Diurnal variation in fish density estimate during acoustic surveys in relation to spatial distribution and avoidance reaction

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Abstract

The diurnal cycle in density measured during acoustic surveys is difficult to investigate quantitatively from the data set of a single survey because the signal depends mainly on the spatial variability and/or horizontal fish migrations. In order to detect the diurnal cycle in spite of the noise due to spatial variability, several acoustic surveys from different tropical countries were combined, after standardization, into a single data base. A diurnal cycle is observed, with the highest values during the night and the lowest during the day. The transition periods are very short (less than one hour). Different hypotheses relative to fish behaviour or to acoustic biases are discussed. Among these hypotheses the lateral avoidance of schools by day and the diurnal change in patchiness seem predominant. Moreover, owing to the extreme skewness of the density distribution the applicability of the Central Limit Theorem is discussed.

Keywords: Acoustic surveys, availability, diurnal variations, quantitative distribution, schooling behaviour, statistical sampling, tropical fish.

Variations nycthémérales des estimations de densité de poissons au cours des campagnes acoustiques en liaison avec la distribution spatiale et l'évitement.

Résumé

Il est difficile d'étudier le cycle nycthéméral de variation de la densité estimée durant les campagnes d'écho-intégration à partir d'une seule campagne car le signal dépend essentiellement de la variabilité spatiale et/ou des migrations horizontales des poissons. Afin de détecter le cycle nycthéméral en dépit du fort bruit provenant de la variabilité spatiale, plusieurs campagnes réalisées dans différents pays ont été réunies dans une base de données, après standardisation. Un cycle journalier est observé, avec les valeurs les plus fortes de nuit et les plus basses de jour. Différentes hypothèses liées au comportement du poisson ou à des biais acoustiques sont discutées. Parmi ces hypothèses, l'évitement latéral des bancs durant le jour et les changements du niveau d'agrégation semblent prédominants. De plus, en raison de l'extrême dissymétrie de la fonction de distribution des densités, l'applicabilité du Théorème Central Limite est discutée.

Mots-clés : Campagnes acoustiques, disponibilité, variations nycthémérales, distribution quantitative, comportement des bancs, échantillonnage, poissons tropicaux.

INTRODUCTION

Diurnal variation in behaviour of pelagic organisms is well documented (Hoar and Randall, 1978; Weston and Andrew, 1990). This variation, which concerns mainly vertical migrations, level of aggregation and spatial orientation, influences the results of acoustic surveys, especially the ratio of apparent biomass measured by echo-integration by day and by night.

Many factors may introduce biases in the density measured by acoustics (see Olsen, 1990; Soria and Fréon, 1991; MacLennan and Simmonds, 1992; Simmonds et al., 1992; Fréon et al., 1993 for review). Some biases, such as those related to seasonal migrations, affect equally day and night estimation and therefore are not considered in this paper. Among the remaining biases, it can be assumed that none is responsible for an overestimation of the total acoustic density (including demersal fish), except in
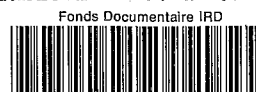
some cases when dense plankton layers during the night may exceed the threshold density. In tropical areas, this problem is limited or solved by appropriate thresholding.

During the day, the factors of underestimation are principally: (1) The lateral avoidance of the vessel which occurs when the fish are in school; (2) The acoustic shadow which refers to the problem of non-linearity in back scattered echo energy when the density increases; (3) The daily horizontal migration which may be responsible for an underestimation of the acoustic density because the fish are located in an inaccessible area (coastal zone for instance); (4) The decrease in target strength (TS) associated with an increase of the tilt angle when the fish dive below the boat; (5) The swimbladder dorsal surface reduction which can reduce the TS of the fish; (6) The bottom blind area when during the day an important part of the demersal biomass is located very close to the bottom. In this case this biomass can be only partially detected (bottom relief, shape of the beam, etc.), while during the night most of this biomass migrates upward and therefore becomes available.

The factors of major underestimation in measured acoustic density during the night are principally: (1) A sub-surface blind area of 4 to 5.5 metre height (or more in case of a strong swell) which may never be sampled according to the depth of the transducer and to its own blind distance. As the biomass is closer to the surface during the night than during the day, the resulting underestimation is predominant during the night; (2) The decrease in TS associated with the variability of the tilt angle of the fish which is greater during the night than during the day; (3) The light on

a vessel which produces a strong reaction, and in some cases changes the echo abundance below the vessel.

Even though these variations are well known by field scientists, in few instances have diurnal variations of these factors been quantified and the variability studied in details (Appenzeller and Leggett, 1992). One of the reasons for this poor documentation is the high spatial variability which can hide the temporal variability, as far as a single survey is concerned. In order to detect the diurnal cycle in spite of the noise due to spatial variability, a large data base of several surveys has been used in this work. Such a quantitative study might define the amplitude of the diurnal cycle and its timing with respect to the main diurnal clue: the sunlight. These results may be useful for deciding the sampling strategy and/or for studying the reliability of weighting factors for a global biomass estimation, in those instances where day and night results can reasonably be mixed.

MATERIAL AND METHOD

The data base was built up from 18 surveys performed in tropical countries. The data come from Venezuela, Indonesia and Mauritania (*table* 1). All the surveys were performed on the continental shelf and concern mainly small pelagic species (principally Clupeidae and small Carangidae). The volume of the data base is equivalent to 112 days of continuous sampling. Different research vessels were used (mainly R/V Nizery, Capricorne and La Salle), from 24 to 48 metre overall-length. All the vessels were using a 120 kHz sounder and a digital echo-integrator AGENOR.

Table 1. − Date, country and duration of the 18 surveys entered in the "synthetic file".

Survey	Date	Country	Total days	Survey duration	
				Number of 6 min record	Equivalent 24 h continuous survey
1	July 83	Indonesia	8	970	4
2	May 85	Indonesia	11	1 629	10
3	Sept. 84	Venezuela	9	936	4
4	Sept. 84	Venezuela	11	1 428	10
5	May 85	Venezuela	12	1 745	7
6	Sept. 85	Venezuela	5	721	3
7	April 86	Venezuela	11	2 052	8
8	May 86	Venezuela	4	693	3
9	Aug. 86	Venezuela	4	851	3
10	Aug. 86	Venezuela	26	3 424	14
11	Sept. 87	Venezuela	6	898	4
12	April 88	Venezuela	7	1 249	5
13	Sept. 88	Venezuela	9	1 305	6
14	Sept. 83	Mauritania	8	1 583	7
15	Feb. 84	Mauritania	9	1 759	7
16	April 84	Mauritania	8	1 484	6
17	Aug. 86	Mauritania	10	1 408	6
18	Oct. 89	Mauritania	9	1 257	5
Total			167	25 392	112

The survey design was generally based on parallel transects regularly spaced except the first ones in Venezuela (spaced according to density dependent stratification). The inter-transect distance varied from 5 to 20 nautical miles. In most of the cases the transects were repeated by day and by night at less than 36 hour interval. The vessel speed varied from 7 to 10 knots, according to the weather conditions and to the vessel; the elementary sampling distance unit (ESDU) is the distance covered by the research vessel in 6 minutes.

When considering the 18 surveys as a whole, observations in 25 392 ESDUs are currently available. The initial values input in the data base were: date, time, minimum and maximum depth, total surface acoustic density index (acoustic energy) measured from the subsurface to the bottom, number of "samples" (number of emissions × number of 10 cm depth layers, which corresponds to the digital sampling frequency of AGENOR, i.e. 7.5 kHz), number of samples above a fixed threshold (usually 50 mV, but up to 100 mV during some surveys where the plankton was dense).

From this initial data three new variables were computed for each ESDU:

- The DSAT: density of samples above the threshold (Marchal, 1988) which is the mean acoustic density of the elementary samples where the density is greater than the threshold previously mentioned; here also a rough standardization was performed in order to eliminate the differences between surveys due to the different thresholds.

- The IVO (index of volume occupation) which is the ratio: samples above the threshold/total number of samples (Marchal, 1988), also standardized.

- SRTI (sun relative time interval). Twenty-five SRTI were defined, according to the times of the sunrise and sunset during the survey (no longitudinal correction was applied within each survey). These time intervals do not have the same duration (fig. 1):

- The shortest intervals last half-an-hour before and after sunset or sunrise, because the main changes of behaviour are supposed to occur during these periods (SRTI 25, SRTI 1, SRTI 13, SRTI 14);

- The longest intervals occur during the middle of the day or of the night. According to the season and the latitude, they vary between 70 and 100 minutes (SRTI 7-8 and SRTI 19–20);

- The remaining intervals are exactly one hour.

We first applied a nested analysis of variance (ANOVA) on the acoustic density index in order to study the effect of the survey, the time and their interactions. Time influence was entered in the model in two different ways: day-night period and SRTI nested within day-night.

Non-parametric tests were also used to compare the daytime and nighttime mean acoustic densities (Wilcoxon, Median and Savage scores) and their Empirical Distribution Functions (EDF) as well (Kolmogorov-Smirnov and Kuiper tests).

Then we computed the relative acoustic density Q' of each ESDU, which is in fact the ratio of the observed acoustic energy Q to its mean during the corresponding survey (this rough standardization allows for the comparison of surveys made with different equipment and different settings). Let $i=1\rightarrow M_j$ denote the number of ESDU per survey, $j=1\rightarrow 18$ the survey number. Consider the data set Q_{ij} of acoustic density observed in each ESDU. Then the relative acoustic density is:

$$Q'_{ij} = Q_{ij} \bigg/ \left(\sum_{i=1}^{M_j} (Q_{ij}/M_j) \right) \qquad (1)$$

Then we intended to normalize the Q' distributions. Following MacLennan and MacKenzie (1988) we used Box-Cox, power and log-normal transformations on nonzero data Q'_{ij}, $l=1\rightarrow N_j$. The Box-Cox transformation $Q'(\lambda) \rightarrow Z'$ is continuous at $\lambda=0$:

$$Z'_{lj} = \left(Q'^{\lambda_i}_{lj} - 1 \right)/\lambda_j \qquad \text{for} \quad \lambda_j > 0 \qquad (2)$$

We used the Box-Cox function (Box and Cox, 1964) to find the values of λ_j which provide the Z'_{lj} distribution closest to a normal distribution (computations were also made for daytime and night-
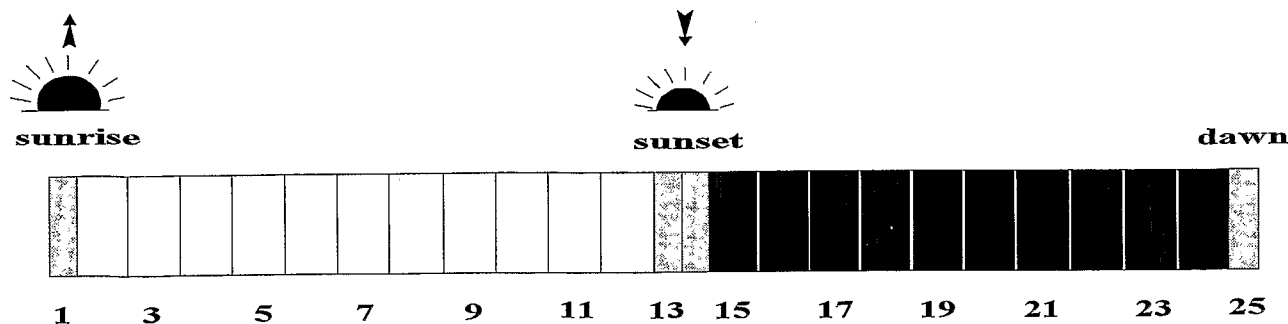

Figure 1. – Diagram of the moving boundaries of the SRTIs (sun relative time intervals).

time data separately). An alternative transformation, not continuous at $\lambda_j = 0$, is the power transformation:

$$Y'_{lj} = Q'^{\lambda_i}_{lj} \qquad \text{for } \lambda_j > 0 \qquad (3)$$

In both cases, for $\lambda_j = 0$ the transformation is $\log_e\left(Q'_{lj}\right)$, which is the usual log-normal transformation on nonzero data. The discontinuous power transformation allows for simple computations of estimators of the mean and the variance, $\widehat{Q}'_j$ and $\widehat{V}'_j$ respectively (Hoyle, 1968; MacLennan and MacKenzie, 1988). As λ_j was always lower than 0.15, estimators for sixth-root normal transformation ($\lambda = 1/6$) were only computed (the very long equation of the variance $\widehat{V}'_j$ estimate is not presented here):

$$\widehat{Q}'_j = m_j^6 + \left(15\, m_j^4\, v_j\right) + 45\, m_j^2[(N_j - 1)/(N_j + 1)]\,(v_j)^2$$

$$+ 15\,(N_j - 1)^2/[(N_j + 1)\,(N_j + 3)]\,(v_j)^3 \qquad (4)$$

where:

$$m_j = \sum_{i=1}^{N_j}\left(Y'_{lj}/N_j\right)$$

$$v_j = \sum_{i=1}^{N_j}\left(Y'_{lj} - m_j\right)^2/N_j$$

Then, in order to take account of those areas where no fish were found, we applied Pennington (1983) formulae for $\widehat{Q}''_j$, the estimate of the mean of the whole zone, and $\widehat{V}''_j$ the estimated variance of the mean:

$$\widehat{Q}''_j = \widehat{Q}'_j\, N_j/M_j \qquad (5)$$

$$\widehat{V}''_j = N_j\,(M_j - N_j)\,\widehat{Q}'^2_j/[M_j^2\,(M_j - 1)]$$

$$+ N_j\,(N_j - 1)\,\widehat{V}'_j\,[M_j\,(M_j - 1)] \qquad (6)$$

When $\lambda = 0$, the log-normal transformation modified to include observations of zeroes is named Δ-distribution. Considering the high number of ESDU (*table* 1) and the moderate proportion of zero values δ_j in the different surveys ($\delta_j < 0.1$ in most of the surveys), the formulation of the estimators can be greatly simplified (Aitchison and Brown, 1957; Owen and DeRouen, 1980). The estimate of the mean was first computed with the usual algorithm using a Bessel Function, but due to the size of our samples, the results converged to the population mean expectation:

$$\widehat{Q}''_j \cong E\,[Q''_j] = (1 - \delta_j)\exp\,[m_j + (v_j/2)] \qquad (7)$$

$$\widehat{V}''_j = \exp\,(2\,m_j + v_j)/N_j[\delta_j\,(1 - \delta_j)]$$

$$+ 0.5\,(1 - \delta_j)\left(2\,v_j + v_j^2\right) \qquad (8)$$

The Kolmogorov D statistic was computed to test the departure from normality of the transformed data. Moreover, we tried to apply other conventional
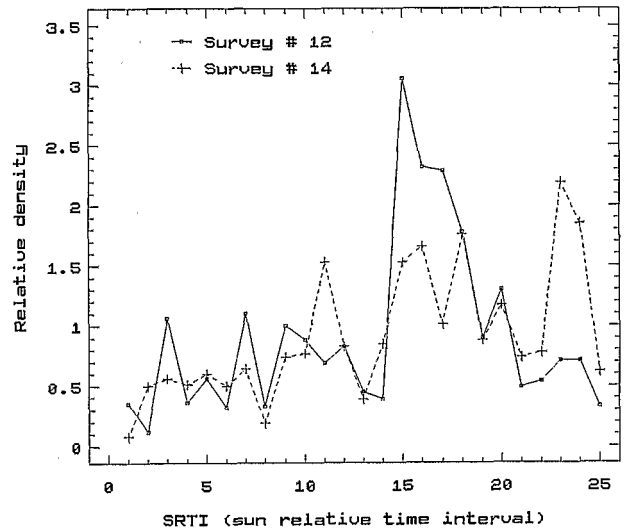

Figure 2. – Example of diurnal variation of the relative acoustic density during surveys 12 and 14 (see *table* 1) illustrating the difficulty of interpretation when considering a single survey.

distribution functions to describe extremely left-skewed distribution (complete or truncated negative binomial, beta, incomplete gamma, Weibull, Gumbel, exponential). We used both the maximum likelihood and moments methods (ALED software, pers. com. J.M. Masson; PARADIS software, G. Pichon and C. Mullon, 1992). Distribution simulations and boot-strapping on the synthetic file were also performed.

The data base does not correspond to a continuous time-series (discontinuity between surveys). We first study the autocorrelation function (AFC) of Q for each survey separately. Nevertheless, in order to study the ACF with as many diurnal cycles as possible, we built an artificial time-series of equal time intervals and without trend as follows. First we use one full hour ESDU instead of the initial 6 minute ESDU in order to eliminate the zero samples from the series (SRTI was not used owing to variable duration). Nevertheless, two surveys performed with a 100 mV threshold still contained series of zero samples appearing periodically during the day, which introduce a particular non-stationarity not suitable for the study of a diurnal cycle; these surveys where eliminated from the time-series. Second, missing observations within survey were replaced by a missing value recognized during the ACF computation. Third, in order to avoid the computation of the ACF on paired data between surveys, series of at least 72 missing values were inserted between each survey (the exact number of the missing values between adjacent surveys was fitted to maintain the 24 hours periodicity). Finally we computed Z'_{lj} transformed data as previously mentioned in equation (1) and (2). The use of relative density indices for each survey provides a global stationarity of the distribution. Nevertheless, one of the 16 remaining surveys presented a strong linear trend which was removed prior to the ACF computation.

Table 2. – Results of a nested ANOVA on the relative density index after Box-Cox transformation ($\lambda = 0.19$), using the SAS General Linear Model procedure (the sequential sum of squares is not presented but give results similar to the partial sum of squares).
Model: Density = Survey (day-night) SRTI (day-night) survey × day-night; STRI nested within day-night.

Source	DF	Partial sum of squares	Mean square	F value	$p > F$
Survey	17	227.871	13.404	143.71	0.0001
Daynight	1	114.855	114.855	1231.43	0.0001
SRTI (daynight)	23	9.410	0.409	4.36	0.0001
Survey×Daynight	17	35.924	1.937	20.76	0.0001

RESULTS

Diurnal variations of mean density estimates, DSAT and IVO

The nested ANOVA on the acoustic densities Q_{ij} (including zero data) was applied to crude data, on $\log_e (Q_{ij} + 1)$ and finally after a Box-Cox tranformation which produced an unskewed distribution of the residuals ($\lambda = 0.19$). The three results are similar and only the last one is presented because the Box-Cox transformation provides the best shape of the distribution (even though far from a normal distribution). The ANOVA indicates the survey has a strong influence for obvious reasons beyond the scope of this study (different seasons, areas, setting), and also a highly significant influence of the period of the day (table 2). The interaction between these two factors and the nested SRTI is not important although it is significant because of the large amount of data available.

Contrary to the typical example presented on figure 2 for a single survey, the relative density in the whole data base shows a more regular pattern of variation (fig. 3) in spite of the large standard deviation observed for each SRTI. Night values are around 50% higher than day values and the difference is highly significant using any of the usual simple linear rank statistics (Wilcoxon, Median and Savage scores give $p < 10^{-3}$). The two intermediate periods of fast change in acoustic density estimates, from day to night and from night to day, are rather short (around half an hour) and comparable to the mean duration of dawn and dusk at the latitude of the studied areas. The graph resulting from the 25 392 observations presents three maximum values. The first one, observed in the morning, two hours after sunrise, is very short. The second and the third ones last at least two hours, after the sunset and before dawn. When removing 0.1% of the highest values (i.e. 25 observations) the first peak disappears. When removing 1% the difference between day and night is maintained and still significant, but the minimum during the night disappears.

The mean DSAT present an inverse pattern, with highest values during the day, which is a consequence of a higher level of aggregation, confirmed by the
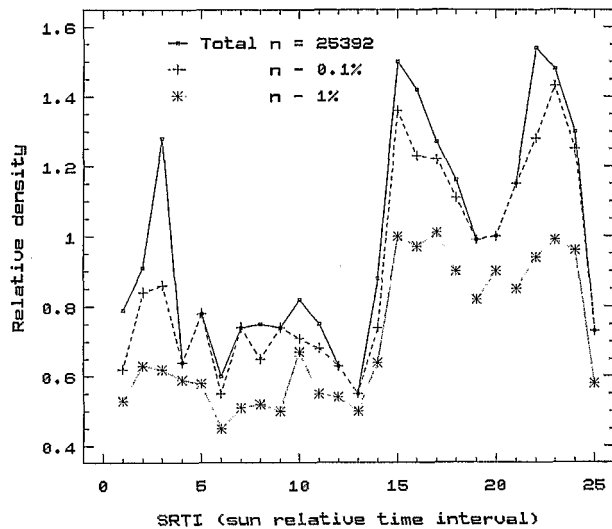
Figure 3. – Diurnal variation of the relative acoustic density in the synthetic file of 18 surveys (25 392 observations, solid line) and influence of the removal of the highest values (0.1% removed, broken line; 1% removed, dotted line).
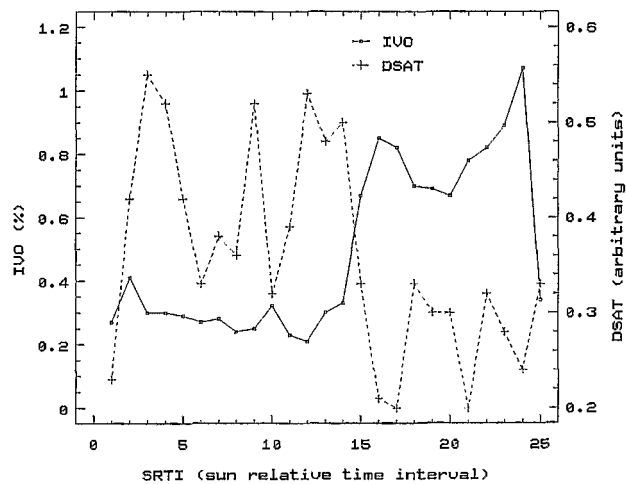

Figure 4. – Diurnal variation of the index of volume occupation (IVO, solid line) and of the density of the samples above a threshold (DSAT, doted line) in the synthetic file.

IVO pattern, which presents lower values during the day (*fig.* 4).

## Difference in day and night acoustic density distribution

In acoustic surveys, it is well known that during the day the spatial variability is higher, owing to the aggregation of fish in schools. The frequency distribution of acoustic density is therefore expected to be very different between day and night. Non-parametric tests comparing the EDF daytime and nighttime confirm this fact for the synthetic file and for any of the 18 surveys as well (Kolmogorov-Smirnov and Kuiper tests give $p{<}10^{-3}$). After logarithmic transformation, the predominance of very low values during the day is responsible for left skewed distributions in the synthetic file (*fig.* 5). This result, which is partially due to the rough method used in the standardization between surveys not having exactly the same skewness, is also found in most of the individual survey distributions. Most of the nighttime histograms look similar to a normal distribution, except for the frequency of null values, which suggests a fit to a Δ-distribution. Box-Cox transformations provide unskewed distributions with λ values ranging between 0.01 and 0.14 according to the survey and the period of the day (*fig.* 6; *table* 3). Nevertheless Kolmogorov D statistics on nonzero data always indicates a departure from normality ($p{<}0.01$).

Table 3. – Optimum values of λ_j in Box-Cox transformations on the density Q'_{ij} for the 18 surveys and for the synthetic file (total).

Survey	Day	Night	Total
1	0.02	0.01	0.03
2	0.07	0.03	0.12
3	0.08	0.02	0.08
4	0.11	0.01	0.06
5	0.06	0.04	0.12
6	0.14	0.02	0.10
7	0.03	0.02	0.02
8	0.10	0.01	0.11
9	0.05	0.01	0.05
10	0.14	0.08	0.10
11	0.05	0.02	0.07
12	0.05	0.01	0.09
13	0.05	0.01	0.01
14	0.05	0.12	0.11
15	0.08	0.10	0.10
16	0.03	0.07	0.05
17	0.08	0.07	0.08
18	0.13	0.09	0.12
Total	0.10	0.10	0.10

The attempts to fit other skewed distribution functions, performed on the synthetic file and on each individual survey as well, were generally unsuccessful, especially for day observations. The truncated negative binomial gives better results: in a few cases it was not

rejected (3/18 files; *table* 4) using the third moment method (but rejected with the other methods).
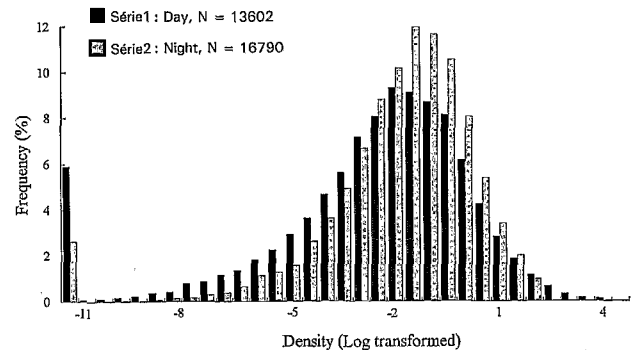
Figure 5. – Frequency distribution of the log-transformed relative acoustic densities ($\log_e (Q' + 0.00001$); synthetic file).
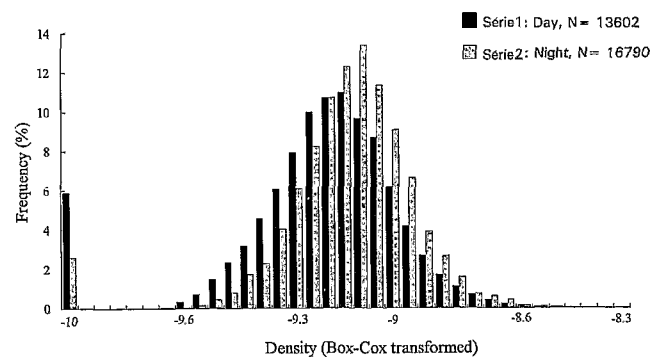
Figure 6. – Frequency distribution of the Box-Cox transformed ($\lambda = 0.1$) relative acoustic densities in the synthetic file.

In cases of strongly skewed distribution it is well known that model-independent parameters (such as the ordinary sample mean) do not give a precise estimator of the mean density (Barbieri, 1981; MacLennan and MacKenzie, 1988; Smith, 1988). A better efficiency is supposedly provided by the use of model-dependent parameters such as those presented in previous equations. Nevertheless, whereas model-independent parameters are unbiased estimators of the population mean, independent of the underlying distribution, model-dependent parameters can be biased or non-robust towards deviations from the model (Smith, 1990). Moreover, the short ESDU used means the samples are not independent of one another, which strongly limits the interpretation of the results.

In spite of these limitations, we computed the estimators of the Δ-distribution and of the sixth-root normal distribution ($\lambda = 1/6$ is the closest value to the λ mean value obtained by Box-Cox function; *table* 3). In both cases variances are very low owing to the high number of observations, but obviously underestimated because these observations are not independent. The difference between the two cases confirms the

Table 4. – Mean and standard deviation (Sd) of the sample, estimators from the Δ-distribution and the sixth-root normal transformation, and night/day ratio of the means for each survey and for the synthetic file (total). Probability (p) of the χ^2 test when fitting a truncated negative binomial distribution (TNB) using the third moment method (see text for the limitations of these results).

| Survey | Period | Sample | | | | Δ-Distribution | | | Sixth-root transformation | | | TNB |
		N	Mean	Sd	N/D	$\widehat{Q}''_j$	$\widehat{\sigma}''_j$	N/D	$\widehat{Q}''_j$	$\widehat{\sigma}''_j$	N/D	p^*
1	Day	683	1.13	4.28	–	1.20	0.15	–	0.79	0.058	–	
1	Night	287	0.69	1.65	–	0.62	0.07	–	0.61	0.051	–	<0.02
1	Total	970	1.00	3.70	0.61	1.00	0.09	0.52	0.72	0.041	0.77	
2	Day	835	0.70	1.25	–	0.87	0.08	–	0.63	0.061	–	
2	Night	794	1.31	2.07	–	1.53	0.13	–	1.25	0.093	–	
2	Total	1 629	1.00	1.73	1.87	1.19	0.08	1.76	0.96	0.060	1.97	
3	Day	438	0.73	1.56	–	0.93	0.10	–	0.52	0.025	–	
3	Night	498	1.24	3.69	–	1.19	0.09	–	1.16	0.050	–	<0.01
3	Total	936	1.00	2.91	1.71	1.11	0.08	1.28	0.82	0.027	2.24	
4	Day	905	1.03	8.01	–	1.10	0.18	–	0.43	0.035	–	
4	Night	523	0.95	3.86	–	1.10	0.21	–	1.28	0.127	–	
4	Total	1 428	1.00	6.79	0.93	1.11	0.14	1.00	0.72	0.047	3.00	
5	Day	943	0.63	1.07	–	0.70	0.04	–	0.59	0.027	–	
5	Night	802	1.43	1.86	–	1.42	0.06	–	1.40	0.049	–	
5	Total	1 745	1.00	1.54	2.25	1.16	0.05	2.03	0.97	0.030	2.37	
6	Day	384	0.68	1.19	–	1.25	0.23	–	0.65	0.045	–	<0.64
6	Night	337	1.36	2.66	–	1.43	0.15	–	1.09	0.065	–	<0.06
6	Total	721	1.00	2.04	2.00	1.64	0.19	1.14	0.88	0.040	1.67	
7	Day	1 059	0.58	1.15	–	0.71	0.05	–	0.49	0.037	–	
7	Night	993	1.45	6.85	–	1.25	0.07	–	0.60	0.057	–	
7	Total	2 052	1.00	4.86	251	1.06	0.05	1.78	0.51	0.030	1.23	
8	Day	308	0.59	1.06	–	0.67	0.08	–	0.56	0.045	–	
8	Night	385	1.33	2.48	–	1.22	0.07	–	1.23	0.065	–	
8	Total	693	1.00	2.01	2.25	1.11	0.08	1.81	0.93	0.045	2.20	
9	Day	499	0.49	1.35	–	0.90	0.15	–	0.46	0.029	–	
9	Night	352	1.72	5.06	–	1.63	0.26	–	0.69	0.036	–	
9	Total	851	1.00	3.47	3.50	1.32	0.16	1.80	0.56	0.023	1.50	
10	Day	1 796	0.87	4.46	–	2.71	0.48	–	0.60	0.033	–	
10	Night	1 628	1.14	4.76	–	1.04	0.10	–	1.30	0.088	–	
10	Total	3 424	1.00	4.61	1.32	2.09	0.21	0.38	0.88	0.038	2.17	
11	Day	516	0.65	1.33	–	0.75	0.06	–	0.29	0.025	–	
11	Night	382	1.47	4.26	–	1.50	0.14	–	1.30	0.089	–	
11	Total	898	1.00	2.98	2.25	1.07	0.07	2.00	0.75	0.043	4.41	
12	Day	643	0.51	2.38	–	0.57	0.09	–	0.47	0.037	–	
12	Night	606	1.53	4.03	–	1.33	0.12	–	1.17	0.068	–	
12	Total	1 249	1.00	3.32	3.01	1.51	0.17	2.35	0.81	0.041	2.47	
13	Day	681	0.62	1.98	–	0.99	0.16	–	0.65	0.036	–	<0.23
13	Night	624	1.41	4.36	–	1.20	0.09	–	1.28	0.074	–	
13	Total	1 305	1.00	3.36	2.27	1.59	0.16	1.21	0.92	0.037	1.96	
14	Day	765	0.64	1.69	–	1.54	0.28	–	0.46	0.038	–	
14	Night	818	1.34	3.06	–	1.98	0.22	–	1.43	0.092	–	
14	Total	1 583	1.00	2.52	2.10	2.26	0.25	1.29	0.90	0.049	3.08	
15	Day	894	1.23	4.70	–	2.10	0.38	–	0.51	0.041	–	
15	Night	865	0.77	3.28	–	1.03	0.15	–	1.22	0.076	–	<0.19
15	Total	1 759	1.00	4.07	0.62	1.49	0.17	0.49	0.87	0.044	2.37	
16	Day	838	0.92	4.53	–	1.43	0.28	–	0.78	0.064	–	
16	Night	646	1.10	3.18	–	1.64	0.25	–	0.56	0.041	–	
16	Total	1 484	1.00	4.00	1.19	1.64	0.21	1.14	0.66	0.036	0.71	
17	Day	719	0.86	3.10	–	1.35	0.23	–	0.59	0.053	–	
17	Night	689	1.14	2.60	–	1.40	0.16	–	0.93	0.074	–	
17	Total	1 408	1.00	2.87	1.32	1.46	0.15	1.04	0.73	0.043	1.58	
18	Day	696	0.58	1.61	–	1.05	0.17	–	0.68	0.063	–	<0.6
18	Night	561	1.53	3.18	–	1.89	0.19	–	1.06	0.075	–	
18	Total	1 257	1.00	2.48	2.65	2.14	0.25	1.80	0.87	0.048	1.57	
	Day	13 602	0.78	3.52	–	1.47	0.06	–	0.58	0.011	–	
Total	Night	11 790	1.26	3.93	–	1.69	0.05	–	1.11	0.018	–	
	Total	25 392	1.00	3.72	1.63	1.80	0.05	1.15	0.81	0.010	1.91	

* $p<0.00$ for the other samples.

sensitivity of the estimators to the model (*table* 4). The Δ-distribution mean estimates are usually greater than the sample means, while the sixth-root normal mean estimates are lower, especially for daytime data. The night/day ratio remains greater than 1 in the synthetic file and in the different surveys as well, even though the Δ-distribution provides night/day ratio closest to one, with remarkable exceptions (but these results do not allow a conclusion on the less unbiased estimate). A combination of the Δ-distribution (night-time data) and the sixth-root normal transformation (daytime) for some surveys, as suggested by the Box-Cox function results, leads to an increase in the night/day ratio. The pattern of the diurnal cycle by SRTI after the sixth-root transformation performed on the synthetic file (*fig.* 7) is similar to the pattern obtained without transformation and after removing the highest values (*fig.* 3).

Figure 8. – Contribution of the highest values of acoustic density in the synthetic file to the computation of the mean biomass, by day and by night (for instance, removing 4% of the highest observed densities obtained during the day reduces the mean biomass to 45% of it initial value).

Figure 7. – Diurnal variation of the estimators of the relative acoustic density in the synthetic file after sixth-root transformation. The points represent the mean expectations for each sun relative time interval (SRTI) and the vertical bars represent two standard deviations.
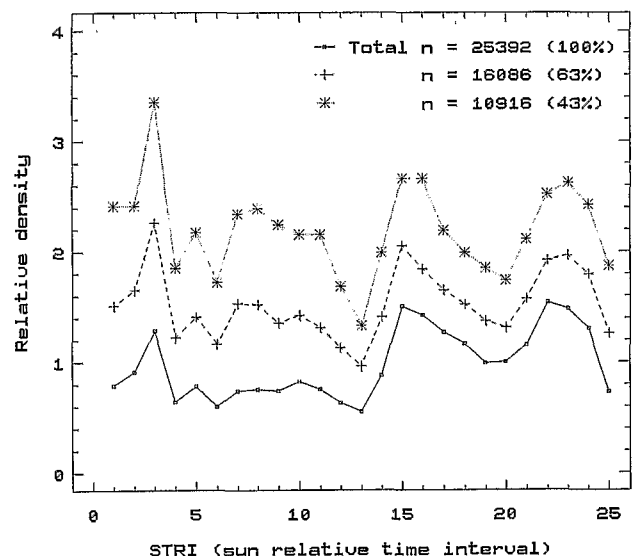
Obviously the different transformations obscure the differences in the right tail of the distribution where few values contribute significantly to the mean estimation: when removing 0.5% of the highest values (i.e. 126 observations), the estimation of the mean is reduced by 24% during the day and only by 15% during the night (*fig.* 8). But it is worth noting that this difference of 9% between day and night remains more or less constant when a higher percentage of highest values is removed, and it never reaches the difference of 50% observed for the total averages. On the contrary, when the lowest values are removed (*fig.* 9), the day/night difference disappears progressively: it is no longer significant when only the values ≥0.3 (43% of the data set) are considered.

Autocorrelation function

The AFC performed on each survey separately indicated in most of the surveys significant positive

Figure 9. – Diurnal variation of the relative acoustic density in the synthetic file (solid line) and influence of the removal of the lowest values: values lower than 0.3 (63%) removed, broken line; values lower than 0.1 (43%) removed, dotted line.

coefficients ($p<0.05$) for lags of one or two hours, and a diurnal cycle of 24 hours which was never significant. The same analysis performed on the artificial time-series of 16 surveys shows a clear diurnal cycle with some significant coefficients up to 59 lags (*fig.* 10) and a slight trend which can be explained by the contagious distribution of the fish within surveys (note that the surveys were separated by at least 72 missing values).
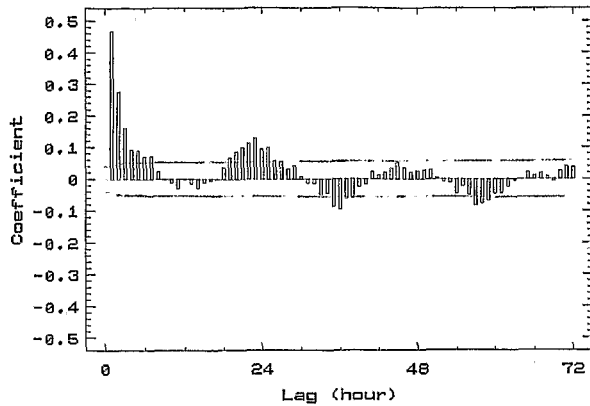
Figure 10. – Autocorrelation function of the relative acoustic density by hour in artificial time series of 16 surveys (see text for details on the construction of this file).

DISCUSSION

Difference between day and night mean density estimates

The lower acoustic density observed during the day is probably primarily due to lateral avoidance by near-surface schools during that period; however, other factors (*table* 5) may be important and are briefly reviewed.

The lateral avoidance occurs mainly during the day when the fish school, and is more important for surface schools (Olsen, 1971; Aglen, 1985; Diner and Massé, 1987; Goncharov *et al.*, 1989; Misund and Aglen, 1992). These last two authors, using a multibeam sonar, estimate that 16 to 41% of the schools avoided the vessel, according to the fish length. During the night it seems that the lateral avoidance is negligible when the vessel is not lit (Gerlotto *et al.*, 1989; Lévénez *et al.*, 1990; Nunnallee, 1991). This difference in behaviour could be the main reason for the low

Table 5. – Tentative classification of the relative importance of biases in biomass estimations by day and by night in tropical areas.

Factors	Over-estimation by night	Underestimation by day	by night
Dense plankton layers	♦		
Acoustic shadow		♦	
Horizontal migration		♦	
Lateral avoidance		♦♦♦	
Vertical avoidance and mean tilt angle		♦♦?	
Variation in swimbladder volume		♦	
Vertical migration and:			
Bottom blind aera	♦		
Sub-surface blind aera			♦
Tilt angle variability			♦
Vessel light			♦
Density distribution function		♦♦♦?	♦♦?

day/night ratio observed in our data. Concerning the avoidance reaction depending on the time of the day, Nephroshin (1979) and Diner and Massé (1987) find significant changes. The apparent changes in acoustic density observed in our study during the day show a pattern which is different from the results mentioned in these two studies (which are not similar to one other). Nevertheless, in our observations the high morning value is caused by a few high values (among which three are adjacent observations) in two surveys. Therefore interpretation of this pattern during the day is in question until more data are available.

Concerning the acoustic shadow, the occurrence of very dense schools in tropical areas is very low (excepting those of anchovies) unlike the high density of herring in temperate areas. Simmonds *et al.* (1992) estimated that the bias due to shadowing was lower than 2% in Venezuela on a whole survey.

A reduction of effective equivalent beam angle might be caused by thresholding of scattered fish distributions and therefore lead to an underestimation of density during the night when using low performance systems (Aglen, 1983). In our cases, where most of the biomass is located above 50 m depth, this bias is minor.

Horizontal migration bias (i.e. migration out of the survey area) may be important in some limited areas (e.g. Gulf of Cariaco in Venezuela) but these areas represent less than 10% of the total surveyed area.

Concerning the vertical fish avoidance, Gerlotto and Fréon (1992) estimated that in Venezuela this behaviour is limited to sub-surface schools, which dive systematically before the vessel passes above them and reach a depth around 5 m greater than the initial one. In this case, the acoustic density underestimation owing to the variation of the tilt angle and the swimbladder volume reduction during this avoidance should be insignificant.

As the demersal biomass in our studied ecosystem never exceeds 25% of total biomass and as most of it is available both in the day and at night, the bias on the day/night ratio related to the demersal biomass upward migration and to their diurnal swimbladder volume change should be relatively low.

Assuming that the whole biomass is closer to the surface during the night than during the day, but that the height of sub-surface blind area is low (4 to 5.5 metres), the bias owing to this volume could be responsible for about 10% on the day/night difference.

The day/night ratio observed could theoretically be explained by a 2.2 dB difference in TS. Using a 120 kHz sounder, a 10° difference between day and night mean tilt angle could lead to such a difference in TS. However, the high variability of the tilt angle during the night is probably limited to deep schools because the shallower fish are probably in polarized position, alerted by night as well as by day, due to the noise of the vessel passing over the school (Gerlotto

and Fréon, 1990). Once more in our case the superficial location of most of the biomass favours a limited bias.

Finally, concerning the light on the vessel, as most of the surveys were done with minimum lighting, it can be supposed that in our cases this bias is limited. Moonlight probably interacts with solar light in the aggregative behaviour of fish, but as the moon cycle is around 28 days, it was considered that the data base currently available was not large enough to study it, even though we verified that the variation of the lunar light intensity hardly explains the variation of acoustic density observed during the night.

Difference between day and night acoustic density distribution

Even though dense schools have been observed during the night in some situations (Woodhead, 1966;

Blaxter and Hunter, 1982), including moonless nights (Fréon *et al.*, 1989), the histogram of density by ESDU is usually expected to be much more skewed to the left in the day than at night. Surprisingly our results do not show such a large difference in the right tail of the distribution, which in both cases (day and night) is strongly skewed, providing a high contribution of the greatest values to the mean. This pattern reflects a high level of patchiness during the night. The EDF is strongly dependent on the size of the ESDU, which in our case is much larger than the size of the schools (but smaller than a concentration of schools). Therefore, it is likely that most of the contraction/expansion of the fish, from dispersed (or in shoal) during the night to school during the day and vice versa, occurs mainly within ESDUs. As the difference in mean acoustic density between day and night is mainly due to the difference in the lowest abundance values, this
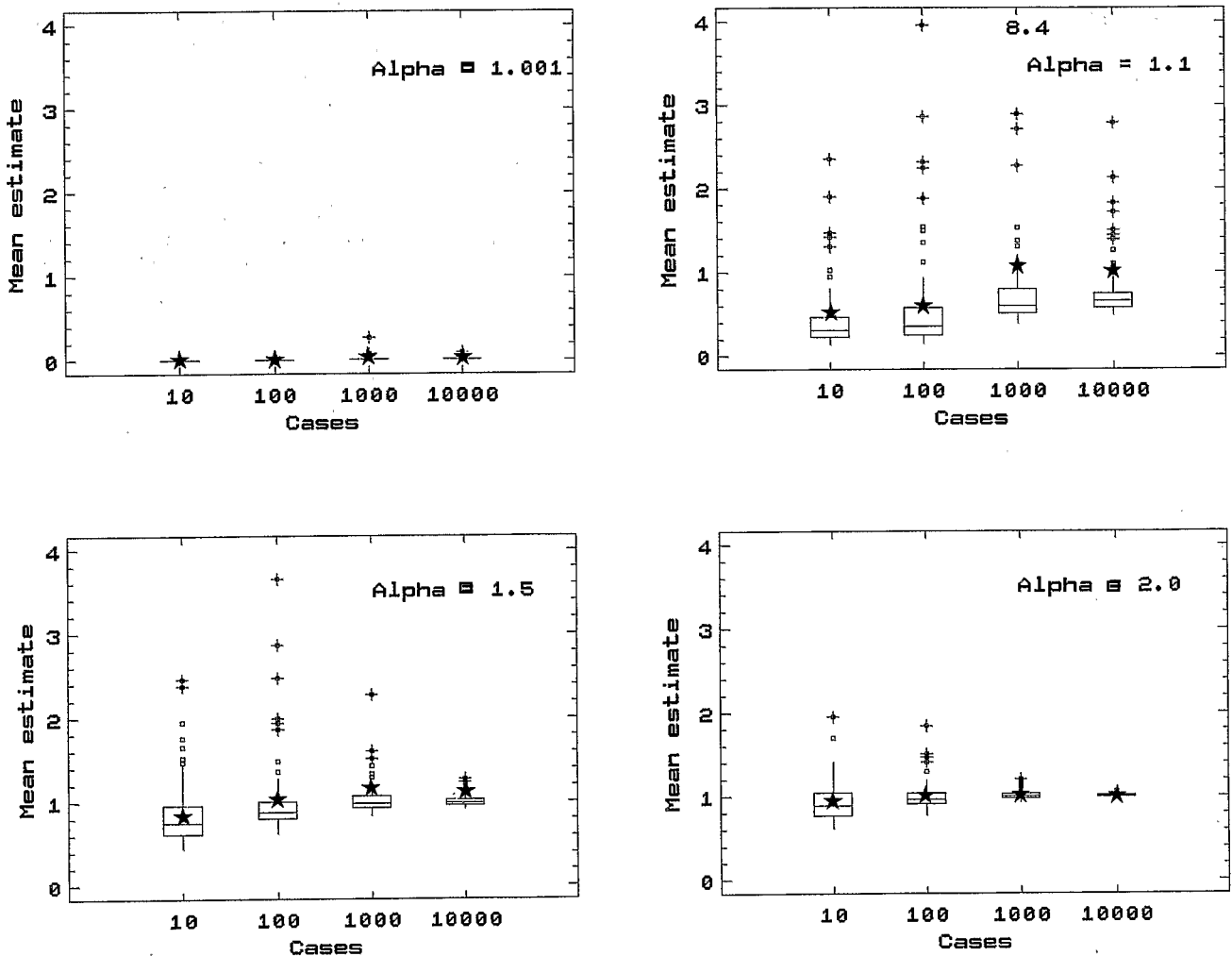
Figure 11. — Simulations of Pareto distributions and difficulty of applications of the Central Limit Theorem: influence of the alpha value and of the number of cases on the mean estimation; note the low convergence to the theoretical mean (= 1) and the resulting bias when alpha <1.1, even when the sample size is large (on these Box-and-Whisker plots the central box covers the middle 50% of the data values, the "whiskers" extend to those points that are within the 1.5 time the interquartile range and other points are outliers; the central line is at the median and the star is at the mean).

suggests either an overestimation of the number of "empty" ESDU during the day (for instance higher avoidance of small schools or low availability of demersal fish) or an underestimation of this kind of ESDU during the night (integration of plankton for instance).

Nevertheless, another interpretation of the day/night ratio is possible: the right tail of the distribution in the population could be different in the day and at night, and our results could reflect an under-sampling of the highest values by day (Anonymous, 1992). In such a case the present difference in the left half of the distribution might be due to a diffusion of the biomass during the night on a larger surface than in the previous hypothesis (over one $ESDU^2$). The applicability of this last hypothesis is limited by the short duration (around half-an-hour) of the expansion and contraction phenomena around dusk and dawn; even though it has nothing to do with the flash expansion or contraction observed in tank (Radakov, 1973) it cannot allow long horizontal migrations.

The Pareto distribution of density studied by Levy (1925) for extremely skewed distributions present interesting properties. The density function $f(x)$ is:

$$f(x) = 0 \quad \text{if } x < \beta \quad \text{or} \quad \beta^\alpha \alpha x^{-\alpha-1} \quad \text{if } x \geq \beta \quad (9)$$

The distribution function is:

$$F(x) = 1 - (x/\beta)^{-\alpha} \quad (10)$$

The first moment is:

$$M(x) = \beta [\alpha/(\alpha - 1)] \quad \text{if} \quad \alpha > 1 \quad (11)$$

The second moment is:

$$V(x) = \beta^2 [\alpha/((\alpha - 1)^2 (\alpha - 2))] \quad \text{if} \quad \alpha > 2 \quad (12)$$

According to the value of its shape parameter α the expectation of mean may theoretically be:

- impossible to estimate $(\alpha < 1)$;
- possible to estimate but with an infinite variance $(1 < \alpha < 2)$;
- possible to estimate with a large $(2 < \alpha < 2.5)$ or reasonable variance $(\alpha > 2.5)$.

According to the Central Limit Theorem, the distribution of the sample mean should tend asymptotically toward normality. Some simulations of the Pareto distributions clearly show that when $\alpha > 1.1$ the computation of the sample mean underestimates the population mean in most of the trials, especially when the number of observations is low (cases $< 1\,000$; fig. 11) but few large values occasionally sampled make the expectation of the mean be the population mean (equal to 1 in our figures). At the opposite, when $\alpha < 1.1$, the convergence of the sample mean to the population mean does not appear in the range of the simulated number of cases. In these particular situations the convergence is very slow because the

probability of sampling the highest values is extremely low. Therefore it can be considered that the Central Limit Theorem hardly applies. We compared the distributions of sample mean given in figure 11 to the distribution obtained from bootstrap on the synthetic file (same number of cases drawn independently with replacement). The figures are comparable to the simulation of Pareto distribution when $1.5 < \alpha < 2$. Nevertheless, it is difficult to draw any definitive conclusion from such a result because it is not sure that the synthetic file, in spite of its large size, gives an unbiased image of the population distribution.

The fitting of the Pareto distribution is made using the theoretical linearity of $F(x)$ after logarithmic transformation $(\log_e(1 - F(x)) = \log_e \beta - \alpha \log_e x)$. These fittings are far from perfect (fig. 12) owing to a curvature of the values which suggests that the distribution is right truncated. This can be easily supported by biological considerations in so far as the maximum fish density has a finite value which can be estimated. The values of β are always greater than zero which forces one to eliminate a substantial part of the lowest values from the fit (but these values do not contribute very much to the mean). The values of α are highly variable (from 0.8 to 1.6) according to the survey and the hour of the day (lowest values during the day). The synthetic file provides the following values of α: day 1.28; night 1.37; total 1.41. However, corresponding values of the mean biomass estimate are unlikely: day 24.8; night 10.6; total 11.2, which once more illustrates the risk of using a wrong by estimated model to estimate the population mean.

The key question is whether the Pareto distribution, or some other heavy tailed distribution, is really suitable for our data. This law is based on the assumption that for logarithmic classes the frequency of class i is proportional to the frequency of class i-1. In our case that would mean that the spatial distribution presents some remarkable characteristics which might
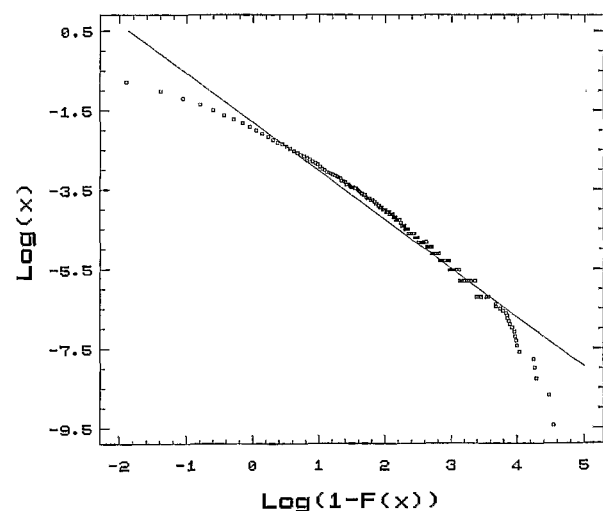

Figure 12. – Fitting of Pareto distribution on the day data of the synthetic file.

strongly structure the statistical distribution of the values. This hypothesis must be confirmed: some preliminary observations made in Venezuela suggest a transitional distribution of the biomass (Fréon *et al.*, 1989), but an opposite conclusion is drawn from temperate areas (Petitgas, 1993). The complexity of actual fish communities is probably another limitation on the inference from a distribution law. Further studies are required on the application of such distribution functions (truncation, influence of the number of class intervals, other functions, etc.). Special attention must be paid to the influence of the ESDU size. An interesting alternative consists in using a routine integration school by school in order to study the school weight distribution. Preliminary results (Scalabrin *et al.*, 1992) indicate an extreme skewness of the school energy distribution (which is usually proportional to the weight), higher than observed in ESDU. At the present stage of our study, the possibility of a difference between the day and night biases due to the distribution cannot be excluded. Aglen (1989) showed that variability in acoustic survey estimates decreases with increasing degree of coverage. Nevertheless his distribution of relative density estimates corresponding to a high degree of coverage still indicates a slight skewness.

Tentative estimation of predominant factors

From these factors of biases listed in *table* 5 it is not easy to decide which factors are predominant and explain our results. Nevertheless some factors have probably a lower influence, especially those decreasing the acoustic density during the night (*table* 5). If not, it would be necessary to admit that in compensation most of the day factors are playing a dominant role, in order to explain the 0.6 day/night ratio. Nevertheless some night factors are necessarily playing a role in our data set, as for instance the sub-surface blind area.

Among the day biases, the lateral avoidance reaction of the schools and the changes in density distribution are probably the most important factors, followed by the bottom blind area. The influence of variation in swimbladder volume is controversial and difficult to estimate from our results.

CONCLUSION

In many countries (temperate and tropical as well), long data series concerning a single stock regularly surveyed at the same season are available. Instead of using a synthetic file of heterogeneous data sets as in the present study, it could be interesting to analyse those homogeneous data from a single area in order to study the occurrence of such diurnal cycles which could be different according to the species, to the biotope and to the season. A lower variability can be expected in such cases, and a proper day/night coefficient estimation could be calculated.

As far as tropical pelagic fish are concerned, it does not seem reasonable to estimate the biomass only from day observations. Using both day and night observations may be controversial, because the variability of any correction factor based on time is very high. It is suggested to use the night values from half-an-hour after sunset to half-an-hour before sunrise in tropical countries (in northern countries where dawn and dusk are longer the definition of the "night-time" should be even more restrictive). This recommendation does not necessarily apply in other areas where day sampling are the only solution (Massé, 1988).

Nevertheless, day observations are often of great interest to collect: they may represent the fraction of the biomass which is accessible to the fishing gear. The daily fluctuation and its mapping is of prime interest. Mixed techniques, using both vertical sounder and single beam or multi-beam sonar, have already been proposed (Lamboeuf *et al.*, 1983). Up to now these techniques have not given practical results, but recent advances in technology may change this status (Misund *et al.*, 1990).

Even though the Pareto distribution we used is not convenient for our data, this study also raises the problem of sample size and the related possible difficulty in applying the Central Limit Theorem because the asymptotic convergence to the mean is very slow. Consequently there might be a risk of systematic underestimation of the biomass by day, and to a lesser extent by night. The application of heavy tailed distribution could be interesting approach but it needs further analyses. Concerning the Pareto distribution, at present it can be stated only that on the one hand the value of alpha depends on the spatial distribution and on the survey design: stratification and probably length of the elementary sampling unit (not studied here), on the other hand its does not fit very well with the highest values observed, which are lower than expected. Further studies on the relationships between the distribution function and the geographical distribution are required (Petitgas, 1993).

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