ESTIMATING ALBACORE MOVEMENT RATES BETWEEN THE NORTH ATLANTIC AND THE MEDITERRANEAN FROM CONVENTIONAL TAGGING DATA

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SUMMARY

A tag attrition model is fit to albacore tag-recapture data in order to estimate albacore movement rates between the Atlantic and the Mediterranean. The estimated transfer rate from the Atlantic to the Mediterranean is not significantly different from zero, and the estimated annual transfer rate in the opposite direction, under the assumptions of the same catchability and reporting rates is 5,49%. Sensitivity tests to assumed reporting rates and relative catchabilities are performed, and observed lower recovery rates in the Mediterranean may suggest either a lower catchability or reporting rate in this area, that would give an even lower estimate of the transfer rate, which is also supported by information from later tag recaptures of fish tagged in the Mediterranean. The small impact of these transfer rates on stock assessment is discussed and a preliminary assessment of the amount of tagged fish needed in order to get accurate and precise estimates of these low transfer rates is also done by simulating different tagging scenarios.

RÉSUMÉ

Un modèle de déperdition des marques est ajusté aux données de marquage-recapture du germon afin d'estimer les taux de déplacement du germon entre l'Atlantique et la Méditerranée. Le taux de transfert estimé de l'Atlantique à la Méditerranée n'est pas sensiblement différent de zéro, et le taux de transfert annuel estimé dans la direction opposée, en prenant comme postulat une capturabilité et des taux de soumission de données identiques, s'élève à 5,49%. On a réalisé des tests de sensibilité aux taux de soumission de données supposés et à la capturabilité relative. Les taux de récupération inférieurs observés en Méditerranée suggèrent éventuellement une capturabilité ou un taux de soumission de données plus faible dans cette zone, ce qui donnerait une estimation encore plus faible du taux de transfert. Cela est également appuyé par des informations provenant de récupérations tardives de marques de poissons marqués en Méditerranée. Le faible impact de ces taux de transfert sur l'évaluation du stock est discuté et une évaluation préliminaire du volume de poissons marqués nécessaire pour obtenir des estimations exactes et précises de ces faibles taux de transfert est également réalisée en simulant différents scénarios de marquage.

RESUMEN

Se ajusta un modelo de tasa de pérdida de marcas a los datos de marcado-recuperación de atún blanco con el fin de estimar las tasas de movimiento del atún blanco entre el Atlántico y el Mediterráneo. La tasa de transferencia estimada del Atlántico al Mediterráneo no se diferencia significativamente de cero, y la tasa de transferencia anual estimada en la dirección opuesta, bajo el supuesto de la misma tasa de capturabilidad y comunicación, es de 5,49%. Se realizaron pruebas de sensibilidad de las tasas de comunicación y capturabilidades relativas

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supuestas, y las tasas de recuperación inferiores observadas en el Mediterráneo pueden sugerir una tasa de capturabilidad o de comunicación más baja en esta zona, lo que proporcionaría una estimación aún más baja de transferencia, que se ve sustentada por la información de recuperaciones de marcas posteriores de peces marcados en el Mediterráneo. Se discute el bajo impacto de estas tasas de transferencia en la evaluación del stock y también se realiza una evaluación preliminar de la cantidad de peces marcados necesarios para obtener estimaciones precisas y exactas de estas bajas tasas de trasferencia mediante una simulación de diferentes escenarios de marcado.

1. INTRODUCTION

The northern stock is considered to be independent from the Mediterranean stock (Bard 1981). Nevertheless, evidence of Atlantic-Mediterranean interchange of some individuals has been recorded through tagging experiments (Aloncle and Delaporte 1976; González-Garcés 1997; Ortiz de Zárate and Cort 1998; Arrizabalaga *et al.* 2002).

When attempting to address stock structure issues and relations between stocks, tagging is a valuable tool both to assess the migratory pattern of a species in a qualitative manner, and also to compute migration rates in a quantitative way. A good experimental design is required especially in the latter case.

In the case of albacore, and like for some other tuna species, maximum tagging effort does not occur at the same time in different areas, difficulting the estimation of transfer rates between them. In table 1 the number of albacore tagged by year and area is reconstructed for the historical period 1960-2001 from ICCAT, IEO, CTC (Dr. Ortiz, pers. comm.) and IFREMER (Dr. Liorzou, pers. comm.) databases, as well as from (Penney *et al.* 1998). It is seen that tagging in the southern Atlantic stock has been very scarce, and the total number of tags in the North Atlantic is an order of magnitude higher than in the Mediterranean. The period 1988-1991 seems to be the only one during which tagging cruises were carried out simultaneously in the North Atlantic and the Mediterranean, being the number of tags released approximately of the same order of magnitude.

Spatially structured tag attrition models (Hilborn 1990; Schwarz *et al.* 1993; Anganuzzi et al. 1994) have been applied to compute migration rates of some more intensively tagged tuna species such as *Thunnus maccoyii* (Hampton 1991), *Thunnus albacares* and *Thunnus obesus* (Sibert *et al.* 2000).

In this study, conventional tagging information for the period 1988-1991 is selected and a spatially structured tag-attrition model is fitted in order to estimate movement rates between the North Atlantic (east and west altogether) and Mediterranean populations. The accuracy and precision of the estimates is also assessed.

2. MATERIALS AND METHODS

Tag release data was stratified in two areas (North Atlantic and Mediterranean) and a yearly basis, so that 8 release groups were identified. Tag recaptures were stratified in subsequent years at liberty. Recoveries up to the end of 1994 were considered in the analysis. Observed releases and recoveries for each release group in each spatial strata up to the end of the study period, reconstructed from Aloncle

and Delaporte (1976, 1980), Aloncle *et al.* (1976), Prince *et al.* (1995), González-Garcés (1997), De Metrio *et al.* (1997) and Ortiz de Zárate and Cort (1998), are given in **Table 2**. Only recoveries with complete information are considered in the database, as described in González-Garcés & Arrizabalaga (2002).

Hilborn (1990) proposed a useful tag attrition model for the estimation of movement rates. Xiao (1996) used a slightly modified form of this model incorporating continuous tag shedding and natural mortality rates. He also constrained the model in the way that no fish could move to areas non considered in the model. We used a similar model as this from Xiao but incorporating tag reporting and immediate tag shedding rates.

$$N'_{i,a,t+1} = \sum_{j=1}^{n} N'_{i,j,t}(1 - q_j E_{j,t}) \exp(-M - w_2) p_{j,a}$$

(1) $N'_{i,a,0} = T_{i,a,t}(1 - w_1)$

$R'_{i,a,t} = N_{i,a,t} * q_a E_{a,t} * \boldsymbol{b}_a$

Where:

i, a and t are subscripts for release group, area and time respectively.

$R'_{i,a,t}$ is the expected number of recoveries from release group i in a specified year t and area a (A=North Atlantic or M=Mediterranean)

$T_{i,a,t}$ is the number of tags released in each release group, area and year

w_1 is the proportion of tag looses due to type I tag shedding

w_2 is the proportion of tag looses due to type II tag shedding

β_a is the tag reporting rate in area a

q_a is the catchability coefficient in area a

$E_{a,t}$ is the fishing effort in area a at time t

M is the instantaneous natural mortality rate

$N'_{i,a,t}$ is the expected number of tagged fish from release group i that is present in strata a in year t

$p_{j,a}$ is the proportion of fish moving each year from spatial strata j to a.

The fishing effort applied to north Atlantic albacore (2001) given in **Table 3** is standardized as in Sibert et al. (2000). As it is assumed that the catchabilities remain constant in time, the effort series reflects the trend for the mean fishing mortality of ages 1-8+ in the area for the period 1988-1994 as estimated in last stock assessment session (2001). The fishing effort in the Mediterranean is not known, so it is assumed that standardized fishing effort is equal to 1 all along the years. At a first step the catchability of both areas is considered to be the same. Natural mortality rate is assumed to be equal to 0.3/year (2001). It is assumed that no migration to other strata non considered here (such as the South Atlantic) occurs, so that the sum of movement parameters ($p_{j,a}$) is equal to 1 for a given tag release group.

$$\sum_{i,j} p_{i,j} = 1$$

(2)

As there are no independent estimates of reporting rates, these are assumed to be equal to 0.8 in both areas, as assumed by Ortiz de Zárate & Bertignac (2002). Tag shedding rates are assumed to be equal to the ones calculated by Laurs et al. (1976) for the north Pacific albacore. It is assumed that no tagging mortality exists. Only movement rates from one site to the other (p_{AM} and p_{MA}) and q_A are estimated in the model, and p_{AA} and p_{MM} are derived from equation (2).

Parameter estimation is achieved by maximizing the poisson maximum likelihood function (Xiao 1996). Maximization was carried out by the quasi-Newton method (Press et al. 1992). In order to compute 95% confidence intervals of the estimates, it was assumed that the observed recoveries follow a Poisson distribution with mean $R'_{i,a,t}$ (Xiao 1996) and 400 parametric bootstrap iterations were carried out.

We tested the sensitivity to the assumptions of equal catchability and reporting rates in both areas, by allowing the catchability in the Mediterranean be 0.4-1.4 times the one in the Atlantic, and allowing each reporting rate to vary independently in the range of 0.1-1. 400 bootstrap iterations were performed in each case.

Finally, in order to assess the accuracy and precision of movement rate estimates, we simulate some tagging scenarios, generate recovery datasets and fit the tag attrition model with 400 bootstraps. For the tagging scenarios, we assume three different levels of p_{AM} and p_{MA} (q_A is held constant at this step), these levels corresponding to the average and extreme values (lower and upper) of the 95% confidence intervals estimated in the previous tag attrition model fit. An equal number of fish is supposed to be tagged in each location and year. Relative bias (RB) and relative standard error (RSE) are computed following Maury (2000) and Xiao (1996):

RB = (p-p')/p
RSE = SE(p')/p

where p is the real value of the parameter and the p' is the estimated parameter value.

3. RESULTS

As stated in Anganuzzi *et al.* (1994) and Xiao (1996), one of the simplest ways to analyse migration rates would be to calculate proportions of recaptures in different areas. Among the 12659 fish tagged in the Atlantic along the study period, 387 were recovered (recovery rate of 3.06%), from which only one was recovered in the Mediterranean, this meaning that only 0.26% of the fish tagged in the Atlantic moved to the Mediterranean. On the other hand, from the 3803 fish tagged in the Mediterranean, only 28 were recovered (recovery rate of 0.74%), from which 2 were in the Atlantic, which would mean a migration rate of 7.14% from the Mediterranean to the Atlantic. However, these estimates are biased as they do not allow for space-time variations in fishing mortality or reporting rates, for instance. The tag attrition model applied takes into account the temporal evolution of the fishing effort in the North Atlantic and sensitivities to catchability and reporting rate differences between areas are tested. Parameter estimates of migration rates and catchabilities are given in table 4. Mean annual movement rates from the northern Atlantic to the Mediterranean and vice versa were 0,59% and 5,49 % respectively, with an average catchability coefficient of 0,0141.

Observed coefficients of variation of the estimates were large, especially for p_{AM} leading to a 95 % confidence interval of 0.00-1.49%.

Observed and predicted number of recoveries for each tag group in each spatial stratum are given in **Figure 1**. **Figure 2** shows that there is no significant correlation between the parameter estimates. The patchiness of p_{AM} values are because only one fish was tagged in the Atlantic and recovered in the Mediterranean, and so many bootstrapped recoveries showed 0, 1, 2 or 3 trans-zonal migrations in this direction, which needed very concrete values of p_{AM}. If bootstrapped recoveries were higher than 3, p_{AM} values were not patchy any more, but more continuously distributed.

Results of the sensitivity tests to assumed area specific reporting rates are shown in **Figure 3**. The average values of the Atlantic-Mediterranean movement rate estimates do not change significantly for reporting rates around the ones that are assumed (0.8). For high reporting rates in the Atlantic, low reporting rates in the Mediterranean would produce a higher estimate of movement rate from the Atlantic into the Mediterranean. On the other hand, migration from the Mediterranean to the Atlantic is higher if tag reporting rates are high in the Mediterranean and low in the Atlantic. The rate of increase is not very high around the values of 0.8 assumed, but increases very rapidly in the upper left

corner of the surface graph (when very low reporting rates in the Atlantic and high reporting rates in the Mediterranean).

The results of the sensitivity tests of migration rate estimates to the assumption of equal catchability coefficients in both areas are given in **Figure 4**, that shows the mean values of migration rates (p_{AM} and p_{MA}) in 400 bootstrap iterations for each qratio value assumed (qratio = qMed/qAtl), run under the assumption of both reporting rates equal to 0.8. Mean p_{AM} estimates and their standard deviations seem to decrease with the q ratio value, while p_{MA} values and their standard deviations increase. In other words, if the catchability in the Mediterranean was lower than in the Atlantic (qratio<1), the rates of fish migrating out of the Mediterranean would be lower.

Figure 5 shows the variation of the mean parameter estimates, the relative bias and the relative standard error with the simulated number of fish tagged each year in each location. We observe that if the transfer coefficient is equal to 0, the estimates are very accurate and precise even if a low number of fish are tagged (obviously, as no evidence of movement is provided in the data). But when transfer coefficients are positive, the lower they are, the more fish we would need to tag in order to achieve estimates with a given accuracy and precision. For the range of movement rates observed for the fit to real data, we would need to tag more than around 5000 fish each year and zone in order to have relatively accurate and precise estimates of transfer rates.

4. DISCUSSION

A good experimental design, with a high amount of fish tagged simultaneously in all the stocks and during several consecutive years is needed to obtain proper estimates of migration rates between stocks from tagging data. The experimental design of the conventional tagging experiments carried out up to now is not optimum for this purpose, as much less individuals have been tagged in the Mediterranean, in which the recovery rates are also much lower. The total number of recoveries is not high, only two fish among the ones tagged in the Mediterranean were recaptured in the Atlantic, and only one fish was observed to migrate from the Atlantic into the Mediterranean. In spite of this, and considering that this is all the available information from conventional tag release recapture experiments, the analysis performed allows having an estimate of the migration rates between both stocks.

The proportion of albacore migrating from the Atlantic to the Mediterranean (under the assumptions of equal reporting rates and catchabilities) is not statistically different from 0. The proportion of fish coming out of the Mediterranean is a bit higher (5,49% of the Mediterranean population size, every year). Nevertheless, the observed confidence intervals are rather wide (1,79%-9,04%). This migration rate could be lower if the catchability or the reporting rate in the Mediterranean was lower than in the Atlantic. The assumption of standardized fishing effort equal to 1 in the Mediterranean makes the catchability value reflect the fishing mortality rate. The fishing mortality rate in the Mediterranean is not properly known, but it seems reasonable to think that it may be somewhat lower than in the Atlantic, were most of the commercial fleets operate. On the other hand, and judging from the low recovery rates of fish tagged in the Mediterranean (0.74 % versus 3,06% in the North Atlantic), it seems reasonable to think that either the reporting rate or the catchability may be lower in the Mediterranean, and so that the percentage of the population that comes out to the Atlantic is much lower than 5,49%.

Only 3 transzonal migrations were observed (2 from the Mediterranean to the Atlantic and 1 from the Atlantic to the Mediterranean) during the studied period, and only 28 fish were recovered among the ones tagged in the Mediterranean. This makes p_{MA} migration rate estimates highly sensitive to the subsequent recoveries of fish tagged in the Mediterranean. More recoveries of Mediterranean tagged fish have occurred after 1994. González-Garcés & Arrizabalaga (2002) describe 39 recoveries from fish tagged in the Mediterranean and according to Liorzou (pers. comm.) up to 62 recoveries have

been recorded. Nevertheless, no more transzonal (from the Mediterranean to the Atlantic) migrations apart from the two occurred during the analysed period have been described. An analysis of data with more recoveries but the same number of transzonal migrations would lead, obviously, to a much lower p_{MA} estimate than the one obtained in the present analysis.

Moreover, it is necessary to take into account the relative size of the populations when attempting to assess the influence of migrations in both the relative abundance and genetic variability between the stocks. In the period 1988-1995, the average reported catches in the Mediterranean were only 4,84% the ones in the north Atlantic. Catch statistics in the Mediterranean present several deficiencies, and there is a lack of a proper stock assessment for the Mediterranean albacore. In spite of this, and judging from the comparison of the reported catches in both stocks, we may think that the Mediterranean stock size may be considerably smaller than the northern Atlantic stock size. In this sense, 5.49% (or less) of the fish in the Mediterranean stock migrating into the north Atlantic may represent a really small number of fish in comparison with the ones present in the north Atlantic stock, which would lead to a minor influence in the relative stock abundance and in terms of homogenising the genetic information of both populations. The finding of genetic differences between samples from the Atlantic and the Mediterranean (Lopez-Rodas 2002) supports the hypothesis of very low mixing rates between both populations.

Good catch and effort statistics would be needed in the Mediterranean, in order to be able to know the relative catchabilities and population sizes of both Mediterranean and North Atlantic stocks studied. Independent reporting rate estimates would also be very helpful.

Given the low movement rates that seem to occur, the cost (and difficulty) of a tagging program to estimate them with a given accuracy and precision is very high. Moreover, the information obtained would probably be of little help for stock assessment purposes, for which it seems reasonable to recommend that tagging efforts be directed to other priorities (natural mortality, growth, etc.), unless future recoveries show higher evidence of transzonal migration (in which case it would be easier to estimate transfer rates with a given accuracy and precision with a properly designed tagging program, and the results would also be more useful for stocks assessment purposes).

5. AKNOWLEDGEMENTS

REFERENCES

ALONCLE, H. and F. Delaporte. 1976. "Marquages de germons par l'istpm, 1967-1974." Collect Vol Sci Pap ICCAT **5**: 216-220.

ANGANUZZI, A., R. Hilborn and J.R. Skalski. 1994. "Estimation of size selectivity and movement rates from mark-recovery data." Can J Fish Aquat Sci **51**: 734-742.

ARRIZABALAGA, H., V. López Rodas, V. Ortiz de Zárate, E. Costas and A. González Garcés. 2002. "Study on the migrations and stock structure of albacore (*Thunnus alalunga*) from the atlantic ocean and the mediterranean sea based on conventional tag release-recapture experiences." Collect Vol Sci Pap ICCAT 54(5): 1479-1494.

BARD, F.X. 1981. Le thon germon (T*hunnus alalunga* bonnaterre 1788) de l'ocean atlantique. De la dynamique des populations à la strategie demographique. France, Universite de Paris **:** 333.

GONZÁLEZ-GARCÉS, A. 1997. Contribución al conocimiento de la dinámica de la población del atún blanco (T*hunnus alalunga*, bonn. 1788) del atlántico norte. Departamento de Biología Animal I (Zoología). Facultad de Biología. Spain, Universidad Complutense de Madrid **:** 200.

GONZÁLEZ-GARCÉS, A. and H. Arrizabalaga. 2002. "Update of albacore tag release-recapture information in the North Atlantic and Mediterranean for the period 1968-1999." Collect Vol Sci Pap ICCAT **54**(5): 1454-1478.

HAMPTON, J. 1991. "Estimation of southern bluefin tuna T*hunnus maccoyii* natural mortality and movement rates from tagging experiments." Fish Bull 89: 591-610.

HILBORN, R. 1990. "Determination of fish movement patterns from tag recoveries using maximum likelihood estimators." Can J Fish Aquat Sci 47: 635-643.

ICCAT. 2001. "Report of the ICCAT SCRS albacore stock assessment session (Madrid, Spain - October 9 to 15, 2000)." Collect Vol Sci Pap ICCAT 52: 1283-1390.

LAURS, R.M.,W.H. Lenarz and R.N. Nishimoto. 1976. "Estimates of rates of tag shedding by North Pacific albacore, *Thunnus alalunga*." Fish Bull 74(3): 675-678.

LÓPEZ-RODAS, V., H. Arrizabalaga, B. Nieto, A. González-Garcés, E. Costas. 2002. "Use of lectins to characterize genetic variability and geographic differentiation in natural populations of *Thunnus alalunga* (Bonn. 1788)." Collect Vol Sci Pap ICCAT 54(5): 1495-1507.

MAURY, O. 2000. "A habitat-based simulation framework to design tag-recapture experiments for tunas in the Indian Ocean. Application to the skipjack *(Katsuwonus pelamis)* population." IOTC WPT Mahe, Seychelles, 29-30 September: 11.

ORTIZ de ZÁRATE, V. and M. Bertignac. 2002. "Analysis of tagging data from North Atlantic albacore (*thunnus alalunga*): Attrition rate estimates." Collect Vol Sci Pap Iccat 54(5): 1438-1453.

ORTIZ de ZÁRATE, V. and J.L. Cort. 1998. Albacore (*Thunnus alalunga*, Bonnaterre) stock structure in the Atlantic Ocean, as inferred from distribution and migration patterns. ICCAT Tuna Symposium, Pta. Delgada. Azores.

PENNEY, A.J., S.Y. Yeh, C.L. Kuo and R.W. Leslie. 1998. Relationships between albacore (*thunnus alalunga*) stocks in the southern atlantic and indian oceans. ICCAT Tuna Symposium, Pta. Delgada. Azores.

PRESS, W., S.A. Teukolsky, W. Vetterling and B.P. Flannery. 1992. Numerical recipes in fortran: The art of scientific computing. Cambridge, Cambridge University Press.

SCHWARZ, C.J., J.F. Schweigert and A.N. Arnason. 1993. "Estimating migration rates using tag-recovery data." Biometrics 49(1): 177-193.

SIBERT, J., K. Holland and D. Itano. 2000. "Exchange rates of yellowfin and bigeye tunas and fishery interaction between cross seamount and near-shore fads in Hawaii." Aquat Living Resour 13(4): 225-232.

XIAO, Y. 1996. "A framework for evaluating experimental designs for estimating rates of fish movement from tag recoveries." Can J Fish Aq Sci 53(06): 1272-1280.

Table 1: Number of albacore tagged by area for the historical period, reconstructed from CTC (Dr. Ortiz, pers. comm.), IFREMER (Dr. Liorzou, pers. comm.), ICCAT and IEO databases, as well as from (Penney et al. 1998). *According to (Penney et al. 1998), 260 fish were tagged during 1985 and 1986. 130 fish have been assigned to each year. The shaded area is selected for the present analysis.

Año	Geographic area			
	Atl N	Atl S	Med	Total
1960	2			2
1961	3			3
1962	2	2		4
1963	4	11		15
1964	1			1
1966	11			11
1968	473			473
1969	315			315
1970	524			524
1971	643			643
1972	1613			1613
1973	691			691
1974	205			205
1975	470			470
1976	806			806
1977	575			575
1978	141			141
1979	115			115
1980	843			843
1981	18			18
1982	57			57
1983	291			291
1984	228			228
1985	133	130*		263
1986	218	130*	6	354
1987	39		95	134
1988	536		239	775
1989	3085		1392	4477
1990	4642		580	5222
1991	4396		1592	5988
1992	41		4	45
1993	129		86	215
1994	77		246	323
1995	14		265	279
1996	20			20
1997	4			4
1998	74			74
1999	1			1
2000	18			18
2001	38			38
Total	21496	273	4505	26274

Table 2: Tag release and recapture information for the study period. $T_{i,a,t}$ = number of tags released in group I and area a at year t. The number of recoveries is the number of fish of a given group recaptured in the same area of release. The number of recoveries in the opposite spatial strata is between brackets.

Release				Recapture						
				Years at liberty						
Tag Group	Area	Year	Ti,a,t	0	1	2	3	4	5	6
1	N Atl	1988	536	30 (0)	7 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)
2	Med	1988	239	0 (0)	0 (0)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)
3	N Atl	1989	3085		54 (0)	32 (0)	8 (0)	5 (0)	0 (0)	0 (0)
4	Med	1989	1392		3 (0)	7 (0)	3 (0)	0 (0)	0 (1)	0 (0)
5	N Atl	1990	4642			36 (0)	38 (0)	11 (1)	1 (0)	0 (0)
6	Med	1990	580			2 (0)	4 (0)	0 (0)	1 (0)	0 (0)
7	N Atl	1991	4396				106 (0)	45 (0)	9 (0)	4 (0)
8	Med	1991	1592				3 (0)	0 (0)	0 (0)	1 (1)

Table 3: Standardized fishing effort for the north Atlantic stock in subsequent years after tagging. As tagging is done approximately at the middle of the fishing season, effort for a given year at liberty is the mean effort of two consecutive natural years.

	Years after tagging						
	0	1	2	3	4	5	6
Ey,a	0,7626	1,0123	1,0644	0,8732	1,0331	1,1543	1,1001

Table 4. Mean, standard deviation and 95% upper and lower confidence intervals (based on 400 bootstraps) for movement rates and catchabilities. p_{AM} = movement rate from the Atlantic to the Mediterranean. p_{MA}=movement rate from the Mediterranean to the Atlantic. q_A=catchability coefficient in the Atlantic. q_M (catchability in the Mediterranean) is assumed to be equal to q_A.

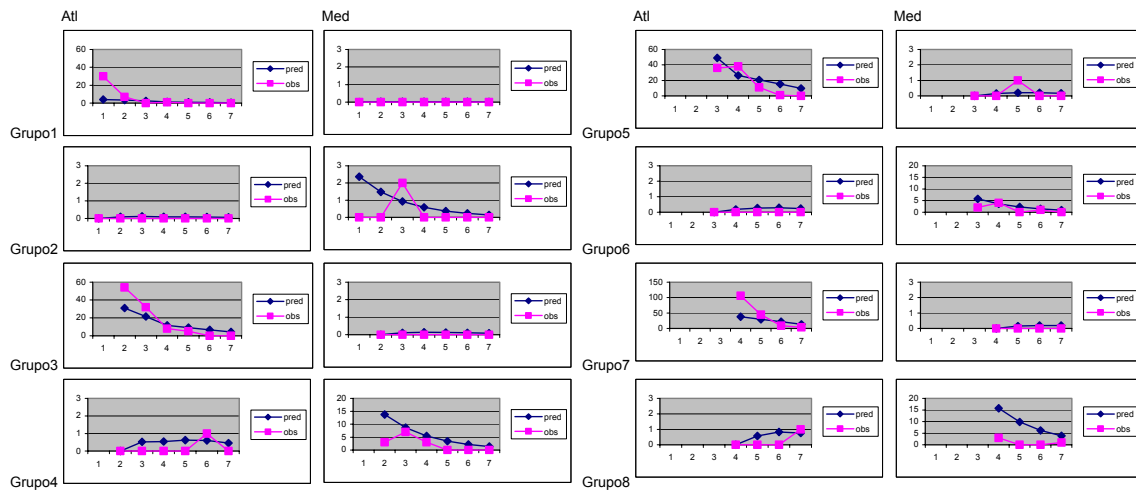|	pAM	pMA	qA
mean	0,0059	0,0549	0,0141
sd	0,0042	0,0190	0,0007
low	0,0000	0,0179	0,0128
up	0,0149	0,0904	0,0154

Figure 1. Observed and predicted number of recoveries for each tag group in each spatial strata.
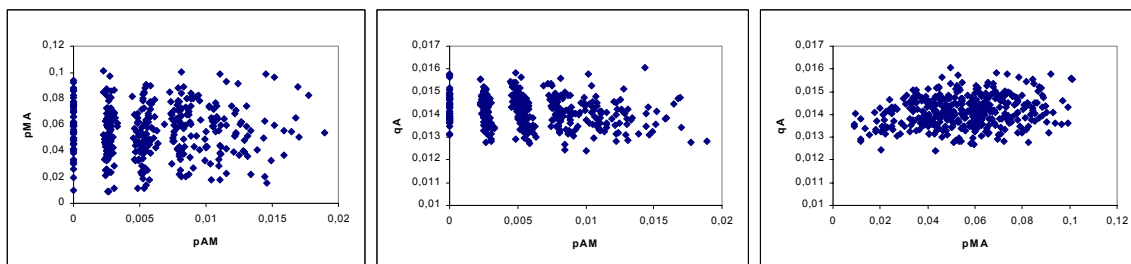

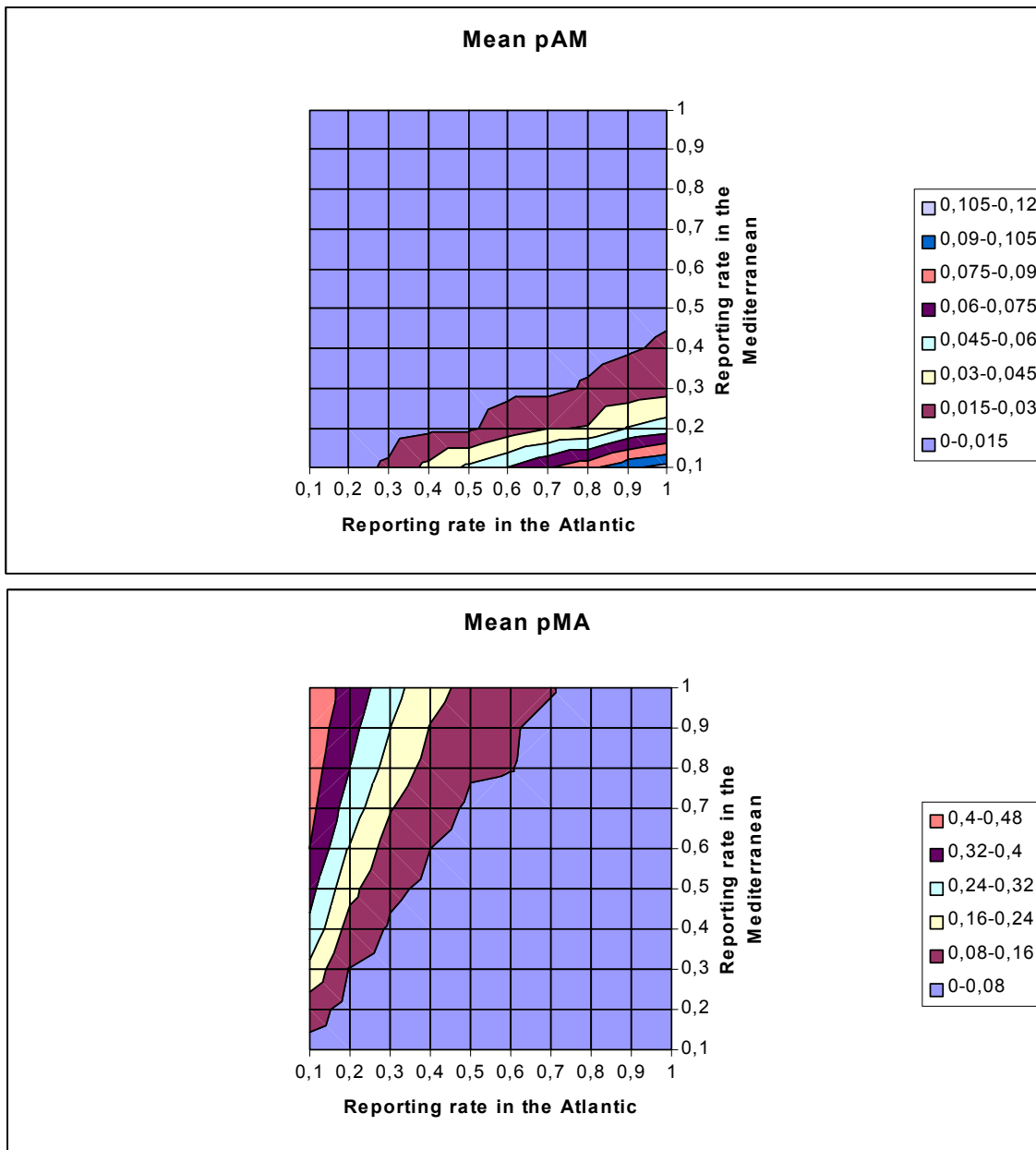**Figure 2.** Correlation plots for estimated parameters (pAM, pMA, qA).

Figure 3. Mean Atlantic-Mediterranean (p_{AM}) and Mediterranean-Atlantic (p_{MA}) migration rates for varying area specific reporting rates. Mean values of the 400 bootstrap iterations in each combination of reporting rates are given.
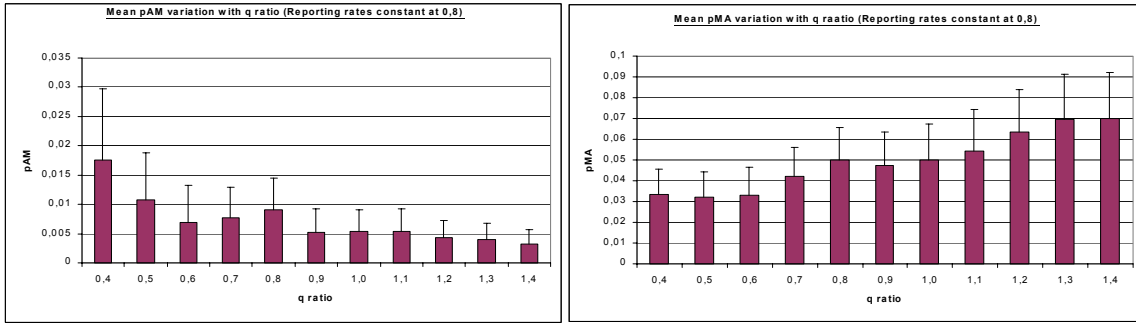
Figure 4. Variation of P_{AM} and P_{MA} with assumed values of q ratio (q ratio = q_M/q_A) at both reporting rates equal to 0,8. Mean values and standard deviations from 400 bootstrap iterations are shown.
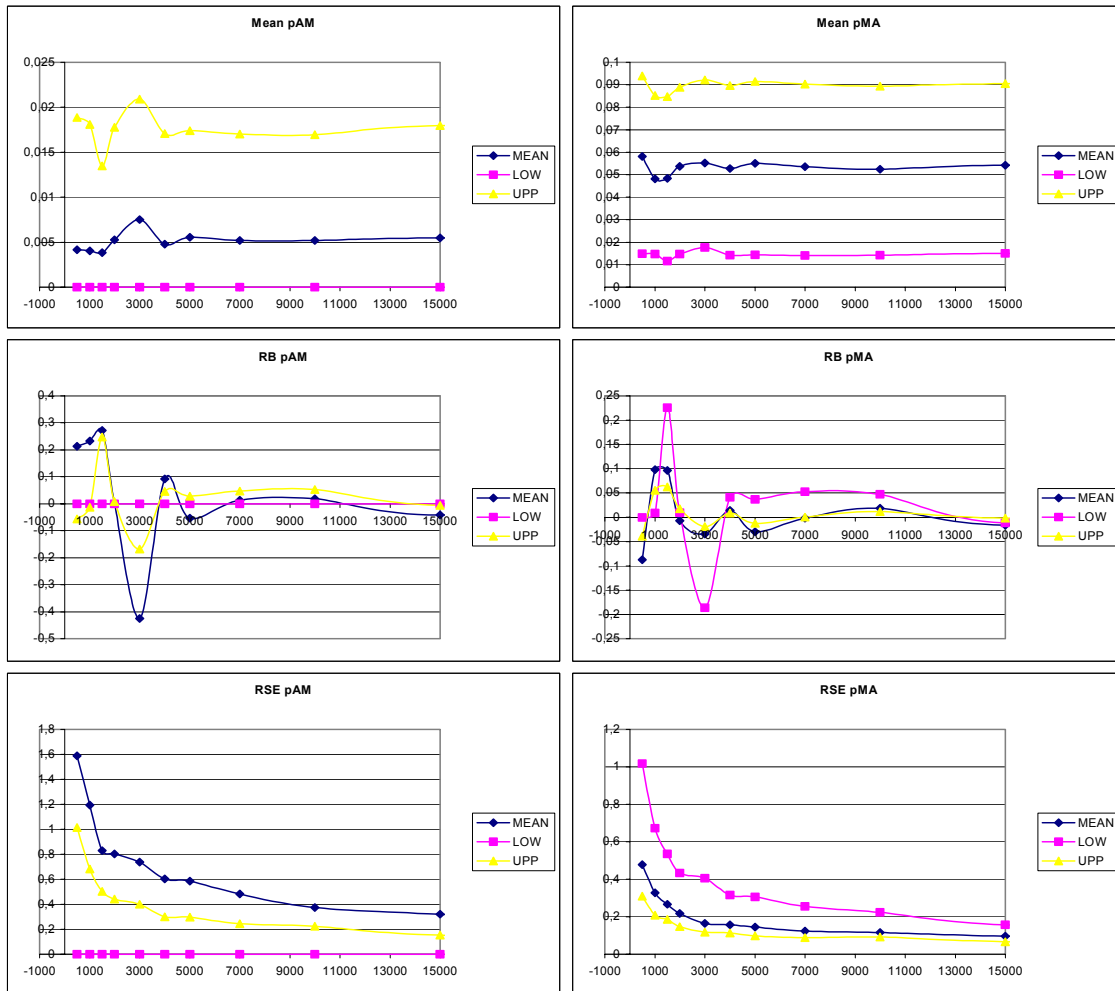

Figure 5. Mean values, relative bias (RB) and relative standard error (RSE) of Atlantic-Mediterranean and Mediterranean-Atlantic movement rate estimates for three levels of assumed true movement rate levels. Mean, Low and Upp indicate the mean movement rate estimate and the lower and upper bounds of the 95% confidence interval given in table 4 for p_{AM} and p_{MA}.