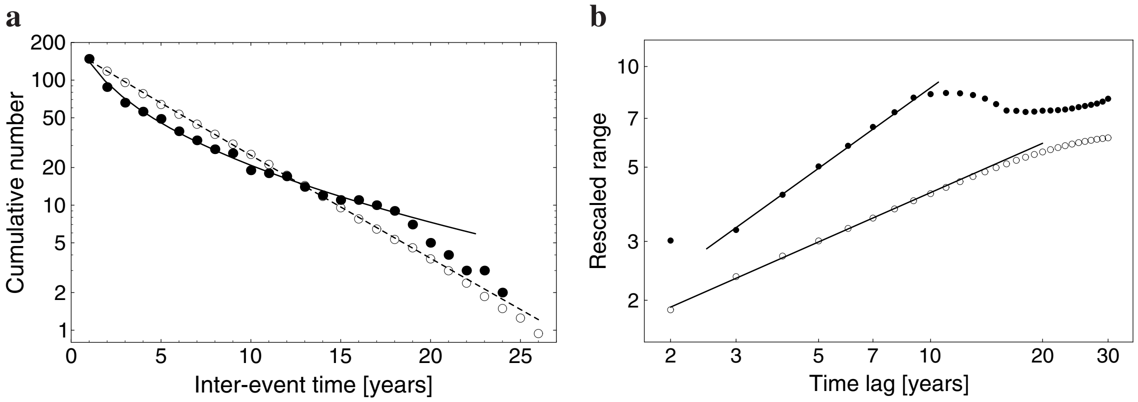

Fig. 8. Memory in recruitment trajectories. (a) Inter-event statistics. Cumulative number of time intervals for extreme events that the recruits exceed the 86% ($= 1-e^{-2}$) level of recruitment in the ICES-ACFM time-series data (ICES Advice 2005). Aggregated inter-event histogram across all the 27 stocks listed in Table 1 is plotted (•) on semilogarithmic scale. The distribution (number of intervals that inter-event times are longer than or equal to τ) is well-described by the stretched exponential (solid line), $P(\text{time} \geq \tau) = \mathfrak{N} \exp[-(\tau/\tau_0)^\gamma]$ with $\mathfrak{N} = 441$, $\tau_0 = 0.73$ years, and $\gamma = 0.43 \pm 0.05$, where the total number of intervals for consecutive events, $N = 148$ (regression through data points after omitting the 5% largest intervals because of truncated tail end). To test whether, after shuffling the recruitment records, the cumulative distribution of inter-event times becomes an exponential, the shuffled data are plotted (○), showing ensemble (100 time-series/ensemble) averages. The dashed line shows the fit (after omitting the 5% largest intervals) to the stretched exponential distribution with $\mathfrak{N}' = 177$, $\tau_0' = 5.05$ years, and $\gamma' = 0.98 \pm 0.02$; the linear plot on semilogarithmic scale represents the pure exponential form of a Poisson distribution for uncorrelated data. The fits are done using the natural logarithm, $\ln P(\text{time} \geq \tau) = \ln \mathfrak{N} - c\tau^\gamma$, to estimate these values (the characteristic scale is given by $\tau_0 = c^{-1/\gamma}$). (b) Rescaled range analysis for recruitment in the ICES-ACFM time-series data (ICES Advice 2005). Double logarithmic scale plot. The mean of rescaled range, $\langle F_{\Delta t}/\sigma_{\Delta t} \rangle$, is calculated over sets of regions across all the 27 stocks. This statistic increases with time lag Δt. The strait-line correlations are with Eq. (19), where $H = 0.80 \pm 0.02$ for the real data (•) and $H = 0.490 \pm 0.007$ for the uncorrelated shuffled data (○). The fits are done by the linear regression using the log-transformed data for $3 \leq \Delta t \leq 10$ years (real data) and $2 \leq \Delta t \leq 10$ years (shuffled data).

and in the uncorrelated shuffled data, showing that the distribution is more frequent for large intervals in the real recruitment trajectories than in the shuffled ones, suggests that the fat-tailed behavior of inter-event time distribution must arise from the correlation in successive recruitment records (Altmann and Kantz 2005; Barabási 2005; Bunde et al. 2005; Yamasaki et al. 2005).

An alternative approach to the quantification of correlations in the succession of year-to-year recruiting events is the rescaled range analysis (e.g. Hurst 1951; Mandelbrot 1983; Ariño and Pimm 1995; Inchausti and Halley 2002). Consider a recruitment trajectory ξ_t, $t = 1, 2, \ldots, N$. Let $\langle \xi \rangle_N$ and σ_N be the mean and the standard deviation of all N values in the time series. The rescaled range for the time series is the ratio F_N/σ_N, where the fluctuation range F_N is defined by

$$F_N = \max_{1 \leq k \leq N} Y_k - \min_{1 \leq k \leq N} Y_k \tag{18}$$

with the running sum of the time series relative to its mean, $Y_k = \sum_{i=1}^{k} (\xi_i - \langle \xi \rangle_N)$. Since we are interested in how F/σ varies with arbitrary subintervals Δt of N, we substitute Δt for N; the mean of $F_{\Delta t}/\sigma_{\Delta t}$, calculated over multiple regions of the data, is expected to satisfy the power-law relation

$$\left\langle F_{\Delta t}/\sigma_{\Delta t} \right\rangle \propto (\Delta t)^H \tag{19}$$

with the Hurst exponent H. The running sum of a Gaussian white noise is a Brownian motion (i.e. for a random walk, successive changes are uncorrelated). The rescaled range of a random walk increases at a particular rate $H = 0.5$. Complex dynamics generate serial correlations over time so that the rescaled range increases more rapidly ($0.5 < H \leq 1$, implying persistence) or more slowly ($0 \leq H < 0.5$, implying antipersistence) than for a random walk. For the ICES-ACFM data, I calculate the rescaled fluctuation range $\langle F_{\Delta t}/\sigma_{\Delta t} \rangle$ averaged across all the 27 stocks, yielding $H = 0.80$, a value considerably larger than 0.5, which implies the existence of long-range correlations (Fig. 8b). To understand the origin of the value of H, the rescaled range analysis is employed after shuffling the recruitment records. For uncorrelated shuffled data, as expected, the rescaled range increases at the rate $H = 0.50$ for a random walk, shown by open symbols in Figure 8b. The rescaled range analysis method confirms the inter-event statistics result. Unusually extreme levels, high or low, come more frequently and more contingently than one might expect from uncorrelated recruitment trajectories: a few good years of recruitment will alternate with a few bad ones.

In summary, I find empirical evidence for temporal correlations in recruitment, while the good fit provided by the Weibull exponential model (Fig. 5b) demonstrates that the independence hypothesis in the succession of year-to-year recruiting events is a rational approximation.

5 Conclusion

The issues surrounding recruitment processes in the early life history remain at heart of critical concerns in resource management. The statistical properties of recruitment fluctuations are of importance for modeling and understanding complex recruitment dynamics. I have found that the Weibull exponential distribution provides an accurate fit to the bulk (95%) of recruitment variations, demonstrating that the no-correlation hypothesis is a reasonable approximation for underlying stochastic survivorship dynamics of recruiting populations in the early life stages. The Weibull exponential distribution arises from a multiplication of independent random factors, i.e. a noisy spawner output (egg supply) and randomly time-varying survival rates. The empirical results are evidence against important regulation on recruitment dynamics in terms of density-dependent processes: the spawner output and (natural) mortality rates of recruiting progeny are, approximately, mutually independent. Shepherd and Cushing (1990) noted that most fish biologists believe in regulation (i.e. deterministic density-dependent processes of recruitment survival), even though they have been able to find remarkably little direct evidence for it. It tends to be regarded by fish biologists as something of a weakly supported generalization.

The remaining 5% of the largest recruits are not explained by the Weibull exponential model. The characterization of the tail of their distribution cannot be based on standard techniques extrapolating from smaller values.

The occurrences of dominant year-classes exhibit intermittent correlations in the recruitment time series. The large recruits occurring with deviation from the Poisson prediction are characteristic of empirical statistical properties of the recruitment time-series in marine fish populations. Time intervals between very large recruitment are well-described by the stretched exponential distribution, which results from the persistence of the magnitude of recruitment, i.e. the "recruitment clustering" effect: a long-term memory exists in the annual recruitment time series, such that small recruits tend to be followed by small ones, and large recruits tend to be followed by large ones. The non-Poisson nature of recruitment clustering features the population dynamics of exploited fishes. Individual survivals on recruitment levels on an inter-annual are independent of initial cohort sizes but year-to-year recruiting events are long-term correlated.

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