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INVESTIGATION OF BIAS IN THE MARK–RECAPTURE ESTIMATE OF TOOTHFISH POPULATION SIZE AT SOUTH GEORGIA

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Abstract

This paper investigates the influence of mixing of fish, and the uneven distribution of tag placements and recapture effort, on bias in the Petersen estimator of population size. It does so by constructing a spatial model of the South Georgia toothfish fishery, simulating fish movements within this system and overlaying various combinations of tagging and recapture effort to investigate bias. The fishable grounds around South Georgia were divided into 77 very small-scale boxes lying along the 1 000 m contour. The uneven distribution of fish was simulated by adjusting an average movement rate downwards when fish entered a high-density box (as indicated by high CPUE) and upwards in a low-density box, so that they tended to be retained in high-density boxes. The model allows simulation of releases by box over multiple years.

The model performed as expected with test situations. It produced a near-perfect estimate of stock size when there was an ideal distribution of tags and/or fishing effort; by 'ideal', it is meant that either tagging or fishing effort was in direct proportion to density (CPUE). When both tagging and fishing effort were non-ideal, e.g. when fishing effort was concentrated away from tag concentrations, or overly concentrated in them, the Petersen estimator either overestimated or underestimated (respectively) the true population size. When run on the real tag–release data, and using average CPUE from 2002 to 2004 and recapture effort in 2003 and 2004, the model indicated that the Petersen estimator produced an underestimate of true population size. Although this paper does not advocate using the magnitude of the estimated bias to correct the tagging estimate of exploitable population size made for Subarea 48.3, it is concluded that the particular distribution of tag releases and recapture effort at South Georgia is likely to lead to an underestimate of the true population size rather than an overestimate of it.

Résumé

Ce document examine l'influence du mélange de poissons et la distribution irrégulière du placement des marques et de l'effort de recapture sur les biais de l'estimateur Petersen de la taille des populations. Pour ce faire, on a procédé à la construction d'un modèle spatial de la pêcherie de légine de la Géorgie du Sud, simulant les déplacements des poissons dans ce système et superposant diverses combinaisons d'effort de marquage et de recapture pour étudier les biais. Les lieux exploitables sont divisés en 77 cases à très petite échelle le long de l'isobathe de 1 000 m. La distribution irrégulière des poissons est simulée en ajustant un taux de déplacement moyen à la baisse lorsque les poissons entrent dans une case de forte densité (indiquée par une forte CPUE) et à la hausse lorsqu'ils entrent dans des cases de faible densité, de telle sorte qu'ils auront tendance à être retenus dans les cases de forte densité. Le modèle permet de simuler la sortie par case sur plusieurs années.

Le modèle a réagi comme prévu dans les situations de test. Il a produit une estimation quasi-parfaite de la taille du stock dans le cas d'une distribution idéale des marques et de l'effort de pêche; par "idéal", il est entendu que l'effort de marquage ou de pêche est directement proportionnel à la densité (CPUE). Lorsque l'effort de marquage et l'effort de pêche n'étaient pas idéaux, par exemple quand l'effort de pêche était concentré loin des lieux de marquage, ou qu'il était trop concentré sur ces lieux, l'estimateur de Petersen surestimait ou sous-estimait (respectivement) la taille réelle de la population. Calibré sur les données réelles de marquage, sur la CPUE moyenne de 2002 à 2004 et l'effort de recapture de 2003 et 2004, le modèle indique que l'estimateur de Petersen produit une sous-estimation de la taille réelle de la population. Bien qu'il ne soit pas recommandé, dans le présent document, d'utiliser l'ampleur du biais estimé pour corriger l'estimation de la taille de la population exploitable fondée sur le marquage pour la sous-zone 48.3, il est conclu que cette répartition particulière de l'effort de marquage et de recapture en Géorgie du Sud conduira probablement à une sous-estimation de la taille réelle de la population plutôt qu'à une surestimation.

Резюме

В этом документе рассматривается влияние смешивания рыб и неравномерного распределения усилия по прикреплению меток и повторной поимке на систематическую ошибку в оценке размера популяции по Петерсену. Для этого используется пространственная модель промысла клыкача в районе Южной Георгии, имитирующая передвижение рыбы в пределах этой системы и рассматривающая различные комбинации усилия по мечению и повторной поимке в целях изучения систематической ошибки. Пригодные для промысла участки вокруг Южной Георгии разделили на 77 очень мелких клеток, расположенных вдоль изобаты 1000-м. Неравномерное распределение рыбы моделировалось путем пересчета вниз средней скорости передвижения вниз, когда рыба входит в клетку с высокой плотностью (о чем свидетельствует высокий CPUE), и вверх – в клетке с низкой плотностью, так чтобы это способствовало удержанию рыбы в клетках с высокой плотностью. Данная модель позволяет имитировать выпуск рыбы по клеткам на протяжении многих лет.

Модель работала, как ожидалось в условиях испытания. Она выдала почти безупречную оценку размера запаса при идеальном распределении меток и/или промыслового усилия; под «идеальным» имеется в виду, что или мечение, или промысловое усилие находились в прямо пропорциональной зависимости от плотности (CPUE). В случае, когда ни мечение, ни промысловое усилие не были идеальными, т.е. когда промысловое усилие концентрировалось далеко от скопления меток или чрезмерно концентрировалось среди них, оценка истинного размера популяции по Петерсену была (соответственно) либо слишком завышенной, либо слишком заниженной. Во время прогона на подлинных данных мечения–выпуска, а также с использованием среднего CPUE за 2002–2004 гг. и усилия по повторной поимке за 2003 и 2004 гг. модель показала, что оценка Петерсена дала заниженное значение реального размера популяции. Хотя в данном документе не поддерживается идея использования величины предполагаемой систематической ошибки для исправления оценки размера облавливаемой популяции в Подрайоне 48.3, в нем делается вывод, что специфическое распределение усилия по выпуску меток и повторной поимке в районе Южной Георгии, скорее всего, приведет к заниженной, а не к завышенной оценке реального размера популяции.

Resumen

Este documento estudia el efecto de la mezcla de peces y de la distribución desigual del esfuerzo, tanto de colocación de marcas como de recuperación de las mismas, en el error del tamaño de la población obtenido con el estimador de Petersen. Para ello se construyó un modelo espacial de la pesquería de austromerluza de Georgia del Sur, simulando el desplazamiento de los peces dentro del sistema, y superponiendo varias combinaciones del esfuerzo de marcado y recaptura para estudiar el error. Se dividió en 77 cuadrículas el área de los caladeros de pesca explotables alrededor de Georgia del Sur, en una escala muy pequeña, a lo largo de la isóbata de 1 000 m. Se simuló la distribución desigual de los peces reduciendo la tasa promedio de desplazamiento cuando los peces entran en una cuadrícula de alta densidad (indicada por una alta CPUE) y aumentándola en una cuadrícula de baja densidad, de modo que tendieron a permanecer en las cuadrículas de mayor densidad. El modelo permite representar el número de peces marcados y liberados por cuadrícula durante muchos años.

Las pruebas con el modelo produjeron los resultados esperados. Se obtuvo una estimación casi perfecta del tamaño del stock cuando la distribución de las marcas colocadas o del esfuerzo de pesca era 'ideal': ideal en este caso quiere decir que tanto el esfuerzo de marcado como el de la pesca son directamente proporcionales a la densidad (CPUE).

Cuando las condiciones del esfuerzo de marcado y de pesca no eran ideales, es decir, cuando el esfuerzo pesquero no se dirigió a las concentraciones de peces marcados, o se concentró casi exclusivamente en ellas, el estimador de Petersen sobreestimó o subestimó respectivamente el tamaño real de la población. Cuando se aplicó el modelo a los datos verdaderos de colocación y liberación de marcas, y utilizando el promedio de la CPUE desde 2002 hasta 2004 y el esfuerzo de recaptura en 2003 y 2004, el modelo indicó que el estimador de Petersen subestimaba el tamaño real de la población. Si bien este estudio no está a favor de utilizar el sesgo estimado para corregir la estimación de la población explotable hecha para la Subárea 48.3 a partir de los datos de marcado, concluye que la distribución particular del esfuerzo realizado en Georgia del Sur, tanto en la liberación de marcas como en la recuperación posterior de las mismas, probablemente llevará a una subestimación del verdadero tamaño de la población, y no a una sobreestimación.

Keywords: toothfish, spatial model, movement model, tagging, mark–recapture, South Georgia, CCAMLR

Introduction

A mark–recapture experiment on toothfish at South Georgia (South Atlantic: CCAMLR Subarea 48.3) has been under way since 2000, and sufficient numbers of fish have now been tagged to enable an estimate of population size to be made. Assessments described by Agnew et al. (2004), Agnew and Kirkwood (2004) and Hillary et al. (2006) have used a modified Petersen estimator that takes account of tag-induced mortality, tag loss and natural mortality as well as length-based differential selectivity. Tagging events and fishing effort appears to be distributed over the whole of the fishing area in recent years (SC-CAMLR, 2004), but in the early years there was a considerable mismatch between the distribution of tagging events and fishing effort (Figure 1).

Mixing rates of tagged toothfish at South Georgia are almost certainly relatively low because, in common with other toothfish populations thus far examined (e.g. Heard Island, (Tuck et al., 2003)), the majority of toothfish typically move only 20–30 km each year (Marlow et al., 2003). This paper investigates the influence of mixing of fish, and the uneven distribution of tag placements and recapture effort, on bias in the Petersen estimate.

A mark–recapture model incorporating mixing effects has previously been developed by Tuck et al. (2003) and used to estimate toothfish population size at Macquarie Island. In this model, the detailed temporal sequence of mark and recapture effort is accounted for, but the spatial distribution of tagging and recovery effort is not modelled explicitly. The model described in this paper does incorporate spatial detail by constructing a spatial model of the South Georgia toothfish fishery, which follows the 1 000 m isobath fairly closely, simulating fish movements within this system and overlaying various combinations of tagging and recapture effort to investigate bias. Consequently, it enables detailed investigation to be made of the effect of spatial mismatches between tag release and recovery effort.

Methods

Spatial model

In order to model small-scale movements of toothfish, the fishable grounds around South Georgia were divided into a number of very small-scale boxes lying along the 1 000 m contour. Movement of toothfish was modelled by moving between these boxes along the contour, so the distance across a box following the contour (approximated by a straight line for this purpose) needed to be sufficiently small that toothfish would have a reasonable chance of crossing into another box. The average distance that tagged fish have moved in the past at South Georgia is 27 km/year, so the distance across the boxes was chosen to be lower than this. On the other hand, longline sets are usually between 8 and 12 km long, so the boxes were chosen to be generally larger than this. Finally, consideration was given to the physical layout of the boxes; for ease of analysis within databases, rectangular areas were chosen, with varying dimensions depending on the trend of the 1 000 m contour at that position around South Georgia or Shag Rocks.

The resultant 77 boxes are shown in Figure 2. The model system was created as a continuous chain around the 1 000 m contour with two junctions, at boxes 18 and 23, joining boxes 1 and 77 respectively. Fish could only move between adjacent numbered boxes except at these junctions, where fish could move in any direction. For instance, a fish could move from box 17 to 1 via box 18 but not directly from box 17 to box 1. The area to the west of Shag Rocks was eliminated to simplify the model; this area in any case has relatively low densities of fish. Likewise, the small extension of the southwestern

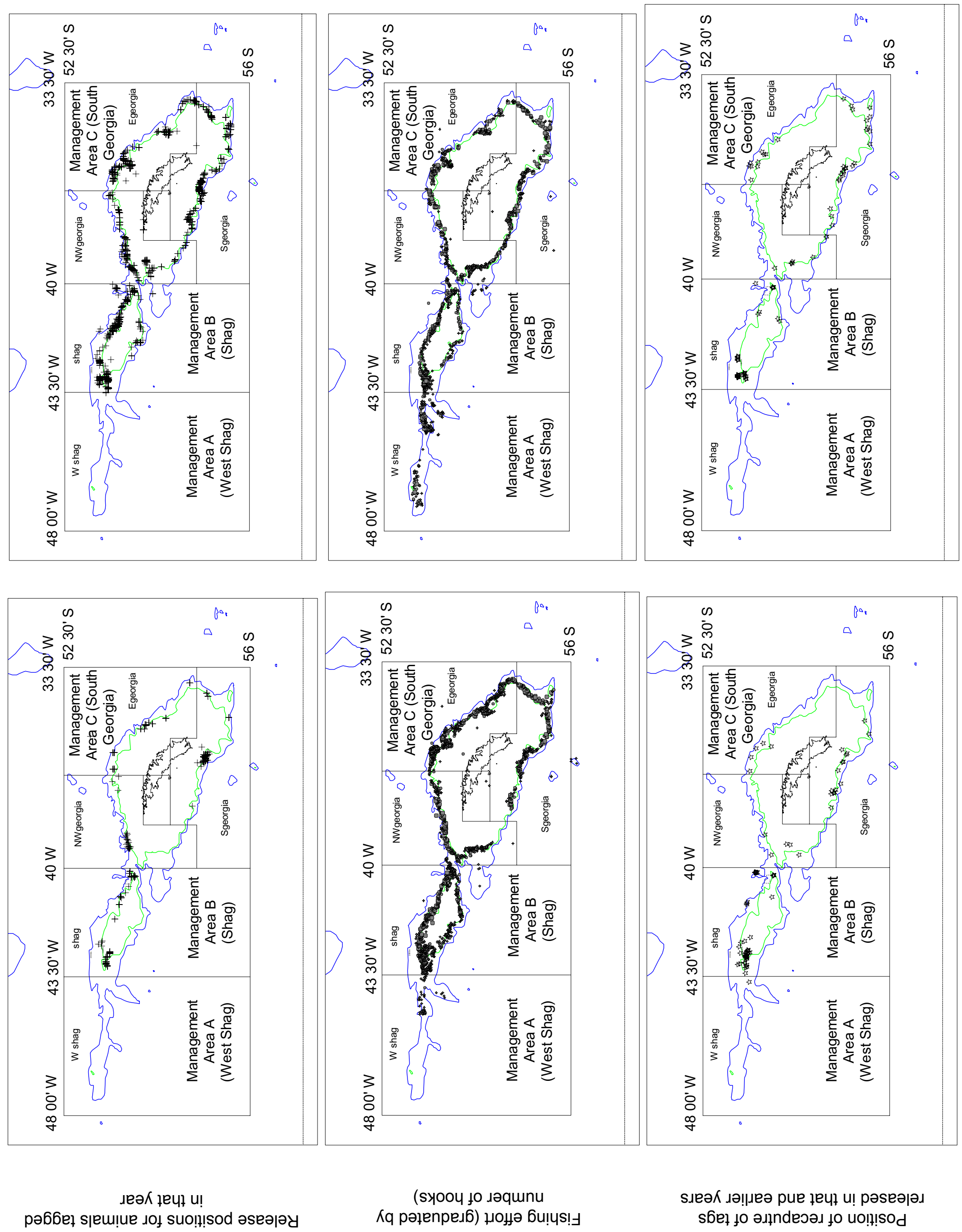

Figure 1: Distribution of tag and release events, fishing effort and recapture events in 2003 and 2004. The areas used for management of toothfish, and the 1 000 and 2 000 m bathymetric contours, are shown.

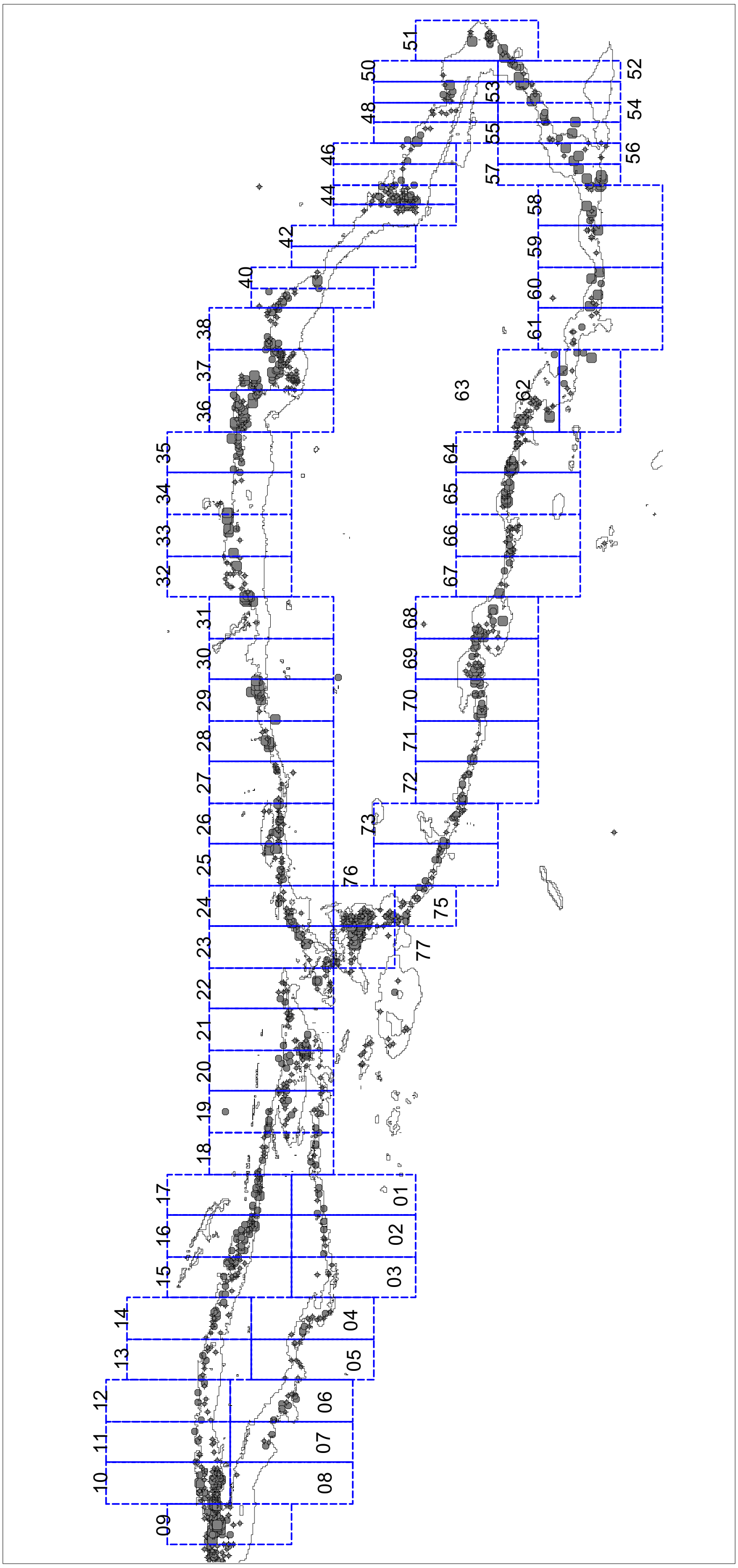

Figure 2: Configuration of the spatial model as a continuous chain of boxes around the 1 000 m contour of South Georgia and Shag Rocks. Plotted data are effort (in hooks) from 2001 to 2004, with the diameter of the circles being proportional to numbers of hooks.

South Georgia shelf adjacent to box 77 was ignored. The distance across each box was calculated as the length of the straight line shown in Figure 3. The boxes on the eastern side of South Georgia were smaller than the others because the 1 000 m contour is trending north-south at this point, so the cross-box distance is greater than where the contour is trending east-west.

The fishable area in each box was calculated as the area between the 500 and 1 500 m contours. Where this did not seem to capture the main fishing pattern, the fishable area was adjusted to fit it.

Modelling movement

Annual fish movement (km/year) was assumed to have a lognormal distribution. Each year, each individual fish was assigned a random distance sampled from this lognormal distribution, and a random direction in which to move. Thus the movement of a single fish could be bi-directional, either clockwise or anticlockwise around the system shown in Figure 2, with the direction able to change between years. The box in which fish ended up was calculated by incrementally moving them along the chain in the direction indicated, with appropriate second choices at the junctions. Fish were always assumed to be in the centre of a box before starting a movement. If their available movement distance D was greater than half the cross-box distance d, they were assumed to move into the next box and the distance between the centre of the old box and the centre of the new box was removed from D. If D was less than $d/2$ the fish stayed in the box. This procedure was repeated until D was exhausted.

The full set of recapture data from South Georgia was used to estimate movement rates, measured as km/year. The available data comprised animals that had been recaptured after 1, 2, 3, 4 and 5 years (40, 41, 12, 5 and 2% of 165 fish respectively). Tags recaptured in the year in which they were released were omitted. The log-transformed mean was 2.304 (equivalent to 10 km/year) and s.d. was 1.51 (CV 0.656).

So far, only a single estimate of movement rate has been considered, but it is clear from the data that some boxes have higher densities of fish than others. Fish are probably congregating in these boxes around, *inter alia*, good local concentrations of food. Ideally the tagged fish in this study should mimic this behaviour and distribute themselves by box in the same proportions as the natural population. There are several ways of simulating this, but the one chosen here reduced the annual movement rate of fish in high-density boxes and increased it in low-density boxes, whilst retaining the average movement for the whole of South Georgia and Shag Rocks at 10 km/year.

To parameterise this variable movement rate, the population size in each box, N, was set as being equal to the product of the average CPUE in the box over the period 2002–2004 and a catchability coefficient, q, which was arbitrary but constant across all boxes (see equation 3). The mean box movement rate was made a function of the linear density of fish in a box, L, where L = box population size N / cross-box distance d (see below for the definition of N). The CV of the movement rate (0.656) was kept constant for all boxes. The slope of the relationship between movement rate and L was determined iteratively by setting a test slope, seeding each box with 100 tags and allowing free movement over 200 years (with zero mortality), and examining the results after this time to see if the test slope produced the required direct relationship (with an intercept of zero) between observed N and model-distributed number of tags in a box. The final equation was

$$\begin{aligned} m_k &= 2.91 - 0.000145L \\ cv_k &= 0.656 \end{aligned} \tag{1}$$

where m_k is the mean movement rate in box k in the log domain, L = known population size N / cross-box distance and cv = coefficient of variation. Thus each box had its own lognormal distribution from which the actual movement of a fish in that box would be sampled.

Figure 4 shows the observed and modelled movement of fish. Observed movement was calculated (above) using tagging data collected over five years, so to compare the model results, a five-year run of the model was chosen. This should correctly capture movement reversals – where an animal moves west one year and back east the next, for instance. It is not known what the frequency of these is, but it was hoped that the model would provide the same results over a long period of observation as is observed in the field. An equally good correspondence between observed and model results was found, with, however, a different pattern of movement, when movement was examined over a single year rather than five years.

Figure 4 also shows the correspondence between observed and modelled distribution of fish. The model was seeded with 100 tags, which were allowed to mix for 200 years to ensure that there was no possibility of transient effects being introduced by the original placement of tags. However,

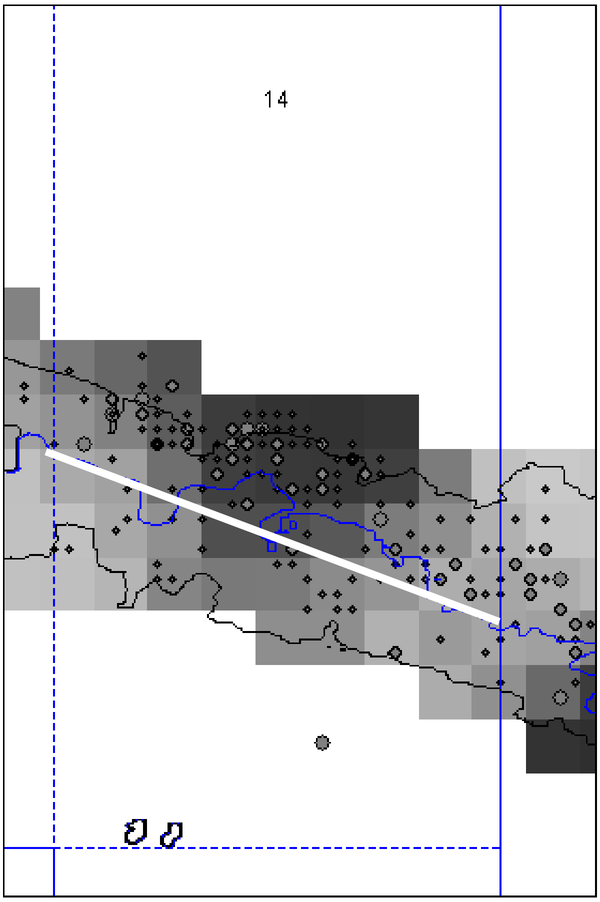

Figure 3: CPUE density interpolated from all data from 2001 to 2004 in box 14, showing also the 500, 1 000 and 1 500 m contours and the direct distance calculated across the box. Open circles represent mean effort (in hooks) from 2001 to 2004, with the diameter of the circles being proportional to the numbers of hooks.

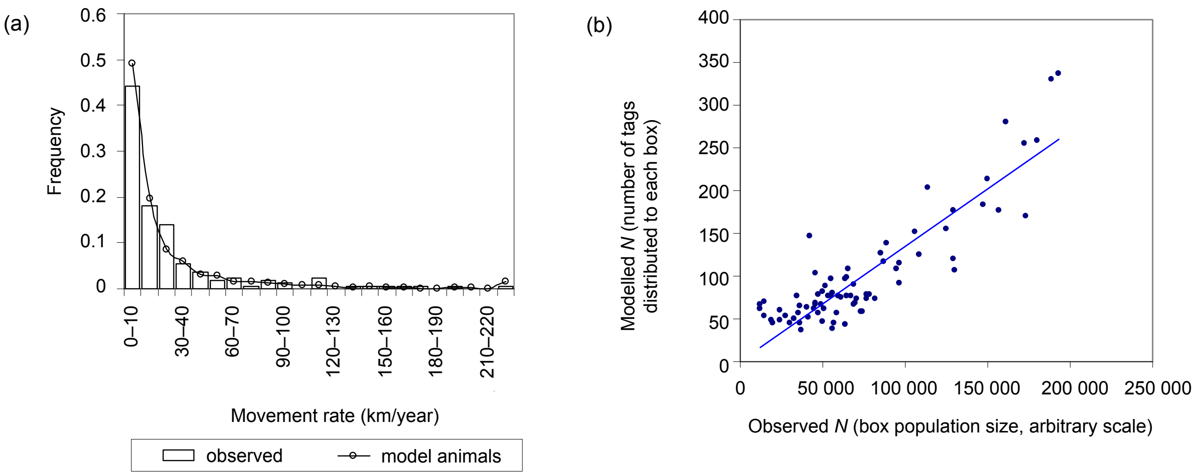

Figure 4: (a) observed (derived from tag returns) and simulated movements of fish, estimated from fish at liberty for five years; (b) relationship between observed total population in a box and the number of tags distributed to the box by the model. The line shown is a regression fitted through the origin. The actual size of *N* is arbitrary, and reflects observed differences in CPUE between boxes.

trials showed that mixing was actually quite rapid, and that within only 10s of years tags were distributed throughout in the required proportions. It can be seen that the correction for box density (equation 1) was able to distribute the fish fairly accurately in proportion to the estimated population size in a box, where population size is the product of observed CPUE and observed size of the box.

Modelling the annual cycle

The model was created to run in discrete time with an annual time step. At each time step, a sequence of four events occur in order: movement, natural mortality, fishing and tag recapture, and tag releases.

After all four events have occurred in time step t–1, there will be $G_{k,t}$ tagged fish alive in the water in box k, for each k. Moving to time step t, first the movement algorithm for each fish in each box was applied. During the annual time step, a proportion of the tagged fish is also expected to suffer natural mortality. In step 2, the expected number of tagged fish that would have died of natural mortality, X, is given by

$$X = \text{smallest integer greater than } (1 - \exp(-M))G_{k,t}. \quad (2)$$

A total of X tagged fish were therefore removed at random from the tagged population, regardless of where they were. No other mortality factors were included in the model, not even the anticipated release mortality, because this would simply be reflected as a proportional adjustment over all tags and years.

The third step is the tag–recapture process in year t. As previously explained, the population size in each box was set as being equal to a product of the average CPUE over the period 2002–2004 and a catchability coefficient, q. The actual population size in each box was assumed to be the same in 2003 and 2004. It is considered that this assumption does not introduce any significant error, since the assessments show that population size did not change significantly between these two years (Hillary et al., 2006). Since the object of the study was to investigate the relationship between real and estimated population size, q was arbitrarily set at 0.1. CPUE in weight is more reliably reported than CPUE in numbers, so the former was used. The total population in box k in 2003 and 2004, N_k, was given by

$$N_k = \frac{A_k U_k}{q w_k} \quad (3)$$

where A_k is the area of fishable ground (500–1 500 m) within box k, U_k is the average CPUE in tonnes/1 000 hooks in box k, q is 0.1, and w_k is the average individual fish weight in tonnes. U_k and w_k were calculated as averages for each box over the period 2002–2004. The average individual weight for the whole area was 6.8 kg.

The catch in a box in year t was calculated as

$$C_{k,t} = \frac{E_{k,t} U_k}{w_k} \quad (4)$$

where $E_{k,t}$ is effort in thousands of hooks actually exerted by the fishery in box k in year t, where t = 2003 or 2004.

To recap, the following were estimated from reported data or the maps for each box:

- U_k average CPUE from 2002 to 2004 (tonnes/1 000 hooks)
- $E_{k,t}$ effort in 2003 and 2004 (1 000 hooks)
- A_k fishable area (km^2)
- d_k cross-box distance (km)
- w_k average weight of fish from 2002 to 2004
- m_k mean movement rate in the log domain
- $G_{k,t}$ the number of tagged fish alive and available for capture in box k in year t.

Two alternative methods were used to recapture tags. In the first (direct) method (A), it was assumed that the ratio of tagged to untagged fish would be the same in the catch as in the population. The number of tags recovered in box k in year t, $g_{k,t}$, was therefore

$$g_{k,t} = C_{k,t} \frac{G_{k,t}}{N_k} \quad (5)$$

where $C_{k,t}$ is the actual catch in numbers in box k in year t, $G_{k,t}$ is the number of tags available for capture in box k and year t, and N_k is the population size of fish in the box.

The second method (B) attempts to mimic the actual fishing operation. Knowing $C_{k,t}$ (in integral numbers of fish), the population in the box N_k was repeatedly sampled for this many fish, each sampling occasion having a chance of selecting a tag which was again the same as the proportion of tags in the population, whilst keeping track of the numbers of tagged and untagged fish captured.

Method A allowed the calculation of a single Petersen estimate of population size:

$$\hat{N}_t = \frac{\sum_{k=1}^{77} G_{k,t}}{\sum_{k=1}^{77} g_{k,t}} \sum_{k=1}^{77} C_{k,t} \qquad (6)$$

with its binomial error variance (Seber, 1982; Agnew and Kirkwood, 2004; Hillary et al., 2006). In method B the fishing operation was repeated 1 000 times, each time generating a single estimate $\hat{N}_t$. Median and upper and lower confidence intervals were calculated from the results. Finally, the ratio of estimated population size to known population size r was calculated for each of methods A and B:

$$r_t = \frac{\hat{N}_t}{N_t}. \qquad (7)$$

Obviously, if r is less than 1, the tagging estimation procedure has underestimated true population size, and if it is greater than 1 it has overestimated true population size.

The fourth and final step in the annual cycle is to add the numbers of fish tagged during the current year to the tagged population in the box in which they were tagged. When simulating the actual tagging at South Georgia, all fish tagged and recaptured during the same season were omitted, because these fish would not have experienced the annual sequence of time steps.

Simulating actual tagging

Agnew and Kirkwood (2004) noted that the numbers of fish released and recaptured prior to 2003 were rather low and the spatial distribution of tagging was rather uneven. Consequently, they did not believe that reliable estimates of population abundance could be obtained until 2003. Nevertheless, it was desirable in the simulation model to have as realistic a depiction of the spatial distribution of tags available for capture at the start of 2003 as possible. The model was initially seeded with the 2000 distribution of tag releases, having first removed any tags that had been recaptured prior to 2003. The annual cycle described above was then simulated for years 2001 and 2002, but without the tag–recapture element. Thus movement and natural mortality of tags released in earlier years and not recovered by 2003 had been properly accounted for. In 2003 and 2004, the full cycle including tag recapture was simulated, allowing Petersen estimates of population abundance to be calculated for those two years.

Results

Model behaviour

The model was subjected to a number of tests to investigate its behaviour (Table 1). Fixing all the box data to be the same and not allowing any movement of fish (i.e. setting U_k, A_k, d_k, m_k, cv_k and w_k to 0.2, 100, 20, 0, 0 and 0.0068 respectively) allowed investigation of the consequences of different distributions of tag deposition and fishing effort (E_k). A series of different scenarios for tag and effort distribution were simulated, with the Petersen estimate being calculated for a single year's fishing. The results are shown in Table 1.

As expected, keeping all parameters constant across all boxes and with a uniform distribution of tags and effort amongst boxes results in perfect estimates of population size (r = 1; case 1 in Table 1). Less expected is the result that if either the tagging or effort distribution is uniform across all boxes, the population is perfectly estimated even if the other distribution is not uniform (cases 2 and 3 in Table 1). This only holds when the population itself is uniformly distributed between boxes, and therefore either tagging or the distribution of effort is directly proportional to population size. If, however, the distributions of tagging and effort are both imperfect, then the population is not well estimated by the mark–recapture experiment: if effort is overconcentrated in areas that have received tags, the true population size is underestimated; and if effort is underconcentrated in areas that have received tags, the true population size is overestimated (cases 4 and 5 in Table 1).

If population size varies between areas, mark–recapture only provides a perfect estimate of population size when either tagging or fishing effort (or both) is distributed in direct proportion to population size (cases 6 to 8 in Table 1). Since both CPUE and fishable area can influence population size, this result considerably complicates the design of an ideal tagging program.

Results with real data

Having established the behaviour of the model, the properties of the existing tagging program were investigated. From the results above, perfect distributions of tags or effort are assumed to be those that are distributed in direct proportion to the population size of each box.

Table 1: Investigation of the effects of different distributions of tags and effort. See text for explanation. 100,…,100 indicates that tags or effort for each of the boxes was 100. Where boxes had unequal distributions, these are shown spatially, for instance in case 3, 0 tags were put into all boxes except three, and 100 effort units were put into all boxes except the three which received all the tags, where zero effort was applied. In cases 1 to 5 the fishable area was held constant in each box, but in cases 7 to 9 this was varied.

Case	Input parameters (U_k, A_k, d_k, m_k, cv_k and w_k were set to 0.2, 100, 20, 0, 0 and 0.06979 unless otherwise stated)	Result
1	Tag : 100,...,100 Effort : 100,...,100	$r = 1$
2	Tag : 100,…,100, 0, 0, 0, 100,…,100 Effort : 0,...,0, 100,100,100, 0,...,0	$r = 1$
3	Tag : 0,...,0, 100,100,100, 0,...,0 Effort : 100,…100, 0, 0, 0, 100,…,100	$r = 1$
4	Tag : 1,…,1, 100,100,100,100, 1,…,1 Effort : 1,…,1, 1, 100,100,1, 1,…,1	$r < 1$: underestimate through overconcentration
5	Tag : 1,…,1, 100,100,100,1,1,1,1, 1,…,1 Effort : 1,…,1, 1,1,1,1,100,100,100, 1,…,1	$r > 1$: overestimation through underconcentration
6	Tag : 100,…,100 Effort : 100,…,100 A : 100,…,100,200,200,200,100,…,100	$r = 0.98$
7	Tag : 100,…,100,200,200,200,100,…,100 Effort : 100,…,100 A : 100,…,100,200,200,200,100,…,100	$r = 1$
8	Tag : 100,…,100,200,200,200,100,…,100 Effort : 100,…,100,200,200,200,100,…,100 A : 100,…,100,200,200,200,100,…,100	$r = 1$

Table 2: Runs of the model with real data. Subscripts for r represent the method of estimating the number of tags, either method A (explicit) or method B (random sampling).

Case	Input parameters (U_k, A_k, d_k, m_k, cv_k, E_k, w_k were set to Appendix 1 unless otherwise stated)	Ratio of estimated to known stock size (95% CI in brackets)
1	Tag : 100,…,100 with 200 years of mixing Effort : ideal – direct proportion to population size	$r_A = 1.003$ $r_B = 1.005$
2	Tag : 100,…,100 with 200 years of mixing Effort : 2004 effort	$r_A = 0.956$ $r_B = 0.954$
3	Tag : as released from 2000 to 2003[1] Effort : ideal – direct proportion to population size	$r_A = 0.975$ $r_B = 0.993$
4	Estimate for 2004 Tag : as released from 2000 to 2003 Effort : 2004 effort	$r_A = 0.821$ (0.69–0.96) $r_B = 0.823$ (0.70–0.93)
5	Estimate for 2003 Tag : as released from 2000 to 2002 Effort : 2003 effort	$r_A = 0.820$ (0.70–0.94) $r_B = 0.826$ (0.74–0.93)

[1] But not including any tags caught prior to 2004

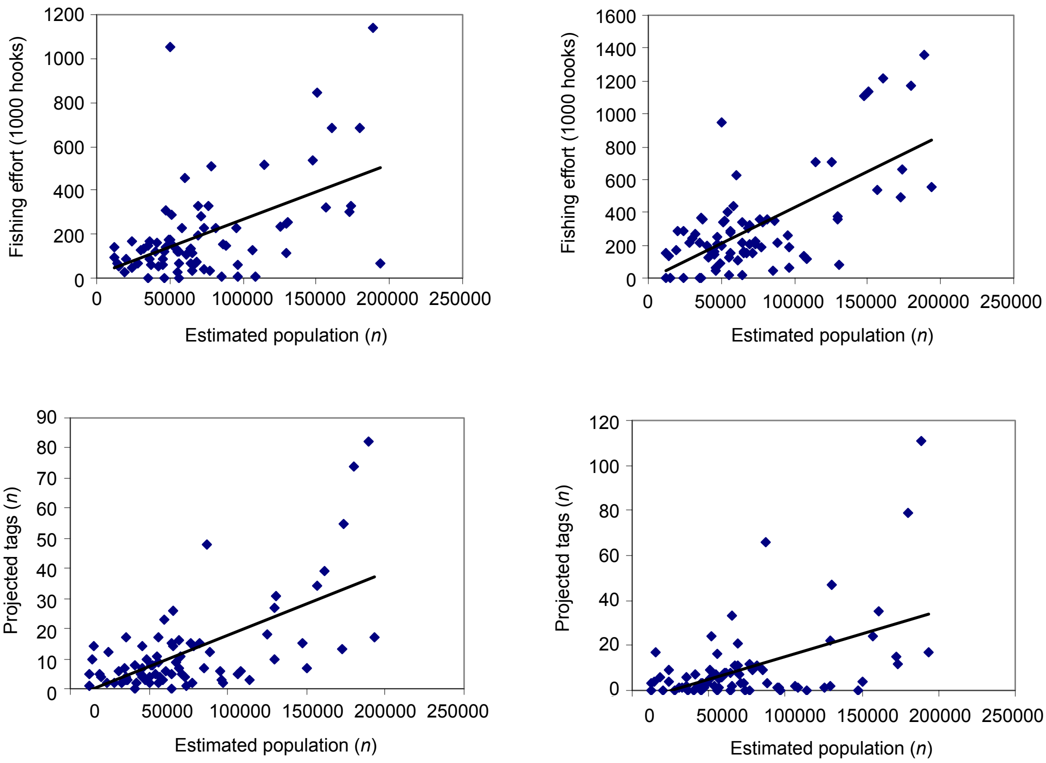

Figure 5: Fishing effort and anticipated tag distribution (produced by applying equation 2 to recorded tag releases) plotted against estimated population size for all boxes for 2004 (left) and 2003 (right).

If an ideal distribution of tags is simulated by seeding the model with 100 tags per box and running the model for 200 years so that they distribute according to equation 1 (producing the plot in Figure 4), and effort is applied in direct proportion to population size, *r* is very close to 1 (case 1 in Table 2). Note that in the previous discussion only one *r* was mentioned, because the results of methods A and B were virtually identical. In all the runs with real data, the different methods gave slightly different results and both are reported.

If a similar ideal distribution of tags is simulated (with 200 years of movement) but effort is applied as it was in 2004, the model predicts that there will be an underestimate of population size by 5% (case 2 in Table 2).

So far only an ideal distribution of tags has been used. This is now replaced with the actual distribution of tags that were released from 2000 to 2003, allowing them to move between years and also allowing for removals due to natural mortality and tag recapture. If the distribution of effort is ideal, it again can be found that the true population size is slightly underestimated (case 3 in Table 2). When both the actual distribution of effort and the actual distribution of tags is used, the extent of underestimation increases to around 21% for both 2003 and 2004 (cases 4 and 5 in Table 2). Note that the 95% confidence intervals are narrower for method B than for method A.

Discussion

This model provides the basis for examining possible biases in the estimation of toothfish population size at South Georgia using the modified Petersen mark–recapture method described in Agnew and Kirkwood (2004). The results suggest that current mismatches between the distribution of tags, the distribution of the population and the distribution of fishing effort are likely to create an underestimate of true population size. The size of these underestimates reflects the size of the mismatch (Figure 5).

In discussion of an earlier version of this paper, it was pointed out that uneven distribution of tag releases and effort could also affect the estimate of movement rate described earlier. Further, the distance between release and recapture boxes is not necessarily a reliable estimator of the actual distance moved by the tagged fish. This is clearly correct, and one potential way to account for this would be to simulate the collection of data on distance moved between release and recapture for a given assumed mean movement rate, and then iteratively estimate the true movement rate that best matched the mean apparent movement rate. This would be worth investigating in the future, but the authors expect that the effect of this adjustment would be relatively minor, compared with the effects of uneven spatial distributions of effort and tagging.

Although natural mortality was incorporated, tagging mortality was not. Since this is likely to be the same for each year of tagging, and is in any case very low (Agnew et al., 2006), it is considered that this omission is most unlikely to affect the results. Similarly, the model was simplified by ignoring fish size, growth and selectivity. These issues may have a part to play in creating further levels of bias but only if these factors are themselves uneven in distribution: for instance, if only small animals are tagged in one area and only large ones in another. It is suspected (but not tested) that the much larger imbalances between tagging effort, population distribution and recovery effort are likely to swamp bias arising from these secondary factors. Nevertheless, reformulation to take account of fish size, growth and selectivity should be considered in future developments of the model.

Another area in which bias could arise is in the calculation of population size per box. It is assumed here that population density is proportional to CPUE and that population size in a box is a product of density and the fishable area. This calculation is currently dependent on calculations of fishable area (500–1 500 m), which is approximately the adult toothfish habitat, but there are discrepancies in the data where fishing has taken place only along one edge of this area, usually the deeper areas. Furthermore, CPUE was calculated by pooling all data from the fishery from a particular box, rather than applying GLM-type modelling. Future work should investigate the sensitivity of the results to estimates of fishable area and area-specific vessel-standardised CPUE.

The model described here was originally conceived specifically to investigate the match–mismatch of distributions of tag release and recapture effort. It has demonstrated that an ideal distribution of both tagging events and recovery effort is in direct proportion to CPUE. The current tagging protocol ensures that tags are released in proportion to CPUE. Although it does not necessarily ensure that fishing effort is in proportion to CPUE, this is a likely result of the behaviour of fishers.

Summary

1. A model of toothfish movement around South Georgia is constructed with the object of examining the consequences of uneven distribution of tags and fishing effort. The model treats the Subarea 48.3 toothfish habitat as a chain of interconnected boxes running around the 1 000 m contour of South Georgia and Shag Rocks.

2. Under ideal conditions, when tagging or recovery effort is in direct proportion to the size of the population in each box, the Petersen mark–recapture method produces near-unbiased estimates of toothfish population size.

3. Given current mismatches between tagging effort, recovery effort and population distribution, the model suggests that the mark–recapture method is likely to produce underestimates of toothfish population size in Subarea 48.3.

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APPENDIX 1

BOX PARAMETERS USED FOR THE FULL MODEL
(EFFORT FOR 2004: CASE 4 IN TABLE 2)

POP.DAT

Box	U_k CPUE (tonnes/1000 hooks)	A_k area (km^2)	d_k distance km	m_k speed	cv_k	E_k effort (hooks in thousands) (2004)	w_k Average weight
01	0.150	57	17	2.79	0.656	69.8	0.00592
02	0.152	60	17	2.81	0.656	93.8	0.00750
03	0.175	81	16	2.75	0.656	27.0	0.00763
04	0.266	173	27	2.62	0.656	120.5	0.00839
05	0.283	123	17	2.53	0.656	60.2	0.00776
06	0.171	282	23	2.38	0.656	4.7	0.00564
07	0.282	316	21	1.58	0.656	69.2	0.00461
08	0.331	268	18	1.62	0.656	680.5	0.00550
09	0.328	367	26	1.86	0.656	1140.9	0.00636
10	0.216	269	17	2.17	0.656	151.5	0.00668
11	0.204	236	17	2.36	0.656	36.5	0.00737
12	0.248	205	17	2.33	0.656	70.7	0.00741
13	0.220	235	17	2.34	0.656	68.8	0.00770
14	0.269	190	20	2.45	0.656	132.4	0.00797
15	0.234	229	19	2.29	0.656	228.6	0.00654
16	0.276	155	19	2.33	0.656	326.5	0.00561
17	0.280	53	17	2.71	0.656	168.9	0.00623
18	0.193	147	17	2.61	0.656	165.1	0.00792
19	0.247	370	23	2.10	0.656	245.7	0.00706
20	0.449	215	17	1.38	0.656	680.6	0.00536
21	0.330	302	22	1.88	0.656	322.8	0.00637
22	0.215	220	16	2.28	0.656	196.1	0.00680
23	0.202	184	17	2.47	0.656	147.0	0.00716
24	0.209	130	22	2.64	0.656	159.4	0.00661
25	0.252	138	16	2.46	0.656	172.0	0.00691
26	0.273	152	18	2.44	0.656	227.8	0.00709
27	0.313	70	17	2.68	0.656	66.0	0.00786
28	0.252	92	19	2.67	0.656	131.5	0.00712
29	0.271	107	17	2.51	0.656	305.8	0.00611
30	0.249	155	17	2.43	0.656	0.0	0.00682
31	0.238	179	18	2.33	0.656	227.9	0.00583
32	0.163	203	18	2.42	0.656	110.6	0.00542
33	0.170	184	19	2.56	0.656	118.9	0.00682
34	0.210	154	19	2.57	0.656	90.0	0.00714
35	0.255	155	17	2.46	0.656	136.7	0.00736
36	0.262	401	25	2.06	0.656	533.4	0.00714
37	0.302	302	18	1.70	0.656	846.2	0.00606
38	0.293	372	17	1.44	0.656	299.4	0.00633
39	0.309	233	26	2.42	0.656	144.8	0.00814
40	0.254	108	9	2.32	0.656	58.0	0.00745
41	0.276	106	15	2.58	0.656	0.0	0.00837
42	0.231	135	16	2.50	0.656	0.0	0.00679
43	0.303	265	12	1.35	0.656	112.9	0.00619

(continued)

Box	U_k CPUE (tonnes/1000 hooks)	A_k area (km^2)	d_k distance km	m_k speed	cv_k	E_k effort (hooks in thousands) (2004)	w_k Average weight
44	0.328	244	17	1.94	0.656	514.4	0.00701
45	0.426	185	10	1.51	0.656	8.3	0.00816
46	0.264	198	9	1.67	0.656	32.5	0.00680
47	0.263	108	24	2.66	0.656	53.7	0.00680
48	0.282	149	10	1.84	0.656	39.7	0.00570
49	0.348	74	8	2.18	0.656	118.5	0.00633
50	0.414	143	16	1.93	0.656	5.5	0.00546
51	0.312	320	21	2.05	0.656	237.3	0.00798
52	0.351	135	20	2.51	0.656	118.0	0.00844
53	0.270	77	10	2.47	0.656	129.9	0.00680
54	0.237	60	9	2.60	0.656	90.2	0.00721
55	0.239	148	9	2.01	0.656	66.7	0.00634
56	0.222	291	23	2.24	0.656	128.0	0.00607
57	0.205	203	8	1.75	0.656	135.9	0.00648
58	0.266	213	16	2.05	0.656	229.9	0.00596
59	0.290	146	18	2.40	0.656	65.9	0.00662
60	0.250	128	17	2.51	0.656	141.5	0.00681
61	0.257	253	20	2.22	0.656	62.1	0.00677
62	0.266	175	20	2.44	0.656	112.8	0.00716
63	0.374	363	28	2.02	0.656	326.4	0.00782
64	0.440	107	18	2.43	0.656	457.2	0.00786
65	0.375	98	17	2.48	0.656	291.0	0.00717
66	0.294	126	16	2.47	0.656	173.3	0.00758
67	0.187	66	18	2.79	0.656	54.4	0.00826
68	0.249	346	21	2.01	0.656	253.3	0.00659
69	0.262	195	16	2.29	0.656	326.7	0.00737
70	0.278	194	17	2.31	0.656	282.2	0.00760
71	0.314	64	18	2.72	0.656	49.2	0.00845
72	0.265	99	17	2.61	0.656	145.1	0.00744
73	0.247	120	21	2.67	0.656	88.5	0.00826
74	0.160	61	18	2.81	0.656	138.3	0.00780
75	0.298	130	25	2.62	0.656	1050.9	0.00769
76	0.193	337	23	2.42	0.656	508.2	0.00833
77	0.169	238	23	2.56	0.656	30.0	0.00725