

## UPDATE OF THE ABUNDANCE INDEX FOR JUVENILE FISH DERIVED FROM AERIAL SURVEYS OF BLUEFIN TUNA IN THE WESTERN MEDITERRANEAN SEA

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### SUMMARY

*The last stock assessment of Eastern Atlantic Bluefin Tuna (EABFT) is showing reassuring trends regarding the status of the stock. However concerns are still raised about the effectiveness of using fisheries-based data as indices of relative abundance. The present manuscript presents a fisheries abundance index for juvenile fish obtained from summer aerial surveys that have been carried out in the western Mediterranean Sea, the Gulf of Lions, since 2000. The dataset amounts to 12 years of data depicting the spatio-temporal variability of EABFT over the Gulf of Lions. Compared to 2016, a line transect approach was applied instead of the strip transect approach to estimate the density. The two density estimates showed very comparable trends but with a reduced inter-annual variability for the line transect approach. Regarding the 2017 stock assessment, there is a need for indices that are (i) fisheries-independent, (ii) for juvenile fish and (iii) from the Mediterranean. As diagnostics from previous VPA sensitivity runs were satisfactory, this index has thus a potential to be included in the runs.*

### RÉSUMÉ

*La dernière évaluation du stock de thon rouge de l'Atlantique Est (EABFT) montre des tendances rassurantes quant à l'état du stock. Cependant, des inquiétudes persistent quant à l'efficacité de l'utilisation de données fondées sur les pêcheries comme indices de l'abondance relative. Ce document présente un indice d'abondance des pêcheries pour les poissons juvéniles obtenu à partir de prospections aériennes effectuées en été dans la Méditerranée occidentale, le golfe du Lion, depuis 2000. Le jeu de données couvre 12 ans de données représentant la variabilité spatio-temporelle de l'EABFT dans l'ensemble du golfe du Lion. Par rapport à 2016, une approche de transect en ligne a été appliquée au lieu de l'approche de transect en bande pour estimer la densité. Les deux estimations de la densité ont montré des tendances très comparables, mais avec une variabilité interannuelle réduite dans le cas de l'approche de transect en ligne. En ce qui concerne l'évaluation des stocks de 2017, des indices (i) indépendants des pêcheries, (ii) concernant les poissons juvéniles et (iii) provenant de la Méditerranée sont nécessaires. Étant donné que les diagnostics des scénarios antérieurs de sensibilité de la VPA étaient satisfaisants, cet indice pourrait être inclus dans les scénarios.*

### RESUMEN

*La última evaluación del stock de atún rojo del Atlántico este (EABFT) muestra tendencias tranquilizadoras sobre el estado del stock. Sin embargo, persiste cierta preocupación en cuanto a la efectividad de utilizar datos basados en la pesquería como índices de abundancia relativa. En este documento se presenta un índice de abundancia de la pesquería para peces juveniles obtenido de prospecciones aéreas realizadas en verano en el Mediterráneo occidental, golfo de León, desde el año 2000. El conjunto de datos reúne 12 años de datos que representan la variabilidad espacio-temporal del EABFT en el golfo de León. En comparación con 2016, para estimar la densidad se aplicó un enfoque de transecto lineal en lugar del enfoque de transecto de franja. Las dos estimaciones de densidad mostraron tendencias muy similares, pero con una menor variabilidad interanual cuando se aplicó el enfoque de transecto línea. Con respecto a la*

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*evaluación de stock de 2017, se requieren índices que sean (i) independientes de la pesquería, (ii) para los peces juveniles y (iii) del Mediterráneo. Dado que los diagnósticos de anteriores ensayos de sensibilidad VPA fueron satisfactorios, este índice tiene potencial para ser incluido en los ensayos.*

#### KEYWORDS

*Juvenile Atlantic bluefin tuna; northwest Mediterranean; fisheries independent abundance index; aerial survey*

## 1. Introduction

The eastern stock of Atlantic Bluefin tuna (*Thunnus thynnus*) have been estimated to be strongly overfished and considered as overexploited during several years, to the point that the 2006 stock assessment suggested a substantial risk of fisheries and population collapse (ICCAT 2007). This situation has substantially changed nowadays as the last stock assessment pointed towards a recovery of the stock (ICCAT 2015). However such a reinsuring trend needs to be confirmed, as the data used for assessing this stock still mainly originate from commercial catches.

Fishery-based data are often used as an index of relative abundance within stock assessments, particularly when a regular survey is not feasible (Hilborn & Walters, 1992; Maunder *et al.* 2006). This is the case for Atlantic Bluefin tuna (ABFT), a highly migratory species that displays an oceanic-wide repartition. Factors such as changes or variations in catchability (e.g. changes in fleet composition and increase in effort vessels) are complex to thoroughly follow and to account for when building such an index of relative abundance, which may lead to inadequate conclusions about trends in abundances (Bishop *et al.*, 2008).

Building CPUE indices based upon Mediterranean purse seine data is therefore problematic, particularly considering the complexity to quantify the effort for this type of fisheries, the management decisions that have affected this fishery during the past decade and the modifications of practices that followed. Relying upon fisheries data for assessment would have been even more problematic in the case of a potential halt in the fishery, for instance resulting from the listing in Appendix I of the Convention of International Trade of Endangered Species (CITES). The lack of index for young fishes and from the Mediterranean as well as the doubts about the biological validity of current trends, all points towards the critical need for an operational fishery-independent index to follow the evolution of the stock. However, in the case of ABFT, only a few scientific or fisheries-independent data are available. This is a recurrent problem for large pelagics, as operational means to acquire fishery-independent data on such mobile species are heavy to implement, costly and/or technically hardly conceivable.

For marine organisms that have a consistent surfacing behaviour, such as turtles and marine mammals, using aerial surveys to estimate density of individuals is a fairly common alternative (Lauriano *et al.* 2011, Panigada *et al.* 2011). As spotting tuna schools from aircrafts was used to improve the efficiency of the purse seine fishery during a long time (Petit *et al.* 1990, Scott & Flittner 1972), it is a natural candidate considered for tuna stock assessment (Hoggard 1995, Polacheck *et al.* 1998, Lutcavage & Newlands 1999, Natale 2011). For example, since 1993, aerial spottings are regularly carried out along the Southern Australian coasts to compute an index of abundance of Southern bluefin tuna juveniles (Cowling & O'Reilly 1999, Eveson *et al.* 2012). Regarding ABFT, only a few attempts of aerial surveys have been made for mature fish along their migration pathways at the Great Bahama Banks (Lutcavage & Kraus 1997, Lutcavage & Newlands 1999, Newlands *et al.* 2006). ICCAT has initiated a research program to develop fishery-independent abundance indices for mature ABFT to improve stock assessment from aerial surveys over Mediterranean breeding areas (GBYP; ICCAT 2012).

The Gulf of Lions, with its large shelf region and numerous canyons is a nursery ground for ABFT (Farrugio 1977). This region is known to be one of the most productive in the Mediterranean Sea. Since the year 2000, aerial surveys have been carried out from June to October in the western Mediterranean Sea, the Gulf of Lions. These aerial surveys initiated for the EU project STROMBOLI (2000-2002) and subsequent surveys (2003 and 2009-2015) were funded by the Agriculture and Fishing Minister, the Agence de l'eau Rhône Méditerranée Corse and IFREMER to monitor the ABFT Mediterranean stock (Fromentin *et al.* 2003). A 5-year gap in the data series (2004-2008) impaired its use as a relative abundance index during past assessments (Bonhommeau *et al.* 2010). The dataset now amounts to 11 years of data depicting the spatio-temporal variability of ABFT over the Gulf of Lions and is worth being considered for stock assessment. This abundance index has been used in past stock assessments as sensitivity runs but is not currently included in the base case run. The diagnostics of the quality of the fit of the VPA to this index actually show that it has a strong potential to be included to the runs.

In 2016 a manuscript presented the available dataset and described the change in the spatio-temporal distributions of the detected BFT schools since the program was implemented (Rouyer *et al.* 2016). In the present manuscript, we use the theory of distance sampling to estimate a time-series of densities to build an index of abundance. Whereas the index presented in 2016 used a strip transect approach, in the present manuscript the line transect approach was applied, which allowed to account for the different factors affecting the detectability. Further improvements that could be implemented to increase the robustness of this index are then presented before discussing the perspectives offered by these data to study the link to environmental conditions and prey abundance and distribution.

The present manuscript argues that these data consistently describe changes that occurred in the ABFT eastern stock since the 2000. In the present context of ABFT stock assessment, this index could be fruitfully used as an index of abundance for ages 2-4 by ICCAT working group for future stock assessments.

## **2. Materials and method**

### **2.1 Data acquisition**

Aerial surveys have been carried out from 2000 to 2003, stopped from 2004 to 2008 because of lack of funding, and the activity has been continuous since 2009. The surveys always take place during the same period, June-October over the Northwestern Mediterranean Sea, in the Gulf of Lions. This period and location correspond to the traditional fishing season of young ABFT by the French purse seiners and is favourable to school detections as ABFT jump and/or swim rapidly at the surface, probably in relation to feeding and/or foraging activity.

Depending on weather conditions, up to 20 flights per year were conducted onboard a Cessna C skymaster 337 “push pull” aircraft at 1000 feet above sea level. This type of aircraft has the advantage to have its wings above the lateral windows, which offers a better overview for the observers. This plane allowed to embark one pilot and two scientists. Thanks to extra funding, from 2012 to 2013 a larger plane, a Cessna Caravan 208 ISR, allowed to embark a larger crew involving two pilots, an IT and video specialist as well as two scientists. This plane allowed for greater flight times, enabling to fly over the whole Gulf of Lions within one day against two with the Cessna skymaster 337. The plane was flying higher, 1500ft, and a high resolution, gyro-stabilized video-camera allowed to record the flight and to obtain accurate geolocation and images for specific school detections.

The aerial surveys take place around noon when the sun is at its highest to avoid glaring and blinding the observers. Flights were constrained to days for which weather conditions suitable, sunny sky and low wind speed (<10nm/h), to avoid confusion between schools and whitecaps and to ensure optimal detections. Such weather requirements make summer the optimal season for the survey, whereas spring and autumn are more constraining.

Four different routes were defined for the surveys (Figure \ref{fig:Routes}), which were comparable in length 667, 648, 580, and 700 km for route 1-4 respectively. The inter-transect distance of 13.8 km reduces chances of double counting schools on subsequent transect lines due to tuna migrations, because tunas are almost exclusively sighted feeding. At the constant speed of 222 km/h employed for the surveys, these routes can be flown in less than 5 hours including distance between airport and transect, which complies with the aircraft fuel autonomy and security requirements. For each flight, the route was randomly selected. However, practical constraints such as weather conditions often interfere. The observers onboard and weather conditions were thus recorded for each survey and transect sections with unsuitable conditions (clouds and/or breaking waves) were skipped. When the route could not be selected randomly, special attention was paid to maximising the coverage of the area and to evening out the amount of times the route were flown.

Tuna schools were spotted by 1 to 3 trained scientific observers, from both sides of the plane/transects, while the pilots provided supplementary sightings on the transect line. A GPS was used to record the position of the plane and detected tuna schools. Each detected school was termed as “tiny”, “small”, “medium”, “large”, “very large” or “aggregation” for high concentrations of schools and rough size estimates were made when possible. For this last class as it is actually impossible for spotters to accurately count the number of schools, it has been decided to delineate an area in which the school density is more or less homogenous rather than a number. The spotting conditions such as the wind strength (beaufort scale) and the number of observers onboard were recorded.

To obtain a reliable index several aspects must be considered and kept in check. First, the objects must be detected at their initial position, prior to any movement in response to the presence of observers. Second, the detectability must decrease with the perpendicular distance from the route and the objects directly on the transect must be detected with a probability of 1. Finally, the perpendicular distances from the route must be measured accurately, the track of plane and the locations of the detected objects must be as precise as possible.

## 2.2 Statistical approach

### 2.2.1 Spatio-temporal distributions

The detected schools for each year were plotted on maps to investigate their spatial distribution. The schools were reported to belong to different size classes and an arbitrary weight was attributed to each school size. The weights were set to 1, 2, 3, 6, 9, and 12 for tiny, small, medium, large, very large schools and aggregation respectively. A kriging method was then applied to obtain a visual representation of the density of the detected schools. All computations were done with the R statistical language and the `mapdata`, `ggplot2` and `distance` packages.

### 2.2.2 Density estimates

The analysis of the aerial survey data was based on the distance sampling theory (Buckland *et al.* 1993). In the distance sampling theory the transects, here the routes, are defined within a given area, here the Gulf of Lions. The object of interest, here a tuna school, is recorded along the route, which is surveyed several times during a given period.

The strip transect method is the simplest to implement, as the width of detection from the line of transect is fixed and directly determined from the histogram. It has been used in the past as it is generally considered as a robust approach as it neither requires a minimum number of observations nor implies the distinction between primary and secondary detection, while being convenient to post-stratify. The implementation of this approach has been recommended to build an index of abundance for Southern Bluefin Tuna (Cowling & O'Reilly 1999).

In the strip transect approach, the density of the replicate  $i$  is estimated as follows:

$$\hat{D}_i = \frac{n_i}{2wL}$$

where  $\hat{D}_i$  is the density estimate, number of schools per unit area, of replicate  $i$ ,  $n_i$  is the number of tuna schools detected in the replicate  $i$ ,  $w$  the width of detection from the line of the transect and  $L$  is the total length of the transect.

The theory allows that some, perhaps many, of the objects remain undetected and that variation in detection due to environment or observer could occur, as soon as  $n$ ,  $L$  and  $w$  are accurately measured. According to the line transect theory,  $w$  is estimated through a detection function, which is a model fitted to the histogram of the perpendicular distances of the detections (Buckland *et al.* 1993; Chen 1996).

The line transect approach aims to estimate the detection probability per distance (detectability  $P$ ) and thus to calculate the percentage of sighted and non-sighted objects:

$$\hat{D}_i = \frac{n_i}{2wLP}$$

The detectability  $P$ , also known as observability or sightability (Pierce *et al.* 2012), is obtained by fitting a 'detection function' to the histogram of distances. It allows to account for other variables, such as school size or environmental conditions (e.g. wind). The shape of the detection function generally is a monotonically decreasing curve, showing a shoulder under which detection remains almost certain and is unaffected by other variables (Buckland 2001; Bauer *et al.* 2015). Here the hazard rate detection function was fitted to account for differences in detectability linked to the size class of the schools, the season of the flight (month), the number of observers onboard and the wind strength (beaufort scale). All possible models were fitted using these available factors. They were then ranked based upon their Akaike Information Criterion.

The mean density,  $\bar{D}$ , from  $r$  replicates is estimated as follows:

$$\bar{D} = \frac{1}{r} \sum_{i=1}^{i=r} \hat{D}_i$$

The variance between replicates is estimated as:

$$Var(D) = \frac{1}{r(r-1)} \sum_{i=1}^{i=r} (\hat{D}_i - \bar{D})^2$$

Time series of densities were computed for each model using an Horvitz-Thomson-like estimator for groups (i.e. clustered population), implemented in the R package *Distance* (Miller 2016). This approach was particularly appropriate for the present case study where schools are classified within different size categories. The models were then compared to each other by computing the sparman-rank correlation coefficient, in order to explore the robustness of the trend to the different models.

### 3. Results

#### 3.1 Spatial distribution of detected schools

The dataset amounted to a total of 2894 observations made over the Gulf of Lions. These observations displayed important differences over time and space. Since 2009, the spatial distribution of the schools detected occupies a wider area than in the early 2000s (**Figure 2**). Whereas schools seemed preferentially concentrated in the southwestern part of the sampled area in the early 2000s, since 2010 the school repartition appears more balanced over the Gulf of Lions. However, due to weather conditions, in 2010 flights were more constrained to the west of the Gulf of Lions. The detections displayed an expansion towards the northwest and the east with more frequent coastal detections made in the recent years. This trend seemed to be even stronger in 2014, 2015 and 2016 and corroborated field reports from small scale and recreative fisheries. For each year surveyed, substantial kernels of density were found to be located on the continental shelf where the oceanic floor plummets from 100m to 1000m. This was further marked for the earlier years of the survey, when higher concentrations were found in a box between 3.5 ° E and 4.5 ° E, and between 42.5 ° N and 43.5 ° N. Even if it generally complies with the previous observations, the low sample size of 2013 impairs an accurate interpretation of the spatial pattern.

#### 3.2 School size distribution

The distribution of school sizes detected over time did not show any substantial trend, excepted for the isolated individual detections that seemed to have increased in the past years (**Figure 3**). But on the contrary the ‘small’ school size seemed to have decreased in the same time. Aggregations were not spotted every year and displayed a uneven distribution across years, with higher percentages in 2009, 2010 and 2011.

#### 3.3 Detectability of schools

In accordance with the distance sampling theory, the number of detected schools decreased exponentially with the perpendicular distance (**Figure 4**) and more than 75% of the schools were detected at a perpendicular distance < 3.7 km (i.e 2 nautical miles). This pattern displayed inter-annual variations that were explained by lower sample sizes, such as 2013, or by a stronger focus on schools within the 3.7 km strip, particularly in 2014, 2015 and 2016 that led to less dispersed histograms. In particular, the large number of observations that were made during the 2016 survey did not allow the observers to focus as much on detections further away from the plane.

### 3.4 Models comparison

A total of 15 models were tested. The Spearman correlation coefficients ranged between 0.66 and 1, and 75% of the values were above 0.9. The p-values ranged between 0 and 0.0308, and 75% of the values were below 0.0002. The density time series displayed very similar patterns that suggested a robust trend (**Figure 5**). The best model selected included all parameters that affected the detection function, school size, number of observers, wind strength and month of flight. The fit of the detection curve and the visual inspection of the residuals were found satisfying (**Figure 6**).

### 3.5 Density estimates

The time series of densities displayed three clear periods (**Figure 7**). The early years of the survey, 2000-2003, displayed low densities, whereas the years 2009-2012 and the more recent years were consistently characterized by higher densities (**Table 1**). The average density of schools during the second period was found three times higher than over the first period, whereas the average density over the third period was almost four times higher than over the second period. The density peaked in 2016, which was a record year for the number of observations. The coefficient of variation did not change drastically over the years, but the early years of the survey were found to display on average higher values than the latest ones. In 2013, adverse weather and reduced availability of the plane substantially reduced the sampling effort. It was thus not believed to be comparable to other years and it was decided to discard it to avoid mis-interpretation.

## 4. Discussion

The present paper shows that the aerial surveys carried in the Gulf of Lions since 2000, is a long enough series suitable to depict the patterns of variations of juvenile ABFT in the Mediterranean. The trend observed in the series of school densities is consistent with recent stock assessment outputs (ICCAT 2014) and the current aerial surveys appear as a prime tool to monitor fish abundance and follow management measure efficiency, even though future improvements are considered to continue to reinforce the robustness of the trend.

In the present work, the line transect approach was chosen, because it allowed to account for differences in detectability linked to the size of the detected school. This did not affect the general trend of the time series, which kept its upward evolution with 2016 being the year with the most numerous schools detected in the history of the index. This approach also allowed to deal with the fact that the observations do not represent variations in individual abundance, but in number of schools. Indeed, the Horvitz-Thomson like estimator from the *Distance* package in R allows to obtain a density estimate for clustered populations (Miller 2016).

Nowadays, including the number of individuals within a school is not possible, although attempts have been made using information from the French PS catch data (Bauer *et al.* 2015). In Bauer *et al.* (2015) including the number of individuals within a school showed to substantially affect the inter-annual variability of the density time series, but the main pattern was found robust to this as recent years were found to be substantially higher than the early ones. This was not unexpected as the inspection of the relative composition of the size-classes of the school did not substantially evolve through time. However, the aggregations were found to be more frequent in 2009, 2010 and 2011.

In any case, stepping up to estimate individual abundance would require at one point or another direct observations to study the link between the size of the school detected at the surface and the actual size of the school beneath it. A perspective could be to use underwater observation with multi-beam echosounders to reconstruct the 3D shape of schools. This would also allow for a better understanding of school dynamics between the surface detections and possibly deeper schools. Alternatively, developments on the attenuation of light in sea waters in the ultraviolet bands (near 365nm) and light detection and ranging (LIDAR) are thus worth being followed as they could also be a strong perspective to follow the number of schools and assess the size of fish from pictures (Bonhommeau *et al.* 2010).

Improving our knowledge on ABFT behaviour and its links to environmental fluctuations and physical oceanography is also a key to obtain a more robust index. The detection of ABFT schools is affected by its behaviour in the water column, but also its availability within the Gulf of Lions. Contrary to marine mammals and reptiles, ABFT does not need to surface to breathe and its surfacing behaviour is rather related to feeding events. The vertical behaviour of ABFT has been documented to be substantially affected by the environmental conditions

and particularly the temperature of the surface layer. For instance, strong northern winds in the Gulf of Lions substantially affect water temperature and local productivity, which may in turn affect the vertical distribution of zooplankton and small pelagic fish, the main prey of juvenile ABFT in the GoL (Bauer *et al.* 2015b). In addition to this vertical movements, ABFT displays horizontal and short-term changes in distribution likely to be linked to changes in environmental conditions, independently from management regulations. Understanding the effect of this process on fish detectability during aerial surveys is of particular interest for a robust index. Additional aerial surveys over the other nursery areas for ABFT in the Mediterranean could partly solve that issue as it would improve the spatial representativeness of the survey and thus reinforce the index of juvenile abundance based on aerial surveys (ICCAT 2012). However, this would be heavy to implement and it would not allow to correct the whole time series. Approaches aiming at understanding short-term distribution changes, such as habitat suitability, constitute important steps for further research to improve the index of abundance. To this end, collecting electronic tagging data and detailed information on the regional oceanography will be pivotal.

The overexploitation of ABFT driven by both high fishing pressure and failure of management regulations (Fromentin *et al.* 2014) led to the enforcement by ICCAT of a multi-annual stock recovery plan in 2007. These measures substantially affected tuna fleets behaviour and impaired fisheries-derived abundance indices, in particular catch per unit effort (CPUE), used to monitor changes in the stock. Current indices available to ICCAT for carrying out stock assessment have now several strong limitations, which will be problematic for the next assessment:

- ⑩ The abundance index for large fish displays very high rates of increases, whose biological plausibility is currently questioned and thus so is the capacity of this index to accurately depict the stock biomass.
- ⑩ Despite the Mediterranean being the area where the largest fraction of the catches for the eastern stock are made, no recent abundance index from the Mediterranean has been used for the stock assessment.
- ⑩ The sole index for young fish used in the assessment is built on data from the Bay of Biscay baitboat fisheries. Since 2012, the Spanish baitboat fishery has sold most of its quota so that this index now comes from only four vessels in the French baitboat fishery.
- ⑩ Indicators from Moroccan and Spanish traps targeting large fish include released individuals. The Spanish trap index is not maintained anymore and the combined index only includes data from the Moroccan trap fishery since 2013.
- ⑩ Indicators from Japanese longliners targeting medium to large fish in the northeast Atlantic showed a strong increasing trend since 2010 and has remained at a substantially high level over the last five years. The combined effects of this high proportion of the 2003 year class, the contraction of the spatial coverage of the Japanese longliners in recent years may affect the ability of this index to track changes in bluefin tuna abundance.

In this context, the Aerial surveys presented in the present study represent a concrete and operational perspective to bridge a major gap in data availability, by providing a fishery-independent index for juvenile ABFT in the Mediterranean.

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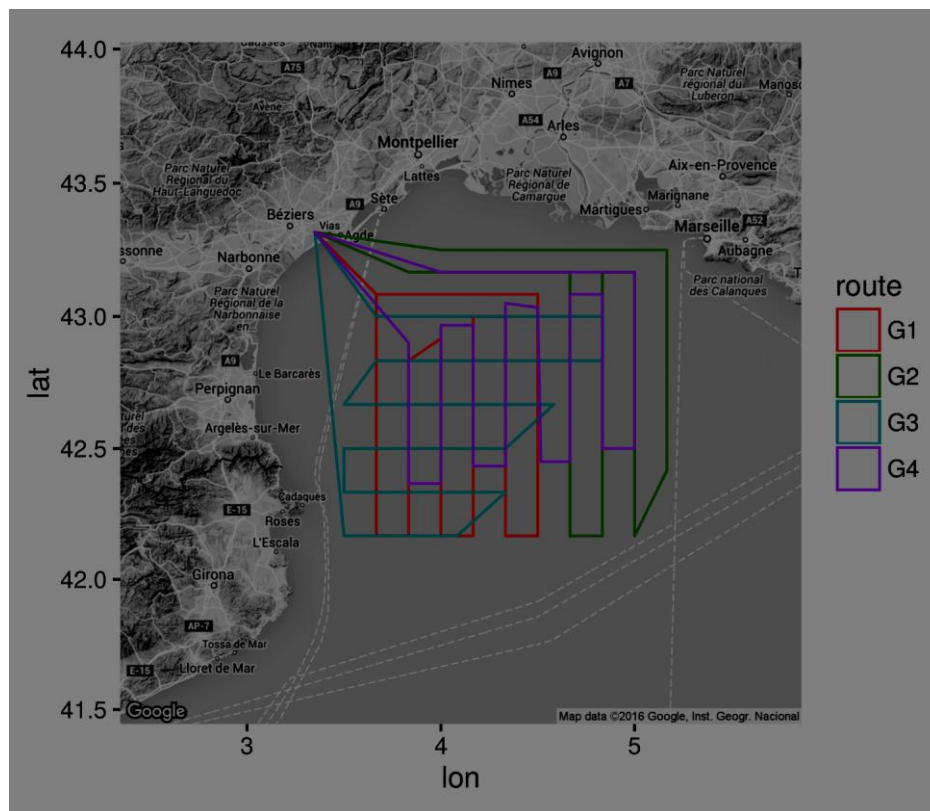
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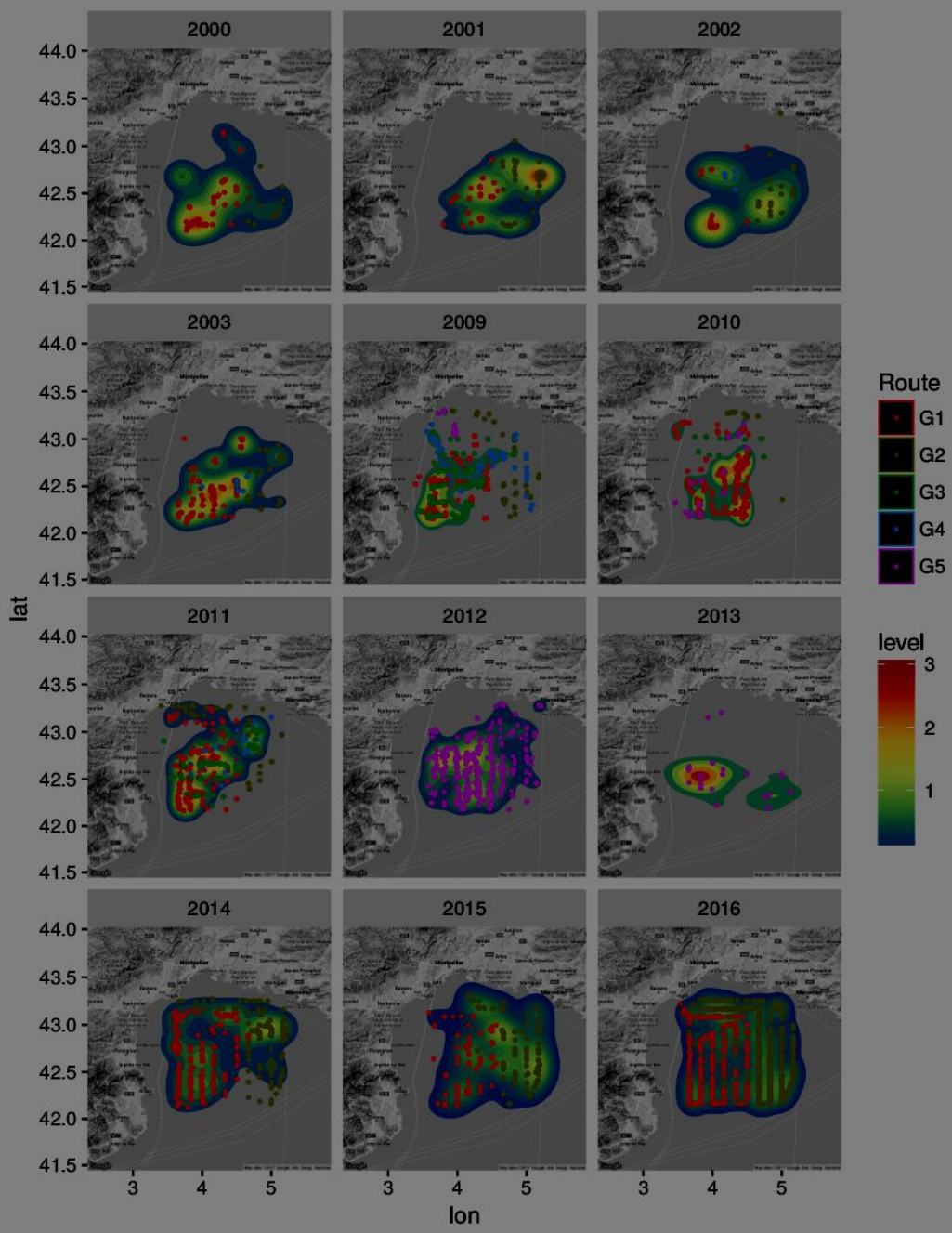
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**Table 1.** Densities and coefficient of variation for the line transect method.

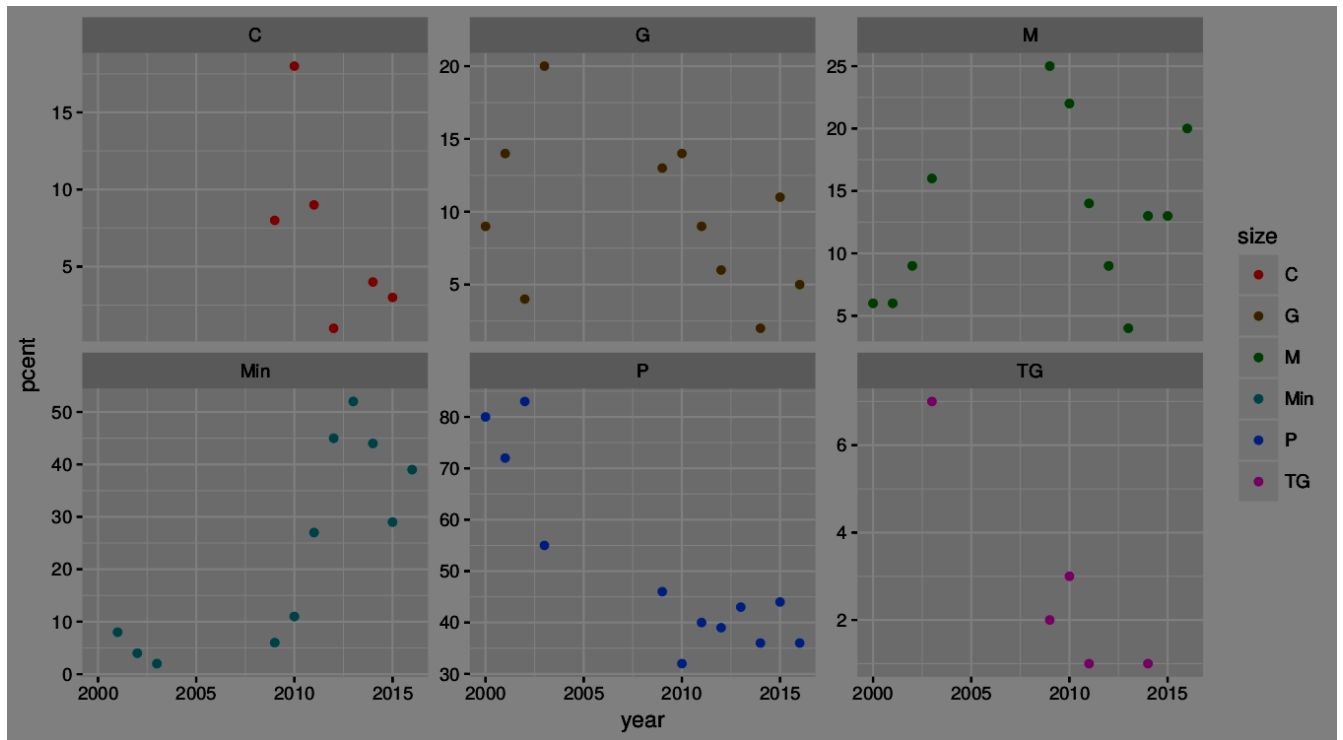
<i>Year</i>	<i>Density</i>	<i>CV</i>
2000	0.024	0.389
2001	0.014	0.374
2002	0.014	0.503
2003	0.015	0.346
2009	0.065	0.423
2010	0.040	0.520
2011	0.088	0.342
2012	0.038	0.316
2014	0.167	0.376
2015	0.087	0.337
2016	0.411	0.280



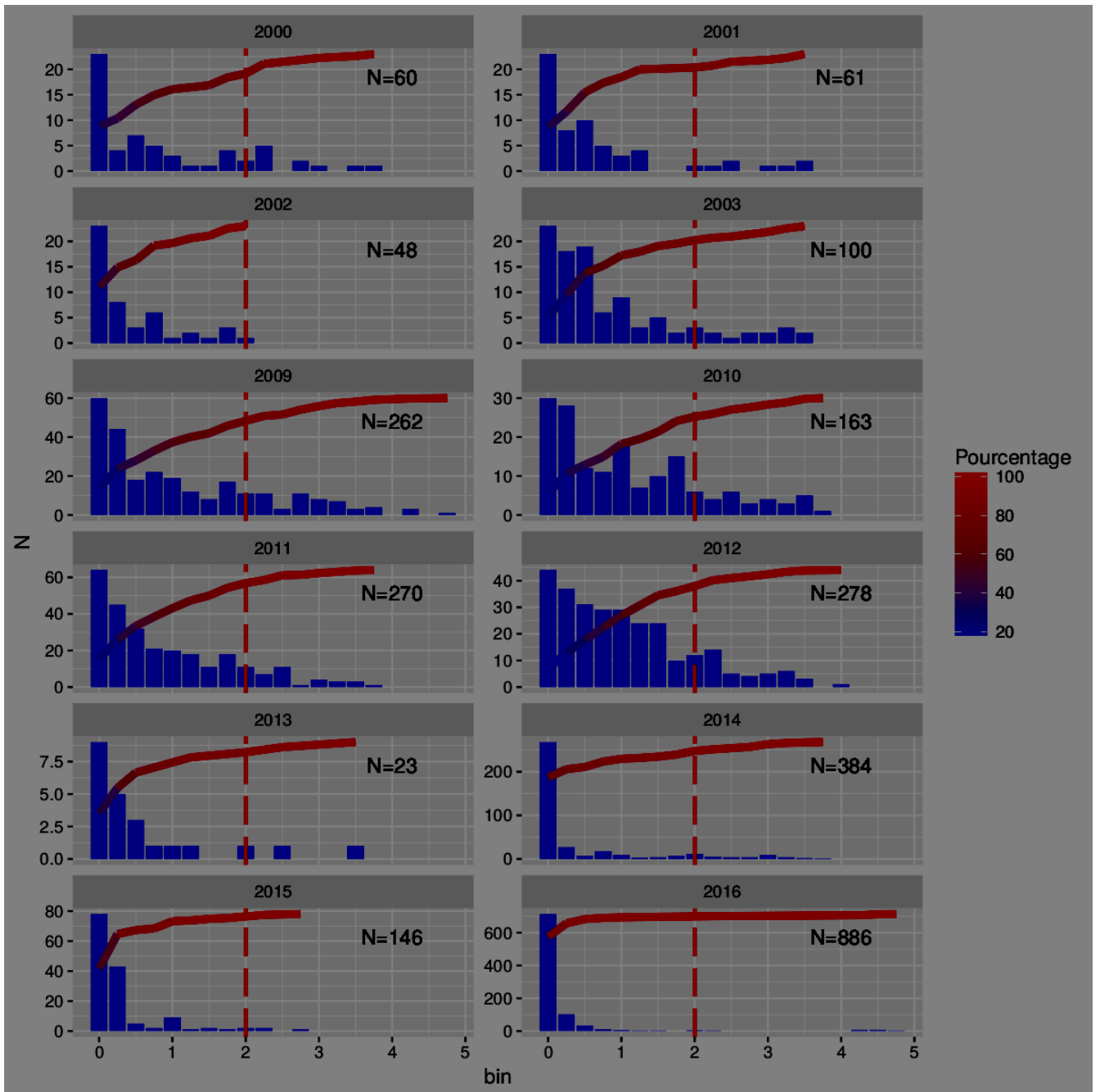
**Figure 1.** Maps of the different routes followed for the aerial surveys above the Gulf of Lions in the Northwestern Mediterranean.



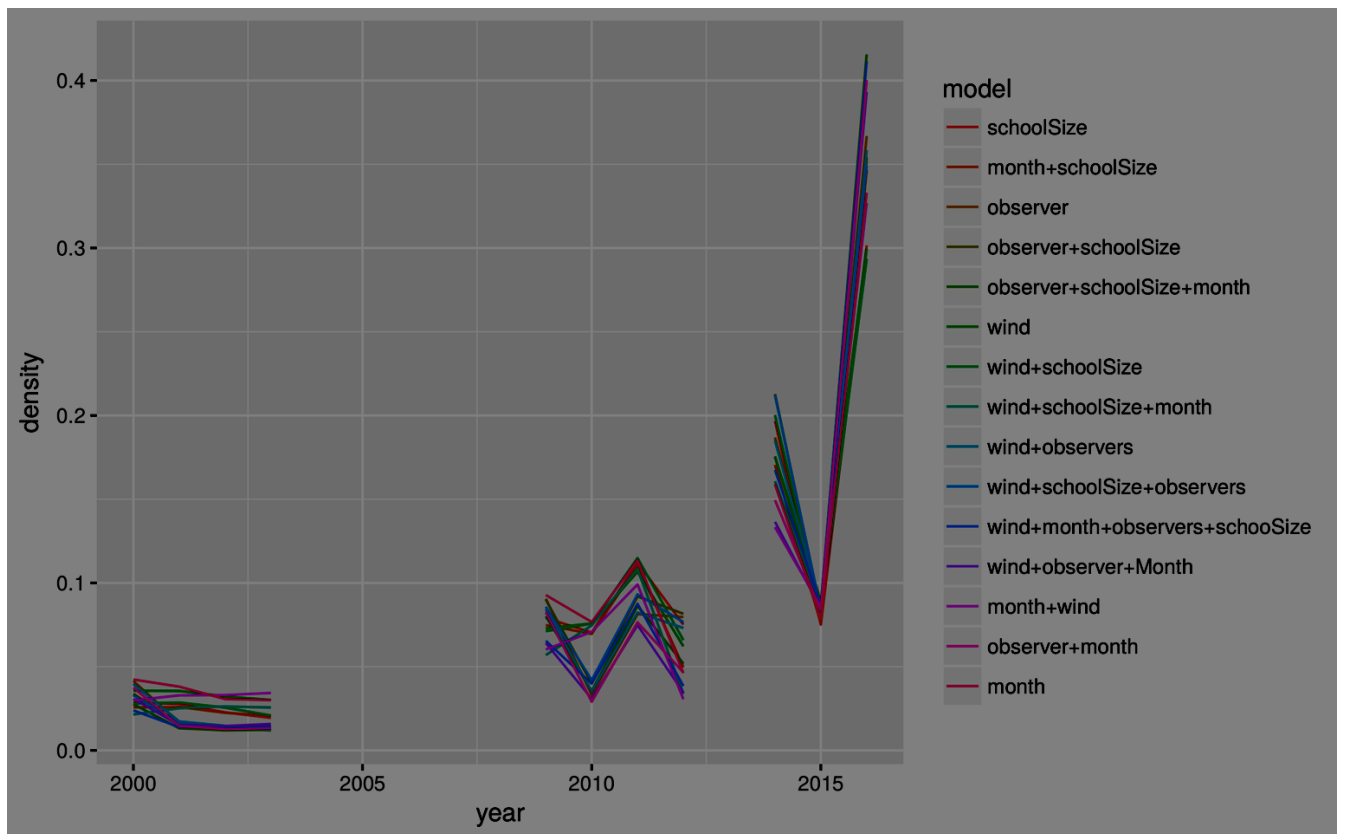
**Figure 2.** Spatial distribution of detected schools of BFT during aerial surveys led between 2000 and 2003 and between 2009 and 2015. As different size of school could be detected, a weight is allocated for each school and a kernel density (kriging method) is calculated to illustrate the relative density observed (colours are dimensionless and for illustration purposes only).



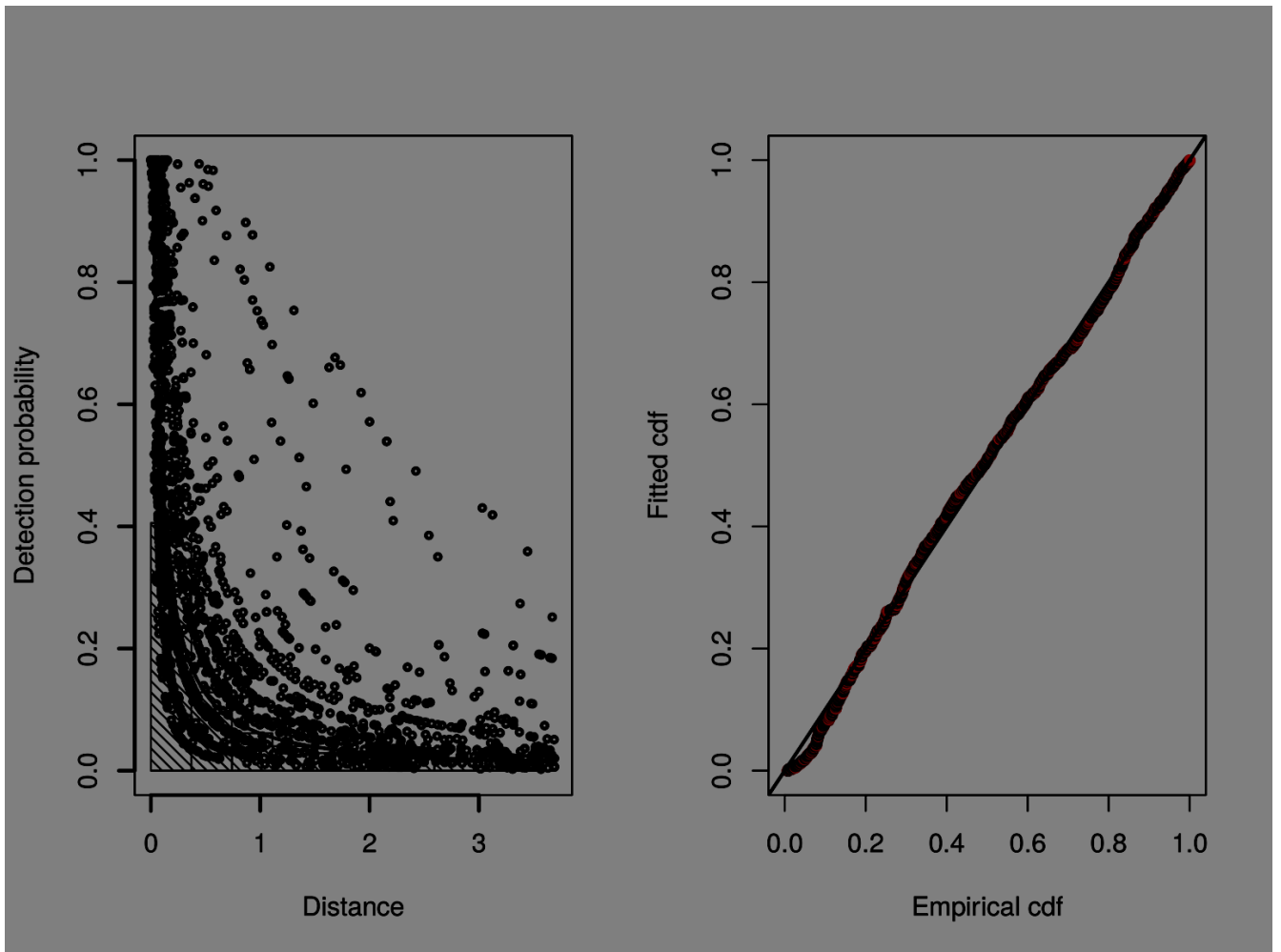
**Figure 3.** Relative importance (percent) of the different size classes of the bluefin tuna schools detected over year. The letters stands for the following school classes: C – Aggregation; TG – Very big; G – Big; M – Medium; P – Small; Min – One individual.



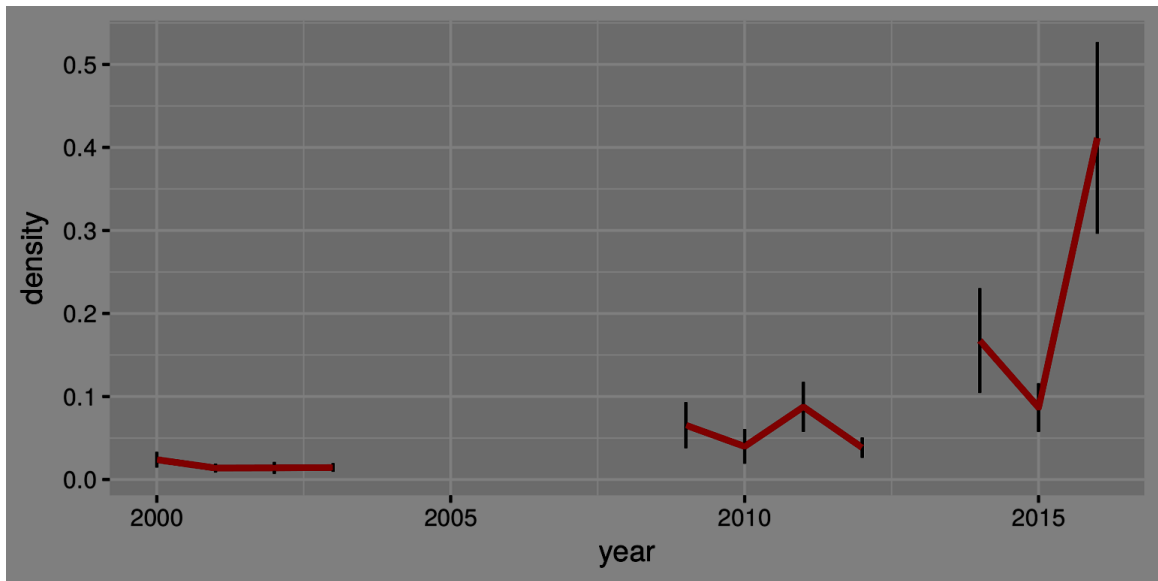
**Figure 4.** Histograms and cumulated percentage (blue to red line) of the number of schools detected, for each class of perpendicular distances to the route. The dashed line indicate the 2 nautical miles distance.



**Figure 5.** Time series of the density estimates for each detection function model tested.



**Figure 6.** Fitted detection functions and distribution of residuals for the best model. The left panel displays the detection functions fitted accounting for the different effects; the right panel displays a q-q plot of the distribution of the residuals.



**Figure 7.** Time series of the density estimates and standard errors between 2000 and 2016 for the best model.