CAN STOCHASTIC VARIATIONS IN RECRUITMENT INDUCE LONG-TERM FLUCTUATIONS IN THE CARRYING CAPACITY?

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SUMMARY

Long-term fluctuations in fish abundance are generally attributed to low frequency processes, such as human exploitation and/or environmental and climatic changes. Based on recent studies and simple simulations, this manuscript shows how long-term fluctuations in the carrying capacity and/or spawning stock biomass of a long-live species, such as the Atlantic bluefin tuna, may simply arise from stochastic variations in the recruitment. The implications of such a feature are discussed and compared among different Atlantic tunas and tuna-like species.

RÉSUMÉ

On invoque communément des processus 'basse fréquence', tels que l'exploitation humaine ou les changements climatiques et environnementaux, pour expliquer les fluctuations à long terme des abondances de poisson. A partir de récents travaux et de modèles de simulation, ce manuscrit montre que les fluctuations à long terme de la capacité de charge et/ou du stock reproducteur d'une espèce à vie longue, telle que le thon rouge atlantique, peut simplement résulter de variations stochastiques du recrutement. Les implications d'un tel processus sont discutées et comparées entre différentes espèces de thonidés.

RESUMEN

Las fluctuaciones a largo plazo en la abundancia de peces suelen atribuirse generalmente a procesos de baja frecuencia, como la explotación humana o los cambios climáticos y medioambientales. Basándose en estudios recientes y simulaciones simples, este documento muestra que las fluctuaciones a largo plazo de la capacidad de transporte y/o de la biomasa del stock reproductor de una especie longeva, como el atún rojo del Atlántico, pueden producirse por variaciones estocásticas del reclutamiento. También se estudia y se realiza una comparación de las implicaciones de dicho proceso en las diferentes especies de túnidos y en especies afines.

KEYWORDS

Long-term fluctuations, recruitment, Atlantic tunas, stochastic variations, life history, lifespan, spawning stock biomass

INTRODUCTION

Long-term fluctuations in fish abundance are generally related to low frequency signals in: (i) human exploitation (e.g. Myers et al. 1996), (ii) environmental and climatic factors (e.g. Cushing 1982, Cushing and Dickson 1976, Dickson and Brander 1993, Ottersen and Sundby 1995), or (iii) in both components (O'Brien et al. 2000). Human exploitation obviously induces a depletion in the spawning stock biomass (SSB), that could, in the most extreme situations, lead to recruitment overfishing (Myers and Barrowman 1996). The SSB of an exploited stock is expected to decline more or less gradually as the exploitation increases, but the relationships between both is often complex and non linear. Since Hjort (1914), it is generally accepted that environmental factors mainly affect fish abundance through variations in recruitment, through: (i) sea temperature, which influences the daily

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development and mortality of the eggs and fish larvae (Pepin 1991) and (ii) the food availability, i.e., the match-mismatch hypothesis (e.g. Cushing 1969, May 1974, Wooster and Bailey 1989) and/or the impact of the wind and current at a large scale (the dispersal of the eggs and fish larvae e.g. Hjort 1926, Lasker 1975) and at a small scale (the turbulence which plays a role on the prey encounter rates, (e.g. MacKenzie and Leggett 1991). When long-term fluctuations in fish abundance are observed and suspected to be fishery-independent, long-term variations or regime shift in recruitment resulting from environmental changes are generally advocated.

However, recent studies have shown that the causes of long-term fluctuations are more complex than previously expected and could be related to high frequency signals. Biotic processes, such as predation, cannibalism and competition resulting from food and habitat limitations, are known to generate cycles in natural fish populations (Caley et al. 1996, Fromentin et al. 2000a), but such processes can also induce long-term fluctuations when noise in the recruitment also occurs (Bjørnstad et al. 1999). Stochastic variations in recruitment are actually sufficient to generate long-term pseudo-cyclic fluctuations in the SSB and the yields (Fromentin and Fonteneau 2001); a feature already stressed by Horwood (1984) two decades ago. Using simple simulations, the purpose of this manuscript is to describe this feature, which is likely to be important for several Atlantic tunas and tuna-like species.

EFFECTS OF SHORT-TERM VARIATIONS IN RECRUITMENT ON SSB

Let's consider the classical equation of population dynamics:

$$N_{a,t} = N_{a-1,t-1} \, e^{-Zt} \tag{1}$$

where, $N_{a,t}$ is the number of fish of age (a) at time (t), and Z the total mortality from age (a-1) to age (a). Z = M+F, with M being the natural mortality and, F the fishing mortality. Let's assume that no density-dependence mortality will occur during the life cycle, but that stochastic variations in the recruitment occur because of changes in the environmental conditions and/or predation (Cushing 1982, May 1974). For simplicity, we won't consider variations in mortality at older ages, neither variations in growth and reproduction. Without fishing mortality, the survival of age 1 at time t may be written as:

$$N_{1,t} = N_{0,t-1} \, e^{-m_0 + e_t} \tag{2}$$

where m_0 is the average natural mortality at age 0, and, e_t, the random noise component being normally distributed, with m=0 and σ=1 and describing stochastic variations in recruitment (e_t could be also Gamma distributed without affecting the results). Considering equation (1) and (2), the survival of age 2 may be written as:

$$N_{2,t} = N_{0,t-2} \, e^{-m_0 - m_1 + e_{t-1}} \tag{3}$$

where m_1 is the average natural mortality at age 1. In the same way, the survival of age 10, for instance, may be written as:

$$N_{10,t} = N_{0,t-10} \, e^{-m_0 - m_1 - \ldots - m_9 + e_{t-9}} \tag{4}$$

In that case, $N_{1,t}$ $N_{2,t}$,…, $N_{10,t}$ lead to time series displaying all white noise and being normally distributed. However, the spawning stock biomass at time t, SSB_t, of a long live species will include various age-classes. Considering, for instance, the East Atlantic and Mediterranean bluefin tuna, which matures at around 4.5 years old and lives until 20 years (Mather et al. 1995), the SSB will include 16 different year-classes and it could be written as:

$$SSB_t = N_{0,t-5} \, e^{-m_0 - \ldots m_4 + \mathbf{e}_{t-4}} + N_{0,t-6} \, e^{-m_0 - \ldots m_5 + \mathbf{e}_{t-5}} + \ldots\ldots + N_{0,t-20} \, e^{-m_0 - \ldots m_{19} + \mathbf{e}_{t-19}} \quad (6)$$

SSB_t will, thus, include a sum of the noise components: e^{et-4}, e^{et-5}, $\ldots e^{et-19}$. Consequently SSB_{t+1} will include the sum of: e^{et-4+1}, e^{et-5+1}, $\ldots e^{et-19+1}$, i.e., e^{et-3}, e^{et-4}, $\ldots e^{et-18}$, so that the SSB time series is similar, in its principle, to a moving average, with a window being equal to the number of year-classes in the SSB. As all the smoothing methods, the moving average alters high frequencies into low frequencies; this modification being proportional to the size of the window (larger the window, more important the smoothing).

To illustrate this, let's take a series of 1000 random numbers, being normally distributed, $N(0,1)$ (Fig. 1a). As expected for white noise, the associated spectrum displays all types of frequency, from low to high, with an equal probability (Fig. 1b). Computing a moving sum on 5 consecutive values of the white noise time series lead to Fig. 1c and its associated spectrum, which is already dominated by a low frequency signal (Fig. 1d). With a larger window (a moving sum over 15 and 25 terms), the time series display clear pseudo-cyclic fluctuations, that are different from simple random variations (Fig. 1e,f). Their associated spectra only display low frequencies (i.e., long-term fluctuations > 50 yr).

Using a simple simulation model, Fromentin and Fonteneau (2001) have shown that this process is sufficient to induce long-term fluctuations in SSB and consequently in the yields of a long live species, such as the Atlantic bluefin tuna (Fig. 2). The SSB and yields of a short live species, such as skipjack, do not, however, display such long-term fluctuations, although the same level of noise has been introduced in its recruitment (Fig. 2). This simply results from the low number of age-classes that constitute skipjack spawning stock (skipjack matures at around 1.5 years and live until 5 years, Fromentin and Fonteneau op. cit.).

Theoretically, stochastic variations in recruitment are, thus, sufficient to induce long-term pseudo-cyclic variations in the SSB and in the yields. This feature is of particular interest regarding the historical data of the East Atlantic and Mediterranean bluefin tuna trap fisheries. Fluctuations in trap catches have been analysed and appear synchronous between locations being far apart, so that they may be considered as a good proxy of those in population abundance (Fromentin et al. 2000b). These fluctuations are largely dominated by a low frequency signal (the long-term fluctuations representing about 66% of the total variance of the time series), which is clearly displayed by the spectral analyses (Fig. 3). Human exploitation, that was largely dominated by trap (a passive gear), from the Middle-Age to the mid-XXth century, is unlikely to induce such secular pseudo-cyclic variations (see e.g., the Formica time series in Fig. 3). However, variations in environmental conditions and/or biotic processes are better candidates to explain such a pattern.

It now remains to understand whether environmental and/or biotic factors could have induced long-term variations in the East Atlantic bluefin tuna through (i) stochastic variations in recruitment (which is probable according to the recruitment strategy of this species: yearly spawning in a few spatially restricted areas, Mather et al. 1995) or through, (ii) long-term changes in recruitment (due to regime shift) or in population abundance (because of an alteration of the migration patterns, see e.g., the case of the West Greenland cod stock, Dickson and Brander 1993).

CONCLUSION

The purpose of this manuscript was to point out that long-term fluctuations in the spawning stock biomass of long live species can simply result from stochastic variations in the recruitment. For the Atlantic tunas and tuna-like species, this process is more likely for temperate and sub-tropical species displaying a recruitment being rather limited both in time and space, such as bluefin tuna, swordfish and secondarily albacore and bigeye tuna. It is less probable for typical tropical tunas, such as yellowfin tuna, for which recruitment occurs over a long period and a large area (the tropical waters being, furthermore assumed, to be more stable).

One may, thus, argue that stochastic variations in recruitment cannot explain long-term fluctuations in a given year-class, especially in a juvenile year-class. However, asymmetric interactions between cohorts due to cannibalism, can resonate stochastic variations in reproduction or recruitment and also generate long-term fluctuations within a single year-class (see e.g., the case of the Norwegian Skagerrak cod stock, Bjørnstad et al. 1999). The extrinsic or intrinsic processes inducing long-term fluctuations in population abundance appear, thus, more complex than generally assumed. Therefore, their study often implies more than simple correlation or regression analyses (the results of these useful exploratory tools being, furthermore, often biased because of autocorrelation or multiple testing, see e.g., Legendre and Legendre 1998), and can necessitate a careful population model.

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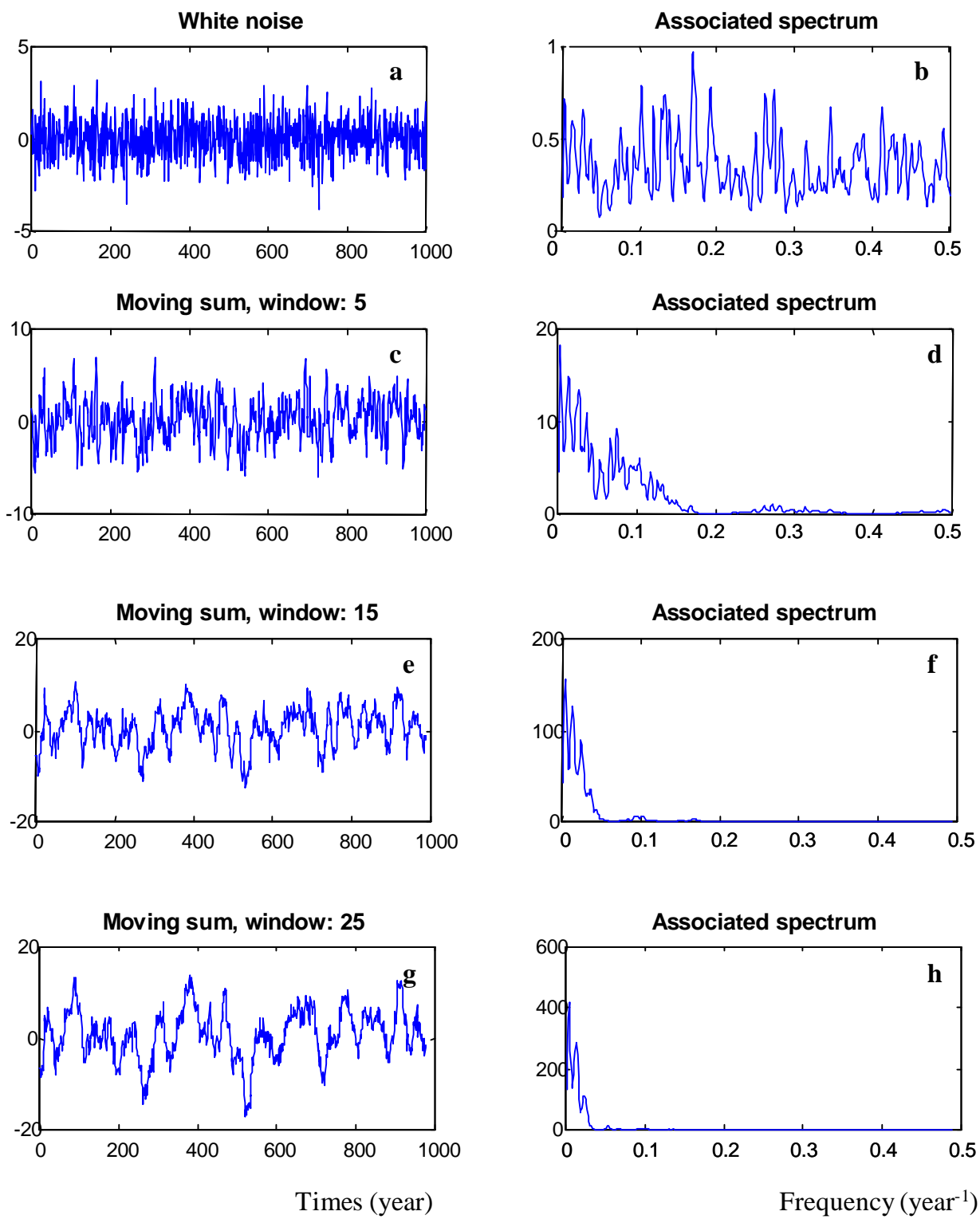
Figure 1. Series of 1000 random numbers, being normally distributed, *N* (0,1): 1a and its associated spectrum: 1b. Series including a moving sum on 5 consecutive values of the white noise time series: 1c and its associated spectrum: 1d. 1e, 1f, 1g and 1h, same as 1e and 1f but with a moving sum over 15 and 25 terms, respectively.
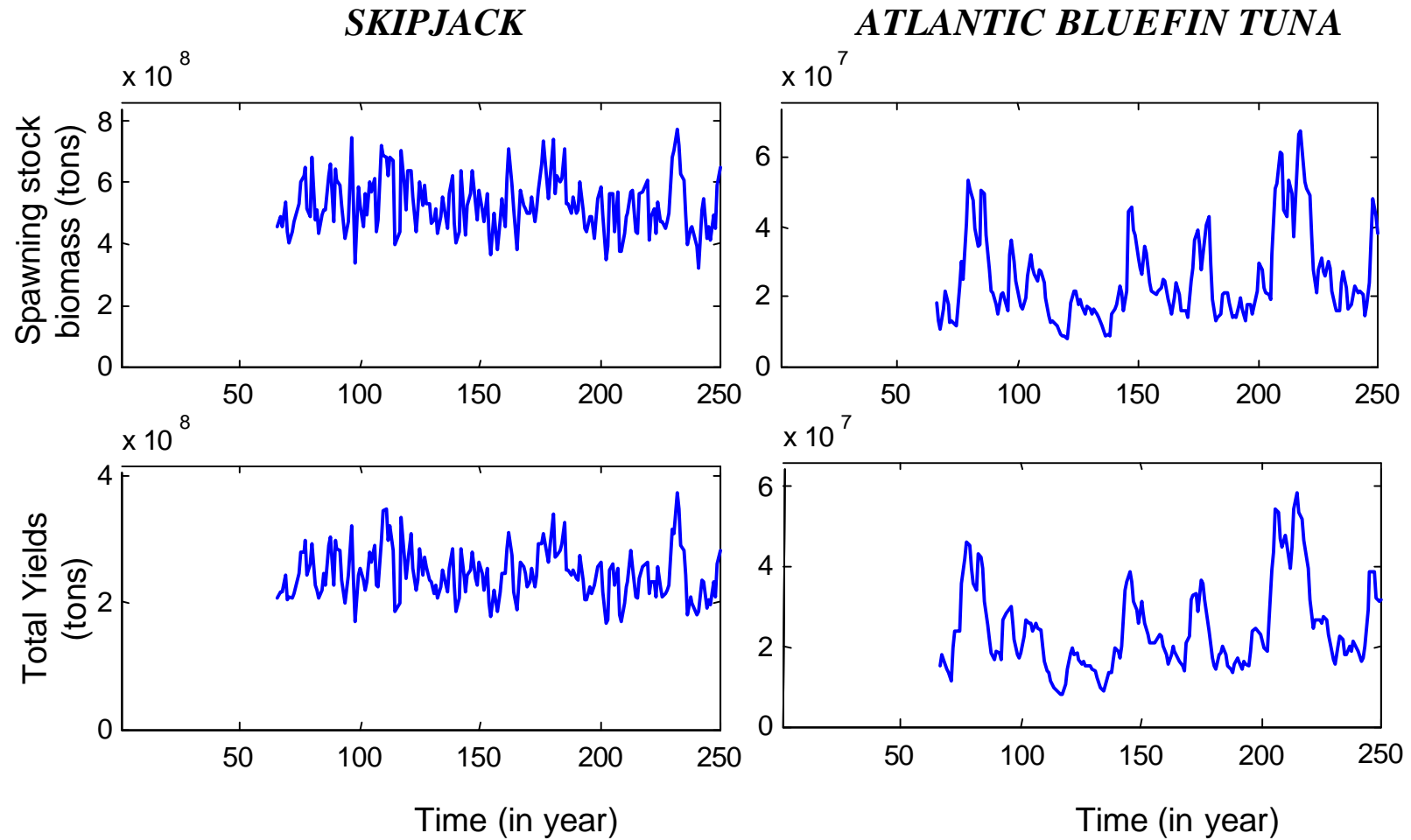
Figure 2. Top plots: simulated time series over 200 years of the spawning stock biomass of skipjack (left) and bluefin tuna (right), according to a same, constant and moderate fishing scenario. Bottom plots: same for yields.
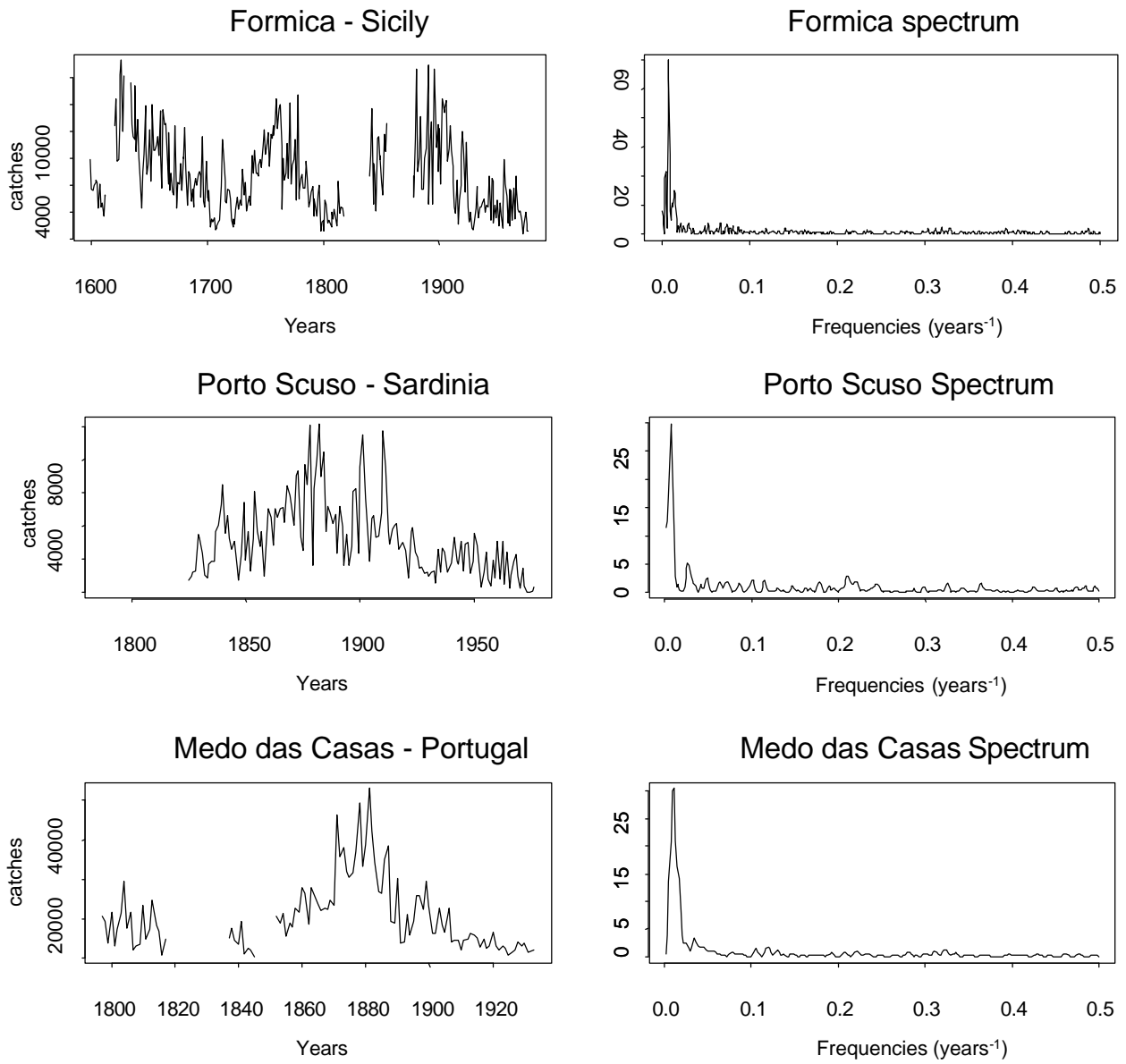
Figure 3. Right plots: long-term catches (in number of fish) of three bluefin tuna traps, operating between 1599 and 1950. Left panels: Associated spectral densities, as estimated by spectral analysis.