

Long-term fluctuations in the eastern Atlantic and Mediterranean bluefin tuna population

Christelle Ravier and Jean-Marc Fromentin



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Long-term time-series of bluefin tuna catches from ancestral Mediterranean and Atlantic trap fisheries are presented and analysed. The trap is a passive gear, little modified for centuries, that catches bluefin tuna *Thunnus thynnus* during their annual spawning migration. These features, together with preliminary analyses, lead us to suggest that long-term fluctuations in trap catches could reflect those in true abundance if they vary in the same manner all around the western Mediterranean and adjacent Atlantic. To test this hypothesis, we investigated 54 time-series more than 20 years long (the longest ones spanning four centuries) of trap catches along the western Mediterranean coasts of Italy, Sicily, Sardinia, Tunisia, Spain, and Morocco, and the adjacent Atlantic coasts of Spain, Portugal, and Morocco. Trends and cycles were identified using Eigen Vector Filtering and spectral analysis, and the synchrony between short- and long-term fluctuations in trap catches was studied with the modified correlogram of Koenig and Knops. The magnitude of fluctuations in trap catches is large, periods of great abundance being up to seven times bigger than those when abundance was low. More interesting was the occurrence of 100-year-long periodic fluctuations as well as 20-year cycles. These medium- to long-term fluctuations, representing more than 50% of the total variability in the time-series, were synchronous all around the western Mediterranean and adjacent North Atlantic. In contrast, short-term variability was synchronous at a local scale only. It is argued that long-term fluctuations in trap catches could be considered as a proxy for those of true abundance, and a synthetic time-series has been computed to depict them. Biological and ecological processes that could cause such long-term fluctuations are also discussed.

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Keywords: periodic fluctuations, *Thunnus thynnus*, time-series, trap fishery, trend.

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Introduction

Fluctuations in fish stock sizes are often ascribed to human exploitation, probably because most studies focus on highly exploited populations (such as the North Atlantic cod *Gadus morhua* stocks) and over relatively short time periods (<50 years, e.g. Garrod and Schumacher, 1994; Hutchings, 1996; Myers *et al.*, 1996; Cook *et al.*, 1997). However, at the beginning of this century, Hjort (1914, 1926) suggested that stochastic processes during the recruitment period could also induce natural fluctuations in stock size. A scarcity of long time-series has probably limited research on this issue, but the number of studies linking long-term

fluctuations in fish populations to variations in environmental conditions (Cushing and Dickson, 1976; Cushing, 1982; Southward *et al.*, 1988; Dickson and Brander, 1993; Fromentin *et al.*, 1998) or to changes in biotic processes (May, 1974; Myers and Cadigan, 1993; Fortier and Villeneuve, 1996; Fromentin *et al.*, 2001) is not negligible.

In this paper, we consider several centuries of catches of bluefin tuna *Thunnus thynnus* (Linné 1758) by trap fisheries, an ancestral Mediterranean fishing technique (Doumenge, 1998). These long-term time-series could help in describing bluefin tuna population dynamics if fluctuations in catches can be considered a good proxy of true abundance. Eastern Atlantic bluefin tuna are

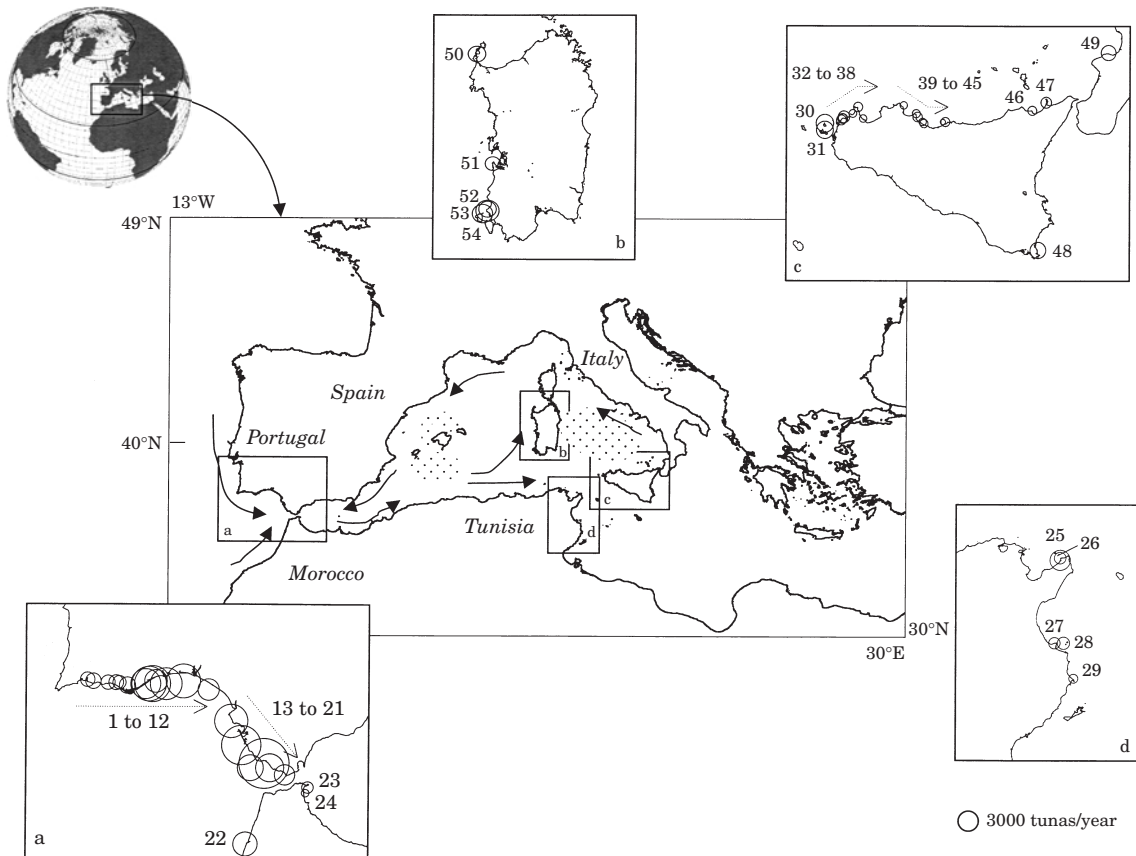


Figure 1. Map of the western Mediterranean and adjacent North Atlantic. Arrows indicate spawning migration routes of eastern Atlantic bluefin tuna and stippled areas its two known main spawning sites, around the Balearic Islands and in the South Tyrrhenian Sea. Insets show the location of traps around (a) Portugal, Spain, and Morocco, (b) Sardinia, (c) Sicily and the South coast of Italy, and (d) Tunisia. Numbers refer to trap names given in Table 1. The diameter of the circle is proportional to the median production of the trap.

large, pelagic, migratory fish that are known to migrate for spawning purposes in the same manner every year. In May, they enter the Mediterranean from the North Atlantic and head for two main spawning areas, north of Sicily and around the Balearic islands (Figure 1; Mather *et al.*, 1995). For centuries, fishermen have used their knowledge of these spawning migrations to set traps along the routes. Fixed and passive gear hardly changed until the middle of the 20th century (Thomazi, 1947; Doumenge, 1998), suggesting that fishing effort may have remained unchanged over centuries. Therefore, a trap can be considered to be a sampler that catches the same proportion of the migrating bluefin tuna population each year. To investigate whether fluctuations in trap catches could be considered as a proxy for true abundance, we tested whether long-term fluctuations in trap catches varied simultaneously around the western Mediterranean and along the Atlantic coasts of Spain, Morocco, and Portugal. Two studies had already documented possible synchrony between long-term

fluctuations in trap catches in different areas. At the beginning of the century, Sella (1929) mentioned possible synchronous fluctuations in catches of Sardinian, Sicilian, and Tunisian traps. Adding Portuguese traps, Fromentin *et al.* (2000a) analysed five long time-series by correlation analysis, and supported the hypothesis of synchrony in long-term fluctuations.

Those studies, however, were confined to a restricted data set. To validate the hypothesis of synchrony, it was necessary to look for additional time-series, and then to carry out more extensive analyses. A data set of 54 time-series from the western Mediterranean and the Atlantic coasts of Portugal, Spain, and Morocco is therefore presented and investigated here. Using time-series analyses, we decomposed the temporal signal and identified trends and cycles in catch, and we further tested whether the fluctuations were synchronous. The aim was to answer the following questions. (1) What are the patterns and the magnitude of long- and short-term fluctuations in catches? (2) Is there evidence of periodic

variation in catches? (3) Do these fluctuations in catches vary in the same manner between different locations? Finally, we discuss possible underlying processes that could lead to such fluctuations.

Material

The Mediterranean trap fishery

For many years, fishers have benefitted from knowledge of the seasonal migration of bluefin tuna, during which the fish migrate close to the coast on their way to their spawning sites (Mather *et al.*, 1995). To catch tuna, fishers traditionally used either traps or beach-seines (Doumenge, 1998), the latter gear sometimes incorrectly referred to also as traps. Unlike traps, beach-seines need many hands to operate, so progressively they have been replaced by fixed gear. The trap system was used throughout the Mediterranean Sea and along the adjacent North Atlantic coasts, from the 14th century in Sicily, the 16th century in Sardinia and Portugal, and the 19th century in Tunisia, Spain, and Morocco (Berthelot, 1869; Pavesi, 1889). The traps are fixed nets set perpendicular to the coast, that stop the migrating tuna and guide them through several enclosures to the final “death room” (Figure 2). There, tuna are gaffed during the “matanza”.

Numerous authors have shown that the name and location of the traps has remained the same over time (e.g. Sarmiento, 1757; Parona, 1919; de Buen, 1925; Sella, 1929; Anon., 1931; Rodriguez-Roda, 1964; Conte, 1985; Figure 1). Migration patterns have been well understood since the Middle Ages, so the most appropriate locations for capturing tuna along their migration routes were selected long ago. Moreover, the installations were often associated with a factory, constituting an establishment difficult to move (Dieuzeide and Novella, 1953; Doumenge, 1998).

The trap was hardly modified between the 17th and the early 20th centuries, as mentioned in the earliest descriptions of traps as well as recent literature (Sañez-Reguart, 1791–1795; Berthelot, 1869; Pavesi, 1889, for Italy; de Bragança, 1899, for Portugal; De Fages and Ponzevera, 1908, for Tunisia; de Buen, 1928, for Spain). However, since the beginning of the 20th century, there have been some modifications. Increasing coastal traffic, noise, and pollution possibly led to a reduction in trap efficiency. Nevertheless, the modifications remained minor until the 1960s (Doumenge, 1998). Then, technical innovations, such as the replacement of the traditional nets of hemp by nylon nets and, above all, the development of modern, active fishing techniques, e.g. purse-seining and long-lining, completely changed the context of the bluefin tuna fisheries and rendered the traps progressively less important (Farrugio, 1981; Addis *et al.*, 1996;

Doumenge, 1998). For these reasons and to avoid any variations that could result from crucial changes in fishing effort and/or catchability, we restricted the time-series analyses to data prior to 1960.

Data

Historically, bluefin tuna fisheries were often economically important establishments. The Royal fiscal administration and collectors of ecclesiastical tithe and salt taxes accurately recorded their receipts. Moreover, bankers were often involved in trap management and for several centuries kept detailed accounts of catches (Doumenge, 1998). For this study, we searched intensively through national and naval archives, scientific libraries and various Mediterranean laboratories for the historical catch data. They were retrieved either from old records published by local authorities or the clergy (e.g. Sarmiento, 1757), in books of historical analyses (e.g. Cancila, 1972), in owners’ archives (e.g. Duchy of Medina Sidonia), or in the personal archives of passionate and relentless scientists (e.g. Sella, Scaccini, Rodriguez-Roda).

Data were collected from beach-seine as well as trap fisheries. As the former are often mistaken for traps, they have to be considered. However, the principle of a beach-seine is quite different from that of a trap: it is an active fishing gear, requiring many hands to operate, and very dependent on the keenness of vision of an observer (who issues instructions on where and when to deploy the net as tuna pass). For this reason, we did not use the time-series of beach-seine catches for the analyses. Characteristics and origins of the different time-series are detailed in the Appendix.

Places and periods of activity of most of the traps are known from the literature (Sarmiento, 1757; Berthelot, 1869; Pavesi, 1889; Parona, 1919; Cancila, 1972). The number of active traps varied over the centuries, but during the period analysed in this paper (early 17th to mid-20th centuries), the main traps were settled and active, so our data collection covered most of the fishing activity. Nevertheless, some information is lacking because some archives were destroyed (such as the information for the middle of the 19th century from the “Formica” and “Favignana” traps, which were destroyed in a fire; Guarrasi, pers. comm.) or lost (such as the detailed information on Portuguese traps after 1930; Vasconcelos, pers. comm.). For the Spanish traps, catches were *a priori* not recorded during the 19th century. There, the oldest data were recorded by the local aristocracy, but it lost its monopoly during the revolution around 1815 and the fishing organization changed completely. As a result, no catches were recorded until the early 20th century.

Most catches (92%) were expressed as the number of tuna caught (see Appendix). In addition, a few data

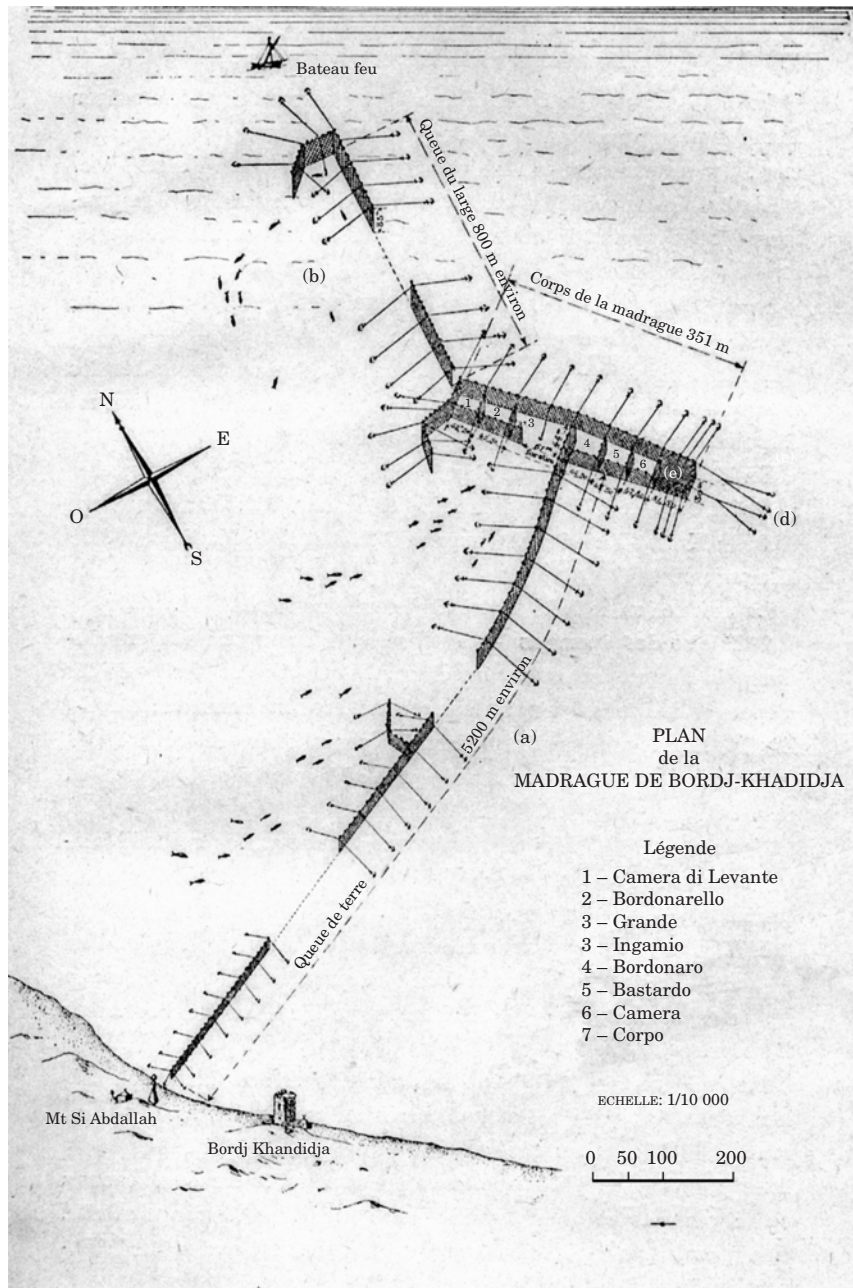


Figure 2. Historical representation of the Tunisian trap “Bordj Khadidja”, after [Parona \(1919\)](#). The traditional trap was made of a net from shore to trap (a), which was on average some 3 km long, and a second leader extending offshore from trap (b), and finally the main trap (c), divided into several compartments. The trap was held by numerous anchors (d). Tuna, hugging the coast during their spawning migration, were shepherded by the two barrier nets up to the main trap. There, they passed through several rooms to the final compartment, the “death room” (e), where the floor, made of net, could be lifted. They were then gaffed by fishers and lifted onto a boat. This simple and efficient fishing technique remained virtually unchanged from the Middle Ages to the early 20th century.

were published as number of barrels (Sicilian production from the 17th to the early 19th century) or in weight (some of the Tunisian time-series). The records generally

also included information on the mean weight of the tuna caught. Most traps caught large tuna (>60 kg), i.e. adults on their spawning migration ([Pavesi, 1889](#);

Sella, 1929; Rodriguez-Roda, 1964; Farrugio, 1981). However, a few traps caught juveniles (<35 kg), which do not, unlike the spawners, have similar patterns of annual migration. In order to be consistent, only the data on traps fishing spawners were retained for this analysis. The literature often distinguished between spawners caught in May during their entrance into the Mediterranean and spawners caught in July during the return trip, but for our purposes, the sum of these two was taken in computing the annual catch.

More than a hundred time-series were gathered, but only the 54 that were at least 20 years long were finally used for the analysis (Table 1). Because of missing values, a few time-series had to be split into several parts (Figure 3). The oldest time-series of trap catches went back to 1599 for Sicily ("Favignana", "Formica"), to 1797 for Portugal ("Medo das Casas"), to 1825 for Sardinia ("Saline", "Porto Scuso", "Porto Paglia", "Isola Piana"), and to 1863 for Tunisia ("Sidi Daoud"). About one-third of the time-series were more than 50 years long, six spread over more than a century, but 42% of them were no longer than 30 years. Most of the Portuguese, Sicilian, Sardinian, and Tunisian series extended from the second part of the 19th century to the early 20th century. Spanish and Moroccan series constituted a particular and problematic case insofar as, unlike others, they mainly covered the 20th century and started in 1910 or 1930. For that reason, they only overlapped Italian, Tunisian, and Portuguese time-series for a few years (Figure 3).

Methods

The methodological procedure is shown graphically in Figure 4. The data were log-transformed (natural logarithm) to stabilize the variance (Sen and Srivastava, 1990). Such a transformation is biologically reasonable because population dynamics are largely governed by multiplicative processes (Williamson, 1972). As mentioned above, about 8% of the catches were published as number of barrels or weight. For consistency, the series in weight or barrels were converted to number of fish, using simple linear regressions or generalized linear models over the periods for which catches were expressed in both number and weight or barrels. The goodness of fit was always highly satisfactory; the multiple r^2 ranged between 0.75 and 0.97 and the p -value was always <0.0002.

Time-series were also plagued by some missing values (lack of data for one or a few successive years either because the trap was temporarily not set for reasons such as war, lack of workers, bad environmental conditions, and/or credits, or because records were lost). As most numerical analyses require time contiguity, missing values were estimated either from additional infor-

mation available during that period, such as data in barrels or in weight (see above), or from time-series modelling. For the latter, empirical analysis was carried out to determine (1) the most appropriate numerical method of filling in missing values (while not distorting the underlying relationships in the data) and, (2) the number of successive missing values that could be estimated satisfactorily. Different smoothing methods (moving average, splines and kernel; S-Plus, 1999) and autoregressive models (ARIMA; Box and Jenkins, 1976) were used and compared in terms of performance. When a significant autoregressive signal was detected, the ARIMA model was selected on the basis of differences between estimated and true values, but otherwise a kernel filter was used. Further, because it appeared that estimates were reliable up to three continuous missing values, we restricted completion of missing values to one, two or three contiguous ones. Finally, 31 of the 54 time-series were considered for the analyses. In 50% of these, the interpolated values represented 1–5% of the total observations and only one time-series had >10% interpolated values (i.e. 14.8%; see also Table 1).

Geographical clustering

To determine homogeneous regions, we classified on the geographic distance matrix (straight line, km) between traps. We used a hierarchical classification with flexible clustering (Lance and Williams, 1967) and grouped the traps on the criterion of Euclidean distance. This clustering technique successively fuses traps into groups and groups into larger clusters, starting with the highest mutual similarity (lowest distance in km), then gradually lowering the similarity level at which groups are formed.

Filtering

To investigate the general trends of the various time-series, data were smoothed by Eigen Vector Filtering (EVF; Colebrook, 1978; Ibanez and Dauvin, 1988). The method consists of constructing, for each time-series, an autocovariance matrix by shifting the series between one and five years (a smoothing window of five years allows for retention only of medium- to long-term fluctuations, i.e. >15–20 years). A Principal Components Analysis (PCA; Hotelling, 1933; Jackson 1986; Legendre and Legendre, 1998) is then conducted on the autocovariance matrix and the first component of the PCA gives the trend of that series. In addition to other smoothing methods (splines, polynomial models, kernel filter, LOESS, or moving average), the EVF evaluates the quantitative importance of the trend, which is given by the percentage of variance explained by the first axis of the PCA.

Table 1. Geographical classification and main characteristics of the time-series of trap catches. Left, cluster resulting from the classification on the geographic distance matrix (in km) between the 54 traps. Columns represent the time-series index, the country ("Por"=Portugal, "Spa"=Spain, "Mor"=Morocco, "Tun"=Tunisia, "Sic"=Sicily, "Ita"=continental Italy, "Sar"=Sardinia), the trap name, the period used in the analyses, the number of actual observations (n), the median values, the coefficient of variation (C.V.), and the percentage of variance associated with the first component of Eigen Vector Filtering.

| Geographic distance index | | | | No. | Place | Trap name | Period | n | Median | C.V. | % First axis EVF |
|---------------------------|------|------|---|-----|-------|------------------|-----------|-----|--------|------|------------------|
| 9000 | 2000 | 1000 | 0 | | | | | | | | |
| | | | | 1 | Por | Sul do Cabo | 1896–1917 | 21 | 1404 | 0.81 | 56.4 |
| | | | | 2 | Por | Senohra da Rocha | 1897–1919 | 23 | 1560 | 0.75 | 46.6 |
| | | | | 3 | Por | Olhos de Agua | 1896–1919 | 24 | 1352 | 0.58 | 53.2 |
| | | | | 4 | Por | Fort Novo | 1896–1920 | 25 | 1435 | 0.65 | 50.8 |
| | | | | 5 | Por | Ramalhete | 1896–1930 | 35 | 1169 | 0.80 | 36.6 |
| | | | | 6 | Por | Cabo Santa Maria | 1896–1933 | 38 | 1730 | 0.72 | 32.4 |
| | | | | 7 | Por | Livramento | 1876–1933 | 58 | 5709 | 0.99 | 68.3 |
| | | | | 8 | Por | Barril | 1867–1933 | 67 | 7606 | 0.87 | 81.2 |
| | | | | 9 | Por | Medo das Casas | 1797–1817 | 21 | 8309 | 0.84 | 35.0 |
| | | | | | | " | 1852–1933 | 82 | | | 82.8 |
| | | | | 10 | Por | Abobora | 1885–1933 | 49 | 3258 | 0.64 | 55.0 |
| | | | | 11 | Por | Sul da Ponta | 1902–1926 | 25 | 4739 | 0.93 | 75.8 |
| | | | | 12 | Por | Torre de Barra | 1897–1917 | 21 | 1404 | 1.00 | 32.7 |
| | | | | 13 | Spa | Reine Regente | 1914–1940 | 26 | 6432 | 0.55 | 44.5 |
| | | | | 14 | Spa | Isla Cristina | 1929–1960 | 32 | 7330 | 0.62 | 79.7 |
| | | | | 15 | Spa | Las Torres | 1902–1923 | 21 | 2967 | 0.61 | 30.9 |
| | | | | 16 | Spa | Arroyo Hondo | 1914–1934 | 20 | 7073 | 0.60 | 45.5 |
| | | | | 17 | Spa | Sancti Petri | 1917–1960 | 42 | 9948 | 0.57 | 65.7 |
| | | | | 18 | Spa | Torre Atalaja | 1914–1934 | 20 | 4317 | 0.58 | 45.1 |
| | | | | 19 | Spa | Barbate | 1910–1960 | 46 | 16090 | 0.49 | 56.9 |
| | | | | 20 | Spa | Zahara | 1910–1936 | 27 | 5102 | 0.63 | 70.0 |
| | | | | 21 | Spa | Tarifa | 1927–1960 | 34 | 2686 | 0.53 | 51.4 |
| | | | | 22 | Mor | Punta Negra | 1936–1960 | 24 | 3845 | 0.58 | 30.1 |
| | | | | 23 | Mor | Aguas de Ceuta | 1940–1960 | 21 | 849 | 0.58 | 32.5 |
| | | | | 24 | Mor | Principe | 1940–1960 | 21 | 384 | 0.92 | 32.3 |
| | | | | 25 | Tun | Sidi Daoud | 1863–1960 | 93 | 5071 | 0.65 | 74.7 |
| | | | | 26 | Tun | Ras El Ahmar | 1905–1941 | 35 | 1689 | 0.81 | 35.8 |
| | | | | 27 | Tun | Monastir | 1894–1926 | 32 | 1628 | 0.79 | 33.8 |
| | | | | 28 | Tun | Conigliera | 1897–1929 | 32 | 1894 | 0.73 | 70.9 |
| | | | | 29 | Tun | Bordj Khadidja | 1903–1929 | 23 | 1017 | 0.96 | 66.0 |
| | | | | 30 | Sic | Formica | 1634–1813 | 175 | 2173 | 0.59 | 71.6 |
| | | | | | | " | 1878–1960 | 78 | | | 63.4 |
| | | | | 31 | Sic | Favignana | 1634–1813 | 168 | 1958 | 0.85 | 62.1 |
| | | | | | | " | 1878–1960 | 80 | | | 78.8 |
| | | | | 32 | Sic | San Giuliano | 1711–1806 | 83 | 715 | 0.84 | 69.3 |
| | | | | | | " | 1885–1914 | 28 | | | 31.0 |
| | | | | 33 | Sic | Osinelli | 1904–1929 | 26 | 890 | 0.64 | 48.2 |
| | | | | 34 | Sic | San Cusumano | 1903–1960 | 58 | 600 | 0.69 | 39.8 |
| | | | | 35 | Sic | Bonagia | 1657–1809 | 141 | 961 | 0.72 | 57.5 |
| | | | | | | " | 1879–1934 | 56 | | | 44.5 |
| | | | | 36 | Sic | Cofano | 1738–1764 | 25 | 495 | 0.60 | 31.2 |
| | | | | 37 | Sic | Secco | 1874–1933 | 73 | 500 | 0.70 | 40.8 |
| | | | | 38 | Sic | Scopello | 1909–1933 | 25 | 369 | 0.68 | 24.7 |
| | | | | 39 | Sic | San Giorgio | 1880–1917 | 38 | 374 | 1.07 | 35.3 |
| | | | | | | " | 1924–1960 | 37 | | | 44.5 |
| | | | | 40 | Sic | San Elia | 1909–1929 | 19 | 425 | 0.77 | 71.0 |
| | | | | 41 | Sic | Solanto | 1909–1929 | 19 | 596 | 0.57 | 31.9 |
| | | | | 42 | Sic | San Nicola | 1909–1929 | 19 | 395 | 0.62 | 29.3 |
| | | | | 43 | Sic | Trabia | 1909–1929 | 19 | 570 | 0.54 | 44.1 |
| | | | | 44 | Sic | Castellamare | 1909–1931 | 21 | 205 | 1.33 | 54.0 |
| | | | | 45 | Sic | Magazzinazzi | 1892–1933 | 42 | 528 | 0.92 | 59.6 |
| | | | | 46 | Sic | Oliveri | 1904–1960 | 57 | 558 | 0.80 | 45.0 |
| | | | | 47 | Sic | Tonno | 1885–1960 | 74 | 757 | 0.90 | 45.0 |
| | | | | 48 | Sic | Marzamemi | 1875–1931 | 57 | 1706 | 0.79 | 73.6 |
| | | | | 49 | Ita | Pizzo | 1876–1932 | 52 | 1595 | 1.01 | 40.0 |
| | | | | 50 | Sar | Saline | 1829–1848 | 20 | 2011 | 0.87 | 38.8 |
| | | | | | | " | 1868–1960 | 92 | | | 75.9 |
| | | | | 51 | Sar | Flummentorgiu | 1829–1848 | 20 | 1316 | 0.74 | 55.0 |
| | | | | | | " | 1868–1914 | 42 | | | 47.6 |
| | | | | 52 | Sar | Porto Paglia | 1825–1960 | 129 | 1826 | 0.72 | 55.6 |
| | | | | 53 | Sar | Porto Scuso | 1825–1960 | 135 | 3155 | 0.63 | 57.8 |
| | | | | 54 | Sar | Isola Piana | 1828–1960 | 135 | 2387 | 0.65 | 59.6 |

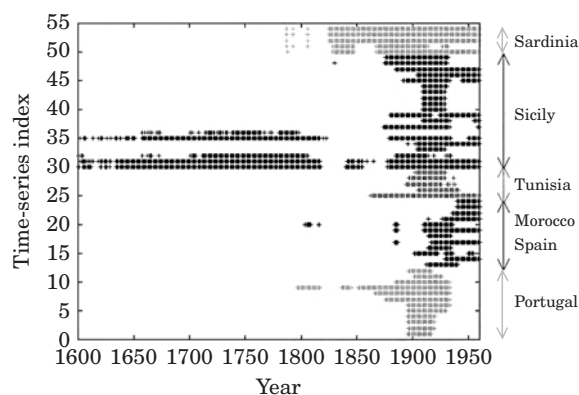


Figure 3. Presence (+) and absence (blank) of data in each of the 54 time-series used (time-series indices identified geographically in Table 1).

Patterns of periodicity

In order to extract patterns of periodicity, spectral analyses were performed on the 12 series that were sufficiently long (at least 80 years). Series were made stationary by extracting a fitted polynomial filter of degree 5 (Legendre and Legendre, 1998). Spectral analysis transforms each time-series into a sum of sine and cosine functions of different period lengths (Wei, 1990). The raw periodogram is the usual means of summarizing this decomposition, but it is a poor statistical descriptor of spectral density, because it has large variance and is not consistent (Priestley, 1981). We therefore used a Parzen smoothing window, and then performed a Principal Components Analysis on these 12 spectral densities to identify the main patterns of periodicity across the 12 long time-series (Bjørnstad *et al.*, 1996; Fromentin *et al.*, 1997).

Synchrony between time-series

It was clearly necessary to test whether fluctuations were synchronous between series collected in the western Mediterranean and the adjacent Atlantic. Because of the particular structure of the data set (series of unequal lengths that did not necessarily overlap), a simple global test of similarity between all time-series could not be computed. To circumvent this problem while gaining information on the spatial scales of the synchrony (if any), we used the “modified correlogram” method proposed by Koenig and Knops (1998). This technique provides a statistical test that measures whether changes through time at sites a given distance apart vary synchronously, defined as yielding a mean r -value greater than zero. The “modified correlogram” is a modification of the Mantel correlogram (Sokal, 1986; Legendre and Fortin, 1989), which allows evaluation of how far spatial autocorrelation, if any, extends geographically and

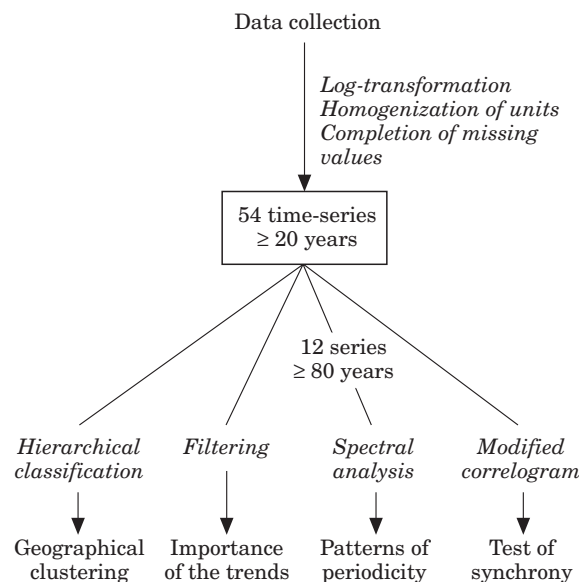


Figure 4. The methodological procedure of the analyses.

whether there is statistically significant cross-correlation between sites located a given distance apart.

To carry out modified correlogram analyses, we first calculated the correlations (r -values) between each pair of sites. We used a non-parametric Spearman correlation coefficient (Zar, 1984) because of the non-normality of some series. These r -values were then divided into appropriate classes of distance, depending on the geographic distance (straight line) between the sites. Within each category, the r -values were tested by performing trials in which sets of correlation coefficients were chosen at random from the entire pool such that individual sites were used only once. For example, if the correlation between A and B was chosen, all other pairwise combinations involving either sites A or B (i.e. not only the correlation between A and B, but also that between A and C, A and D, B and C, etc.) were eliminated from the remaining pool of available values. This procedure was continued until all combinations had been tried, and then the mean r -value was calculated. After 1000 trials, statistical inference was determined using the standard z -value. As tests were performed on more than one distance category, corrections for multiple comparisons were applied using the sequential Bonferroni method (Rice, 1989; Peres-Neto, 1999).

To test whether synchrony was attributable to trends alone or to both trends and year-to-year fluctuations, analyses of both original series (log-transformed data) and detrended series (the series of log-transformed data minus the trend estimated by EVF) were carried out. As length of series can affect the ability to detect synchrony (i.e. the longer the series, the better the diagnostic), we first analysed series with at least 15 years in common,

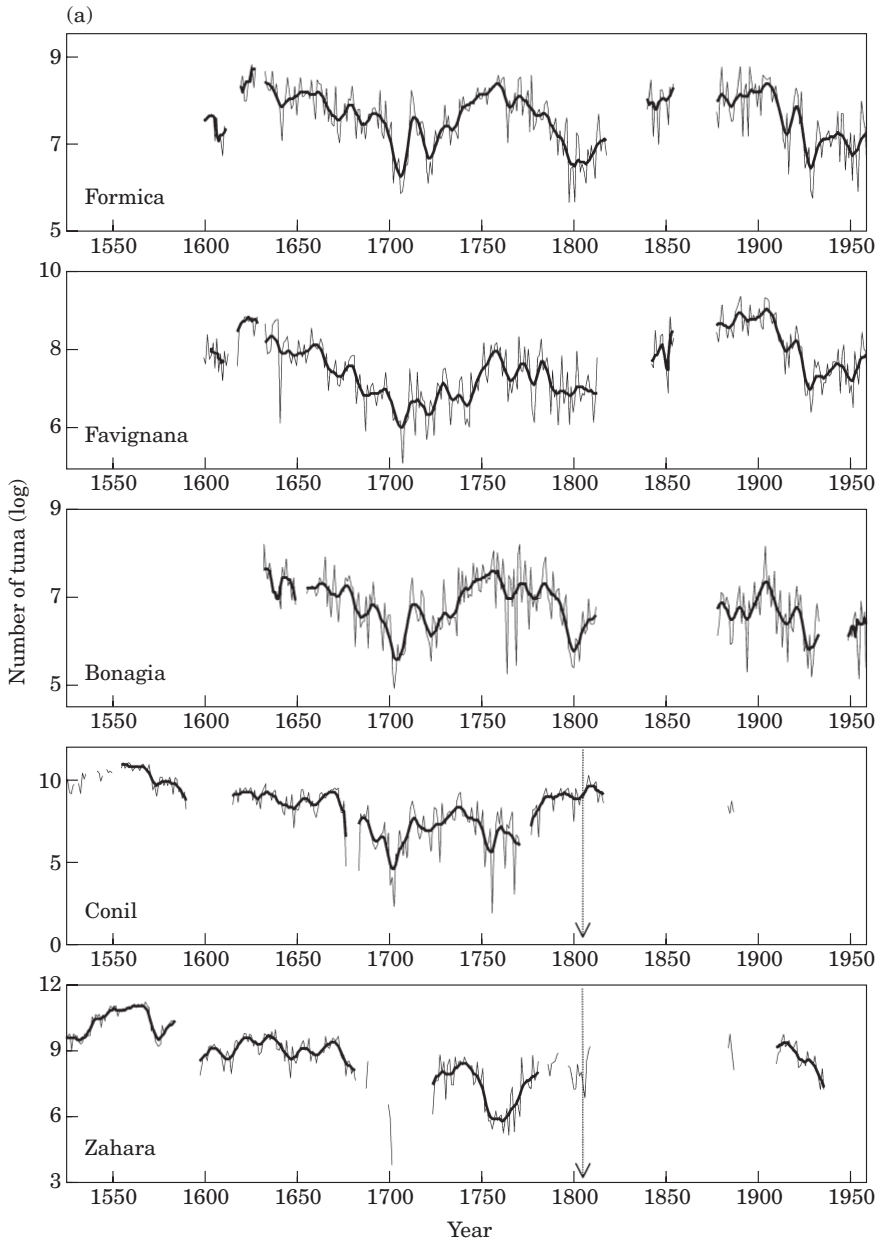


Figure 5a.

then series with at least 50 years in common. The first set of analyses allows comparison of the greatest number of series, whereas the second allows comparison of the longest time-series.

Synthetic time-series

A synthetic time-series was calculated to depict the general temporal pattern in Mediterranean bluefin tuna abundance. The most common way of computing such a

summarized series would be to implement a PCA on all the series, then to extract the first axis, i.e. the dominant temporal pattern (or the mean pattern) shared by all traps. However, such a method requires the same length and the same starting date for all time-series, which is not the case here. Therefore, we simply computed an average of each year from the standardized (mean divided by the standard deviation) values of all available time-series in that year. This procedure is not totally consistent from a statistical viewpoint, but our purpose

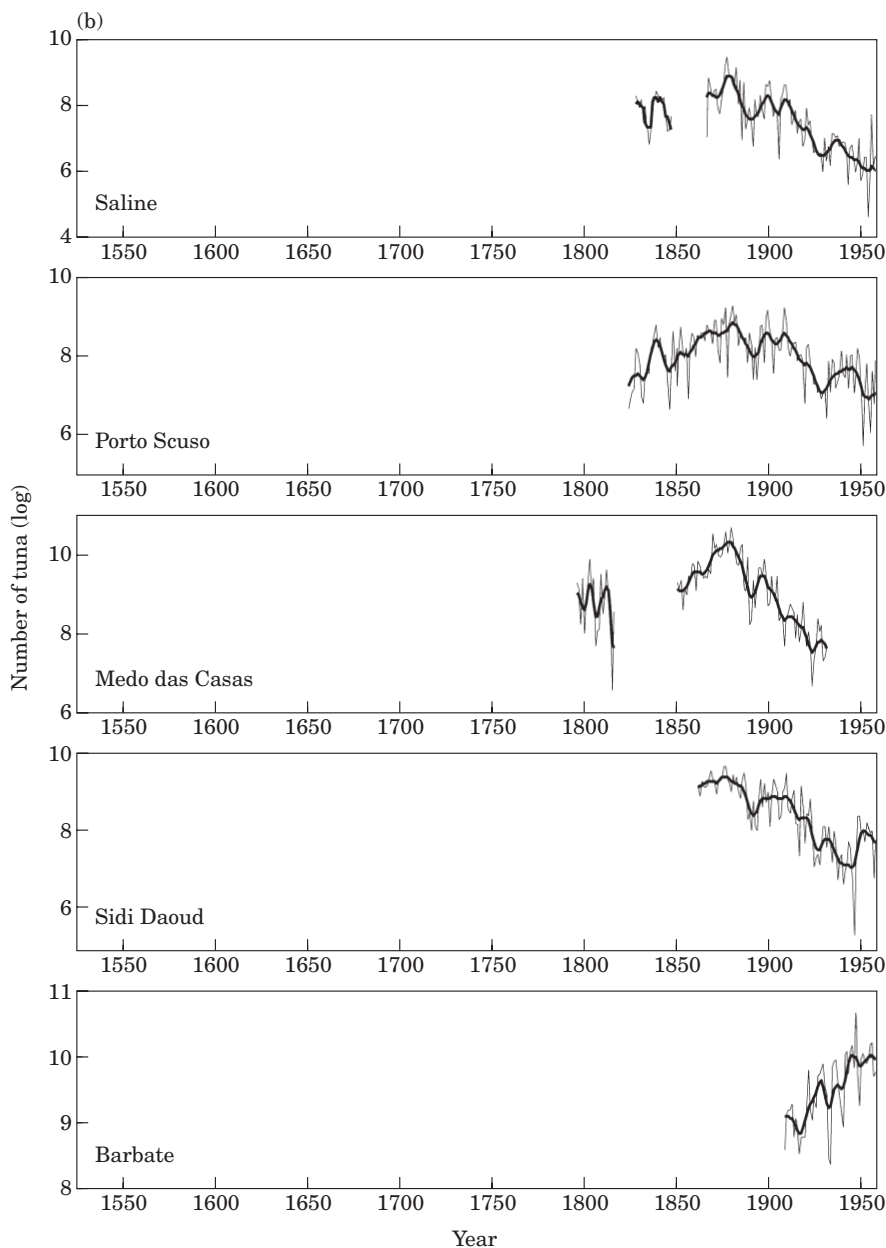


Figure 5b.

Figure 5. Examples of 12 time-series of trap catches (thin lines, log data; bold lines, smoothed data). (a) Catches of the three longest Sicilian (“Formica”, “Favignana”, “Bonagia”) and two longest Spanish (“Conil”, “Zahara”) time-series. For the two latter, the time of change in gear from beach-seine to trap is indicated by the arrow (1804 for “Zahara”, and 1806–1809 for “Conil”). (b) Catches of two Sardinian (“Saline” and “Porto Scuso”), one Portuguese (“Medo das Casas”), one Tunisian (“Sidi Daoud”) and one Spanish (“Barbate”) time-series. For time-series longer than 20 years, the trend is estimated by EVF (see the text), in other cases by a running median.

is simply descriptive and not inferential. An EVF was performed on this time-series to depict the long- and medium-term fluctuations.

All numerical analyses were performed using [Matlab \(1999\)](#) and [S-plus \(1999\)](#) software.

Results

According to the classification on the distance matrix (in km), the 54 traps were classified into five areas corresponding to: Portugal, Spain and Morocco,

Tunisia, Sicily and Sardinia (Table 1). These five areas were gathered within two main areas, the area around Gibraltar, and the eastern end of the western Mediterranean. The most productive traps were on the southern coasts of Spain and Portugal (Figure 1). They caught 4300 tuna per year (median value). The most productive trap was “Barbate” which caught about 16 000 tuna annually, and the least productive was “Ramalhete”, which caught about 1100 bluefin tuna annually. Some traps at the eastern end of the western Mediterranean were also productive; the median annual catches (for the period 1880–1930) were about 6200 tuna for the Tunisian trap “Sidi Daoud”, 3800 and 3000 tuna for the Sardinian “Porto Scuso” and “Isola Piana” respectively, and 3000 and 5200 tuna for the Sicilian “Formica” and “Favignana” respectively.

Amplitude of fluctuations

Trap catches displayed remarkable temporal fluctuations: coefficients of variation of the 54 series of trap catches ranged from 0.49 to 1.33 (Table 1). The amplitude of variation between periods of low (1690–1710, 1790–1810, 1910–1930) and high abundance (1630–1650, 1750–1770, 1870–1890) was large, with factors of 2–4 on Tunisian, Sicilian, and Sardinian traps and 4–7 on Portuguese traps (Figure 5). For example, mean annual catches of the “Formica” trap were only 1000 tuna in periods of low abundance and up to 3500 tuna during periods of high abundance.

Patterns of periodicity

Quick visual inspection of the series of trap catches indicated periodic fluctuations of about a century; they are clearly outlined by Eigen Vector Filtering (Figure 5). On the three longest series (Sicilian traps “Formica”, “Favignana”, and “Bonagia”), years of high annual catches (1630–1650, 1750–1770, 1870–1890) alternated with years of low annual catches (1690–1710, 1790–1810, 1910–1930), with a period of about 100–120 years. The other long time-series (“Porto Scuso”, “Isola Piana”, “Porto Paglia”, “Medo das Casas”) also displayed pseudo-cyclic variation of about 100–120 years, with a peak at the end of the 19th century, which was common to all traps.

More careful inspection revealed a shorter cycle of about 15–25 years superimposed on the 100-year fluctuations (Figure 5). This secondary periodicity was further investigated by spectral analysis on the 12 series more than 80 years long (from ten different traps, “Favignana” and “Formica” being split up in two parts because of missing values). To summarize the patterns of periodicity, a PCA was performed on these 12 series of spectral densities. The first principal axis encompassed 67% of the variance, so it captured the bulk of the

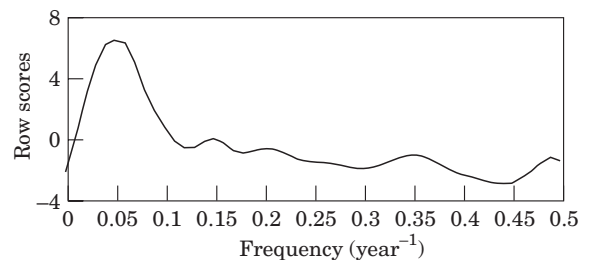


Figure 6. Plot of the first principal component of the PCA, computed on the spectral densities of the 12 time-series >80 years long. This axis encompassed 67% of the total variance and depicted a main peak at around 0.035–0.07 year⁻¹, i.e. a cycle of about 15–30 years.

variability. It displayed a peak for frequencies around 0.05 year⁻¹ (0.035–0.07 year⁻¹) i.e. periods around 20 years (30–15 years; Figure 6). All 12 series were highly positively correlated with this axis ($r > 0.7$), confirming the cycle to be common to all the series. The two following axes explained only 11 and 8% of the total variability, respectively, and detected short-term fluctuations. Hence, temporal variability may be decomposed into three main components: (i) pseudo-cyclic fluctuations of about 100–120 years, (ii) cycles around 20 years, and (iii) annual fluctuations.

Importance of the trends

The percentage of variance explained by medium- to long-term fluctuations (≥ 15 years) was high for most of the series (Table 1). The trends represented an average of 51% of the total variance in the series, and about 68% when the series were longer than 80 years (for comparison, smoothing time-series of random numbers would lead to a trend explaining 20–30% of the total variance). As expected, the percentage of variance attributable to the low frequency is related to the length of the series; the longer the series, the greater the percentage of variance. Although, the year-to-year fluctuations appeared non-negligible (Figure 5), they remained secondary in comparison to the long- and medium-term fluctuations.

Synchrony of the series

Simple graphical observation of the time-series shows synchrony between the long-term fluctuations of the different traps (Figure 5). From 1620 to 1700, the three Sicilian time-series declined in parallel, then increased up to 1750 before declining again until 1800. The time-series covering the 19th and 20th centuries also displayed synchrony, with low catches in the early 19th century, then an increasing trend from 1850 through the end of the 19th and into the early 20th centuries.

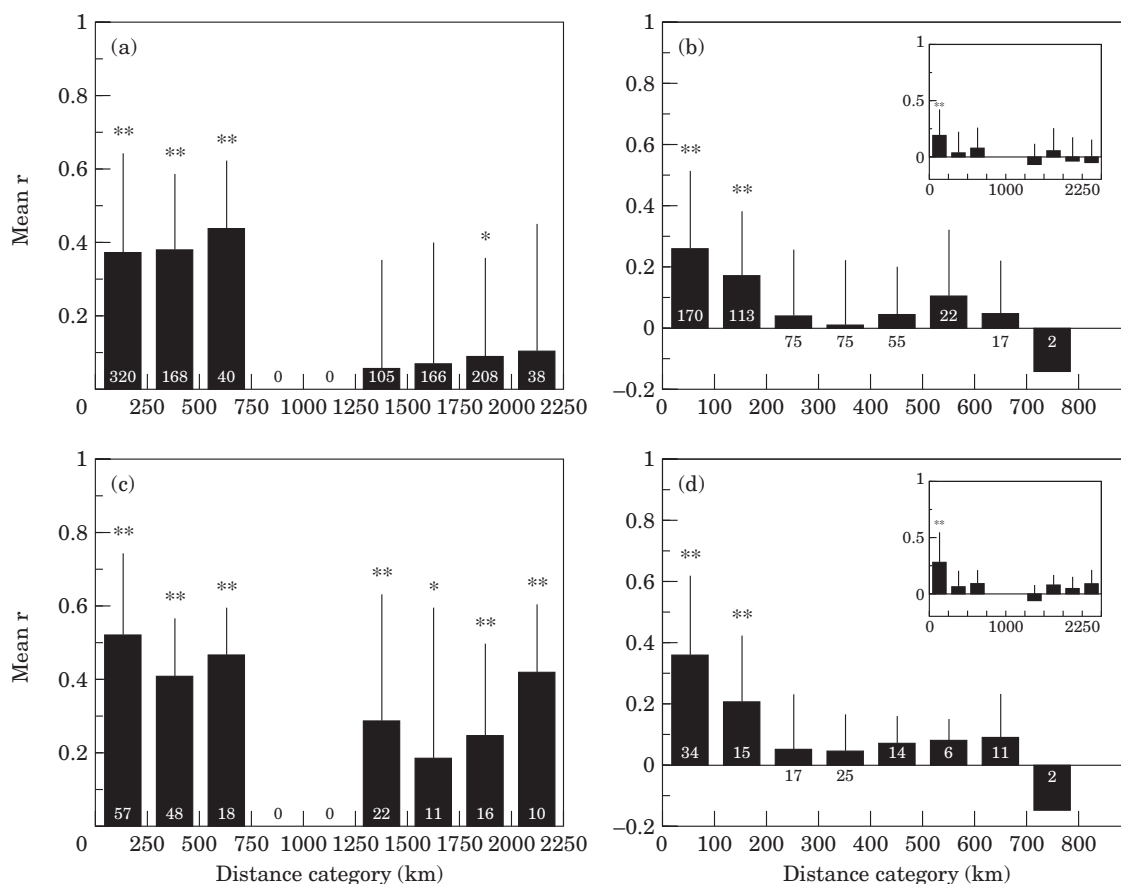


Figure 7. Modified correlograms computed on log data (a, c) and detrended time-series (b, d), overlapping over at least 15 years (a, b) or 50 years (c, d), i.e. 1045 and 182 pairwise comparisons respectively. Pairwise correlations were divided into distance categories of 250 km for a, c, and inserts of b and d, and categories of 100 km for b and d. The number is of pairwise correlations for each distance category. Mean (+standard deviation) r -values are plotted. Significance is indicated by asterisks, * = $p < 0.05$, ** = $p < 0.01$.

Thereafter, there was by a rapid decline and a plateau from the 1930s to the 1950s (Figure 5). Some Spanish traps, e.g. “Barbate”, did not, however, conform to this general pattern, catches increasing from 1920 to 1960. Nevertheless, if we except some of the Spanish traps (that only cover the 20th century), brief graphical examination indicates that the long-term fluctuations were globally synchronous between traps.

To check this crude examination, “modified correlograms” were computed to test for significant autocorrelation, i.e. synchrony, between sites located within any given range of distances apart. The first correlogram was computed on the correlation matrix between original time-series overlapping by at least 15 years (Figure 7). Whatever the distances between the traps, all time-series appeared to be positively correlated with each other. The time-series from traps less than 750 km apart, i.e. within the Sardinian-Sicilian-Tunisian group and the Gibraltar area group, were particularly, and

significantly, positively correlated (mean $r = 0.4$, $p < 0.01$). Mean correlation between time-series from the two groups were, however, low and non-significant (mean $r \in b [0.06-0.11]$). A second correlogram was then computed between detrended time-series overlapping by at least 15 years (Figure 7b). The time-series appeared to be significantly correlated only up to 200 km apart (mean $r = 0.21$), those more than 700 km apart being weakly or not correlated (mean $r \in b [-0.14-0.05]$). Removing the trends therefore led to a significant drop in spatial autocorrelation, indicative that the long-term trend is the feature most common to all series. However, these results highlighted a regional structure to the short-term variability: short-term fluctuations appeared to be synchronous at a local scale (≤ 200 km), i.e. within each area highlighted by the classification (Portugal, Spain-Morocco, Tunisia, Sicily, Sardinia).

Analyses of the time-series having at least 15 years in common allowed the maximum number of time-series to

be used, but 15 years is probably too short to describe synchrony between long-term fluctuations. Therefore, correlograms were also computed on time-series having at least 50 years in common. Original time-series showed significant spatial autocorrelation over the whole area studied (Figure 7c). Whatever the distance between them geographically, time-series were significantly positively correlated, with mean r of 0.40–0.51 within groups (traps from either the eastern Mediterranean area, or from the western Mediterranean/adjacent Atlantic), and mean r of 0.18–0.42 between groups (traps from Sardinian-Sicilian-Tunisian group against traps from the Gibraltar area). The correlogram on detrended time-series showed that they were only positively correlated up to 200 km apart (Figure 7d). Therefore, correlograms on long-term series emphasized the synchrony between long-term trends and confirmed that short-term variability was only structured at a scale <200 km.

In conclusion, long-term fluctuations in trap catches appeared significantly synchronous all around the western Mediterranean and adjacent North Atlantic, whereas the year-to-year fluctuations were only synchronous on a local scale.

Discussion

Data

Mapping of the studied sites reveals strong disparity in the location of traps around the western Mediterranean and adjacent North Atlantic, which does not result from incomplete data collection. The traps constitute important fisheries along the southern coasts of Portugal and the Atlantic and Mediterranean coasts of Spain and Morocco, and along the Tunisian, Sicilian, Sardinian, and western continental Italian coasts, i.e. along the migration routes of spawning bluefin tuna (Berthelot, 1869; Farrugio, 1981). Elsewhere, along the Algerian, French, and Adriatic coasts, traps were of minor importance and only caught juveniles and/or sporadically some adults, so such information was not used in this study. Graphic representation of the data set also reveals temporal disparity in the availability of trap data. This mainly reflects the availability of historical records and the fact that some of the catches were not recorded (e.g. in Spain during the 19th century) or were destroyed (e.g. Sicilian data in the mid-19th century). Nevertheless, we believe that the data presented in this study are trustworthy and of good quality, because most historical documents give extensive information about the catches, including mean weight of tuna, dates of the “matanza” (collecting tuna from the “death room”), environmental conditions, and number of fishers and boats.

Fluctuations in trap catches as a proxy for fluctuations in abundance

The results of the correlograms showed that long-term trends in trap catches were synchronous over more than 2000 km, from southwest Portugal to east of Sicily and from north of Sardinia to south Tunisia. Bluefin tuna migrate annually from the North Atlantic to reproduce in two main areas of the western Mediterranean, hugging the coast on their way to their spawning sites (Aristotle, 4th century B.C.; Mather *et al.*, 1995). If the traps did not catch a representative proportion of the bluefin tuna population, there would have been no reason for the apparent long-term fluctuations to be synchronous around the whole western Mediterranean basin and along the southern coasts of Spain and Portugal. This result would support the hypothesis of Fromentin *et al.* (2000a) that long-term fluctuations in trap catches are a good proxy for variation in population abundance.

It may be argued that synchronous historical social and economic events (wars, plagues, changes in trade and industry) could explain such a pattern. However, such events are rarely (if ever) common and/or synchronous between the different countries of the study area, and those in common were too short to explain the long-term fluctuations. Moreover, there is no information in the literature that indicates the possible influence of historical social and economic events on trap fisheries over decades or centuries (Hjort, 1914; Hersart de la Villemarqué, 1995). Nevertheless, these events can affect short-term variability, which in turn may be related to local and/or regional variations in environmental conditions, fish behaviour (tuna migrating farther offshore in one area than in another in a given year), and fishing effort (accidental damage to nets, variation in the ability of the “Reis”, the lead fisher). All these short-term variations, which tend to be on a local scale only, could explain why the year-to-year fluctuations appear synchronous within areas <200 km.

The literature (Berthelot, 1869; Pavesi, 1889; de Bragança, 1899; de Buen, 1928; Thomazi, 1947; Doumenge, 1998) highlights the similarity between the traps over the whole studied area and the absence of meaningful technical modification until the 20th century. However, notable changes during the 20th century resulted in increased human perturbation and crucial changes to fishing gear and technology after the Second World War. The total number of active traps varied slightly over time, though most operated from the 16th century. The Spanish bluefin tuna fishery was, however, less stable than elsewhere. First, beach-seines were used until the early 19th century and then replaced by traps. Second, the aristocracy surrendered its rights on traps around 1815, traps being auctioned and scattered between numerous owners. From 1804 to

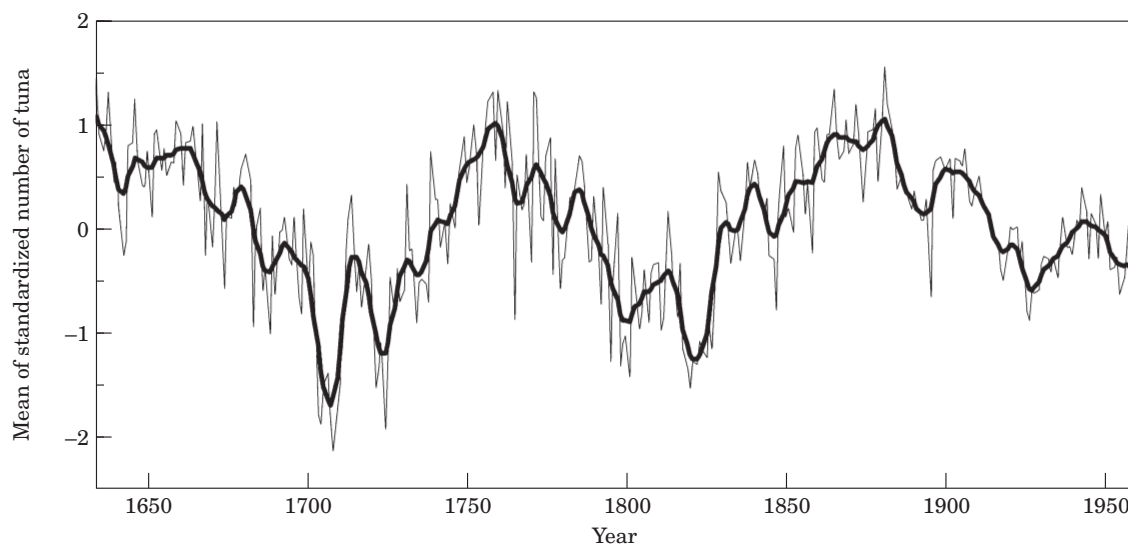


Figure 8. Synthetic series (thin line) computed as mean of the standardized values of the different time-series. The trend (bold line), estimated by Eigen Vector Filtering (see the text), constitutes an index of long-term fluctuations in abundance.

1880, the number of active traps varied between 14 and 19 along the Mediterranean and Atlantic Spanish coasts (Berthelot, 1869; Pavesi, 1889). Franco restored exclusive rights on traps around 1930–1940, which led to a reduction to some ten traps. This local change could explain why the catches of the Spanish traps increased between 1930 and 1960, while the catches of all the other traps remained approximately constant. Unfortunately, information on the catches of Spanish and Moroccan traps during the 19th century was not available, precluding our ability to check this hypothesis. Nevertheless, the two Spanish time-series of beach-seine catches in the 17th and 18th centuries, “Zahara” and “Conil”, tend to show fluctuations similar to the Sicilian time-series of the same period.

Finally, because long-term fluctuations were synchronous throughout the western Mediterranean and adjacent Atlantic (at least until the 20th century), a synthetic time-series could be constructed and smoothed by an EVF (Figure 8). The trend in this series, which explained 78% of the total variance, summarizes the long-term fluctuations in Mediterranean bluefin tuna abundance from 1634 to 1960, i.e. three 100–120 years cycles with peaks around 1635, 1760, and 1880, and troughs around 1710, 1820, and 1930. Cycles of about 20 years are superimposed on these long-term fluctuations. If our results provide strong evidence of synchrony in fluctuations and lead to the conclusion that trap data give a reasonable indication of the frequency of long-term fluctuations in abundance, it must be stressed that trap data do not provide unbiased estimates of the relative amplitude of the fluctuations. Indeed, the differences in the amplitude of fluctuations in catches among traps

suggests that the catchability of different traps may vary with population size.

Cycle and trend

Several authors have observed and documented periodic fluctuations in bluefin tuna catches. Parona (1919) noted a cycle of five years, in phase or in contrast according to the geographical site monitored. Ten years later, Sella (1929) documented periodic fluctuations of large amplitude (about 50 years) as well as short-term variations. Similar observations were made at the same time on a Portuguese trap (“Medo das Casas”) by Neuparth (1925), who postulated that catches varied with cycles of eight and 80 years. De Buen (1925) wrote that the catches of the Spanish traps “Conil” and “Zahara” displayed 100 years fluctuations, whereas Rodriguez-Roda (1966) and Lozano Cabo (1958) estimated that the catches of the Spanish and Moroccan traps varied over periods of six to eight years.

The numerical and statistical analyses carried out here indicate that the eastern Atlantic bluefin tuna population displayed long-term fluctuations with a period of about 100–120 years, together with cyclic variations of about 20 years. Decomposing the variance of the series showed that the long-term trend accounted for a large part of the total variability (45–80%). Such a feature has been rarely documented, in either marine or terrestrial ecology, presumably because of the lack of long time-series (Hjort, 1914; Cushing, 1975; Hassell *et al.*, 1989). This fact stresses the importance of retaining time-series of population abundance (or proxies of abundance) over long periods if the aim is to detect and describe the

principal sources of variability (Fromentin *et al.*, 1998; Bjørnstad *et al.*, 1999).

Long-term fluctuations in fish abundance have been demonstrated for several Atlantic fish populations (see Cushing and Dickson, 1976; Cushing, 1982; Alheit and Hagen, 1997). They have been commonly related to three main factors:

- (1) human activity, mainly through overexploitation and pollution of spawning and nursery areas,
- (2) environmental changes,
- (3) biotic processes, such as predation, cannibalism and competition.

Overexploitation is a well known feature of many North Atlantic fish populations (Myers *et al.*, 1996; Cook *et al.*, 1997). However, it is unlikely to explain the 100–120 years cycle of variations in bluefin tuna abundance because, first, exploitation cannot lead to cycles of about the same length (more than a century) over different periods and in different locations, second, traps are passive gear, and third, the number of traps remained more or less constant over the period analysed, so effort is likely to have been constant. In the case of bluefin tuna, therefore, it is likely that factors (2) and/or (3) were more influential. Biotic and environmental factors can effect long-term variations in bluefin tuna trap catches, through enhancing or impacting recruitment. Environmental events mainly affect fish recruitment through changes in:

- sea temperature, which influences the daily development and mortality of the eggs and fish larvae (Pepin, 1991; Ottersen and Sundby, 1995),
- food availability, i.e. the match-mismatch hypothesis (Hjort, 1926; May, 1974; Cushing, 1990) and/or the impact of the wind and current at a large (dispersal of fish eggs and larvae, Hjort, 1926; Lasker, 1975) and small scale (turbulence playing a role in prey encounter rates; MacKenzie and Leggett, 1991; MacKenzie *et al.*, 1994; Kiørboe and MacKenzie, 1995).

Biotic processes, such as predation, cannibalism, and competition resulting from food and habitat limitations, can also generate cycles and long-term fluctuations in fish stocks, through density-dependent-mortality/growth and resonant effects (Caley *et al.*, 1996; Knell, 1998; Bjørnstad *et al.*, 1999; Fromentin *et al.*, 2000b).

The environment certainly influences migration patterns of fish populations (e.g. the West Greenland cod stock; Cushing, 1982). It could therefore be argued that the 100–120 years cycle in catches of bluefin tuna by the trap fishery may have been the result of a switch between Mediterranean and West Atlantic spawning sites attributable to changes in oceanographic conditions and/or food availability. Past research and mark-recapture studies indicated that bluefin tuna migrate annually to well-defined spawning areas, i.e. they con-

duct established “homing behaviour” (Cury *et al.*, 1998). Moreover, Polovina (1996) demonstrated decadal variations in the trans-Pacific migration of northern bluefin tuna in relation to climate-induced change in prey abundance, but also stressed that the spawning areas never changed. Such arguments tend to dismiss a hypothesis of changes in migration patterns, but it must be kept in mind that most of studies cited were performed over a short period and covered recent trends only.

Our main hypothesis is therefore based on the old, but still pertinent, concept of Hjort (1914, 1926), according to which the 100–120 years cycle in bluefin tuna abundance would result from annual fluctuations in recruitment. Eastern bluefin tuna are widespread and only reproduce in a small spatial and temporal window (around the Balearic islands and in the south Tyrrhenian Sea from mid-May to June, Mather *et al.*, 1995). Therefore, recruitment of bluefin tuna is more likely to vary from year to year than recruitment of tropical tuna populations, which reproduce over large areas and in more stable waters (Fromentin and Restrepo, 2001). This feature is of particular interest, because Bjørnstad *et al.* (1999) demonstrated that short-term variability in recruitment of fish combined with cannibalism between juveniles may induce long-term fluctuations because of the resonant effects. Furthermore, Fromentin and Fonteneau (2001) showed that noise in recruitment combined with a large number of classes of spawners could also lead to long-term variations in spawning stock biomass and yields, as well as to regular cycles, depending on the lifespan of the species. These last theoretical findings appear consistent with the present results, which show a 15–30 years cycle concomitant to the bluefin tuna lifespan. This feature could further provide an hypothesis to explain the collapse of the Nordic fishery for bluefin tuna in the mid-1960s (Tiews, 1978; Marsac, 1998) and its reappearance after 30 years (Olafsdottir and Ingimundardottir, 2000).

Fisheries implications

Atlantic bluefin tuna are mainly managed by quotas and size limits (ICCAT, 2001). In the long term, the Convention upheld by the International Commission for the Conservation of Atlantic Tunas (ICCAT) as well as the precautionary approach imply that Atlantic tuna stocks should be managed by strategies based on maximum sustainable yield, i.e. based on models that often assume that the population is at an equilibrium or steady state (Hilborn and Walters, 1992). The current results have shown annual and long-term variations in abundance of bluefin tuna, so the concept of maximum sustainable yield may be irrelevant for the eastern Atlantic population. The temperate life history traits of the species (slow growth, late age at maturity, short

spawning duration, long lifespan) make it more vulnerable to exploitation than tropical tuna (Fromentin and Fonteneau, 2001). Therefore, definition of a suitable precautionary approach that would take into account the natural variability of the stock by determining, for instance, a level of reference that is time-dependent instead being a simple reference point, is crucial in terms of fisheries management.

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Appendix

Columns represent the time-series index of the trap, the total period over which data are available (including missing values), the total number of observations during that period, the units of the original data (N=number of fish, B=number of barrels, T=weight in tons), and the sources of the data (* personal archives of A. Scaccini and M. Sella provided by C. Piccinetti, Fano Laboratory, Italy; ** personal archives of J. Rodriguez-Roda given by his widow to the ICCAT secretariat; *** archives of Medina Sidonia duchy provided by the duchess).

| No. | Trap name | Period | Total observations | Units | Source |
|-----|------------------|-----------|--------------------|-------|--|
| 1 | Sul do Cabo | 1896–1917 | 21 | N | Scaccini & Sella* |
| 2 | Senohra da Rocha | 1897–1919 | 23 | N | Scaccini & Sella* |
| 3 | Olhos de Agua | 1896–1919 | 24 | N | Scaccini & Sella* |
| 4 | Forto Novo | 1896–1920 | 25 | N | Scaccini & Sella* |
| 5 | Ramalhete | 1896–1930 | 35 | N | Scaccini & Sella* |
| 6 | Cabo Santa Maria | 1896–1933 | 38 | N | Scaccini & Sella* |
| 7 | Livramento | 1876–1933 | 58 | N | Scaccini & Sella* |
| 8 | Barril | 1867–1933 | 67 | N | Scaccini & Sella* |
| 9 | Medo das Casas | 1896–1933 | 112 | N | Scaccini & Sella* |
| 10 | Abobora | 1885–1933 | 49 | N | Scaccini & Sella* |
| 11 | Sul da Ponta | 1902–1926 | 25 | N | Scaccini & Sella* |
| 12 | Torre de Barra | 1897–1917 | 21 | N | Scaccini & Sella* |
| 13 | Reine Regente | 1914–1940 | 26 | N | Scaccini & Sella*, Rodriguez-Roda** |
| 14 | Isla Cristina | 1929–1965 | 37 | N | Rodriguez-Roda** |
| 15 | Las Torres | 1902–1954 | 34 | N | Scaccini & Sella*, Rodriguez-Roda** |
| 16 | Arroyo Hondo | 1914–1934 | 20 | N | Scaccini & Sella*, Rodriguez-Roda** |
| 17 | Sancti Petri | 1884–1971 | 57 | N | de Buen (1925), Scaccini & Sella*, Rodriguez-Roda** |
| 18 | Torre Atalaja | 1914–1934 | 20 | N | Scaccini & Sella*, Rodriguez-Roda** |
| 19 | Barbate | 1884–1980 | 69 | N | Scaccini & Sella*, Rodriguez-Roda** |
| 20 | Zahara | 1804–1980 | 43 | N | Medina Sidonia***, Pavesi (1889), Scaccini & Sella*, Rodriguez-Roda** |
| 21 | Tarifa | 1914–1971 | 46 | N | Rodriguez-Roda** |
| 22 | Punta Negra | 1936–1971 | 34 | N | Rodriguez-Roda** |
| 23 | Aguas de Ceuta | 1940–1970 | 31 | N | Rodriguez-Roda** |
| 24 | Principe | 1940–1972 | 32 | N | Rodriguez-Roda** |
| 25 | Sidi Daoud | 1863–1997 | 130 | N; T | Scaccini & Sella*, Hattour (pers. comm.), Mather <i>et al.</i> (1995) |
| 26 | Ras El Ahmar | 1905–1941 | 35 | N; T | Scaccini & Sella*, Hattour (pers. comm.) |
| 27 | Monastir | 1894–1938 | 37 | N | Scaccini & Sella*, Hattour (pers. comm.) |
| 28 | Conigliera | 1897–1937 | 33 | N | Scaccini & Sella* |
| 29 | Bordj Khadidja | 1903–1929 | 23 | N; T | Hattour (pers. comm.), Piccinetti & Omiccioli (1999) |
| 30 | Formica | 1599–1978 | 305 | N; B | Cancila (1972) |
| 31 | Favignana | 1599–1997 | 321 | N; B | Scaccini & Sella*, Doumenge (pers. comm.) |
| 32 | San Giuliano | 1600–1934 | 131 | N | Cancila (1972) |
| 33 | Osinelli | 1904–1929 | 26 | N; T | Scaccini & Sella*, Heldt (1931, 1937) |
| 34 | San Cusumano | 1896–1964 | 63 | N | Scaccini & Paccagnella (1965a) |
| 35 | Bonagia | 1599–1964 | 241 | N; B | Cancila (1972) |
| 36 | Cofano | 1657–1798 | 74 | N | Scaccini & Sella*, Pavesi (1889), Heldt (1930, 1931, 1932, 1937), Hamre <i>et al.</i> (1966) |
| 37 | Secco | 1874–1964 | 64 | N | Cancila (1972) |
| 38 | Scopello | 1909–1967 | 36 | N; T | Scaccini & Paccagnella (1965a), Heldt (1930, 1931, 1932, 1937), Hamre <i>et al.</i> (1966) |
| 39 | San Giorgio | 1880–1963 | 78 | N; T | Scaccini & Paccagnella (1965b) |
| 40 | San Elia | 1909–1929 | 19 | N | Scaccini & Sella*, Gamberini (pers. comm.) |
| 41 | Solanto | 1909–1929 | 19 | N | Scaccini & Sella*, Scaccini & Paccagnella (1965b) |
| 42 | San Nicola | 1909–1929 | 19 | N | Scaccini & Sella* |
| 43 | Trabia | 1909–1929 | 19 | N | Scaccini & Sella* |
| 44 | Castellamare | 1909–1931 | 21 | N | Scaccini & Sella*, Heldt (1930, 1931, 1932) |

Appendix *continued*

| No. | Trap name | Period | Total observations | Units | Source |
|--------------------|----------------|-----------|--------------------|-------|--|
| 45 | Magazzinazzi | 1892–1961 | 60 | N; T | Scaccini & Sella*, Scaccini & Paccagnella (1965a, b), Hamre <i>et al.</i> (1968) |
| 46 | Oliveri | 1904–1967 | 62 | N | Piccinetti & Omiccioli (1999), Scaccini & Paccagnella (1965b) |
| 47 | Tonno | 1885–1963 | 77 | N | Piccinetti & Omiccioli (1999), Scaccini & Paccagnella (1965b) |
| 48 | Marzamemi | 1830–1931 | 58 | N; T | Scaccini & Sella* |
| 49 | Pizzo | 1876–1932 | 52 | N | Scaccini & Sella* |
| 50 | Saline | 1788–1964 | 116 | N | Pavesi (1889) |
| | | | | N | Scaccini & Sella*, Pavesi (1889), Rubino (1995) |
| 51 | Flumentorgiu | 1787–1932 | 69 | N | Pavesi (1889) |
| | | | | N | Scaccini & Sella*, Heldt (1930, 1931, 1932, 1937) |
| 52 | Porto Paglia | 1787–1973 | 143 | N | Pavesi (1889), Conte (1985) |
| 53 | Porto Scuso | 1787–1976 | 153 | N | Pavesi (1889), Conte (1985) |
| 54 | Isola Piana | 1787–1980 | 155 | N | Pavesi (1889), Conte (1985) |
| Beach-seine | | | | | |
| | Zahara | 1503–1804 | 184 | N | Medina Sidonia*** |
| | Conil | 1503–1809 | 221 | N | Medina Sidonia*** |
| | Conilejo | 1525–1722 | 32 | N | Medina Sidonia*** |
| | Rio del Terron | 1741–1768 | 28 | N | Medina Sidonia*** |
| | Carboneras | 1743–1766 | 24 | N | Medina Sidonia*** |