



New insights on European hake biology and population dynamics from a sustained tagging effort in the Bay of Biscay

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Following a pilot experiment that fundamentally challenged the knowledge of European hake life traits (growth and age at first maturity), a sustained tagging effort was carried out in the Bay of Biscay from 2004 to 2007. Out of 27 690 fish tagged between 2002 and 2007, 1199 (4.3%) have been recovered to date. These data have permitted a refinement of the growth parameters of the species, analysis of interannual variability, improved understanding of movements and migrations, and an examination of natural (M) and fishing mortality (F). Both L_{∞} and K of a von Bertalanffy growth model could be estimated using a robust non-linear regression procedure. Growth varied significantly between years, which is likely related to variation in environmental factors such as temperature. Data did not reveal seasonal movements of fish perhaps because of poor tag return rates from offshore fleets. However, results clearly revealed homing behaviour and/or inshore residency. Confounding factors hindered the estimation of mortality, which resulted in high estimates of M . The outcomes of this experiment led to substantial changes in the stock assessment conducted by ICES and call into question the findings of previous studies that have used erroneous age-based data to address topics on the ecology and dynamics of this species.

Keywords: age validation, attrition model, fishing mortality, growth, maturity, migration, natural mortality.

Introduction

European hake (*Merluccius merluccius*) is widely distributed over the Northeast Atlantic shelf from Norway to Mauritania, with a larger density from the British Isles to south of Spain, and in the Mediterranean and Black Sea (Casey and Pereiro, 1995). It is one of the most important demersal species in the Northeast Atlantic, exploited mainly by Spain (around 60% of the current landings) and France (around 25%), whereas the UK, Denmark, Ireland, Norway, Belgium, Netherlands, Germany, and Sweden account for the remaining landings. Genetic studies (Roldan *et al.*, 1998; Cimmaruta *et al.*, 2005; Pita *et al.*, 2011) have not shown clear evidence of multiple populations in the Northeast Atlantic. However, since the end of the 1970s, ICES has assumed two different stock units: the so-called northern stock (Division IIIa, Subareas IV, VI, and VII, and Divisions VIIIa, b, and d) and the southern stock (Divisions VIIIc and IXa) along the Spanish and Portuguese coasts. Both stocks have recently suffered from overexploitation, and the European Commission has implemented emergency plans

for the recovery of the stocks since 2001 (ICES, 2010a). The perception of the population dynamics has long been impeded by two main shortcomings: (i) the controversial estimation of critical life traits (including growth) and (ii) the lack of reliable discard series. Both limitations are being addressed through dedicated data collection and research. Regarding the latter, conventional tagging recently opened new avenues for a better understanding of the biology and population dynamics of the species (de Pontual *et al.*, 2003). Tagging data provided evidence of substantial growth underestimation due to age overestimation (de Pontual *et al.*, 2006), thus challenging the internationally agreed age estimation method. The implications of such a finding on the perception of past stock dynamics and fishery management were addressed through simulations (Bertignac and de Pontual, 2007). Results were consistent with previous simulation studies based on age-structured stock assessment models (e.g. Kimura, 1990; Coggins and Quinn, 1998) and showed a significant impact of bias on medium- and long-term predictions, which impeded the efficiency of management measures

(e.g. those aimed at a reduction in fishing mortality). This is especially unacceptable in the context of the international commitment (United Nations, 2002) to move stocks to levels where they produce maximum sustainable yield by 2015. More tagging efforts, off the northwest Iberian Peninsula (Pineiro *et al.*, 2007) and in the Mediterranean Sea (Mellon-Duval *et al.*, 2010), have recently proved that growth underestimation was not a regional issue. Besides, a large tagging effort was sustained in the Bay of Biscay from 2004 to 2007 to (i) refine the growth estimation of the species and investigate potential interannual growth variability, (ii) learn about movements and migrations, (iii) investigate natural and fishing mortality, and (iv) evaluate the accuracy and precision of the age estimation method by examination of otoliths recovered from tagged fish. This latter goal was dealt with through an international otolith exchange and workshop on age estimation of European hake (ICES, 2010b). These specific results will only be briefly discussed in this paper in support of the other outcomes that have provided new benchmarks in terms of assessment and resource management and new questions that will need to be addressed by further research.

Material and methods

Tagging surveys

Five tagging surveys were carried out in northern Bay of Biscay between 2002 and 2007 (Table 1). Fish were caught in a bottom trawl equipped with a codend specially designed to minimize mortality (de Pontual *et al.*, 2003). Hauls lasted 10–15 min at a speed of 3 knots and were performed on the continental shelf at depths of 16–98 m. On board, the swimbladder of fish was perforated when necessary to enhance survival, and the fish were placed in a tank supplied with flowing cooled (12–13°C) seawater. All fish were tagged using numbered FD-94 or FD-68B (depending on fish length) Floy® tags inserted at the base and in front of the second dorsal fin. Fish were also tagged internally by injection with Terramycin® (oxytetracycline) at a dosage of 60 mg kg⁻¹ for subsequent otolith analysis (see de Pontual *et al.*, 2006). After tagging and measurement of total length (L_T), fish were allowed to recover in tanks from 30 min to ~4 h. Releases were made using a pipe connecting the resting tank to a bottom-open cage designed to help the fish descend away from the surface and to prevent predation by birds. Releases were made twice a day at different locations, selected to limit immediate recapture. Experiments were advertised in media (newspapers, radio, and TV) and via posters and mailings to fishers and stakeholders. A reward of 50€ was offered for each tagged fish returned to the laboratory as well as an additional 1000€ awarded following a random draw among all participants.

Modelling growth

The suitable form of the von Bertalanffy growth model (VBGM) for fitting to tag–recapture data has been described by Fabens (1965) and gives the expected change in size (ΔL) as:

$$\Delta L = (L_\infty - L_1)(1 - e^{-K\Delta t}), \quad (1)$$

where L_∞ is the asymptotic maximum length reached when t tends to infinity, K the growth coefficient, L_1 the initial fish length (at tagging), and Δt the time elapsed between tagging and recapture (subsequently referred to as time at liberty).

Modelling was performed using AD Model Builder IDE (Fournier *et al.*, 2012), which provides robust non-linear regression procedures together with standard ones. Because it does not rely on the assumption that model errors are normally distributed (Fournier, 2011), the former performs much better than least-squares estimators when there are large outliers in the data being analysed. Growth increments (original scale) were fitted for both combined sexes and separated sexes using the entire dataset (all surveys). Residual analysis and precision of the estimates were used to assess the quality of the models. Data (original scale) were subsequently analysed to look at the interannual variability of growth through an ANCOVA (sex and year of tagging as fixed factors and length at tagging and time at liberty as covariates). This was possible for three surveys for which data were well balanced.

Movements and migrations

Most tag recoveries were received with precise positions of recapture allowing analysis of apparent fish movements between release and recapture. To analyse potential seasonal trends in fish movements, maps were derived from data aggregated over 2-month periods from the time of tagging (referred to as month 0, which corresponded to June–early July whatever the survey).

Investigating natural and fishing mortality

The model used for this analysis is a tag attrition model (e.g. Seber, 1973; Kleiber *et al.*, 1987) that deals with the decline in the rate of tag recapture as the population of tagged fish declines with time following release. It is thus able to estimate parameters of that decline, specifically fishing and natural mortality. The model used here is spatially aggregated and thus predicts total tag recaptures in a given month from anywhere within the region. Movement outside the region is not specifically addressed. The emigration of tagged fish from the region, therefore, appears to the model as another component of mortality and is confounded with natural mortality.

Table 1. Synopsis of the tag–recapture experiments carried out in the Bay of Biscay.

Year	No. tagged	Size range at tagging (L_T cm)	No. recoveries	Recovery rate (%)	Recoveries maximum L_T (cm)	Time at liberty (maximum d)
2002	1 307	13–58	41	3.14	67.0	1 066
2004	3 128	9–84	46	1.47	62.5	716
2005	7 361	15–63	334	4.54	51.2	517
2006	6 523	14.5–59	366	5.61	78.8	1 555
2007	9 112	16.5–64	403	4.42	72.0	785
2006 DST	115	30–39.5	4	3.48	35.1	81
2007 DST	144	28.9–39.2	5	3.47	33.7	65
Total	27 690	13–84	1 199	4.33	78.8	1 555

DST, data storage tags; L_T , total length. Year 2002 was a pilot experiment.

Various other tag losses such as tag shedding and extra mortality due to carrying a tag also contribute to apparent natural mortality.

The model predicts tag recoveries based on the catch equation and is fitted to the observed tag return results by maximizing a goodness-of-fit function, which in this case is a multinomial likelihood function. What the model specifically calculates are the probabilities of all possible fates of a tag that is released at the beginning of a given month. The probability that a tag from a release set s is recaptured in month i (counted from the tagging time of release set s) and is subsequently returned with recapture month information is given by:

$$p_{i,s} = \frac{\alpha \gamma F_{t(i,s)}}{F_{t(i,s)} + M} (1 - e^{-(F_{t(i,s)} + M)}) \prod_{k=1}^{i-1} e^{-(F_{t(k,s)} + M)}, \quad (2)$$

where $F_{t(i,s)}$ is the fishing mortality at time $t(i,s)$ and $t(i,s)$ denotes the point in time (given by a specific year and month) to which (i,s) corresponds. The $F_{t(i,s)}$ parameters are thus common across release sets. M is the natural mortality (assumed constant), α a combined parameter comprising the instantaneous survival from being tagged and the proportion of recaptured tags that are returned, and γ the proportion of returned tags for which the month of recapture is known.

Besides the probability categories for return with known recapture month, we have the probability of return with unknown month, $p_{NA,s}$ which is given by:

$$p_{NA,s} = \frac{1 - \gamma}{\gamma} \sum_{i=1}^{n_s} p_{i,s}, \quad (3)$$

where n_s is the number of months for release set s in the analysis. The final category is the non-returns, $p_{NR,s}$, given by:

$$p_{NR,s} = 1 - p_{NA,s} - \sum_{i=1}^{n_s} p_{i,s}, \quad (4)$$

which includes all tagged fish not otherwise accounted for. It comprises survival beyond the available data and losses to the population of tags in the tagging area by other than local fishing including emigration, death, and tag slippage.

The parameter γ , the probability that a returned tag has recapture month information, is calculated from the observed overall number of returned tags that had known recapture month:

$$\gamma = 1 - \frac{\sum_{s=1}^S r_{NA,s}}{\sum_{s=1}^S (r_{NA,s} + \sum_{i=1}^{n_s} r_{i,s})}, \quad (5)$$

where $r_{i,s}$ and $r_{NA,s}$ are the observed numbers of tags that have been returned with and without recapture month, respectively. There are no independent estimates of reporting rates and instantaneous survival from being tagged for hake tags; we thus tested the sensitivity of our results to values of α in the range of 0.05–1.0.

To estimate M and $F_{t(i,s)}$, the model was fitted to tag datasets with different dates of release by minimizing the negative log of the multinomial likelihood function. The function to minimize is then:

$$L(F_i, M) = - \sum_{s=1}^S \sum_{i=1}^{n_s+2} r_{i,s} \ln(p_{i,s}), \quad (6)$$

where the probabilities $p_{i,s}$ depend on the parameters $F_{t(i,s)}$ and M by virtue of the model, and the $r_{i,s}$ are the observed number of tags in the corresponding recovery (or lack thereof) categories. The combinatory factor of the multinomial function is ignored in this formulation because it is independent of the parameters and, therefore, has no effect in fitting the model. Minimization was carried out with a quasi-Newton routine using AD model builder (Fournier et al., 2012).

Results

Modelling growth

A synopsis of tag–recapture data is given in Table 1. In all, 27 690 hake were tagged and released between 2002 and 2007; to date, 1199 have been recovered, corresponding to a recovery rate of 4.33%. This rate actually varied from 1.47 to 5.61% depending on the tagging year. The time-at-liberty (ΔT) ranged from 1 to 1555 d. Recoveries showed a maximum length of 78.8 cm for a male tagged at 31.5 cm and recaptured more than 4 years later. Besides conventional tagging, a pilot experiment with data storage tags was carried out in 2006 and 2007. It is worth noting that corresponding recovery rates were close to those of conventional tagging.

Whatever the tagging survey, most recoveries were tagged as juveniles (mode at 25–30 cm L_T), although some were tagged as adults. About half of the recoveries had a short time at liberty. Fish recovered within 30 d after tagging had null growth and were excluded from subsequent analysis. In addition, missing or dubious data for 57 fish (tag return without a fish, questionable information on the recapture date, measurement errors, etc.) were also excluded. This led to a primary dataset of 565 recoveries, subsequently referred to as D30. Figure 1 describes the structure of the data through relationships between lengths at release and recapture with respect to time at liberty displayed. A second dataset was then constructed, excluding fish that were at liberty for less than 60 d (D60, $n = 413$). Summary information regarding the two datasets (fish length at tagging, growth, time at liberty, and sex distribution) is provided in Table 2.

Each dataset was used to estimate growth by both standard and robust non-linear regression procedures leading to four growth models subsequently referred to as standard30, robust30, standard60, and robust60. Estimates of L_∞ and K are provided in Table 3, together with parameter values reported in previous studies. The corresponding models were plotted to allow graphical comparisons (Figure 2). Note that for all four models, the fitted curves are nearly identical up to ~ 70 cm in length (whereas the maximum L_T of any recovery was 78.8 cm). Thus, a clear-cut choice between these models is not obvious.

However, for both D30 and D60, standard regressions provided higher values of L_∞ together with higher standard errors compared with robust regressions analyses. Q–Q normal plots of standardized residuals (Figure 3, column 1) show that the residuals of both standard30 and standard60 are not normally distributed, suggesting that some outliers might alter the parameter estimations when using a standard non-linear regression procedure. These results argue in favour of the choice of the robust60 growth model for European hake, with $L_\infty = 125.2 \pm 12.8$ cm and $K = 0.170 \pm 0.025$ year⁻¹. It is worth noting that this new K estimate is more than twice the ICES (1993) reference for comparable L_∞ values. Residuals were evenly distributed around zero when plotted against size at release (Figure 3, column 2), time at liberty (Figure 3, column 3), and predicted growth (data not shown), which constitute additional

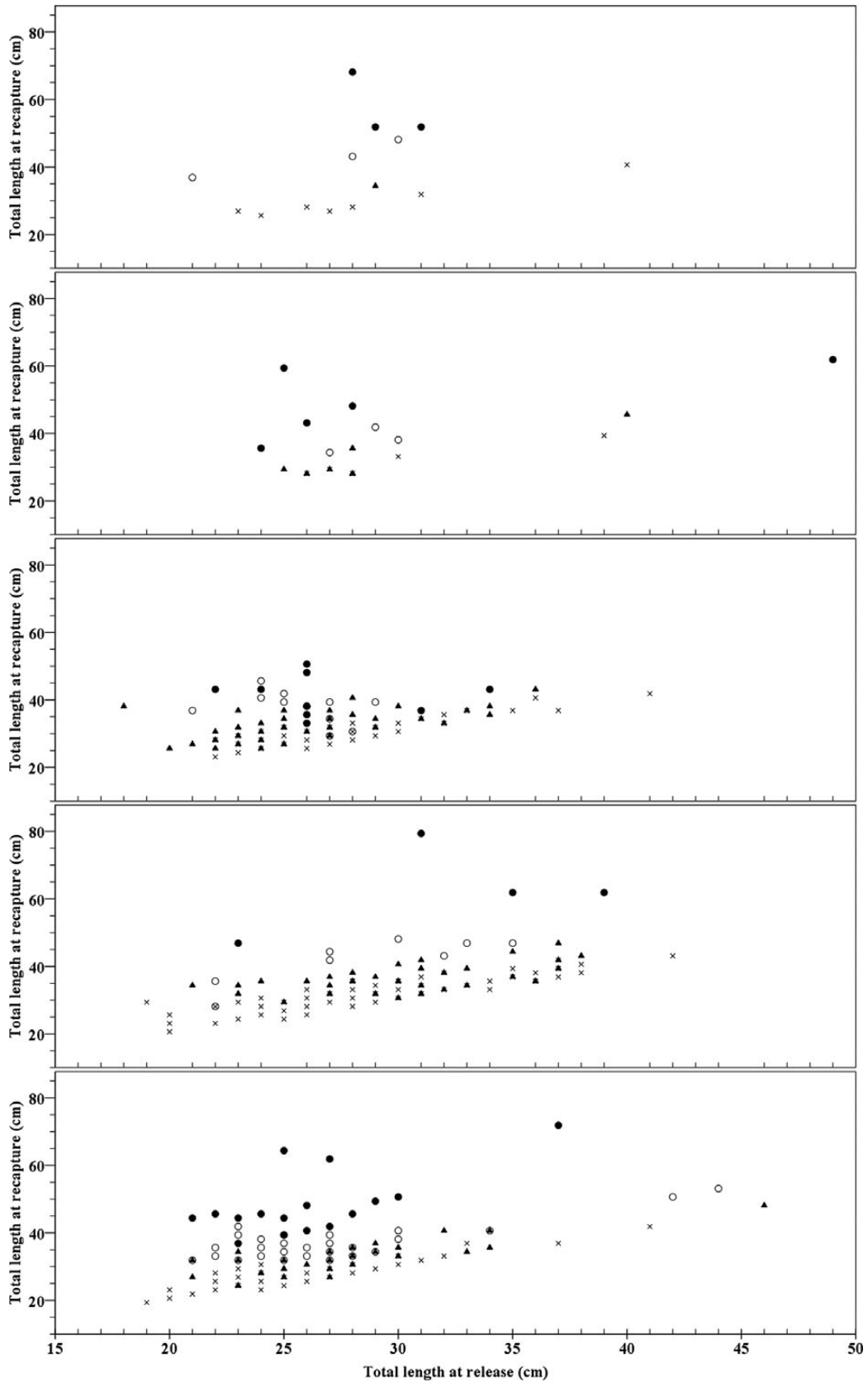


Figure 1. Relationships between lengths at release and recapture with respect to time at liberty: cross [30–99]; triangle [100–199]; open circle [200–365]; close circle ≥ 366 . Data are shown for each release set (top to bottom panels: years 2002, 2004, 2005, 2006, 2007).

Table 2. Summary information on datasets used for modelling growth.

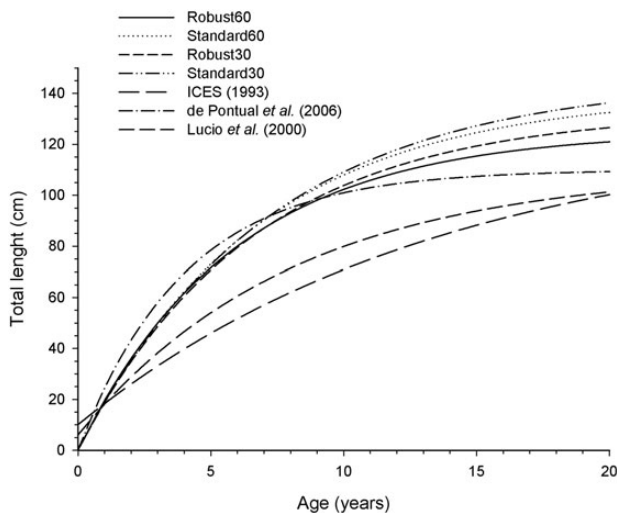
Dataset	Statistic	L_T tag (cm)	ΔL (cm)	Time at liberty (d)	Sex	n
D30 ($n = 565$)	Mean \pm s.e.	27.58 ± 0.18	5.36 ± 0.26	133.3 ± 5.7	Male	238
	Median	27.00	3.40	86	Female	286
	Range	18.0–48.5	0.1–47.3	31–1555	Und.	41
D60 ($n = 413$)	Mean \pm s.e.	27.61 ± 0.22	6.82 ± 0.33	165.6 ± 7.2	Male	167
	Median	27.00	4.90	114	Female	213
	Range	18.0–48.5	0.1–47.3	61–1555	Und.	33

D30, fish at liberty for at least 30 d; D60, fish at liberty for at least 60 d; L_T tag, total length at release; ΔL , somatic growth; und, undetermined sex.

Table 3. von Bertalanffy growth parameters estimated for the four models fitted on sex-combined data [see Equation (1) for the significance of the parameters].

Model	L_∞	s.e.	K	s.e.	t_0	r
Standard30	145.31	17.93	0.139	0.023	–	–0.996
Robust30	132.91	13.16	0.152	0.021	–	–0.991
Standard60	139.75	18.56	0.148	0.027	–	–0.995
Robust60	125.16	12.84	0.170	0.025	–	–0.990
ICES (1993)	127.5	–	0.073	–	–1.13	–
de Pontual et al. (2006)	110.0 (fixed)	–	0.250	0.012	–	–
Lucio et al. (2000)	110.0	–	0.124	–	–0.452	–

Model in bold characters is considered as the best fit. Previous estimates for the northern stock are also provided for comparison.

**Figure 2.** VBGMs derived from tagging data considering combined sexes. Comparisons of robust vs. standard non-linear regressions on both datasets D60 (fish at liberty for at least 60 d) and D30 (fish at liberty for at least 30 d). Previous estimates are also drawn for comparison. Note that care must be taken for direct comparison of growth estimated by different methods (the exact location of growth curve derived from tagging data is not determined along the age axis, as in this case, the von Bertalanffy parameter t_0 is implicitly set to zero).

indicators regarding the quality of the fits. However, residual values can be high (more than 10 cm in absolute value) and slightly increased with time at liberty, mainly in the first months post-tagging, which reflects either high individual growth variability and/or differential ability to recover from tagging.

Fitting the VBGM onto data separated by sex did not provide consistent results if both L_∞ and K were simultaneously estimated.

Unrealistic values of L_∞ together with high standard errors were obtained using either standard or robust non-linear regression procedures due to insufficient numbers of recoveries, especially large fish. Therefore, we fixed L_∞ at (i) the value estimated on sex-combined data, i.e. 125.2 cm for both sexes and (ii) the values given by Lucio et al. (2000) then considered in de Pontual et al. (2006), i.e. 80 and 110 cm for males and females, respectively. Estimated parameters are provided in Table 4 and corresponding models are plotted in Figure 4.

Based on known sizes at first maturity in the Bay of the Biscay ($L_{50} = 37.9$ and 48.8 cm for males and females, respectively; Lucio et al., 2000), the models indicate that males would first mature at age 2, whereas females would mature at ages 2–3 depending on the model under consideration.

The ability of tagging data to capture potential interannual growth variability was supported by the number and relatively well-balanced observations obtained from three surveys (2005, 2006, and 2007, Table 5). However, variables such as time at liberty and total length at tagging had different statistics between years (Table 5), indicating that they should be considered when analysing interannual variability of growth.

An ANCOVA was thus fitted with sex and year of tagging as fixed factors and length at capture and time at liberty as covariates ($r^2 = 0.764$). Errors of variance were homogeneous between groups (Levene's test; $p = 0.147$). There was no significant interaction between fixed factors. Covariates (length at tagging and time at liberty) had significant contributions to the model ($p < 0.001$), and both year of tagging ($p = 0.001$) and sex ($p = 0.01$) had significant effects. Estimated marginal means plotted against year of tagging (Figure 5) show that somatic growth was significantly higher for fish tagged in 2006.

Learning about movements and migrations

Most tag recoveries were received with precise positions of recapture, allowing analysis of apparent fish movements between release and recapture. Overall, most fish were recovered near their release locations (Figure 6), confirming the preliminary observation of de Pontual et al. (2003). However, some fish travelled long distances, suggesting that some exchange at a population level would be possible. Further, Figure 6 highlights two points that support this hypothesis. First, the apparent travelled distance is not proportional to time at liberty; for instance, two fish that had a relatively short time at liberty (labelled 50 and 54 on Figure 6) travelled quite long distances southwards, whereas one fish that had more than 3 years at liberty (1066 on Figure 6) was recovered not far off the west coast of Brittany. Moreover, the fish that had 1555 d at liberty was recovered at only 26.1 km from the release position. The second point concerns the very small number of fish that were returned by Spanish fishers, a result which is not consistent

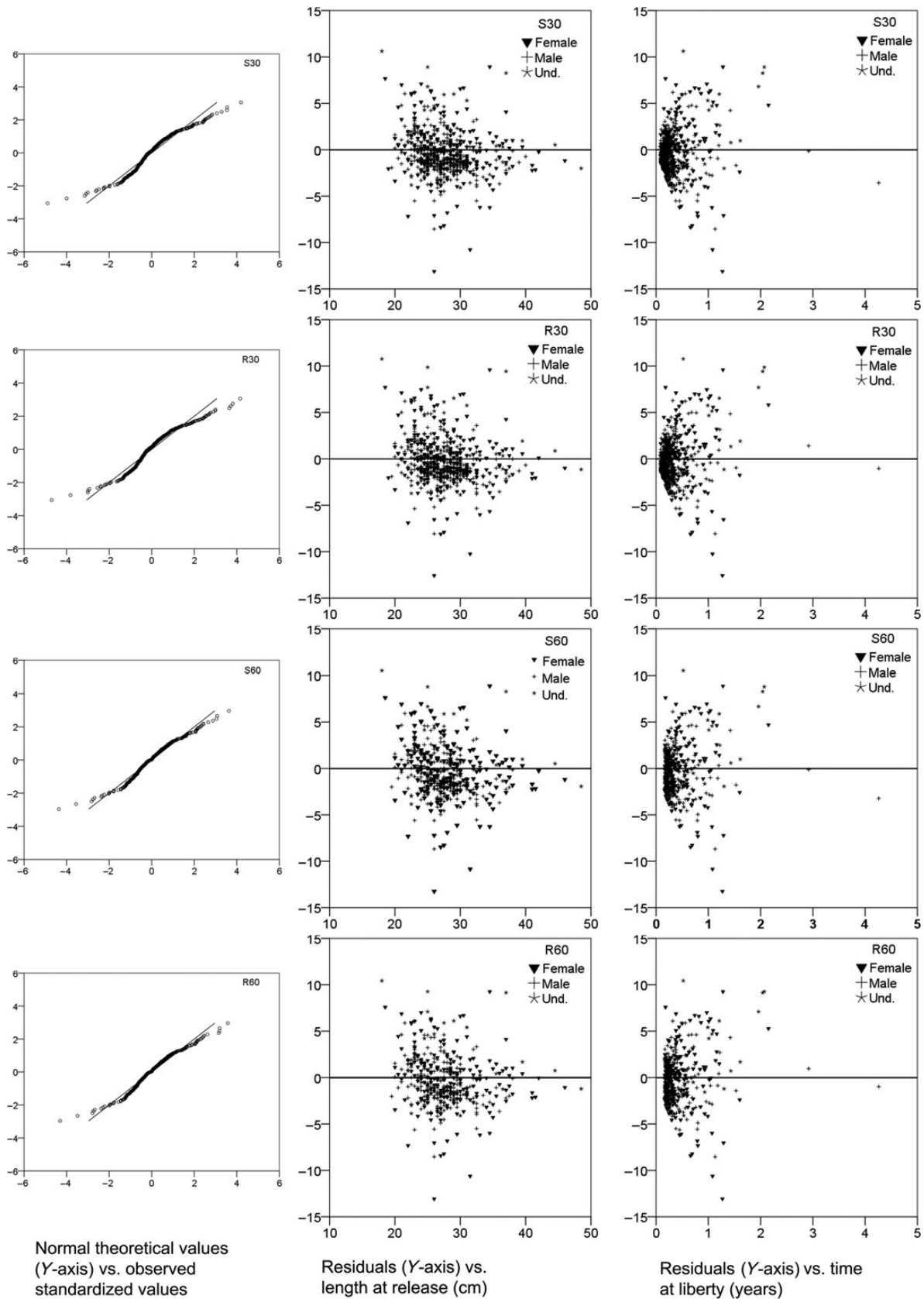


Figure 3. Residual analysis of the four models described. From top to bottom row: standard30 (S30), robust30 (R30), standard60 (S60), robust60 (R60). From left to right column: normal Q–Q plot for standardized residuals, residuals vs. length at release, residuals vs. time at liberty.

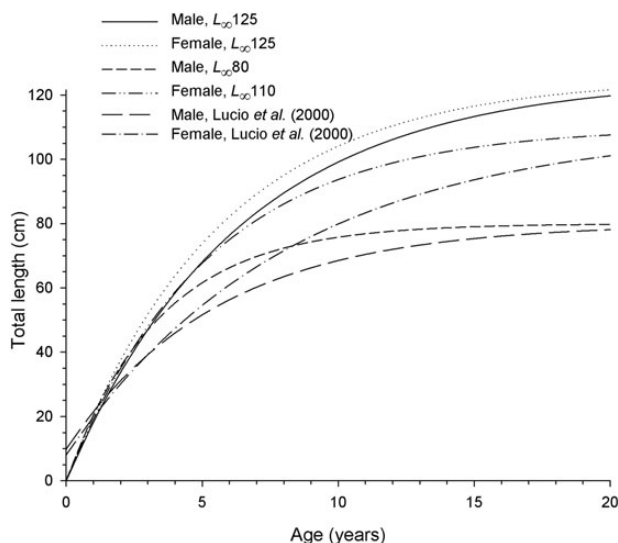


Figure 4. VBGM derived from tagging data considering separate sexes. Results are shown for different setting of L_{∞} . Models $L_{\infty}80$ and $L_{\infty}110$ for males and females, respectively, were constructed for comparison with estimates of Lucio et al. (2000). Note that care must be taken for direct comparison of growth estimated by different methods (the exact location of a growth curve derived from tagging data is not determined along the age axis as, in this case, the von Bertalanffy parameter t_0 is implicitly set to zero).

Table 4. European hake growth parameters estimated for separate sexes, based on the D60 dataset [see Equation (1) for the significance of the parameters].

Sex	Model	L_{∞}	K	s.e.	t_0
Female ($n = 213$)	L_{∞} fixed	125.2	0.178	0.005	
	L_{∞} fixed	110.0	0.191	0.006	–
	Lucio et al. (2000)	110.0	0.122	–	–0.619
Male ($n = 167$)	L_{∞} fixed	125.2	0.157	0.005	
	L_{∞} fixed	80.0	0.294	0.011	
	Lucio et al. (2000)	80.0	0.181	–	–0.724

Previous estimates for the northern stock are also provided for comparison.

Table 5. Descriptive statistics (mean \pm s.d.) of tagging data used to analyse interannual growth variability.

Year	Sex	Somatic growth (cm)	Time at liberty (d)	Size at release (cm)	n
2005	Female	6.14 \pm 4.93	147.01 \pm 106.53	27.01 \pm 3.89	72
	Male	4.75 \pm 4.65	118.30 \pm 87.57	26.69 \pm 3.17	61
	Total	5.50 \pm 4.83	133.84 \pm 98.97	26.86 \pm 3.57	133
2006	Female	5.90 \pm 5.11	130.04 \pm 82.81	30.29 \pm 4.77	67
	Male	6.13 \pm 8.02	144.62 \pm 245.23	27.76 \pm 5.09	37
	Total	5.98 \pm 6.26	135.23 \pm 159.57	29.39 \pm 5.01	104
2007	Female	7.92 \pm 7.10	200.95 \pm 135.55	27.28 \pm 5.02	59
	Male	6.47 \pm 4.78	179.86 \pm 104.06	25.94 \pm 2.64	59
	Total	7.20 \pm 6.07	190.41 \pm 120.78	26.61 \pm 4.05	118

The first two surveys (2002 and 2004) were excluded from the analysis because of insufficient data.

with the exploitation rate of the stock by Spanish fleets. This probably induced some bias in the perception of the movement and migration of the species.

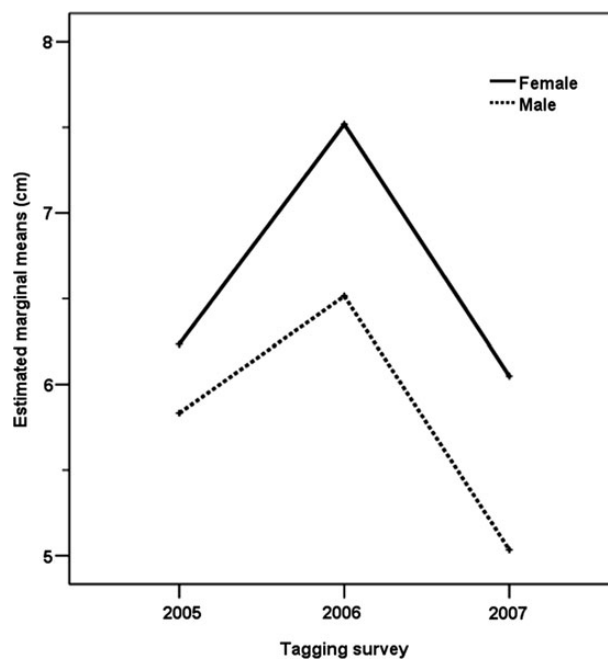


Figure 5. Interannual variation in somatic growth (cm). Marginal means were estimated considering covariates assessed in the model as follows: length at tagging = 27.5 cm, time at liberty = 153.0 d.

The temporal variation of the apparent fish movements (Figures 7 and 8) also supports the hypothesis of an unbalanced contribution to recaptures from the fleets that operate far off the coast. Data do not reveal the expected seasonality of fish movements either north–south along the continental shelf slope or west–east from deep to shallower waters after spawning (Casey and Pereiro, 1995). Very few fish were recaptured on the slope, while some fish were recaptured near shore in winter (see months 5–8, Figure 7 and months 15–18, Figure 8). Despite this likely biased perception of seasonal movements, an interesting finding is the very little apparent movement of some fish that had a long time at liberty regardless of the season (Figure 8).

Estimating fishing and natural mortality: using a tagged fish attrition model

Data stratification

The structure of the analytical model is such that tagged fish are presumed to be released at the start of a given calendar month. To make the observed data correspond to that scenario as closely as possible, the release data were aggregated into release sets by rounding the date of release to the nearest first of the month. Nine release sets were defined. The returns were aggregated by month by truncating the recapture date to month rather than rounding, as with the release date. Thus, the recoveries assigned to a given month are those with recapture dates any time within that month. Again, this corresponds to the structure of the analytical model, which predicts the number of returns within each whole month following the release date. On some occasions with the above scheme, tags released in the last half of a month would be recaptured in that same month, which would result in these recoveries being assigned a recapture one month before the assigned release month. Recoveries such as these were reassigned to the following month. The considered stratification (not including DST data) is given in Table 6.

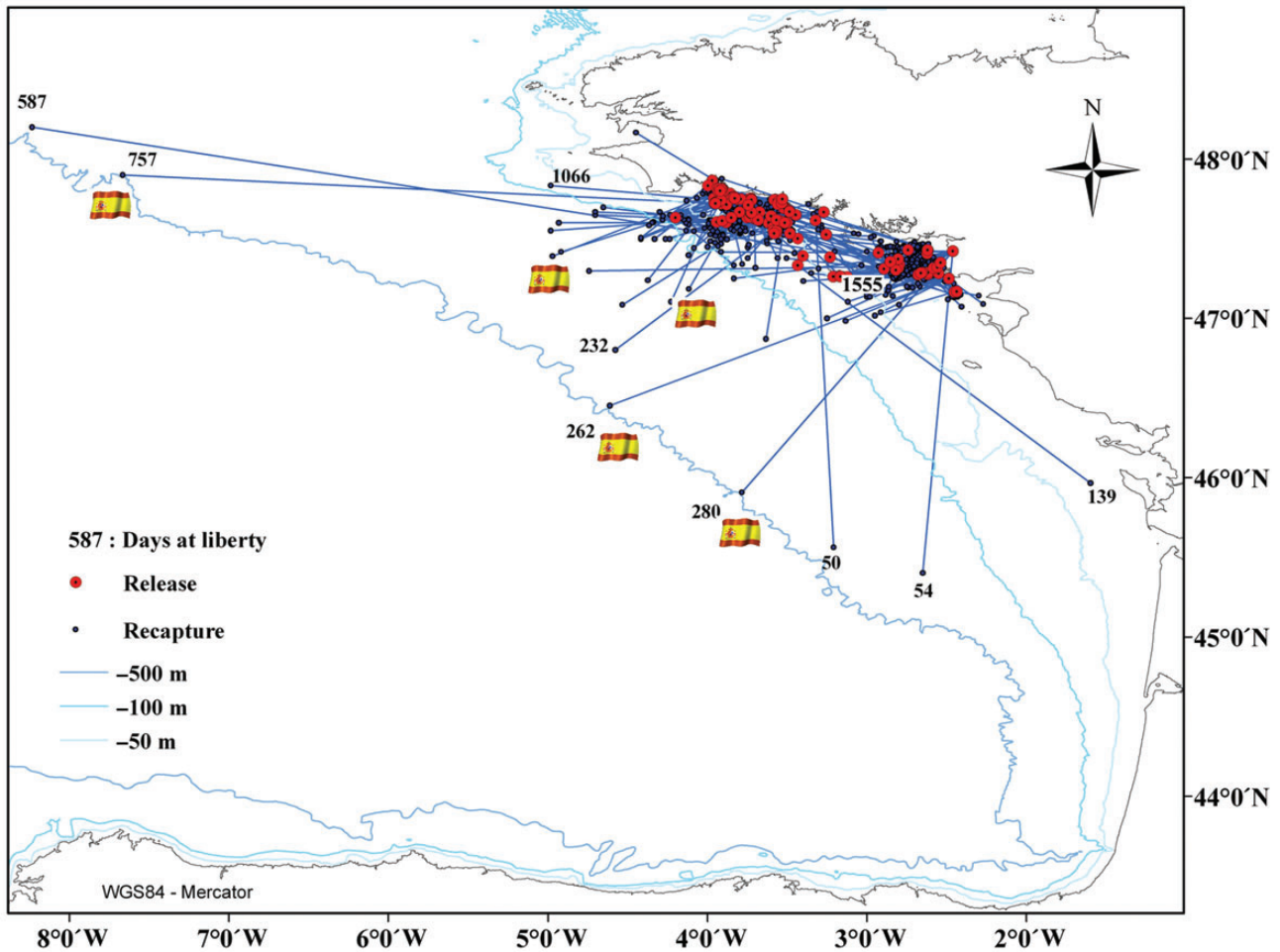


Figure 6. Comprehensive view of apparent movements of tagged fish. For each recovery, release point (red circle) and associated recapture location (blue circle) are reported. Some fish are labelled with the time elapsed between tagging and recapture. Spanish flags highlight fish that were reported by Spanish fishers.

M estimates

Iterative fits converged readily with α fixed. Figure 9 shows predicted (solid line) and observed tag returns for $\alpha = 0.5$ aggregated over the release sets. An attempt to estimate α was also carried out, but the model could not find a solution in the interval $[0, 1]$, and the value obtained for α was equal to the upper bound.

The sensitivity of the results for *M* estimates to different values of α is presented in Figure 10. The estimates of *M* were directly related to α , but the sensitivity was slight for $\alpha > 0.5$.

Whatever level of assumed reporting rate, model estimates of *M* are very high (e.g. $M = 0.26 \text{ month}^{-1}$ for $\alpha = 0.5$). Average *F* over the period of the analysis was estimated low compared with *M* ($F = 0.03 \text{ month}^{-1}$ for $\alpha = 0.5$), leading to a value of $F = 0.33$ yearly.

Discussion

Somatic growth

Conventional tagging of European hake recently opened new avenues for a better understanding of the species' biology and population dynamics that have remained controversial for decades (de Pontual *et al.*, 2003). Despite limited data (41 recoveries were obtained), these first tagging results provided strong evidence of

substantial growth underestimation (by a factor ~ 2) due to bias in the agreed method of age estimation (de Pontual *et al.*, 2006). More tagging efforts, off the northwest Iberian Peninsula (Pineiro *et al.*, 2007) and in the Mediterranean Sea (Mellon-Duval *et al.*, 2010), have since proved that growth underestimation was not a regional issue. The results of a large tagging effort in the Bay of Biscay between 2002 and 2007 clearly confirm that European hake grow fast. Over the 27 690 released tagged fish, 1199 fish have been returned to date (time at liberty up to 1555 d, maximum L_T of the recoveries: 78.8 cm). Importantly, this is the first time that there are sufficient tagging data for estimating both L_∞ and *K* of the VBGM in a consistent way, although large fish with significant time at liberty still remain relatively scarce. This limitation is revealed by the four models fitted with sex-combined data (Figure 2, Table 3), which slightly diverge for fish $> \sim 70\text{--}80$ cm, a result clearly related to the maximum size of recoveries of 78.8 cm, low compared with the largest reported size of 140 cm for this species (Cohen *et al.*, 1990). The proposed choice of the Robust60 model ($L_\infty = 125.2 \text{ cm}$; $K = 0.170 \text{ year}^{-1}$) is driven by several arguments. First, the choice of a robust model is driven by the existence of some outliers (Figure 3) likely to impede the quality of estimates derived from standard non-linear regression. Second, excluding fish that had less than 60 d at liberty is supported

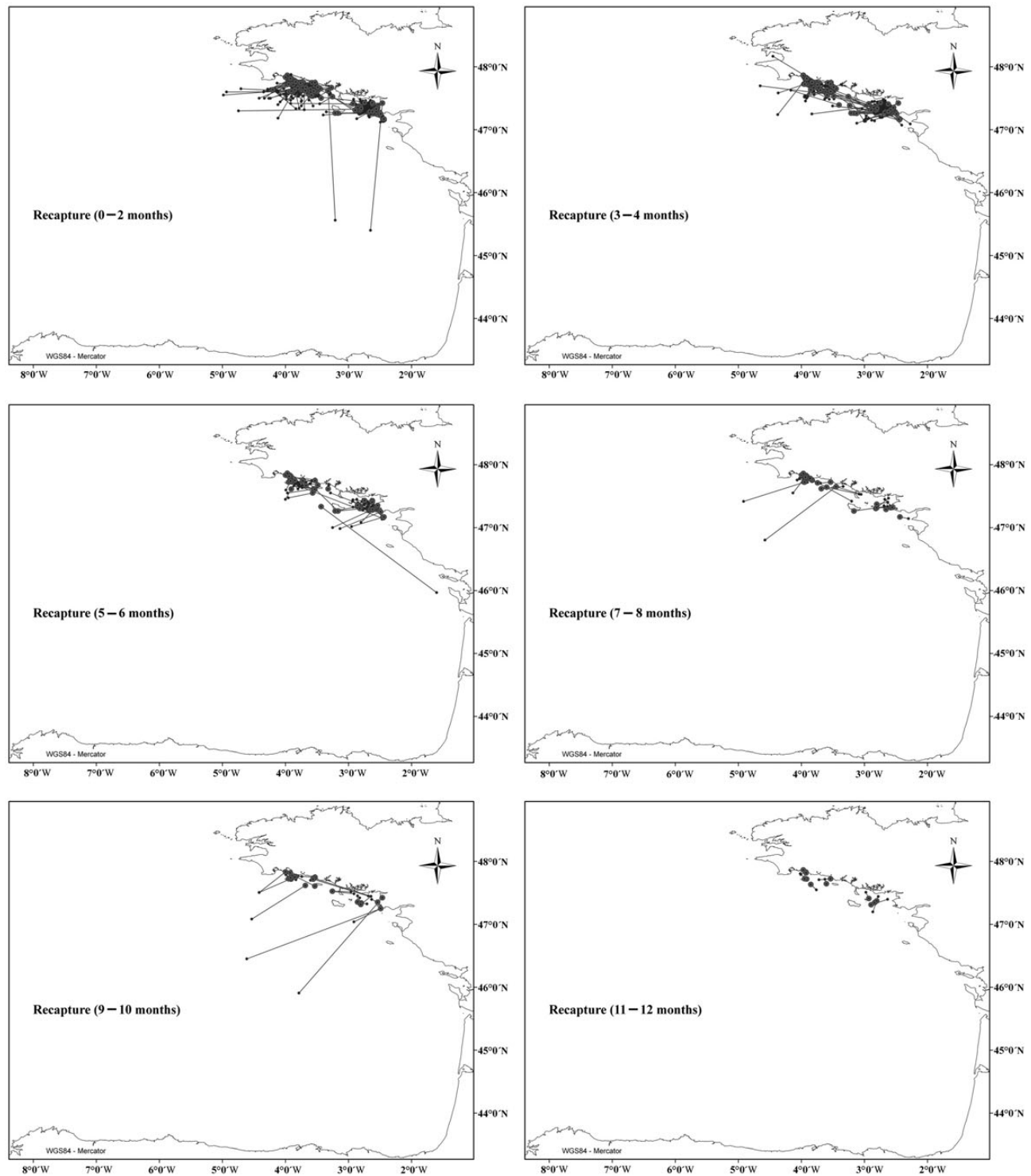


Figure 7. Temporal variations in apparent movement. Data were grouped by 2-month periods from the tagging period (referred to as month 0, which corresponded to June–early July depending on the fish). For each recovery, release point (large circle) and associated recapture location (small circle) are reported.

by the residual analysis (Figure 3). It is also relevant from a biological point of view because of probable bias due to the effects of tagging on survival and growth, as already observed (Hampton, 1991; de Pontual et al., 2003). Although such effects are difficult to quantify, controlled experiments have shown that post-tagging mortality of

European hake can extend to more than 50 d (Jolivet et al., 2009), whereas growth is also affected in a range that still needs to be specified. Acclimatization of European hake is still in its infancy (Iglesias et al., 2010; Jolivet et al., 2012) and controlled experiments thus remain challenging. Lastly, as claimed by Francis (1995) and

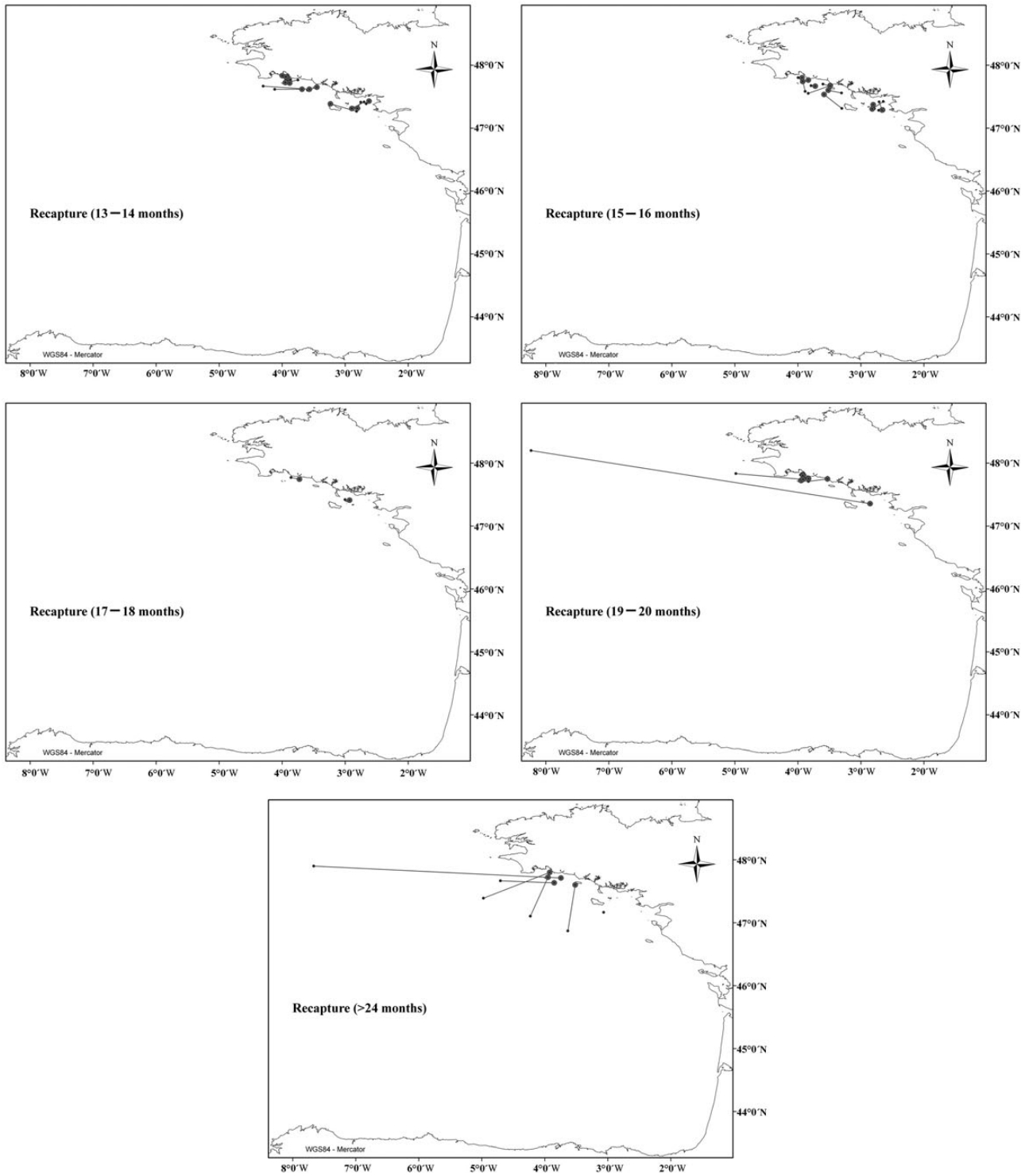


Figure 8. Temporal variations in apparent movement of recoveries with more than one year at liberty. Data are grouped by 2-month periods from the tagging period (referred to as month 0, which corresponded to June – early July depending on the fish). The bottom panel refers to fish that had more than 2 years at liberty. For each recovery, release point (large circle) and associated recapture location (small circle) are reported.

shown by Haddon (2011) through simulations, tagging data may be biased high for L_{∞} and low for K . This was an additional reason for preferring the robust60 model, which provided the lower estimate of L_{∞} together with the highest precision.

Differential growth in males and females has been extensively reported (e.g. Casey and Pereiro, 1995; Pineiro and Sainza, 2003). Tagging data confirm this statement, as shown by the models fitted for separated sexes. An insufficient number of large fish was

Tagging data did not reveal any seasonality of fish movements, either north–south along the continental shelf slope or west–east from deep to shallower waters after spawning, as discussed in Casey and Pereiro (1995). Our tagging data neither corroborate nor contradict these hypotheses. The inability to capture spatio-temporal structure may result from several factors. First, as already mentioned, offshore fleets, specifically the Spanish fleet (accounting for 70% of the landings), poorly contributed to the tagged fish recovery. Second, tagging operations were limited to the northern Bay of Biscay, which is far from covering the spatial distribution of the species. Despite this limitation, the data show very little apparent movement for most fish, even for winter recoveries (see months 5–8, Figure 7 and months 15–18, Figure 8) and for fish that had a long time at liberty. This may suggest the existence of a contingent of non-migrating fish and/or the existence of homing behaviour, as already hypothesized from DST analysis (de Pontual *et al.*, 2012). Such behaviour should be further investigated as it has important consequences in terms of management and conservation (Righton *et al.*, 2001; Solmundsson *et al.*, 2005).

Model estimates of M are very high (e.g. $M = 0.26 \text{ month}^{-1}$ for $\alpha = 0.5$) compared with $F (=0.03 \text{ month}^{-1}$ for $\alpha = 0.5$). It must be noted, however, that in this model, M is an apparent natural mortality that combines several sources of attrition (tag shedding and extra mortality due to carrying a tag, emigration of tagged fish from the region), which are confounded with natural mortality. Available data do not permit a separation of those different sources of apparent mortality. From survival experiments conducted in captivity (Jolivet *et al.*, 2009), however, it is clear that the mortality rate is substantially higher for tagged than for untagged hake, which probably leads to a strong positive bias in the estimation of M .

In the absence of other information, the tag-reporting rate was assumed to be constant over time. However, reporting could have varied over time, due to the variation in the effectiveness of tag-recovery procedures or cooperation of fishing fleets. There are indications that the reporting rate may have been low for the Spanish fleets operating in the area of tagging. There were only 5 returns from Spanish fleets during the period (2003–2009) for tagged fish having spent more than 5 months at liberty, while the French fleet reported 145 tagged fish recaptured. During the same period, the Spanish catch in the Bay of Biscay was ca. twofold that by the French. Furthermore, most tags recovered from Spanish boats were from boats with observers onboard. Although this inconsistency can partly be because those fleets are not fishing the same areas, this may not be the only cause of such discrepancy; a differential reporting rate probably exists. It is then possible that unreported tag recaptures by the Spanish fleet, which reported relatively few recaptures, have resulted in a further positive bias in our estimate of M .

Although informative, these results show the limitations of the current tagging experiments to address hake movement, migration, and mortality. Tagging locations were limited to the northern Bay of Biscay, a small part of the population distribution area. To better address the issues, future tagging experiments need to be extended to a larger area so that exchange rates between main areas (Porcupine Bank, Great Sole, northern and southern Bay of Biscay, and Iberian Atlantic) can be estimated. If such a tagging programme were carried out, it would be essential to ensure stakeholder (particularly fishers) participation to maximize return rates from all the major fleets contributing to the catch. Estimation of tag-induced mortality and tag shedding would also be needed. This could be carried out through double tagging experiments and survival

experiments in captivity. The latter could be used to improve the tagging protocol, if required (e.g. Morales-Nin *et al.*, 2011). Furthermore, coupled individual markers (Fromentin *et al.*, 2009) and particularly otolith chemistry (Swan *et al.*, 2006; Chang *et al.*, 2012) should help to unravel the spatial structure of European hake. Knowledge of the spatial structure of this widely distributed species as well as a better estimation of its natural mortality rate are critical to better understand the species' population dynamics and, in turn, facilitate better stock assessment and management of this heavily exploited resource.

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