

## A FRAMEWORK FOR ESTIMATING MOVEMENT AND FISHING MORTALITY RATES OF THE BLUE SHARK, *PRIONACE GLAUCA*, IN THE NORTH ATLANTIC FROM TAG-RECAPTURE DATA

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### SUMMARY

*Previous attempts to conduct a stock assessment for the blue shark (Prionace glauca) in the North Atlantic have been handicapped by the lack of reliable catch and effort data. The use of tag-recapture data is among ICCAT's recommendations for future assessment work. This paper proposes a statistical framework for estimating blue shark movement and fishing mortality rates from the tag-recapture data of the National Marine Fisheries Service Cooperative Shark Tagging Program (NMFS-CSTP). The model considers four geographical regions. Blue sharks can stay in the region in which they were tagged and they can move among regions. The parameters of the model are the intra- and inter-region movement probabilities and the catchability coefficients that relate the probabilities of capture and the ICCAT longline fishing effort data. Bayesian estimation methods are used to estimate and quantify the uncertainty associated with the values for these parameters. The dataset of the NMFS-CSTP shows potential for use in a blue shark stock assessment and should be investigated further. Areas of interest for future research are identified.*

### RÉSUMÉ

*Les tentatives antérieures visant à réaliser une évaluation du stock de requin peau bleue (Prionace glauca) dans l'Atlantique Nord ont été entravées par le manque de données fiables de prise et d'effort. Le recours aux données de marquage-récupération figure parmi les recommandations de l'ICCAT pour les évaluations futures. Le présent document propose un cadre statistique destiné à estimer les déplacements et les taux de mortalité par pêche du requin peau bleue à partir des données de marquage-récupération obtenues dans le cadre du Programme coopératif de marquage de requins du National Marine Fisheries Service (NMFS-CSTP). Le modèle envisage quatre régions géographiques. Les requins peaux bleues peuvent rester dans la région où ils ont été marqués et ils peuvent se déplacer entre les régions. Les paramètres du modèle sont les probabilités de déplacement intra et inter-régions et les coefficients de capturabilité qui relient les probabilités de capture et les données d'effort de pêche palangrière de l'ICCAT. Des méthodes d'estimation bayésiennes sont utilisées pour estimer et quantifier l'incertitude associée aux valeurs de ces paramètres. Le jeu de données du NMFS-CSTP pourrait éventuellement être utilisé dans une évaluation du stock de requin peau bleue et devrait faire l'objet d'une étude plus approfondie. Les zones d'intérêt pour la recherche future ont été identifiées.*

### RESUMEN

*Los intentos anteriores de realizar una evaluación de stock para la tintorera (Prionace glauca) en el Atlántico norte se han visto obstaculizados por la ausencia de datos fidedignos de captura y esfuerzo. La utilización de datos de marcado y recaptura está incluida en las recomendaciones de ICCAT para el futuro trabajo de evaluación. Este documento propone un marco estadístico para la estimación del movimiento y de las tasas de mortalidad por pesca de la tintorera partiendo de los datos de marcado y recuperación de marcas del National Marine Fisheries Service Cooperative Shark Tagging Program (Programa de marcado cooperativo de*

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*tiburones del Servicio de Pesca, NMFS-CSTP). El modelo considera cuatro regiones geográficas. La tintorera puede permanecer en la región en la cual se colocó la marca o puede moverse entre las regiones. Los parámetros del modelo son las probabilidades de movimiento interregional o intrarregional y los coeficientes de capturabilidad que relacionan las probabilidades de captura y los datos de ICCAT sobre el esfuerzo pesquero del palangre. Se utilizaron métodos de estimación bayesianos para estimar y cuantificar la incertidumbre asociada con los valores de estos parámetros. El conjunto de datos del NMFS-CSTP muestra potencial para su utilización en la evaluación del stock de tintorera y debería ser objeto de nuevos trabajos de investigación. Se identifican los campos de interés para futuras investigaciones.*

#### KEYWORDS

*Bayesian methods, Blue shark, Migrations, MCMC, North Atlantic, Tagging*

### 1. Introduction

The blue shark, *Prionace glauca* Linnaeus 1758 (Carcharhinidae) is an oceanic-pelagic species exhibiting a cosmopolitan distribution (Gubanov and Grigr'yev 1975; Compagno 1984). The identification of different population units of this elasmobranch in the world's oceans and their degree of intermixing remains poorly understood. This knowledge gap has been partially narrowed via several tag-recapture programs (Stevens 1976, 1990; Casey 1985; Fitzmaurice and Green 2000; Kohler *et al.* 1998, 2002) in the North Atlantic Ocean, where the species is regarded as the most abundant among pelagic sharks (McKenzie and Tibbo 1964; Draganik and Pelczarski 1984).

Tag-recapture records show seasonal north-south migratory movements related to size and sex on both sides of the North Atlantic, as well as long distance west-to-east/east-to-west transatlantic movements (Stevens 1976; Casey, 1985; Fitzmaurice and Green, 2000; Kohler *et al.* 2002). Observations of trans-equatorial movements are extremely rare. Combination of these tagging results with reproductive and length-frequency data suggest that blue sharks segregate by life-stage and sex in the North Atlantic and that complex movement patterns exist among areas (Pratt 1979; Casey 1982, 1985; Connet 1987; Vas 1990; Castro and Mejuto 1995). The assumption of a single stock of blue sharks in the North Atlantic has been adopted for fishery management purposes (Casey 1985; Kohler *et al.* 2002).

Blue sharks are a major by-catch in the pelagic longline fisheries carried out by several nations in the Atlantic Ocean (Bonfil 1994). Baum *et al.* (2003) recently described significant declines in shark populations in the Northwest Atlantic including blue sharks. The responsibility for data collection and analysis of Atlantic multi-national pelagic shark stocks has been assumed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) and the Sub-Committee on By-catch was established in 1996 (Kebe *et al.* 2001). A stock assessment meeting to discuss the stock status of the blue shark in the Atlantic Ocean was scheduled by ICCAT for 2004. The Sub-Committee on By-catch recommended that tag-recapture data be included in the stock assessments.

Within this context, it is important to describe the movement patterns and degree of intermixing of blue sharks among different areas of the North Atlantic where fisheries of several nations occur. Kohler *et al.* (1998, 2002) reported on the results of the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program (CSTP) including a description of blue shark movement patterns. This was done by using the traditional technique of plotting vectors from where the sharks were initially tagged to where they were recaptured and calculating proportions of area-specific recaptures to total releases. This method is useful for obtaining a qualitative description of migration patterns. However, its use is not appropriate if unbiased quantitative analyses are planned (Hilborn 1990; Xiao 1996). The approach does not allow for variables that potentially explain the observed number of recaptures by area (e.g., differential fishing effort, tagging mortality, tag loss and reporting rate). Furthermore, the treatment of uncertainty is limited. Alternative statistical methodologies are available (e.g., Ishii 1979; Cormack 1981; Sibert 1984; Hilborn 1990; Schwarz *et al.* 1993; Schweigert and Schwarz 1993; Anganuzzi *et al.* 1994; Xiao 1996) and some of these allow for the joint estimation of movement and fishing mortality parameters.

In this paper we propose the use of the tag-recapture data from the NMFS-CSTP to estimate movement and fishing mortality rates for the blue shark in the North Atlantic. A statistical framework based upon the method of

Hilborn (1990) was evaluated using the CSTP data. A Bayesian estimation procedure was implemented to estimate uncertainty in model parameters. Areas of interest for future research are identified.

## 2. Materials and methods

### 2.1 Tag-recapture data and geographical areas

A description of the tagging program and its results is given in Kohler *et al.* (1998, 2002). We adopted the geographical strata system of the North Atlantic assumed in Kohler *et al.* (2002). This system was defined solely based on tag release distributions, which largely reflects the fishing effort patterns of cooperative taggers, primarily recreational fisherman. Alternative systems should be discussed within ICCAT, particularly with respect to area designations that would account for fleet distribution patterns and oceanographic/bathymetric characteristics. The model assumes four geographical regions in the North Atlantic Ocean, defined as north of the Equator: area 1 - northwestern North Atlantic (NW) (west of 30°W and north of 25°N); area 2 - southwestern North Atlantic (SW) (west of 40°W and south of 25°N); area 3 - northeastern North Atlantic (NE) (east of 30°W and north of 25°N); and, area 4 - southeastern North Atlantic (SE) (east of 40°W and south of 25°N). The Mediterranean Sea was not considered in this paper due to the low number of tag releases and recoveries in the area.

A blue shark tag-recapture dataset covering the period from 1962 to 2001 (including 92,306 tag releases and 5,559 recaptures) was investigated to illustrate the approach. The recapture distribution of blue sharks tagged by the CSTP is presented in **Figure 1**. The time series of tag releases and recoveries by area are given in **Figure 2**.

### 2.2 Fishing effort data

Tag recaptures from a harvested population are related to fishing effort, and this information is therefore necessary for any attempt to derive unbiased estimates of movement parameters and exploitation rates. The fishery exploitation of blue sharks in the North Atlantic has been considered a data-limited situation with respect to catch and effort data (ICCAT 2001; ICES 2003; Hessen 2003).

The longline fishing effort database available from ICCAT was used in the present experimental analysis. This multi-national database provides information on fishing effort (in numbers of hooks) by longline fishery (tuna and swordfish) in a 5°x5° geographical quadrature system. At this early stage of the research, we assumed a single “fleet” fishery with the effort data from different nations being pooled. No attempt was made to standardize between effort targeting swordfish versus effort targeting tunas.

Initial model runs with the pooled ICCAT effort dataset resulted in poor fits to the tag-recapture data. This suggests that standardization of fishing effort might be required before pooling or that a fleet-specific model is more appropriate. Also, there may be problems with the dataset since the total longline effort was likely not reported (Personal commun. ICCAT secretariat). For this exploratory analysis, we adopted a linear fit to the effort data in each area as a proxy of the actual exploitation pattern (**Figure 3**). Harvest rates derivable from the present exercise are therefore meaningless in absolute terms, reflecting the experimental nature of this research.

### 2.3 Model Description

The maximum likelihood based framework of Hilborn (1990) for estimating movement rates from tag returns was evaluated using the CSTP blue shark tag-recapture dataset. We used Hilborn’s population dynamics and movement model revised by Xiao (1996), which explicitly includes terms for instantaneous natural mortality ( $M$ ) and tag loss ( $\lambda$ ). The model is written as

$$\hat{N}_{i,a,t+1} = \sum_{j=1}^n \hat{N}_{i,j,t} (1 - q_j E_{j,t}) e^{-(M+\lambda)} p_{j,a} + T_{i,a,t} \quad (1)$$

where,

$\hat{N}_{i,a,t}$  = the predicted number of tagged fish of group  $i$  present in area  $a$  at time  $t$ ;

$q_j$  = catchability coefficient in area  $j$ ;

$E_{j,t}$  = fishing effort in area  $j$ , time  $t$ ;

$p_{j,a}$  = probability of movement from area  $j$  to  $a$ ;

$T_{i,a,t}$  = the number of tags released from group  $i$ , area  $a$ , time  $t$ .

A tag group  $i$  is defined in Hilborn (1990) as a group of fish tagged in the same space and time stratum. However, his framework is flexible and can be extended to include age-, size- or sex- related tag release groups, or whatever criteria are thought to be relevant in the dynamics of the tagged population. Also, the approach allows for recruitment in a tagged group through the addition of new tag releases into that group in subsequent years, instead of considering the new tags as new individual tag groups. For this research, we considered four tag groups released independently in the four geographical areas, with recruitment of new tags occurring in the following years. A one-year time step was assumed in our model.

An estimate of instantaneous natural mortality for the blue shark was obtained using the empirical method of Hoenig (1983). The technique provided an estimate of  $M=0.2$  by assuming a longevity of 20 years (Stevens, 1975; Skomal and Natanson, 2003). At the moment, there is no estimate of tag loss in the CSTP. For this reason, we assumed no tag loss ( $\lambda=0$ ).

Blue sharks are an important part of the by-catch in international tuna and swordfish fisheries in the North Atlantic (Bonfil 1994). However, there seems to be variation in the retained catch proportions and the status (alive vs. dead) of releases by different fleets. For this reason, the quantity  $q_j E_{j,t}$  of equation (1) represents a probability of capture and not necessarily the actual fishing mortality rate as in Hilborn's method. The true harvest rate in area  $j$  at time  $t$  ( $u_{j,t}$ ) can be derived from the product of the "capture rate" and a "killing rate" ( $K_{j,t}$ )

$$h_{j,t} = q_j E_{j,t} K_{j,t} \quad (2)$$

Estimates of  $K$  were not available for this research. The parameter was fixed at 1 (all animals die) for the purpose of this experimental analysis.

An observation model must specify the relationship between the numbers of tagged sharks present in an area under equation (1) and the tags that are actually recaptured and reported to the agency ( $R_{i,a,t}$ ). The Hilborn (1990) observation model was made more flexible by adding a tag-reporting parameter

$$\hat{R}_{i,a,t} = \hat{N}_{i,a,t} q_a E_{a,t} \psi_{a,t} \quad (3)$$

where  $\hat{R}_{i,a,t}$  is the predicted number of tags recovered from tag group  $i$ , area  $a$ , time  $t$ ;  $\psi_{a,t}$  is the tag-reporting rate in area  $a$ , time  $t$ . Estimates of  $\psi$  are still not available. The parameter was fixed at 1 (100% reporting rate) for the experimental analysis.

Finally, a statistical likelihood model is necessary to compute the likelihood of the observed number of tag recoveries given that the population dynamics and observation models are true. The multinomial was approximated by a Poisson likelihood function considering that the recovery of a tagged fish in any space/time stratum is a rare event. The Poisson distribution for fish from tag group  $i$  in area  $a$  at time  $t$  can be written as

$$L(R_{i,a,t} | \hat{R}_{i,a,t}) = \frac{e^{-\hat{R}_{i,a,t}} \hat{R}_{i,a,t}^{R_{i,a,t}}}{R_{i,a,t}!} \quad (4)$$

where  $R_{i,a,t}$  is the actual number of tags recovered from tag group  $i$ , area  $a$ , time  $t$ .

The total likelihood function is

$$\prod_{i,a,t} \frac{e^{-\hat{R}_{i,a,t}} \hat{R}_{i,a,t}^{R_{i,a,t}}}{R_{i,a,t}!} \quad (5)$$

Model parameters are estimated by minimizing the total negative log-likelihood

$$\sum_{i,a,t} \left[ \hat{R}_{i,a,t} - R_{i,a,t} \log(\hat{R}_{i,a,t}) \right] \quad (6)$$

A quasi-Newton minimization procedure was implemented to find the maximum likelihood estimates (MLE) of the parameters (AD Model Builder<sup>©</sup>, Otter Research Ltd., 2000).

#### 2.4 Case Study Hypothesis – a “Clockwise Movement Gyre”

The framework presented above offers a convenient way to represent different movement hypotheses. This can be done by manipulating the movement rate elements of the transition matrix  $\mathbf{M}$ ,

$$\mathbf{M} = \begin{pmatrix} p_{11} & p_{21} & p_{31} & p_{41} \\ p_{12} & p_{22} & p_{32} & p_{42} \\ p_{13} & p_{23} & p_{33} & p_{43} \\ p_{14} & p_{24} & p_{34} & p_{44} \end{pmatrix} \quad (7)$$

where  $p_{ij}$  represents the probability of movement from area  $i$  to area  $j$ .

A full Markovian model allowing movement from one area to all other areas can be implemented by freeing all the parameters of the matrix. Alternatively, one can assume a simpler hypothesis (i.e., constraining movement patterns) by fixing some of the elements of  $\mathbf{M}$  to 0.

In this experimental research, we sought a simpler model based on the knowledge available on the biology and ecology of the species. Results of the NMFS and European tagging programs suggest a clock-wise cyclical movement pattern for blue sharks in the North Atlantic (Stevens 1976; Casey 1985; Kohler *et al.* 1998; 2002; Fitzmaurice and Green 2000). This migration pattern seems associated with large oceanic gyres (Carey and Scharold 1990). Considering this information, our case study hypothesis allows blue sharks either to remain in the area of tag release or to move to the adjacent area following a “clockwise movement gyre” (**Figure 4**). The transition matrix  $\mathbf{M}$  representing the case study hypothesis is,

$$\mathbf{M} = \begin{pmatrix} p_{11} & p_{21} & 0 & 0 \\ 0 & p_{22} & 0 & p_{42} \\ p_{13} & 0 & p_{33} & 0 \\ 0 & 0 & p_{34} & p_{44} \end{pmatrix} \quad (8)$$

This case study parameterization of  $\mathbf{M}$  is convenient because one of the two movement parameters for each area is the complement of the other. We set the diagonal elements of  $\mathbf{M}$  (probabilities of staying in the area) as derived quantities and the off-diagonal elements (probabilities of moving to the adjacent area) as estimated parameters. The reparameterized transition matrix is,

$$\mathbf{M} = \begin{pmatrix} 1-p_{13} & p_{21} & 0 & 0 \\ 0 & 1-p_{21} & 0 & p_{42} \\ p_{13} & 0 & 1-p_{34} & 0 \\ 0 & 0 & p_{34} & 1-p_{42} \end{pmatrix} \quad (9)$$

The case study reduced model has eight estimated parameters (four catchabilities and four movement rates).

## 2.5 Bayesian Framework

A Bayesian estimation procedure was applied to evaluate uncertainty in the model parameters and the derived quantities (movement rates). Uniform priors were assigned to all of the parameters. The marginal posterior distributions of the parameters were generated based on 1,000 samples taken from 50 million MCMC simulations (thinning to 1 draw out of 50,000 simulations).

## 3. Results and discussion

### 3.1 Model fit

The model fit to the NMFS-CSTP blue shark tag-recapture data is in **Figure 5**. The parameter estimates (MLE), their standard errors and the correlation matrix are presented in **Table 1**.

A reasonable model fit was obtained for the NW, NE and SW Atlantic areas. The model fits the recapture data of the SE Atlantic poorly. This might be related to a tag recapture reporting problem in this region. The data for the SE region shows two pulses of tag releases in the early 80s which became immediately reflected in the recapture time series of the area (see **Figure 2**). This reflected a unique exploratory fishing survey by the Polish R/V *Wieczo* that had been engaged in cooperative research with NMFS for several years. However, very low numbers of recaptures occurred in the region during the mid 80s despite the continuous tagging taking place in the remaining areas. This signal seems to have been modeled as a movement pattern in the SE Atlantic where emigration predominates. This is shown by an MLE of 0.990 for the rate of movement from the SE to the SW Atlantic. A contradictory signal, however, is given by the data during the late 1990s. In this period, tag recaptures in the SE Atlantic show a strong peak with no releases taking place in the region during the decade. This suggests a differential pattern of tag reporting rates in the SE Atlantic during the 80s and 90s. Good estimates of tag-reporting rates ( $\psi$ ) by different nations are required to resolve these problems.

The catchability coefficients that relate the capture probabilities and the ICCAT longline fishing effort data are estimated parameters in the model. The values obtained in this analysis are meaningless in absolute terms since the multi-nation effort data was pooled with no standardization process being implemented. Estimates of blue shark exploitation rates are therefore not available at this early stage. However, it seems that these quantities could easily be estimated in a multi-fleet model if reliable time series of fishing effort exist for the different nations. A multi-fleet model is already under construction. Estimates of the proportion of sharks retained or discarded dead (the “killing rate” parameter  $K$ ) are also needed if accurate fishing mortality rates are desired. Catch disposition information is currently available at least for the northwest Atlantic (Diaz and Serafy SCRS/2004/107; Beerkircher SCRS/2004/106). These estimates could be incorporated into the model for this area and approximated for other areas. Size (age)-specific catch disposition information could also be incorporated to some extent into an age- or stage-based implementation of our model.

A low correlation between movement parameters was found (see **Table 1**). High correlations ( $r > 0.85$ ) were found between the catchabilities and emigration parameters (**Table 1, Figure 6**). An exception to this was the SE Atlantic area, again suggesting that the model was forced at the upper bound for this parameter. This strong correlation represents a problem with the current model parameterization since the catchability coefficients cannot be estimated analytically. New parameterizations are being investigated.

A Bayesian analysis was carried out to estimate uncertainty in model parameters. The strong correlations between the catchabilities and emigration parameters are clearly shown in the posterior correlations plots (**Figure 6**). However, the trace plots of our MCMC runs suggest no major problems in the convergence to the posterior distributions (**Figure 7**).

The marginal posterior distributions of the movement rate parameters are presented in **Figure 8**. The informative nature and potential of the NMFS-CSTP for investigating movement patterns of the blue shark is shown. The uncertainty level of the parameters for the NW Atlantic was found to be less than for all other areas. This is not a surprising result since most of the tagging effort of the program occurs in this region. Emigration was found to be the predominant movement component in the four areas under the assumed movement hypothesis. This supports the highly migratory behavior of this oceanic pelagic species and the need for international management.

### 3.2 Future research

Future research will include the following topics:

- Full use of the information available for all year- and area-specific tag release groups in the CSTP database;
- Testing different movement hypothesis and time-steps (e.g., counter clockwise movement patterns, seasonal movement);
- Assuming different geographical strata systems, particularly with respect to area designations that would account for fleet distribution patterns and oceanographic/bathymetric characteristics;
- Constructing a multi-fleet model using more detailed effort data from other national sampling programs;
- Implementing of the framework at the age- or stage-based level;
- Using of catch disposition information (estimates of the proportion of sharks retained or discarded dead, the “killing rate” parameter  $K$  in the model) to estimate fishing mortality rates;
- Using simulation to investigate the failure of important model assumptions (e.g., natural mortality, tag loss and reporting rates).

Pooling the datasets of the NMFS-CSTP and European tagging programs (Stevens 1976, 1990; Fitzmaurice and Green 2000) would likely increase the precision of the model parameters. Also, this cooperative work would allow new geographical areas to be considered.

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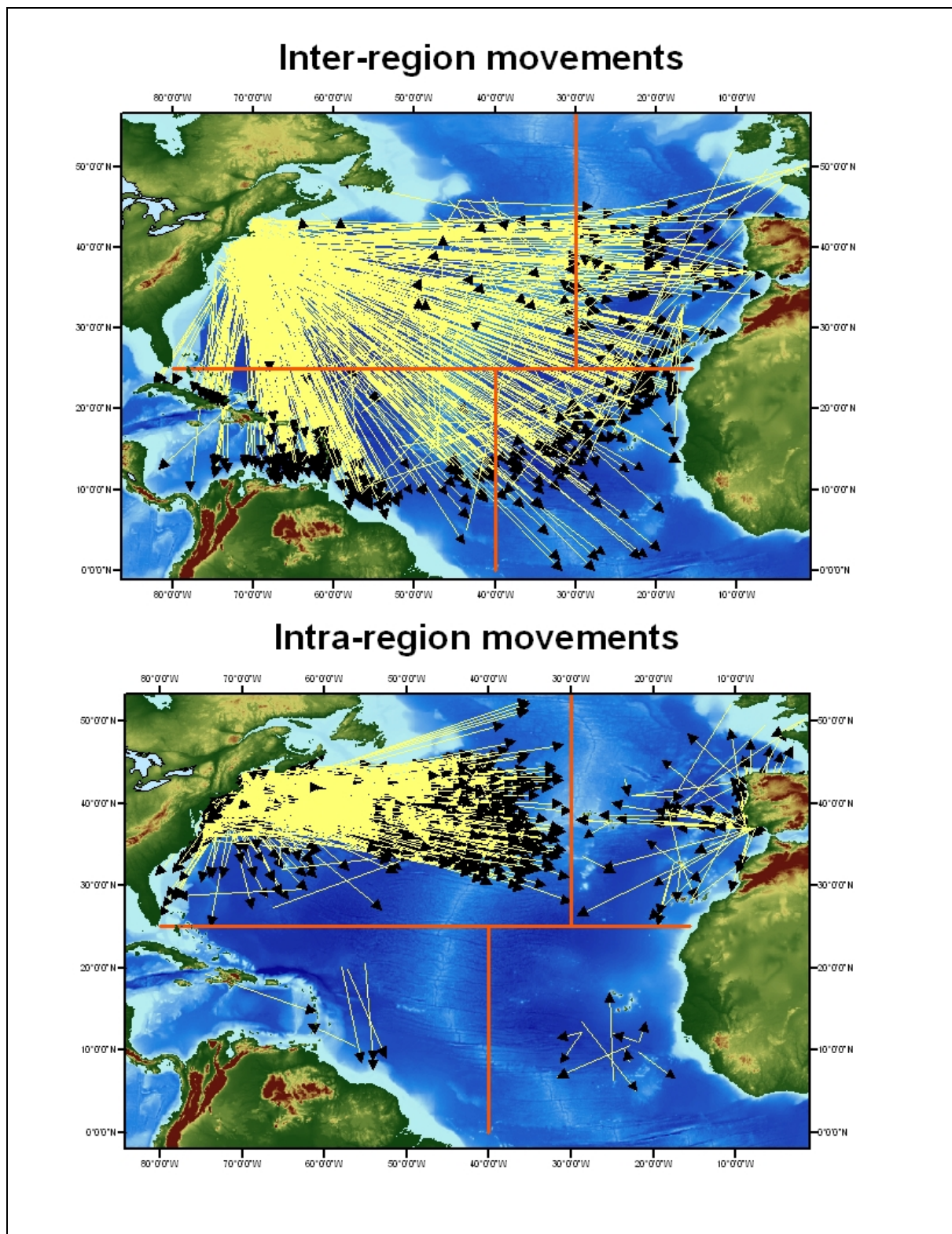
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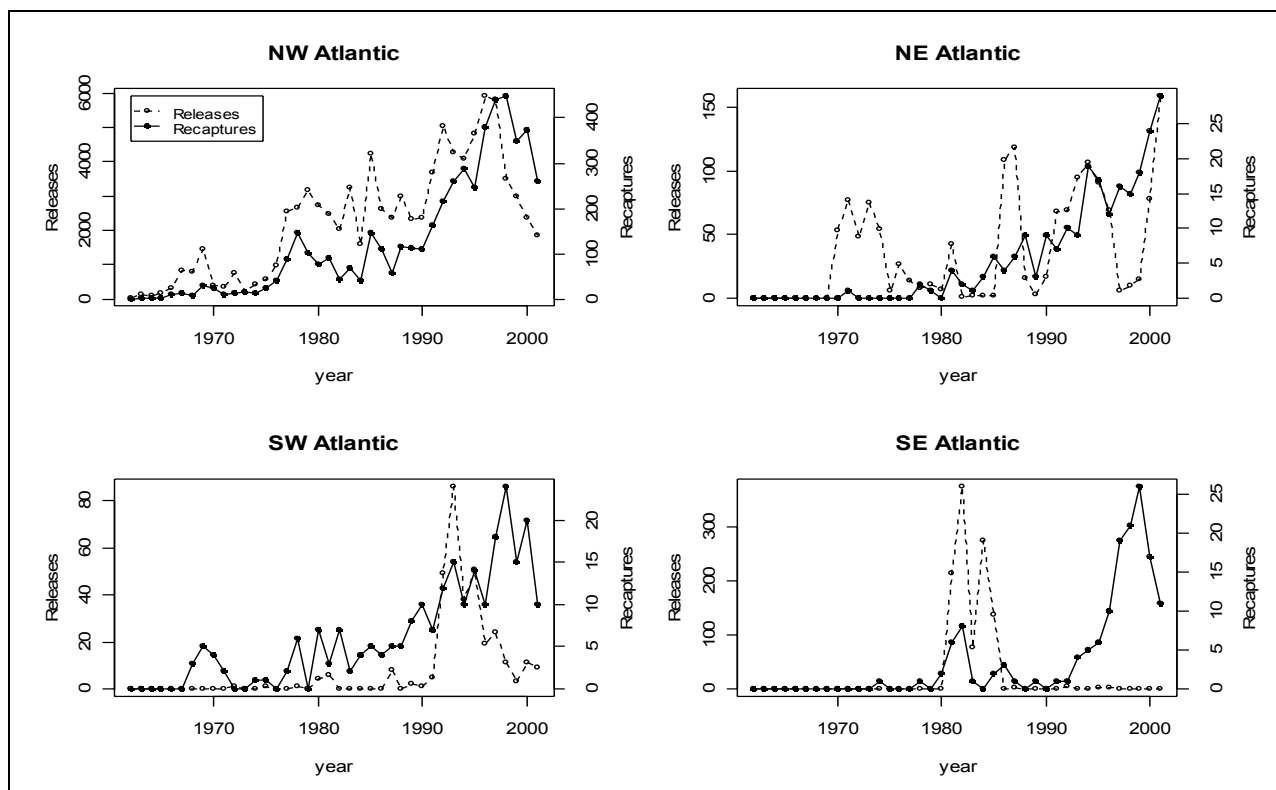
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**Table 1.** Parameter estimates (MLE), standard errors and the correlation matrix obtained for the case study model. A “clockwise movement gyre” hypothesis for the blue shark, *Prionace glauca*, in the North Atlantic was assumed. High parameter correlations ( $r > 0.85$ ) are highlighted. Geographical areas: 1- NW North Atlantic; 2 – SW North Atlantic; 3 – NE North Atlantic; and, 4 – SE North Atlantic.

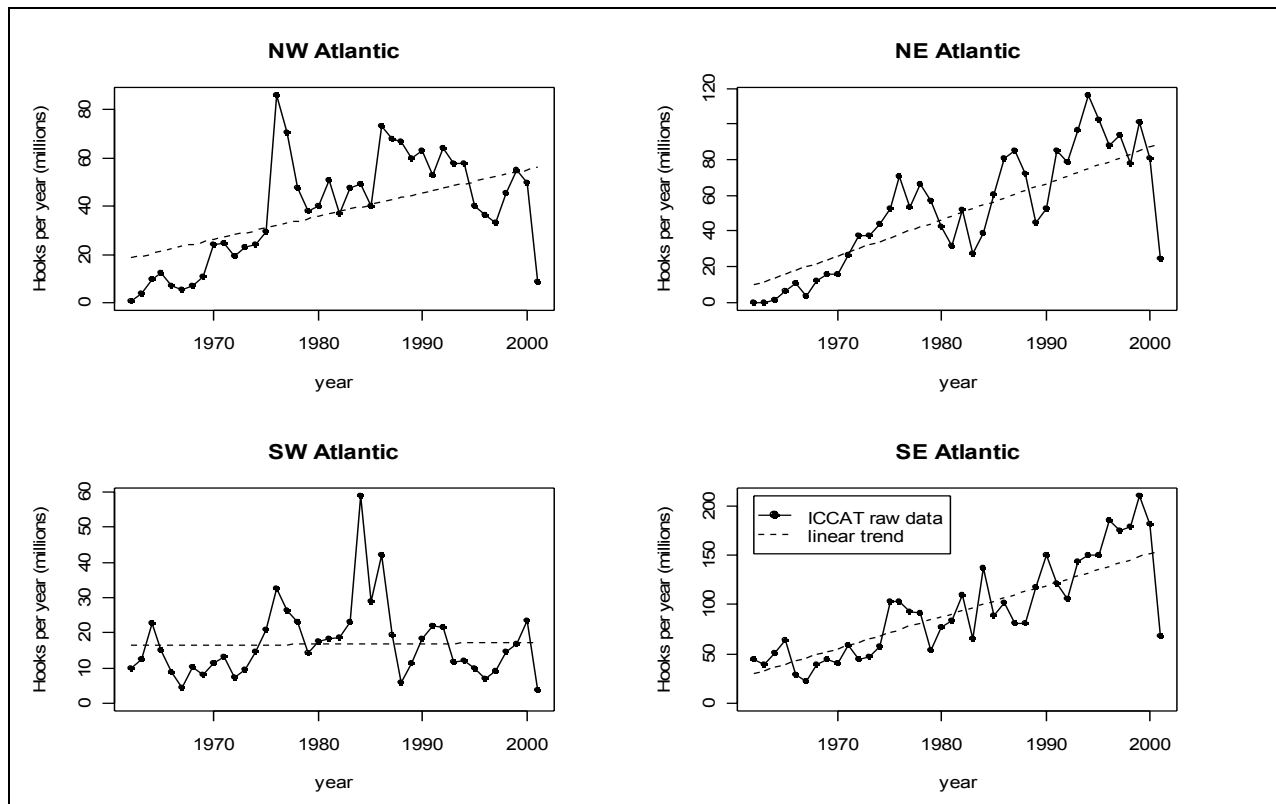
| Parameter | value   | std   | logq_1 | logq_2 | logq_3 | logq_4 | mov_13 | mov_21 | mov_34 | mov_42 |
|-----------|---------|-------|--------|--------|--------|--------|--------|--------|--------|--------|
| logq_1    | -7.180  | 0.069 | 1      |        |        |        |        |        |        |        |
| logq_2    | -8.470  | 0.244 | -0.088 | 1      |        |        |        |        |        |        |
| logq_3    | -10.438 | 0.200 | -0.329 | -0.792 | 1      |        |        |        |        |        |
| logq_4    | -10.816 | 0.126 | -0.036 | 0.445  | -0.498 | 1      |        |        |        |        |
| mov_13    | 0.763   | 0.078 | 0.883  | 0.024  | -0.318 | -0.232 | 1      |        |        |        |
| mov_21    | 0.588   | 0.172 | -0.087 | 0.883  | -0.672 | 0.183  | 0.187  | 1      |        |        |
| mov_34    | 0.657   | 0.172 | -0.235 | -0.810 | 0.911  | -0.649 | -0.132 | -0.593 | 1      |        |
| mov_42    | 0.990   | 0.002 | 0.000  | -0.004 | -0.002 | 0.016  | 0.000  | -0.003 | -0.002 | 1      |



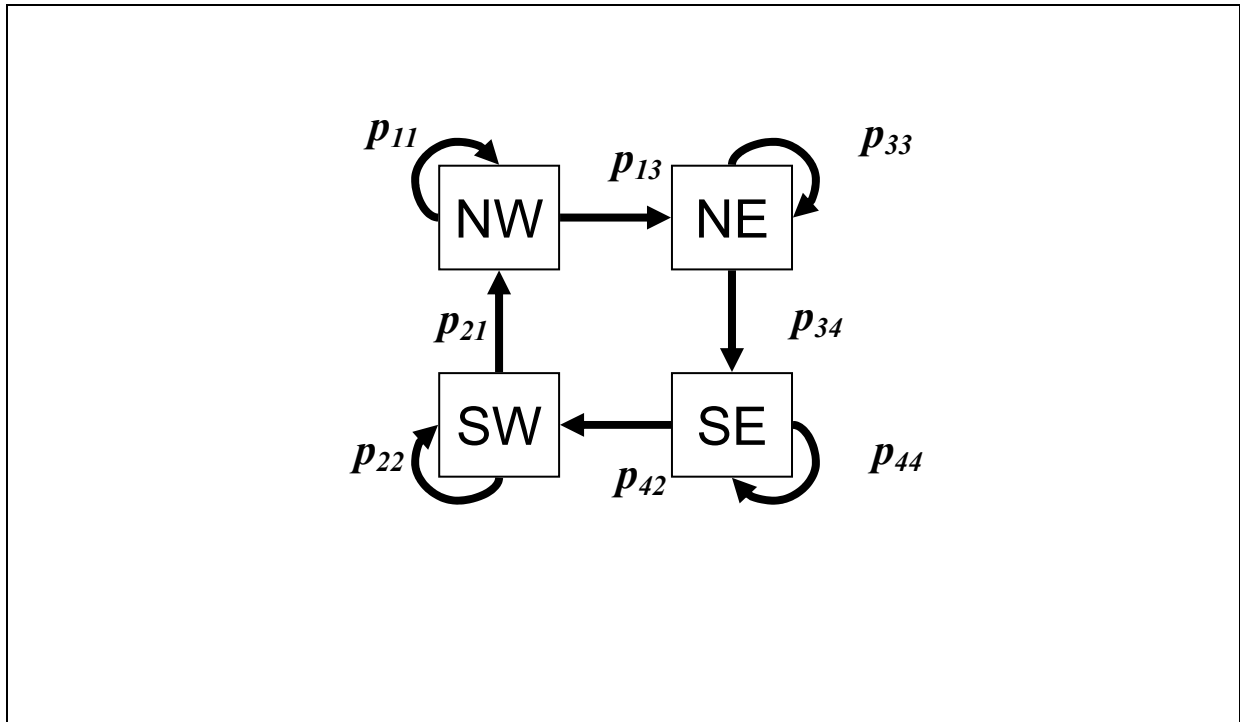
**Figure 1.** Tag-recapture distribution for the blue shark (*Prionace glauca*), from the NMFS Cooperative Shark Tagging Program (1962-2001). Geographical area definition can be found in text.



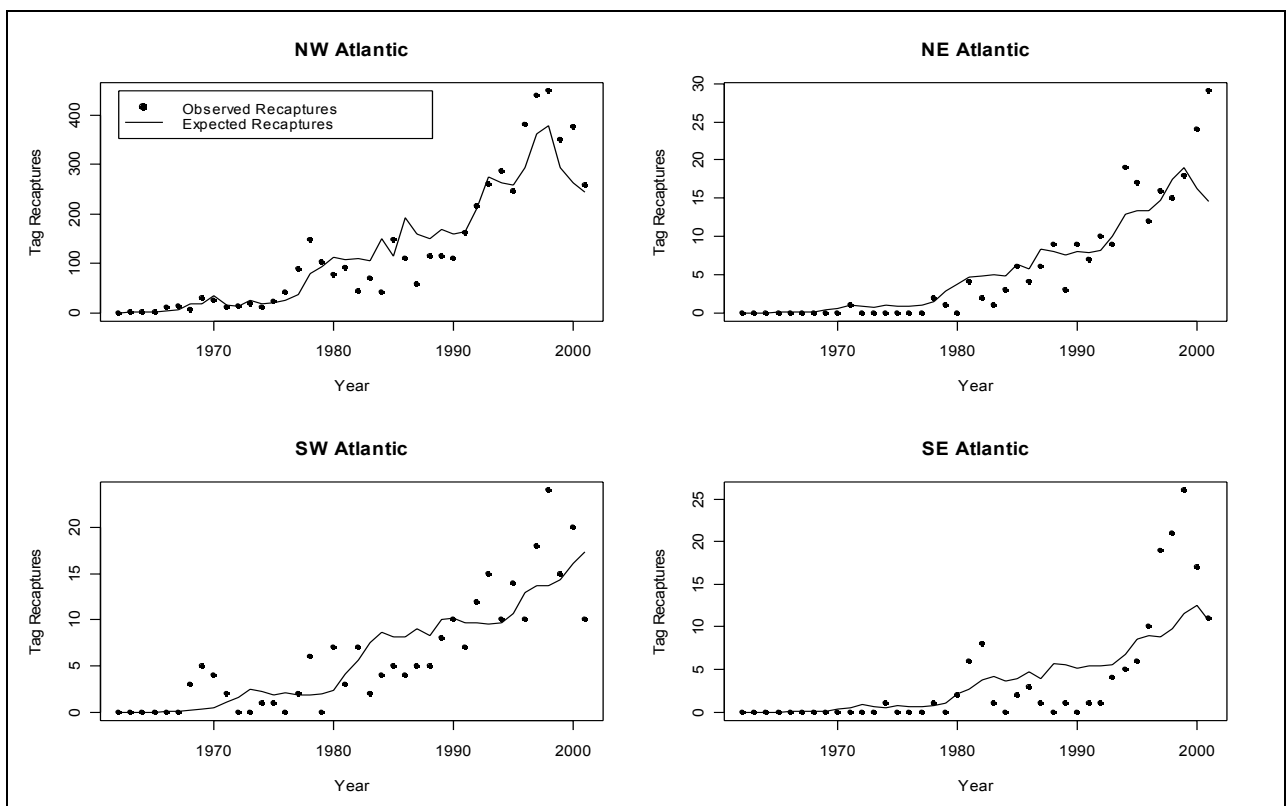
**Figure 2.** Time series of tag releases and recaptures for the blue shark (*Prionace glauca*), from the NMFS Cooperative Shark Tagging Program, 1962-2001.



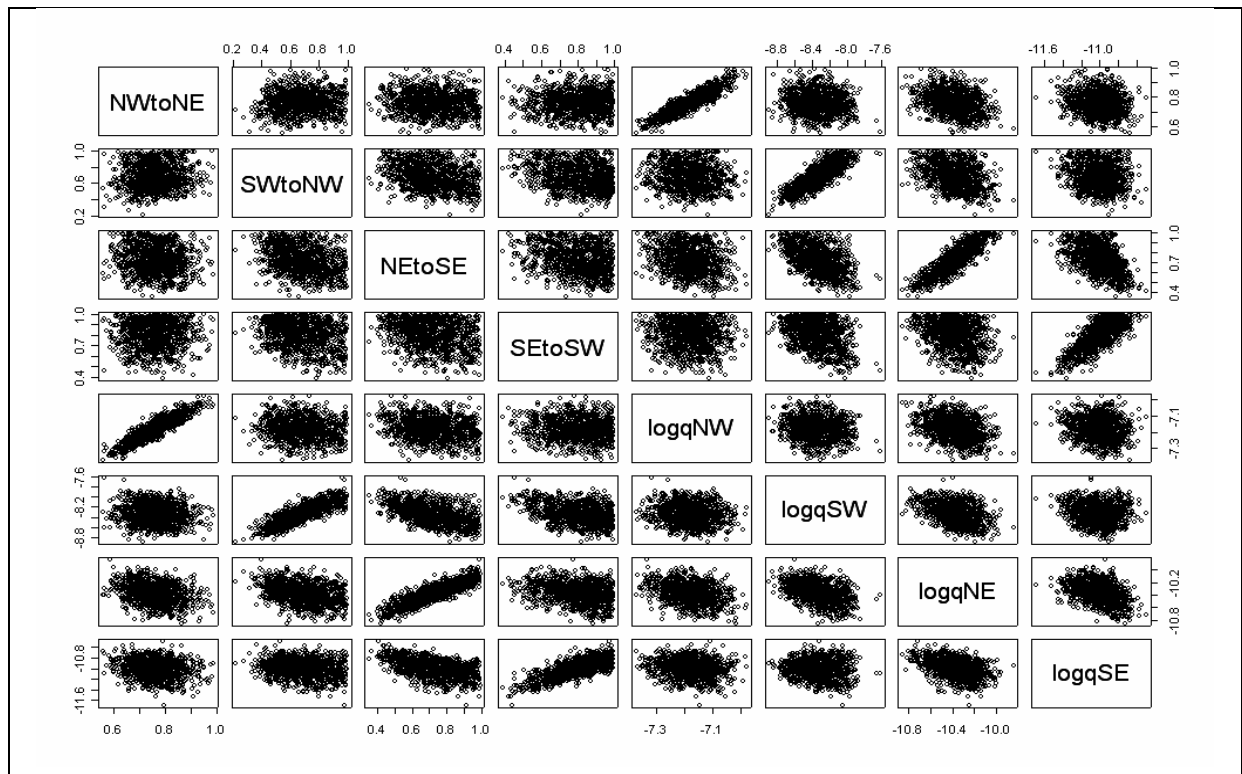
**Figure 3.** Fishing effort data provided by ICCAT. A linear trend of the raw data was assumed for the case study model.



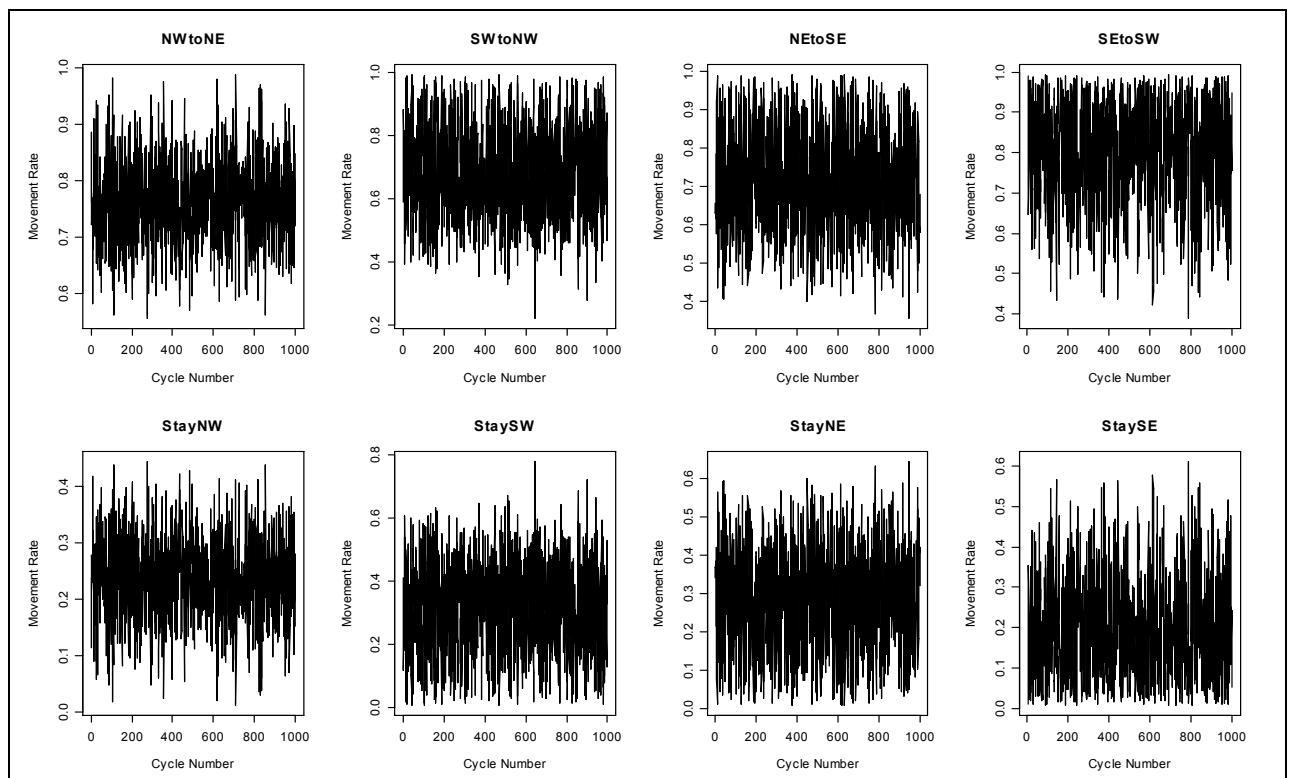
**Figure 4.** Diagram illustrating the “clockwise movement gyre” hypothesis assumed in the model. Four geographical areas are assumed: 1 – NW North Atlantic; 2 – SW North Atlantic; 3 – NE North Atlantic; and, 4 – SE North Atlantic. The estimated movement parameters ( $p_{ij}$ , probability of movement from area  $i$  to  $j$ ) are illustrated.



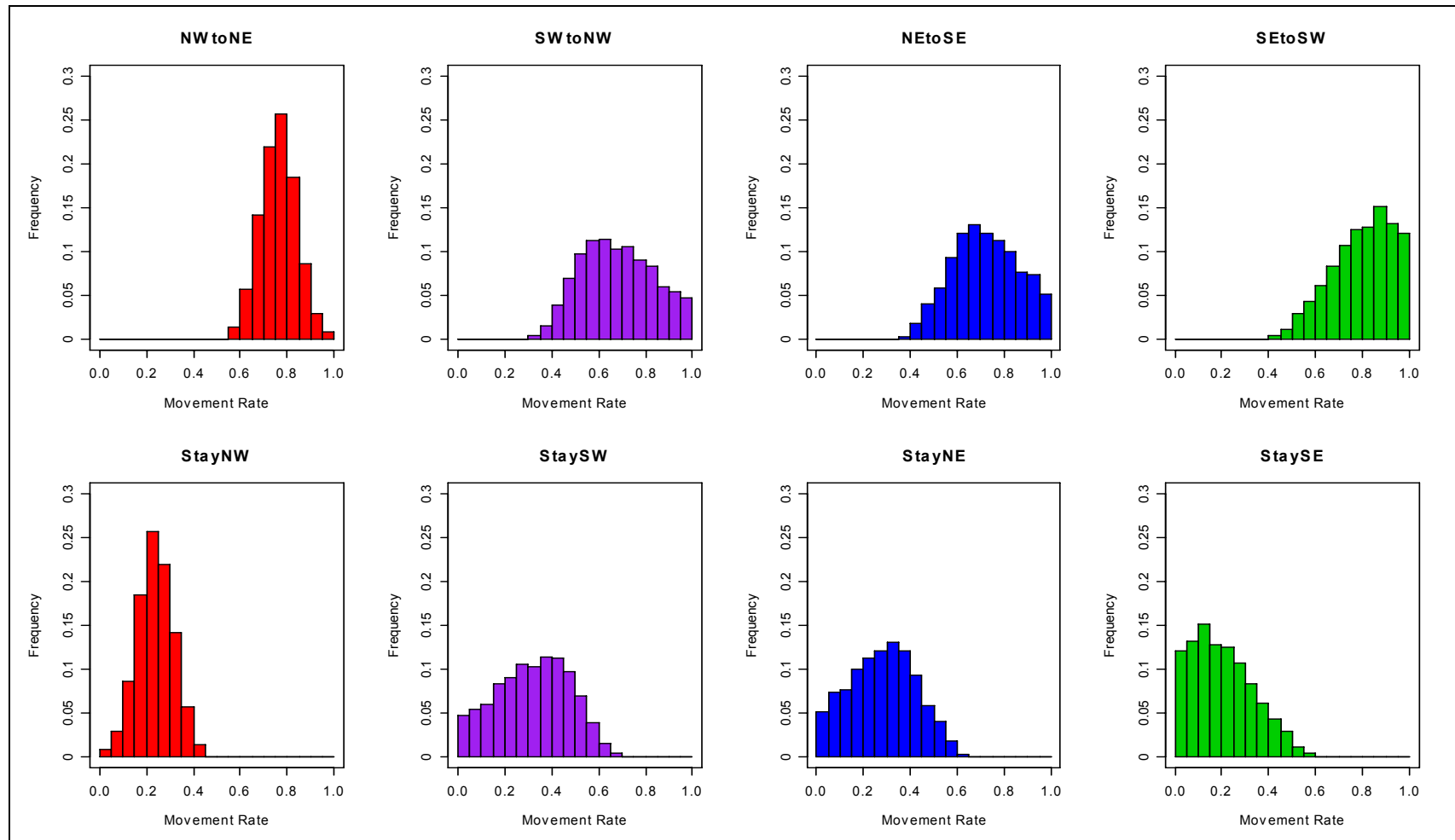
**Figure 5.** Model fit to the NMFS-CSTP tag-recapture data of blue shark, *Prionace glauca*.



**Figure 6.** Posterior correlations of model parameters.



**Figure 7.** Trace plots from the MCMC runs for the case study model with 1000 samples from 50 million draws.



**Figure 8.** Marginal posterior distributions of the movement rate parameters for the blue shark (*Prionace glauca*) in the North Atlantic. The case study movement hypothesis is explained in the text.