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1 **Abundance estimation of Northeast Atlantic Mackerel based on tag recapture data - a**
2 **useful tool for stock assessment?**

3

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8

9 **Abstract**

10 In the present study we utilize tag recapture data to estimate year class abundance and
11 spawning stock biomass of mackerel (*Scomber scombrus* L.) in the Northeast Atlantic for the
12 period 1986-2008. On average 20 000 jigged mackerel have been tagged annually with
13 internal steel tags in the spawning area west of Ireland and the British Isles, and the tags have
14 been recaptured in commercial catches screened through metal detectors. The spawning stock
15 biomass estimates derived from two different tag-based models were highly variable but were
16 on average 2 and 2.3 times higher than the ICES official estimate. The official estimate is
17 considered uncertain and most likely an underestimate of the actual biomass, due to
18 unregistered mortality in the fisheries and lack of fishery-independent, age-disaggregated
19 data. Hence, tag-based estimates could potentially improve the current assessment if included
20 in the ICES stock assessment on a regular basis. These estimates also involve some
21 uncertainty that needs consideration, especially related to variable tagging mortality, detector
22 efficiency and migrations of the stock.

23 *Keywords: tagging, abundance, biomass, mortality, uncertainty*

24

25

26 **1. Introduction**

27

28 The Northeast Atlantic (NEA) mackerel supports a very valuable fishery, with landings that
29 have ranged between 470 000 and 820 000 tonnes (t) since the mid 1990s (ICES, 2009a).

30 Based on their respective spawning grounds the stock is divided into three spawning
31 components; the western, southern and North Sea components, and these are managed as one
32 stock; the Northeast Atlantic Mackerel (ICES, 2009a). At present, the official International
33 Council for the Exploration of the Seas (ICES) assessment is based on an integrated catch-at-
34 age model (ICA, Patterson and Melvin, 1996) and a triennial egg survey estimate of spawning
35 stock biomass (ICES, 2009a; Lockwood et al., 1981). The stock assessment is heavily
36 dependent on catch-at-age data and since 2005, ICES has recognized that the level of
37 unaccounted mortality in the fishery may be significant (ICES, 2006). There are strong
38 indications that large amounts of landings are unregistered (ICES, 2009a) and discarding and
39 slipping of unwanted mackerel at the fishing grounds may be significant (Borges et al., 2008;
40 ICES 2009a). While some discard sampling has been carried out since 2000 and is included in
41 the assessment, there is not enough data to capture the full scale of discarding (ICES, 2009a).

42 Due to the lack of fishery-independent data and unreliable catch data there is a need
43 for alternative fishery-independent estimates of stock biomass. The egg surveys are an
44 important part of the assessment, but are only carried out every third year and do not provide
45 age-structured data. There is also ongoing work with the use of acoustic methods for
46 abundance estimation of the mackerel stock, but at the moment the estimates are not reliable
47 enough to be used in the assessment as indicators of abundance (Gorska et al., 2007; ICES,
48 2009b; Nesse et al., 2009; Slotte et al., 2007).

49 Tagging studies are commonly used to estimate fish population abundance and
50 mortality rates (for a review see Pine et al., 2003; Schwarz and Seber, 1999) and may be a
51 useful tool for stock assessment (Cadigan and Bratney, 2001; Kleiber et al., 1987; Schwarz
52 and Taylor, 1998). The Institute of Marine Research in Norway (IMR) has used internal metal
53 tags to tag NEA mackerel since 1969 (Hamre, 1970) and these data have been used for
54 mortality estimates (ICES, 2009a). The Norwegian tagging data and data from experiments
55 conducted by other countries have also been very valuable for tracing the mackerel migrations
56 and distribution (Rankine and Walsh, 1982; Uriarte and Lucio, 2001). Until the late 1970s
57 Norwegian tagging data were also used to estimate stock size (Hamre, 1978). Tags were then
58 recovered by magnets installed at reduction plants, but as the use of mackerel changed from
59 fish meal to mainly human consumption very few tags were recovered and the tag data could
60 no longer be used for stock assessment. Since 1986 metal detectors have been installed at
61 Norwegian fish factories making it possible to estimate stock abundance from tag data again.

62 The main objective of this paper is to use tag recapture data to provide age-structured
63 abundance and biomass estimates for the NEA Mackerel stock for the period 1986-2008, and
64 to compare these tag-based estimates with official ICES estimates of SSB based on the ICA
65 model and the triennial egg survey SSB estimates.

66

67 **2. Methods**

68

69 *2.1. Tagging experiments*

70

71 Tag releases from 1984 to 2006 were included in the analysis. Between 5600 and 34000
72 mackerel were tagged in each year, except in 1987 and 2005 when no tagging experiments

73 were carried out (Table 1). The same personnel have been involved in the tagging operations
74 since 1984, thereby reducing the variation in mortality caused by the tagging operation. The
75 3-4 week long tagging experiments have been carried out between May and the middle of
76 June in the spawning area west of Ireland and west of the Hebrides (Figure 1).

77 Mackerel were caught by jigging (manual until 2005 and automatic since 2006) and
78 the tags used were individually numbered pieces of steel, rounded at the ends, 20 mm long, 4
79 mm wide and 1 mm thick. The fish were unhooked and released into vats with running sea
80 water. Damaged individuals were discarded while the ones in good condition were allowed to
81 swim for a maximum of 30 minutes in the tank before tagging. The total length was measured
82 and the tag number was recorded before the tag was inserted into the abdominal cavity or
83 muscle tissues through a small cut. After tagging, the fish were immediately released back to
84 the sea. Individuals that were injured during the fishing and tagging process were used for
85 age-length keys (ALK), by measuring individual lengths and removing otoliths for age
86 reading. The age was read from the otoliths according to the standard age reading
87 methodology used for mackerel at the Institute of Marine Research, IMR. The method
88 involves examination of whole otoliths with a light microscope and determination of age by
89 counting annuli. ALKs consisting of 500 to 1000 fish were available for each tagging year.

90

91 *2.2. Tag recaptures*

92

93 Every year since 1986 between 4000 and 45000 tonnes of mackerel have been screened
94 through metal detectors at Norwegian fish factories (Table 2). All catches landed at one of
95 these factories were screened through the detector. If a tagged fish was detected, a batch of
96 10-40 fish, including the one tagged, was automatically removed from the conveyor belt into

97 a vat. A handheld detector was then used to screen the fish in the vat, and the recovered
98 tagged individuals were sent frozen to IMR where the individual tag numbers with associated
99 data were recorded. The individual fish were weighed, the total length was measured and the
100 age was read from otoliths as described in section 2.1. On some occasions the otoliths were
101 lost or unreadable and length at release and the relevant ALK were used to age the fish. At
102 each factory there was one person employed by IMR who made sure the detector was
103 working properly and estimated the efficiency of the detector. The efficiency was measured in
104 most of the screened landings by marking between 5 and 10 fish and counting how many of
105 these were detected by the instrument. Percentage efficiencies were then given for each
106 landing (Table 2). The body lengths and the total weight were measured manually in a sample
107 of about 100 fish from each screened catch, and sometimes samples were shipped to IMR for
108 aging.

109

110 *2.3. Numbers screened per year class*

111

112 The numbers of fish screened per age class and year were calculated by first converting the
113 amount of fish screened in tonnes to number of fish using the average individual weight in the
114 sample from the catch. The length distribution of the sampled fish was applied to the whole
115 landing and then converted to an age distribution using ALKs from the same year, quarter and
116 area. The numbers of fish screened per age class and year were then corrected for the
117 efficiency of the detector.

118

119

120

121 2.4. Abundance-at-age

122

123 Age structured abundances were estimated for the years 1986-2008 for mackerel between 2-
124 12 years. Two different models were used for the calculations, both based on the Lincoln-
125 Petersen model (Ricker, 1975).

126

127 2.4.1. Software

128

129 A computer program called MERKAN, developed specifically for this project, was used to
130 both extract and organize relevant data from raw data files and to perform analyses.

131 The program selects data related to tag release at specified time and area, and recaptures in
132 landings screened for tags at specified time and area. Each tag has a unique number that
133 allows linking the information at recapture to information at release. Data on screened catches
134 are also selected according to time and location. All information on tagged fish, recaptured
135 tags and screened landings are allocated to year classes as described in sections 2.1, 2.2 and
136 2.3.

137 The result of this data extraction is assembled in 3 tables in the program:

138 $R_{ycl,i}$: Number of tags released from year class ycl in year i in the selected area

139 $r_{ycl,i,j}$: Number of tags recaptured from year class ycl , released in year i in the selected area and
140 recaptured in year j at the selected time and location

141 $N_{scrycl,j}$: Numbers screened in the selected time in year j , belonging to year class ycl .

142 These tables were used in the subsequent calculations.

143

144

145 2.4.2. Model 1 - MERKAN

146

147 The abundance at release time (Year i) by year class was calculated as:

148

$$N_{ycl,i} = R_{ycl,i} * s_i * \left(\frac{\sum_{j=i+1}^{2008} N_{scr ycl,j}}{\sum_{j=i+1}^{2008} r_{ycl,i,j}} \right)$$

149

150 where s_i is the assumed fraction of tagged individuals that survive the tagging operation and

151 the other notations are as described in section 2.4.1. The calculations were done within the

152 MERKAN program and tags recaptured the same year they were released were excluded to

153 allow for one year of mixing of the tags among the population. The lowest age at release

154 included in the calculations was two years. Mackerel abundance was estimated with this

155 method between 1986 and 2006, with the exception of 1987 and 2005, as no tagging

156 experiments were completed in these years. 2006 was the last year in which abundance was

157 estimated because two years of recoveries is the minimum required to estimate abundance.

158 Except for the loss of tags due to fish not surviving the tagging operation, the mortality in the

159 tagged population was assumed to be the same as in the untagged population. We will refer to

160 this model as MERKAN in the following sections.

161

162 2.4.3. Model 2 – HAMRE (Hamre, 1978)

163

164 This model estimates abundance in the tag recapture years rather than in the release years as

165 in MERKAN. The calculations were carried out in excel and the following model was used to

166 estimate abundance in the year classes:

167

$$N_{ycl,j} = N_{scr\ ycl,j} * \left(\frac{\sum_{i=1986}^{j-1} R_{ycl,i} * s_i * e^{-Z_{ycl,i,j}}}{\sum_{i=1986}^{j-1} r_{ycl,i,j}} \right)$$

168

169 where $Z_{ycl,i,j}$ is the cumulative total mortality in the year class, ycl , between tag release and
170 recapture and the other notations are the same as were explained for the MERKAN. An initial
171 tagging survival rate, s_i , was assumed and thereafter the natural and fishing mortality rates
172 estimated by the ICES assessment for the NEA mackerel stock (ICES, 2009b) were applied to
173 the tagged individuals by year class. The abundance was estimated for the years 1986-2008
174 for 3-12 year old mackerel. We will refer to this model as HAMRE in the following sections.

175

176 2.5. Biomass estimates

177

178 The biomass was estimated by converting the numbers-at-age to total weight in each year by
179 using the mean weight-at-age in the stock as estimated by ICES (2009 b). The total weights of
180 3-12 year old fish were then summed for each year.

181

182 2.6. Tagging survival

183

184 The initial tagging survival rate was set at a constant 60% in all years and for all ages. This
185 assumption was based on tagging survival experiments carried out by Hamre (1970) and
186 Lockwood *et al.* (1983). In the experiment carried out by Hamre (1970) 100 internally tagged
187 mackerel were kept in a keep net for three weeks, together with a control group of 100
188 mackerel. The survival rate of the tagged mackerel was 82% and the control group survival

189 was 91%. In the Lockwood et al. (1983) experiment 93 tagged and 92 untagged mackerel
190 were kept in a keep net for 15 days. The survival of the tagged group was 81.7% and control
191 group survival was 95.7%. The same tagging methodology was used in the survival
192 experiments as has been used in this study, but additional mortality is caused by releasing the
193 fish in the sea, occasional bad weather conditions, sea bird predation on the newly tagged
194 mackerel and long term mortality. There is no available data on the mortality resulting from
195 releasing the fish in the field and to assess the implications of over- and underestimation of
196 the survival rate the biomass estimates were also calculated for tagging survival rates of 70%
197 and 50%.

198

199 *2.7. Uncertainty*

200

201 Some of the uncertainties in the MERKAN results were estimated by bootstrap. Two sources
202 of uncertainty were covered: the age distribution of the released mackerel and the landings
203 which were screened for tags. The terms $R_{ycl,i}$ were recalculated for each bootstrap replicate
204 by reallocating the total number of released tags to year classes with a new age distribution.
205 This age distribution was drawn according to a multinomial distribution with the original
206 fractions at age as expectation values, and with a sampling size that was set at 100, which is
207 the normal number of individuals that are length sampled by IMR. This was done separately
208 for each experiment (release year). The landings were redrawn randomly with replacement,
209 for each bootstrap replicate, from the material of single landings until the number of redrawn
210 landings matched the actual number of landings for all the years included in the material. The
211 amount screened and the tags found in the drawn landings were used. The abundance and

212 biomass estimates from MERKAN are presented as medians with 25th and 75th percentiles
213 based on 1000 bootstrap replicates.

214

215 *2.8. Length and age distributions of discarded, tagged and screened mackerel*

216

217 Length and age distributions were compared to examine whether the ALKs, used to age the
218 tagged mackerel, were representative of the tagged population and whether the tagged
219 population was representative of the commercial catches. Age distributions of the tagged and
220 screened mackerel were used rather than lengths to avoid the influence of growth in the time
221 between tagging and screening. Due to very large sample sizes and the use of ALKs for the
222 screened and tagged mackerel the statistical analyses were complicated. The sample sizes
223 were therefore standardized to 100 and the significances of group differences were
224 statistically tested with factorial ANOVA. By reducing the sample sizes the statistical
225 precision was reduced, but the statistical analyses became biologically more meaningful. The
226 results from a power analysis (power = 0.8, standardized effect = 0.5, using the observed
227 means and standard deviations) showed that between group differences of about 1.5 cm in
228 length and slightly less than one year in age would result in statistical significance when using
229 sample sizes of 100.

230

231

232

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234

235

236 **3. Results**

237

238 *3.1. Abundance-at-age*

239

240 The tag recapture models indicated higher abundances compared with the official estimates
241 based on the ICA model in most of the analyzed year classes (ICES, 2009b, Figure 2).

242 Exceptionally high abundances were estimated for the 2001–2004 year classes. The tag
243 estimates fluctuated from year to year, especially for the old and young year classes. There
244 were also high levels of uncertainty in the estimates. More stable estimates were produced for
245 the intermediate year classes, 1988-1994. The estimates of 2-year old mackerel by MERKAN
246 and correspondingly 3-year olds by HAMRE were low in many of the assessed year classes
247 when considering the general trends in the time courses.

248

249 *3.2. Biomass estimates*

250

251 The biomass estimates based on MERKAN ranged from 3.1 to 7.2 million tonnes in the years
252 1986-2006, while the estimates from the HAMRE model ranged from 1.2 to 9.5 million
253 tonnes (Figure 3). The estimates for 2007 and 2008 from the HAMRE model were 13.5 and
254 26.5 million tonnes respectively (due to the exceptionally high values these years estimates
255 have been excluded from Figure 3). The ICA model estimates were well below the lower
256 confidence limit of the tag model estimates (Figure 3, ICES, 2009a). SSB estimates from the
257 triennial egg survey were also about 15% below the tag estimates (Figure 3, ICES, 2008). The
258 tag recapture estimates indicate a reduction in biomass in the 1990s, which is not indicated by
259 the ICA estimates. The ICA model on the other hand indicates a decrease in the SSB from the

260 late 1990s to 2002 and then an increase from 2002 to 2006, also indicated by the egg surveys.
261 This increase can also be seen in the tag estimates that indicated a substantial increase in the
262 stock biomass from 2002/2003.

263 The choice of tagging survival rate between 50-70% influenced the biomass estimates
264 by between 0.4 million tonnes in the lowest estimate to 3.2 million tonnes in the highest
265 estimate (Figure 4).

266

267 *3.3. Length and age distributions of discarded, tagged and screened mackerel*

268

269 The mean lengths of the ALKs and the tagged mackerel differed by less than 1.5 cm in all
270 years, except for 1990 when the difference was 2 cm (Figure 5). The mean lengths were lower
271 in the ALKs in 15 out of 22 years and the difference between the groups was statistically
272 significant ($p < 0.001$). The mean ages of the tagged and screened mackerel differed by less
273 than one year in all years and there was no consistent bias in the data (Figure 5). The
274 differences in the age distributions of the two groups were not statistically significant.

275

276 **4. Discussion**

277

278 Both tag recapture models produce abundance estimates that are larger and more variable than
279 the official estimates (ICES, 2009a). These results are in accordance with previous studies
280 (ICES, 2008, Simmonds et al., 2010). Simmonds et al. (2010) used Bayesian state-space
281 models to investigate the agreement between data from egg surveys, tagging data and catch-
282 at-age and the results indicate a SSB that is substantially higher than the official ICES
283 estimate. The triennial egg survey SSB estimates have on average been 30% higher than the

284 official SSB estimates (ICES, 2008). The survey estimates are furthermore believed to
285 underestimate the stock size by up to 40% due to incomplete coverage of the egg distribution
286 and unaccounted egg mortality before first capture (ICES, 2005; Portilla et al., 2007).

287 One of the main assumptions in this study is complete mixing of the tagged individuals
288 with the whole NEA mackerel stock. This assumption may be difficult to satisfy when
289 considering the highly migratory and widely distributed NEA mackerel stock. Migration and
290 distribution studies do, however, indicate that the whole stock is present in the northern North
291 Sea and Norwegian Sea in autumn and winter (Uriarte and Lucio, 2001) when most of the
292 landings have been screened. The fisheries are also selective and tend to target larger
293 individuals (Kvalsvik et al., 2002), but the age distributions of the tagged and screened
294 mackerel did not indicate any bias in the samples. The size selectivity of the fisheries should,
295 anyhow, not influence the tag based estimates because year classes are treated separately, both
296 with respect to the numbers released, the numbers recaptured and the numbers screened, and
297 the year class abundance is determined by the concentration of tags in the screened catches.
298 Likewise, the cumulated mortality is summed over ages within the year class.

299 A substantial increase in biomass is indicated by the tag models from 2002 to 2006 and
300 2008 respectively. The official estimates (ICES, 2009a) and the egg surveys (ICES, 2008)
301 also indicate an increase in the stock in these years, but the reduction in tag recapture rate
302 since 2005 is too distinct to be explained by solely an increase in the stock size. Mackerel
303 distribution areas during spawning and summer feeding have expanded and moved further
304 north and northwest in the more recent years (ICES, 2009b). These changes may indicate an
305 increase in the stock, but may also have introduced a bias in the tag based estimates if the
306 changes result in variation in the mixing rate of the tags with the whole population. It is,
307 however, also likely that methodological issues have introduced a source of error. First, the

308 change from manual to automatic jigging in 2006 may have involved a decrease in the
309 survival rate of the tagged mackerel. Secondly, there is reason to believe that the detection of
310 tags and testing of detector efficiency has become less reliable at some of the factories during
311 the last years resulting in loss of tags and overestimation of the detector efficiency. Small
312 sample sizes may also have resulted in highly uncertain estimates in the last years of the study
313 period. Nevertheless it is important to improve the temporal and spatial coverage of the
314 fisheries and increase both the number of tagged individuals and the screened landings.
315 According to Robson and Regier (1964) the tagged sample size times the size of the sample
316 examined for tags should be at least three or four times the expected population size to avoid
317 bias in the estimates. Samples of that size may be difficult to reach when the stock is as large
318 as the NEA mackerel, but at the moment between 20 000 and 40 000 tonnes are screened each
319 year while the total catch is around 600 000 t and there is therefore potential to substantially
320 increase the amount screened. Given international co-operation detectors could be installed
321 internationally and by installing two detectors at the large mackerel ports in the UK, for
322 example, the amount screened could be doubled.

323 The MERKAN model estimates were not affected by uncertainty in catch data as no
324 assumption on mortality was required other than initial tag loss, but the estimates varied
325 substantially among years. The uncertainty related to the level of tagging survival rate and
326 how it varies between years and sizes is probably the greatest uncertainty source in these
327 estimates, and an assumption of a constant rate is highly unrealistic. The mean lengths of the
328 age-length keys were significantly lower than the mean lengths of the tagged mackerel and
329 the difference seems to be due to a larger proportion of small mackerel (below 25 cm) in the
330 ALKs. These mackerel are mainly 0- and 1-year olds and not included in the data and should
331 thereby not introduce any bias in the age distribution of the tagged mackerel, but this may

332 indicate that small mackerel are more vulnerable to the tagging operation and therefore have
333 lower tagging survival rate. An attempt was made to study the variation in wind strength and
334 sea bird predation pressure on the newly tagged mackerel and how these influenced recapture
335 rates, but no effect was found, although the data were of too poor quality to be assessed
336 properly. Some of the uncertainty related to variation in tagging survival rate is reduced in the
337 HAMRE model as several tag release experiments are summed.

338 Some of the uncertainty was estimated by bootstrapping some of the raw data. The age
339 distribution of the tagged fish at release is based on samples of the fish caught for tagging.
340 The uncertainty due to the relatively small sample size was included in the bootstrap,
341 assuming a multinomial distribution. Furthermore, the potential uncertainty caused by few
342 landings screened and low numbers of tags found in each landing, was included by randomly
343 drawing (with replacement) the landings to be used in the analysis. Clearly, these sources,
344 although important, do not cover the whole range of sources of uncertainty. To cover all
345 relevant sources adequately would be a major task, in particular because their distributional
346 properties often are poorly known.

347 In order to improve the dataset in the future and to reduce the uncertainty involved in the
348 estimates a more automatic tagging and recapture method should be introduced. Passive
349 integrated transponder tags (PIT) are presently considered to be more successful than the
350 traditional tagging method. The technology does not require constant surveillance and manual
351 data collection, which seem to cause problems in the current method. Automatic detection of
352 tags and data collection would also make it easier to install more detectors, also
353 internationally.

354 Given the lack of fishery independent, age-structured data, tag recapture estimates could
355 be of great value, and perhaps be included in the stock assessment of the Northeast Atlantic

356 mackerel on a regular basis. The tag recapture dataset provides age-structured abundance
357 estimates that are not directly influenced by the unreliable catch data, and the stock estimates
358 can be carried out on a yearly basis at a relatively low cost. One disadvantage with the
359 MERKAN estimates in an assessment is that they do not cover the most recent years. The
360 HAMRE model, on the other hand, requires fishing and natural mortality rates as input and
361 these are derived from the assessment model. However, if the tag-based estimates were used
362 in the assessment, the fishing mortality rates would probably change themselves. One possible
363 way forward is to feed the mortality information embedded in the tag recapture data into the
364 HAMRE model, and use either the resulting index as a relative measure of abundance, or
365 derive expected recaptures from the assessment model and fit that to the data. Such
366 approaches would require further modelling work and a careful evaluation of the effect of the
367 noise in the data. Further studies of the survival rate of the tagged mackerel and an improved
368 understanding of the migration and distribution patterns and changes in these patterns are
369 essential.

370

371 **Acknowledgements**

372

373 We would like to thank the whole mackerel tagging team at the IMR, especially Sigmund
374 Myklevoll who has been the leading man from the start of the tagging program. Thanks to
375 Knut Hestenes and Helga Gill for excellent help with data processing and Aud Vold and
376 Johannes Hamre for constructive comments on the manuscript.

377

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449

450 **Tables**

451

Table 1. Tags released in the years 1984-2007 and yearly recaptures one year after release (R_{y+1}) to 10 years after release (R_{y+10}).

Release year	N. released	Recaptures									
		R_{y+1}	R_{y+2}	R_{y+3}	R_{y+4}	R_{y+5}	R_{y+6}	R_{y+7}	R_{y+8}	R_{y+9}	R_{y+10}
1984	708	2	1	1	3	1	0	1	0	0	0
1985	408	7	3	4	3	3	0	1	1	0	0
1986	16983	5	5	1	5	2	2	0	1	0	0
1988	20068	10	9	6	3	3	8	4	0	0	1
1989	20789	14	8	2	5	2	2	2	1	3	0
1990	19744	10	6	14	11	2	2	3	3	2	1
1991	21382	11	24	17	2	3	3	2	1	2	1
1992	15800	17	17	5	4	6	3	1	1	0	1
1993	22279	32	22	8	11	14	3	1	3	2	0
1994	26934	26	30	17	25	12	9	7	2	1	0
1995	24448	30	36	46	24	20	8	12	2	1	0
1996	18858	33	52	26	21	13	11	7	1	1	0
1997	34375	108	68	50	32	28	11	2	2	1	0
1998	21900	60	40	41	20	15	6	0	1	0	0
1999	12379	30	26	16	9	3	2	0	0	0	
2000	5552	17	16	13	6	0	0	0	0		
2001	20623	72	50	27	10	2	5	0			
2002	17272	55	34	11	4	3	0				
2003	11806	32	8	4	5	2					
2004	13649	23	13	10	8						
2006	27312	29	11								
2007	27678	4									

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Table 2. Mackerel screened for tags in the years 1986–2008 and the efficiency of the detector.

Year	Screened (t)	Eff. (%)
1986	3966.7	97.8
1987	7376.9	89
1988	7391.7	96.9
1989	5866.1	99.6
1990	10855.4	97.8
1991	9483.4	99
1992	10831.2	90.3
1993	21086	95.2
1994	25536.2	92
1995	16332.7	91.1
1996	18481.6	92.2
1997	20898.8	90.9
1998	26280.9	95.4
1999	22846.7	96.6
2000	26647.2	95.6
2001	26984.4	98.8
2002	29089.6	96
2003	45592	92.2
2004	44918.7	96.6
2005	30819.6	95.2
2006	24039.6	97.7
2007	22669.6	97.2
2008	18946.6	97.7

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470 **Figures**

471

472 Figure 1. Tag releases (squares) in the spawning area west of Ireland and recaptures (circles)
473 from fisheries in the northern North Sea, 1986-2008.

474

475 Figure 2. Mackerel year class abundance (numbers at age 10^9) estimated by the MERKAN
476 (filled circles) and the HAMRE (filled squares) models compared with the official ICA
477 estimates (open squares, ICES, 2009b). The MERKAN estimates are presented as bootstrap
478 medians with 25th and 75th percentiles.

479

480 Figure 3. Stock biomass estimates of 3-12 year old mackerel, 1986-2006, based on the
481 MERKAN and the HAMRE models. The estimates are compared with the official SSB
482 estimates (ICES, 2009a) and the triennial egg survey SSB estimates (ICES, 2008). The
483 MERKAN estimates are presented as bootstrap medians with 25th and 75th percentiles.

484

485 Figure 4. The influence of various tagging survival rates (50, 60 and 70%) on the biomass
486 estimates based on the MERKAN (a) and the HAMRE (b) models, 1986-2006.

487

488 Figure 5. Comparisons of the mean lengths with 95% confidence intervals of the ALKs used
489 to age the tagged mackerel and the tagged mackerel (Figure a) and the mean ages with 95%
490 confidence intervals of the tagged and screened mackerel (Figure b).

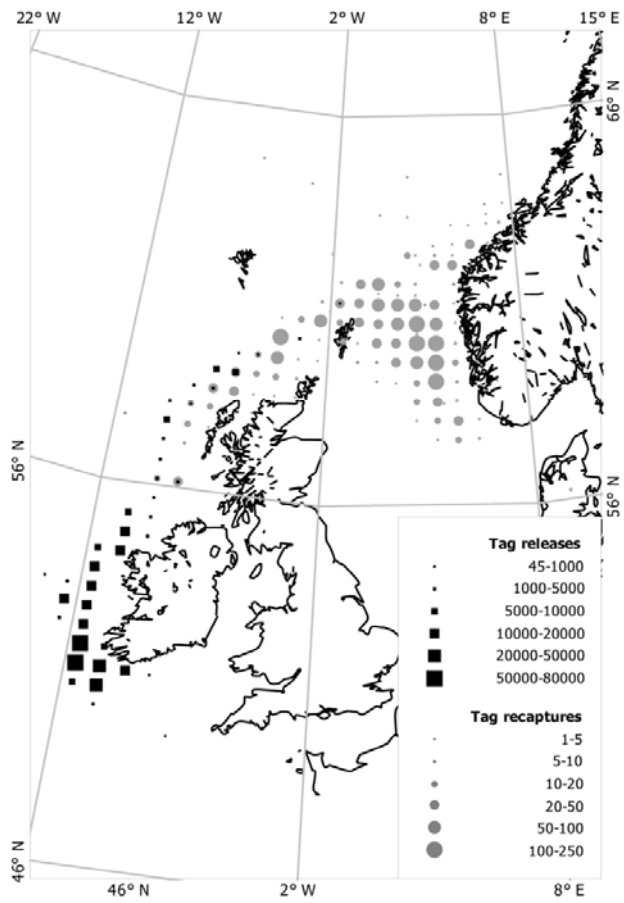
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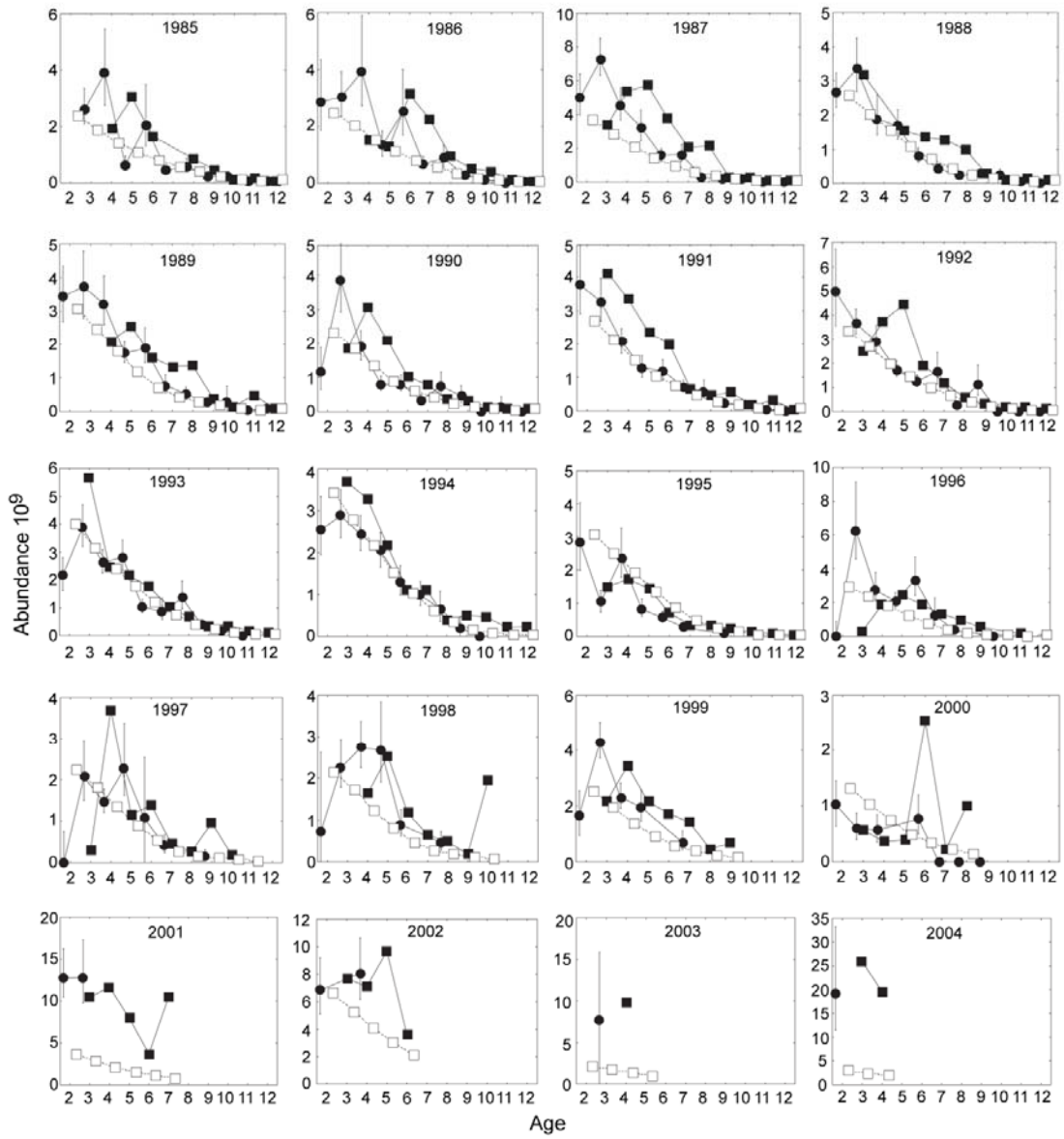
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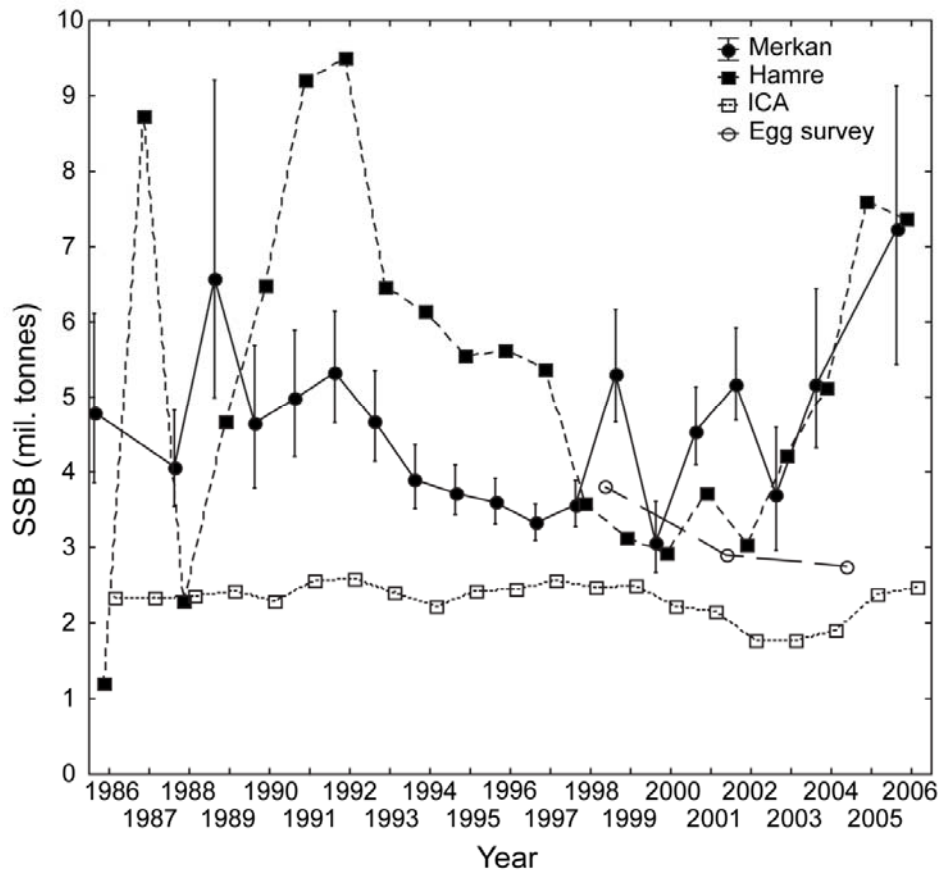
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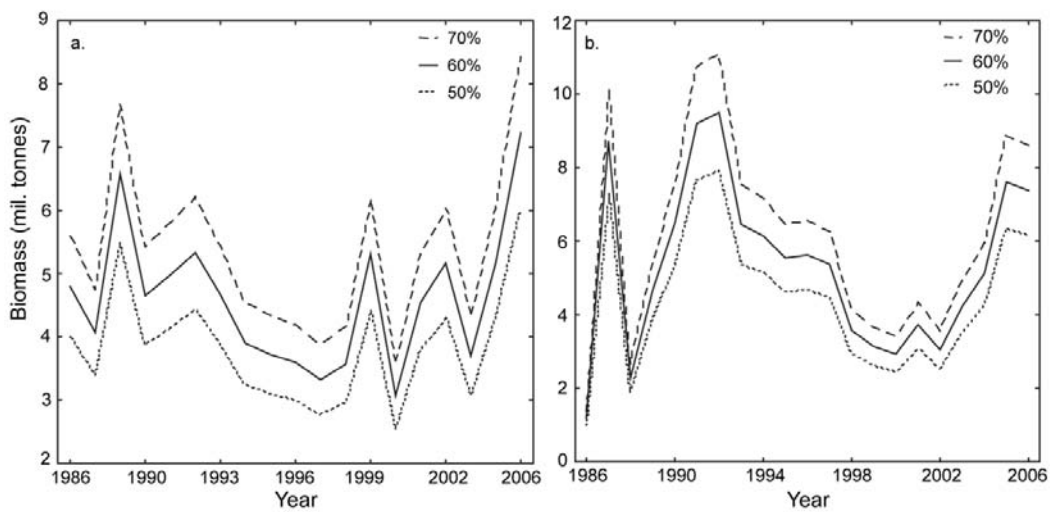
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 498 Figure 1.
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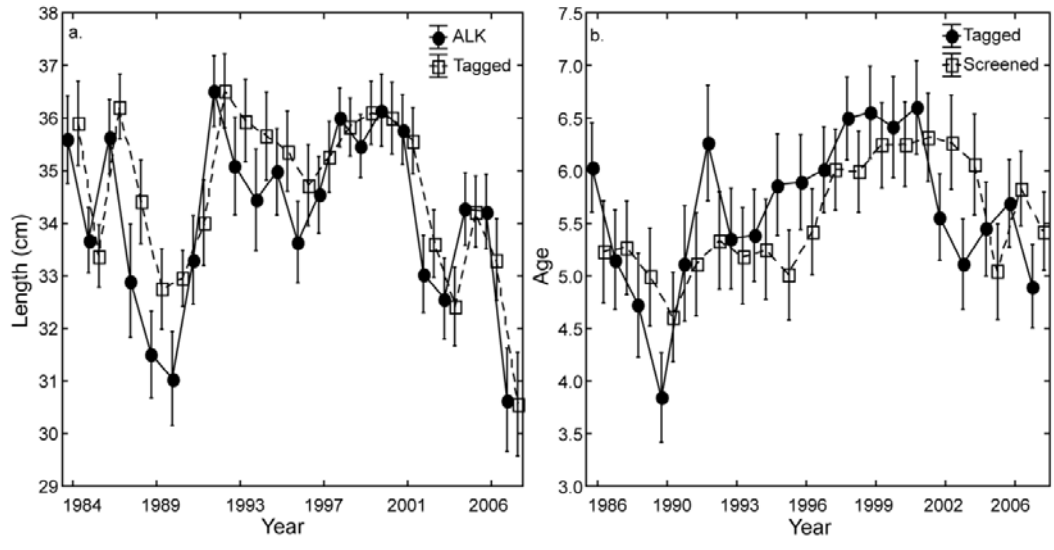
500
 501 Figure 2.
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