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Spatial Dynamics of Scallops in Relation to the Orkney Dive Fishery

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Introduction

The principal method of fishing for king scallops, *Pecten maximus*, in Orkney waters is hand collection by divers. Divers typically target areas at a relatively small spatial scale (tens of m^2) and catchability of scallops at this scale is considered to be very high. Divers nevertheless observe that exploited areas are re-populated by fishable scallops over very short time periods, often over periods of weeks, meaning that sites can repeatedly be targeted within the same fishing season. Given high visibility of individual scallops coupled with a high efficiency of removal by divers, this re-population seems most likely to be accounted for by immigration. This inference is, however, difficult to reconcile with the usual assumption that the mobility of scallops is very limited. Moreover, suitable sources of immigration are sometimes separated from fished sites by areas of apparently unsuitable habitat. The extent to which scallops are mobile between areas and can re-colonise areas of local depletion could be a crucial mediating factor controlling the availability of scallop stocks to exploitation and potentially of great importance in defining a sustainable fishery for scallops in Orkney waters.

The objective of the project was to determine spatial turnover rates of scallops at two spatial scales: (i) at the scale of individual fishing patches (tens to hundreds of metres), determining immigration rates following fishing; and (ii) at the local fishery scale (1-10 km and greater), determining potential sources of immigration to fishing patches from more distant areas. This report addresses the first of these spatial scales, using depletion fishing experiments coupled with tagging to estimate size-specific population size and site-fidelity to small experimental areas.

Methods

Depletion Fishing Experiments

Depletion fishing experiments were undertaken to estimate the density and size-composition of scallop populations at a local scale. Depletion fishing involves repeated removal of catch on a defined sample plot, measuring the rate at which the catch rate declines as the total catch accumulates.

Fifteen depletion experiments were conducted in Orkney waters during 2013 and 2014, comprising five fishing occasions at a location to the south of Wyre, five in Scapa Bay and five close to Fara (Figure 1). The results of the Wyre experiments are reported here, undertaken on board the fishing vessel *Three Boys* (K905, skipper

Emlyn Grieve) at a location to the south of the island (59°6.48'N, 2°57.93W). The survey line was marked out by a heavy sinking rope, left in situ between fishing occasions. Fishing covered a strip of 2 m either side of the rope, and the length of rope covered (and marked for future reference) was 178 m, determined by the coverage of the first bout of fishing. The survey area was thus 712 m^2. Fishing was undertaken by a team of four divers employing their usual hand-gathering technique but collecting all sizes of scallops encountered. All scallops captured on each bout of fishing were counted and measured (shell height and width). All scallops not retained for landing were returned to the survey area, distributed along the line by a diver placing scallops on the sea bed. Three fishing bouts were completed on each occasion, limited by dive time and diminishing catch rates. The five depletion fishing occasions were 25 June, 8 August, 7 October and 18 November 2013, and 13 June 2014. Other than the depletion experiments, no fishing activity is thought to have occurred on the Wyre grounds over the duration of the survey series.

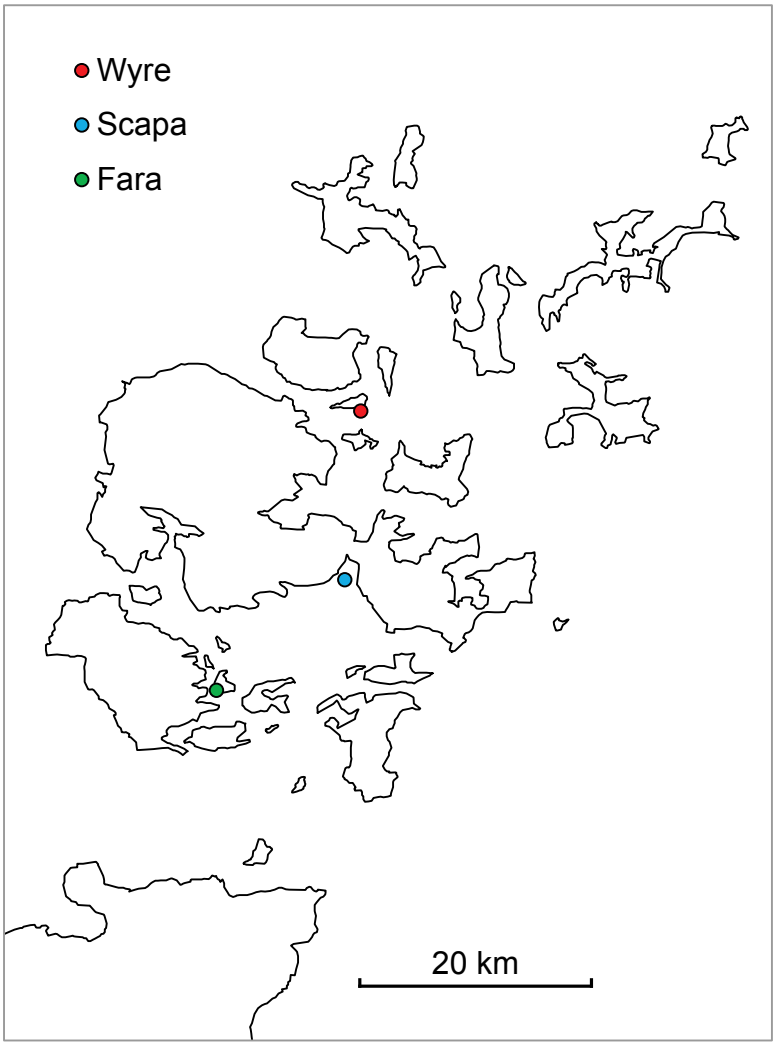

Figure 1: Locations of depletion fishing plots in Orkney waters during 2013 and 2014.

Depletion Modelling

Modelling of the changes in catch rate measured over the course of a depletion experiment allows estimation of capture probabilities for a unit of fishing effort and hence of the size of the population from which the catch was drawn. Traditionally this is accomplished using a simple method developed by Leslie and Davis (1939), based on regression of catch rates on cumulative catch. A statistically more rigorous maximum likelihood approach has been developed for the analysis of data from these experiments, allowing likelihood-based inferences about parameter uncertainty and variability of capture probabilities between size-groups and survey occasions. Population estimates and capture probabilities were constrained within feasible bounds by log - and logistic transformation respectively. Five models were considered for variation in capture probability between size-groups and survey occasions:

(i) *time * size*, in which separate capture probabilities are estimated for each size-group and survey occasion independently – this is equivalent to fitting a separate model to the data for each size-group on each occasion;

(ii) *time + size*, in which the effects of size-group and survey occasion on capture probability are additive on a logistic scale – this means that differences among size-groups are modelled as being consistent between survey occasions (or, equivalently, that differences among survey occasions are consistent between size-groups);

(iii) *time*, in which capture probabilities are modelled as differing between survey occasions but the same in all size-groups;

(iv) *size*, in which capture probabilities are modelled as differing between size-groups but the same on all survey occasions; and

(v) *constant*, in which capture probabilities are modelled as being the same on all survey occasions and in all size-groups.

Population numbers were treated as free parameters in all models, being the outcome of catch scaled by capture probability. The simplest adequate model for the data was selected by minimum value of the Akaike Information Criterion, adjusted for small sample size according to Burnham & Anderson (2002). Catch numbers, being count data, were modelled as Poisson distributed. Overdispersion in

the count data was accounted for by estimating a dispersion coefficient (*c*, variance inflation factor) based on the Pearson χ^2 statistic for the full *size * time* model:

$$\hat{c} = \chi^2 / \mathrm{df} \text{ , Eq. 1}$$

where df is the degrees of freedom for the model (number of catch observations minus the number of separately identifiable model parameters). Given a value of $\hat{c}$ significantly greater than its expectation (value of one) under a Poisson distribution, model selection and estimation of parameter uncertainty followed Burnham & Anderson (2002) in using a quasi-likelihood approach, i.e. the quasi-likelihood version of the Akaike Information Criterion, adjusted for small sample size ($QAIC_c$) was used, and all variances and covariances were inflated by a factor $\hat{c}$ before calculation of standard errors and confidence intervals.

The maximum likelihood depletion model is described briefly in Appendix 1, together with code for implementing the model in the R statistical package (R Core Team, 2014). This shows how expectations for catch numbers are formulated in terms of capture probabilities *P* for an individual fishing pass (dive) over the experimental plot. For comparison with parameters estimated from tag-recapture data (see below), the cumulative probability *P′* over the course of an experiment is then calculated as:

$$P' = \sum_{i=1}^{nd} P(1-P)^{i-1} \text{ , Eq. 2}$$

where *nd* is the number of dives. *P′* is directly comparable with capture probabilities for each occasion modelled for the tagging data (see below). Appendix 1 also shows code for implementing the model in the R statistical package (R Core Team, 2014).

Tagging During the Depletion Experiments

Legal scallops (≥100 mm shell width) were (mostly) retained for landing and a sample of (mostly) sub-legal scallops was tagged. Subsequent recaptures of scallops that had grown to legal size were returned to the survey ground rather than being retained for landing. Three different tagging methods were trialled (Figure 2): numbered disk tag wired to one ear of the scallop; numbered disk tag glued to the flat valve near the umbo; numbered cable tie inserted through a hole drilled through one ear of the flat valve. In addition to tagging, some scallops were marked with black mastic, enabling untagged resident scallops to be recognised on subsequent occasions.

(a) Glued disk tags

(b) Wired disk tags

(c) Cable tie tag

Figure 2: Tagged scallops of three different types used in Orkney during 2013-2014.

The depletion fishing experiments provide spot estimates of the scallop population (both tagged and untagged) present in the survey area on each occasion, whilst recaptures of tagged scallops provide a perspective on population dynamics between occasions. Application of the Cormack-Jolly-Seber (CJS) model (Lebreton *et al.*, 1992) allows recaptures to be modelled as a function of survival/fidelity and recapture probabilities. Recapture data are pooled between dives within survey occasions, thus recapture probabilities estimated from tagging are equivalent to the depletion estimates cumulated over the dives (Equation 2)[1]. The CJS model was implemented in Excel for this project, based on determining cell probabilities in 'reduced m-arrays' (Burnham *et al.*, 1987). The reduced m-array format is a summary of the recapture data where rows of the array refer to release cohorts and columns refer to occasions of first recapture. Re-releases of tag recaptures are treated alongside new releases in following release cohorts (this is the 'reduced' element of the m-array). Data on release numbers, first recaptures and numbers never recaptured from each release cohort are sufficient for maximum likelihood estimation of all the parameters of a CJS model (Burnham & Anderson, 1987). Allowance was made for unequal sampling intervals (42-207 days) between occasions, so that meaningful equality constraints could be made for survival/fidelity probabilities, i.e. on a per day rather than per interval basis. Similar to the depletion model, 16 different CJS-type models were considered, based *time * size*, *time*, *size* and *constant* constraints on either or both of the survival/fidelity and capture probabilities. Logistic transformation was used to constrain all probabilities within feasible bounds. Model fitting was by maximum likelihood, with the kernel of a multinomial log-likelihood (l) defined as:

$$l = \sum m_{ij} \ln p_{ij} \text{ , Eq. 3}$$

where m_{ij} is an observed element of the reduced m-array, p_{ij} is the probability of that observation, formed in terms of survival/fidelity and capture probabilities and the summation is over the rows (i) and columns (j) of the reduced m-array. This log-likelihood was maximised using the Solver add-in in Excel.

A goodness-of-fit test for the full model (*time * size* for both survival/fidelity and capture probabilities) was based on a Pearson χ^2 statistic for the reduced m-array, with pooling of expectations <2 within rows. A non-significant value for this statistic

[1] In principle, this equivalence of model parameters provides a means of defining a joint model for depletion and tag recaptures, maximising the sum of log-likelihoods for the two components of the data. To avoid double-counting of data this would require disaggregation of the tagged and untagged captures in the depletion model. Implementation of this combined model has not been possible within the resources available for this project.

(see below) indicates that the CJS model is a suitable basis for inference about recapture probabilities and that the tagging data were not over-dispersed with respect to the assumptions of a multinomial likelihood. Selection of the simplest adequate model as a basis for further inference was based on minimum value of the Akaike Information Criterion adjusted for small sample size (AIC_c). Given several models with AIC_c values differing from the minimum by about two or less, final survival/fidelity and capture probability estimates were obtained by model averaging following the approach of Burnham & Anderson (2002). Survival/fidelity and capture probabilities from all models were estimated for each size-group and occasion, and weighted averages across the models were calculated using relative model likelihoods as weights ('Akaike weights'). The final probability estimates are thus most strongly influenced by the most likely model (model with lowest value of AIC_c), with other models contributing according to their relative likelihoods.

Given the use of Excel to fit the CJS-type models to the data, a variance-covariance matrix is not available for the model estimates, so a full exploration of uncertainty around model parameters is not yet possible. An implementation of the model in the R statistical package will allow this to be explored in future.

Permanent emigration cannot be distinguished from mortality in these CJS-type models, hence the reference to survival/fidelity probabilities. Given an assumed value for the instantaneous rate of natural mortality (M) of 0.15 yr^{-1} for Scottish scallop populations (e.g. Dobby *et al.*, 2012), it is possible to partition the two components. Given a survival/fidelity of ϕ, expressed on a daily basis, an assumed daily probability of fidelity f to the survey area can be calculated as:

$$f = \exp\left[\left(\ln(\phi^{365}) + M\right)/365\right]. \text{ Eq. 4}$$

This then allows the probability of permanent emigration E to be estimated for any given time interval to be calculated as:

$$E = 1 - f^t, \text{ Eq. 5}$$

where t is the interval duration in days.

Small Scale Movement Patterns

Estimates from the depletion and tagging experiments can be used to provide a complete picture of scallop population dynamics in the survey plot. As summarised in Figure 3, these processes are:

(i) *Losses due to emigration and mortality*. Removals of legal-sized scallops (≥100 mm shell width) by fishing are known. For size-group *j*, losses of scallops from the survey area due to permanent emigration or natural mortality between occasions *i* and *i*+1, L_{ij}, are given by:

$$L_{ij} = (N_{ij} - F_{ij})(1 - \phi_{ij}^{t_i}), \text{ Eq. 6}$$

where N_{ij} is the population number in size-group *j* estimated by depletion model for occasion *i*, F_{ij} is the number of scallops of that size-group removed by fishing, ϕ_{ij} is the daily survival/fidelity probability of scallops in that size-group during the interval between occasions *i* and *i*+1, and t_i is the duration of that interval in days.

(ii) *Transition between size-groups owing to growth.* The sizes of tagged scallops measured on consecutive occasions can be used to estimate the probabilities of transitions between size-groups. Growth between occasions can be represented by a linear relationship:

$$W_{i+1} = a + bW_i, \text{ Eq. 7a}$$

where W_i and W_{i+1} are shell widths on occasions *i* and *i*+1 respectively, and *a* and *b* are the intercept and slope of the relationship, estimated by linear regression. The threshold shell width above which scallops grow into the next size-group is then estimated by inverting this relationship:

$$W_{threshold,ij} = \frac{W_{boundary,j+1} - a}{b}, \text{ Eq. 7b}$$

where $W_{threshold,ij}$ is the threshold for shell widths in size-group *j* measured on occasion *i*, and $W_{boundary,j+1}$ is the lower length boundary of the recipient size-group *j*+1. The probability of transition between size-groups *j* and *j*+1 between occasions *i* and *i*+1, $T_{ij,}$ is then:

$$T_{ij}^{j+1} = \frac{\sum_{w=W_{threshold,ij}}^{W_{boundary,j+1}} C_{iw}}{\sum_{w=W_{boundary,j}}^{W_{boundary,j+1}} C_{iw}}, \text{ Eq. 8}$$

where C_{iw} is the number of scallops of size w caught on occasion i (note that w indexes the multiple sizes that are grouped within a size-group). Note that transition probabilities estimated in this way are conditioned on the scallop size composition measured in the survey catches. This is appropriate for the accounting of population processes between surveys, but does not generalise to populations differing in size structure. Too few data are available to allow construction of a generalised transition matrix between size-classes defined at a finer level. Using the transition probabilities defined in Eq. 8, the number of scallops growing between size-group is calculated as:

$$G_{ij} = T_{ij}\left(N_{ij} - F_{ij} - L_{ij}\right), \text{ Eq. 9}$$

where G_{ij} is the number in size-group j on occasion i that remains in the survey area on occasion i+1, having grown to size-group j+1.

(iii) *Residency within the survey area and size-group*. The number of scallops of size-group j that remain in the survey area between occasions i and i+1, without growing into the next size-group during that interval, R_{ij} is given by:

$$R_{ij} = N_{ij} - F_{ij} - L_{ij} - G_{ij}, \text{ Eq. 10}$$

where all quantities are subscripted by occasion i and size-group j. This represents the starting population number from which fishery removals, emigration and growth of the remainder are subtracted.

(iv) *Immigration into the survey area from outside*. Once the processes of losses due to emigration/mortality, growth between size-groups and residency within the survey area have been projected between survey occasions, any discrepancy between the projected population and that estimated by the depletion model should in principle be accounted for by immigration of new scallops from outside the survey area:

$$I_{i+1,j} = N_{i+1,j} - R_{ij} - G_{ij}, \text{ Eq. 11}$$

where $I_{i+1,j}$ is the number of immigrants into the population in size-group j measured at occasion i+1.

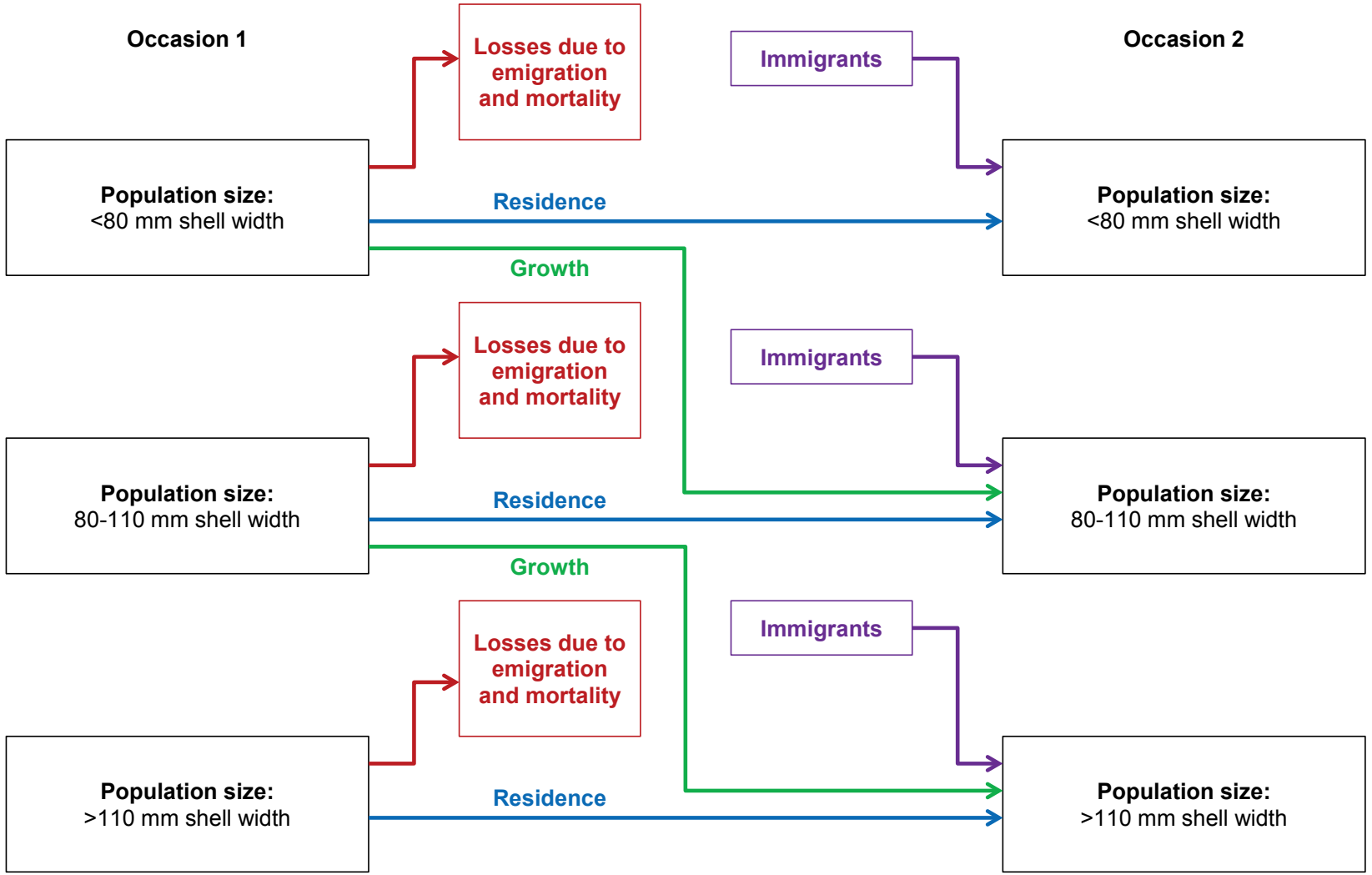

Figure 3: Diagram of population dynamic processes affecting changes in numbers of scallops in each size-group within the survey area between survey occasions. Note that emigration accounted for among the losses is permanent within the time-scale of the survey series. Mortality of scallops larger than 100 mm shell width includes known fishery removals.

Results

Depletion Experiments at Wyre

The outcomes of the five depletion fishing experiments at Wyre are summarised according to three scallop size-groups in Table 1 and Figure 4. Convincing patterns of declining catch per dive are shown in most cases, the notable exception being the smallest size group (<80 mm shell width) in June 2014, for which the catch rate increased from 10 to 31 scallops between the first and second dives. Inspection of fitted values from the full maximum likelihood model (*time * size*) indicated no obvious patterns of lack-of-fit by the model, but the Pearson statistic for goodness-of-fit was significant (χ^2=50.474, df=16, P<0.001), taken to indicate over-dispersion in the count data rather than a structural failure of the model. This statistic was used to estimate a variance inflation factor $\hat{c}$=3.155 that was taken forward into quasi-likelihood-based model inference. Sample size for the model was 45, being the number of survey occasions (five) × the number of size-groups (three). After accounting for this over-dispersion, and adjusting for small sample size, the 'best' (most parsimonious) model was selected by minimum value of $QAIC_c$ as representing variation in capture probabilities between size-groups but not between occasions (*size*, Table 2). Model selection was unambiguous, with relative likelihoods for alternative models being negligible, thus no need was seen for model averaging to account for model uncertainty. Accordingly, the estimates in Table 1 and the depletion lines in Figure 4 are based on capture probabilities and population estimates from the *size* model.

As might be expected, estimated capture probability increased with scallop size, being 0.33, 0.68 and 0.79 per dive for scallops in the <80 mm, 80-110 mm and >110 mm shell width size-groups respectively (Table 1). It is likely that differences in fishing efficiency between individual divers contributed to variability of the catch rates about the overall depletion trends shown in Figure 4, but comparisons of model residuals between individual divers show no obvious patterns.

Population estimates were lowest in the >110 mm shell width size-group, varying from 16 (0.023 .m^{-2}) in June 2014 to 87 (0.12 .m^{-2}) in June 2013 (Table 1), the difference being due, at least in part, to fishery removals during the depletion experiments. Smaller size-groups were higher in abundance, the highest estimate being 173 (0.24 .m^{-2}) for scallops in the 80-110 mm size-group in October 2013. Overall numbers estimated to be in the survey area ranged from 168 (0.24 .m^{-2}) in June 2014 to 339 (0.48 .m^{-2}) in October 2013.

Table 1

Summary of scallop catches for depletion fishing experiments at Wyre. Capture probabilities per dive and population estimates are from the selected maximum-likelihood depletion model (see Table 2). 95% confidence intervals are shown in brackets. Lower limits for population size are given as the sum of catches on each occasion, which in all cases exceeded the statistical lower 95% confidence limit. Density estimates are calculated for the plot area of 712 m^2.

(a) 25 June 2013

	<80 mm shell width		80-110 mm shell width		>110 mm shell width	
Dive	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**
1	0	41	0	56	0	74
2	41	15	56	6	74	6
3	56	13	62	0	80	4
Capture probability per dive:	0.327 (0.193-0.497)		0.678 (0.588-0.756)		0.794 (0.659-0.884)	
Population estimate:	99 (69-169)		64 (62-102)		87 (84-129)	
Scallop density (.m^{-2}):	0.139 (0.097-0.238)		0.090 (0.087-0.143)		0.122 (0.118-0.181)	

(b) 8 August 2013

	<80 mm shell width		80-110 mm shell width		>110 mm shell width	
Dive	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**
1	0	47	0	53	0	8
2	47	32	53	15	8	12
3	79	34	68	10	20	0
Capture probability per dive:	0.327 (0.193-0.497)		0.678 (0.588-0.756)		0.794 (0.659-0.884)	
Population estimate:	162 (113-257)		81 (78-122)		20 (20-46)	
Scallop density (.m^{-2}):	0.228 (0.159-0.361)		0.113 (0.110-0.171)		0.028 (0.028-0.064)	

(c) 7 October 2013

	<80 mm shell width		80-110 mm shell width		>110 mm shell width	
Dive	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**
1	0	57	0	94	0	11
2	57	21	94	27	11	5
3	78	3	121	4	16	1
Capture probability per dive:	0.327 (0.193-0.497)		0.678 (0.588-0.756)		0.794 (0.659-0.884)	
Population estimate:	116 (81-193)		129 (125-179)		17 (17-42)	
Scallop density (.m^{-2}):	0.164 (0.114-0.272)		0.182 (0.176-0.252)		0.024 (0.024-0.058)	

(d) 18 November 2013

	<80 mm shell width		80-110 mm shell width		>110 mm shell width	
Dive	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**
1	0	32	0	112	0	39
2	32	30	112	43	39	1
3	62	25	155	12	40	1
Capture probability per dive:	0.327 (0.193-0.497)		0.678 (0.588-0.756)		0.794 (0.659-0.884)	
Population estimate:	125 (87-205)		173 (167-229)		41 (41-73)	
Scallop density (.m^{-2}):	0.176 (0.122-0.288)		0.243 (0.235-0.322)		0.058 (0.058-0.103)	

(e) 13 June 2014

	<80 mm shell width		80-110 mm shell width		>110 mm shell width	
Dive	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**	**Cumulative Catch**	**Catch per Dive**
1	0	10	0	43	0	12
2	10	31	43	22	12	2
3	41	9	65	12	14	2
Capture probability per dive:	0.327 (0.193-0.497)		0.678 (0.588-0.756)		0.794 (0.659-0.884)	
Population estimate:	72 (50-131)		80 (77-121)		16 (16-40)	
Scallop density (.m^{-2}):	0		10		0	

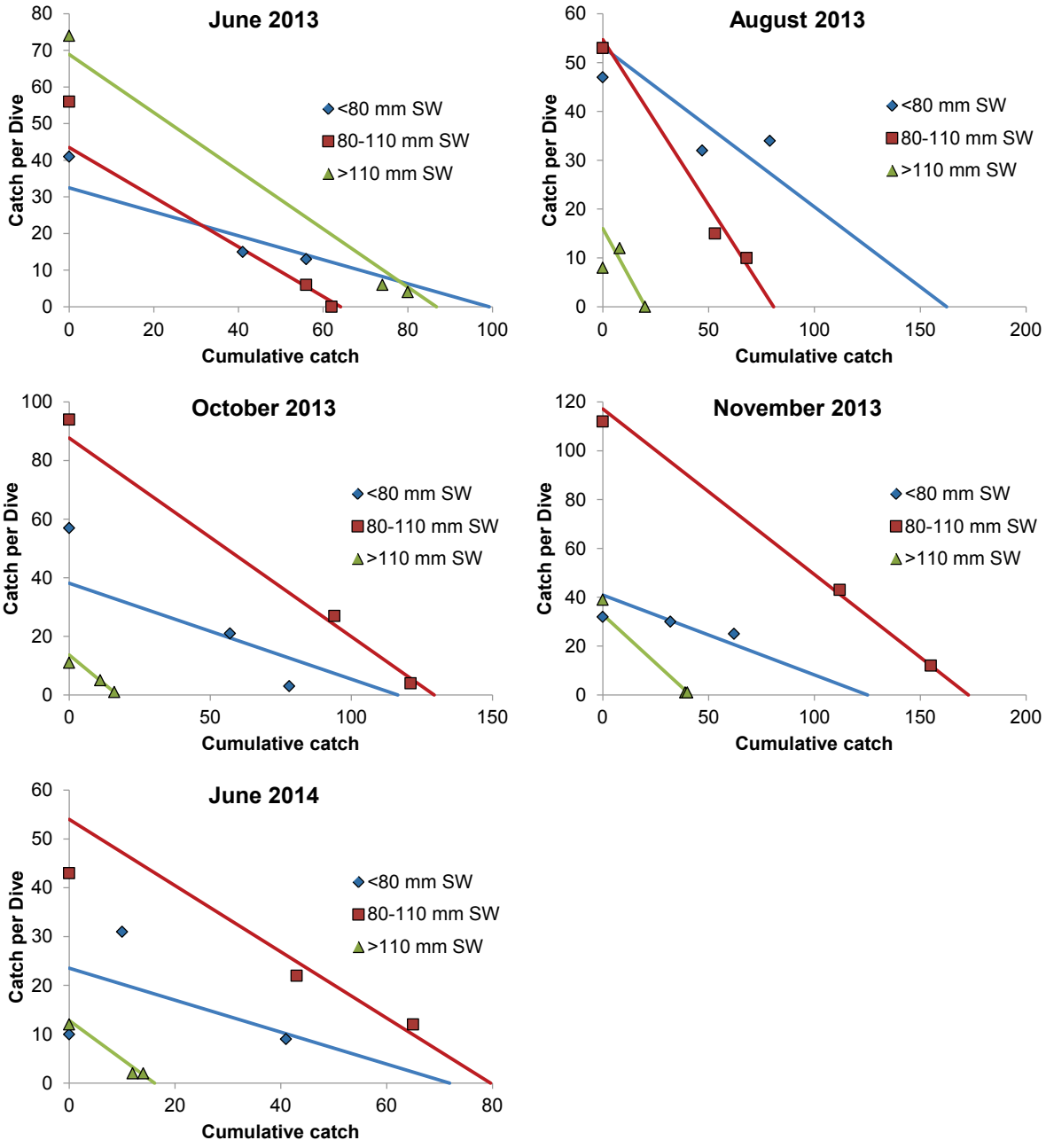

Figure 4: Leslie plots for scallop depletion experiments at Wyre; the negative slope of each line represents the probability of capture per dive for each size group; the point at which each line intercepts the horizontal axis (x-axis) represents the estimated population size of scallops within the survey area. Capture probabilities and population estimates were derived from the selected maximum-likelihood model fitted to the data (see Tables 1 and 2) rather than by regression using the Leslie method.

Tagging and Recapture at Wyre

Size-frequency data for scallops tagged and recaptured at Wyre are shown in Figure 5, and recapture data are shown in Table 3 summarised for three size groups using the 'reduced m-array' format (Burnham *et al.*, 1987). Recapture rates were very high, without significant patterns of difference between tag types (Figure 6; χ^2=2.74, df=6, *P*=0.841). Goodness-of-fit testing indicates that the time- and size-structured CJS model framework (*time* * *size* for both survival/fidelity and capture probabilities) is a suitable basis for inference (χ^2=0.113, df=3, *P*=0.990, based on cell expectations for the reduced m-array, with pooling across expected values <2). Effective sample size for the tagging and recapture data is 450, calculated as the total number of releases included in the reduced m-arrays (Table 3). This figure was used in the adjustment for small sample size in model selection. The model with the lowest value of AIC_c represents differences between sampling intervals in survival/fidelity probabilities and variations between size-groups in capture probabilities (*time*, *size*, Table 4). The capture probability model is consistent with the pattern of variation determined in the modelling of depletion data (Table 2). However, several alternative models appear equally defensible for the model (differences in $QAIC_c$ of around 2 or less), such that it is appropriate to consider model uncertainty in deriving final estimates of demographic rates and recapture probabilities. Model average values of capture probabilities on each survey occasion and size-group, and survival/fidelity probabilities for each survey interval and size-group, were calculated using the weights in the right-hand column of Table 4). These are shown in comparison with estimates from the 'best' model (*time*-dependent survival/fidelity probabilities, *size*-dependent capture probabilities) in Figure 7. For ease of interpretation, the daily survival/fidelity probabilities, ϕ, have been converted into monthly (30-day) loss rates as $1-\phi^{30}$. In general the estimates are similar in scale. A possible explanation of the apparent trends of decline in capture probabilities over the survey series shown in the model average estimates is given below. Loss rates appear to be lowest during the late summer to autumn period, being highest for the November 2013 to June 2014 interval, possibly indicating higher rates of mortality and/or emigration during winter and/or spring.

Figure 7 also shows comparable estimates of capture probability derived from the depletion model, cumulated over the three dives on each occasion by using Eq. 2. These are consistently higher than the estimates from tag-recapture, by about 22% for scallops <80 mm shell width and 26-27% in larger scallops. Aside from statistical lack of precision in the estimates, there are two likely explanations for this discrepancy. The first possibility is that a proportion of scallops may be effectively invisible to divers on any given survey occasion, so that the depletion capture

probabilities refer only to the non-cryptic portion of the population. Provided that the visibility of individual scallops varies between occasions, the cryptic portion of the population would be 'visible' over the longer term in the tag recaptures. This perhaps also accounts for the trends of decline in capture probability apparent in the model average values from tag recapture, since the opportunity for cryptic scallops to become visible to divers declines as the end of the survey series becomes evident. A second possible explanation, is that the definition of 'population' differs subtly between the depletion and tag recapture experiments: in the depletion experiments, the population is strictly contained within the survey plot, whereas emigrants from this survey plot are visible to the tagging experiment provided that that emigration is temporary. The two explanations, heterogeneity of capture probabilities and temporary emigration, are both plausible and not mutually exclusive. Both point to a possible incompatibility between the population estimates from the depletion experiments and the population dynamics represented by the tag recapture modelling. This incompatibility is explored in the next section, considering spatial and population dynamics at a small spatial scale.

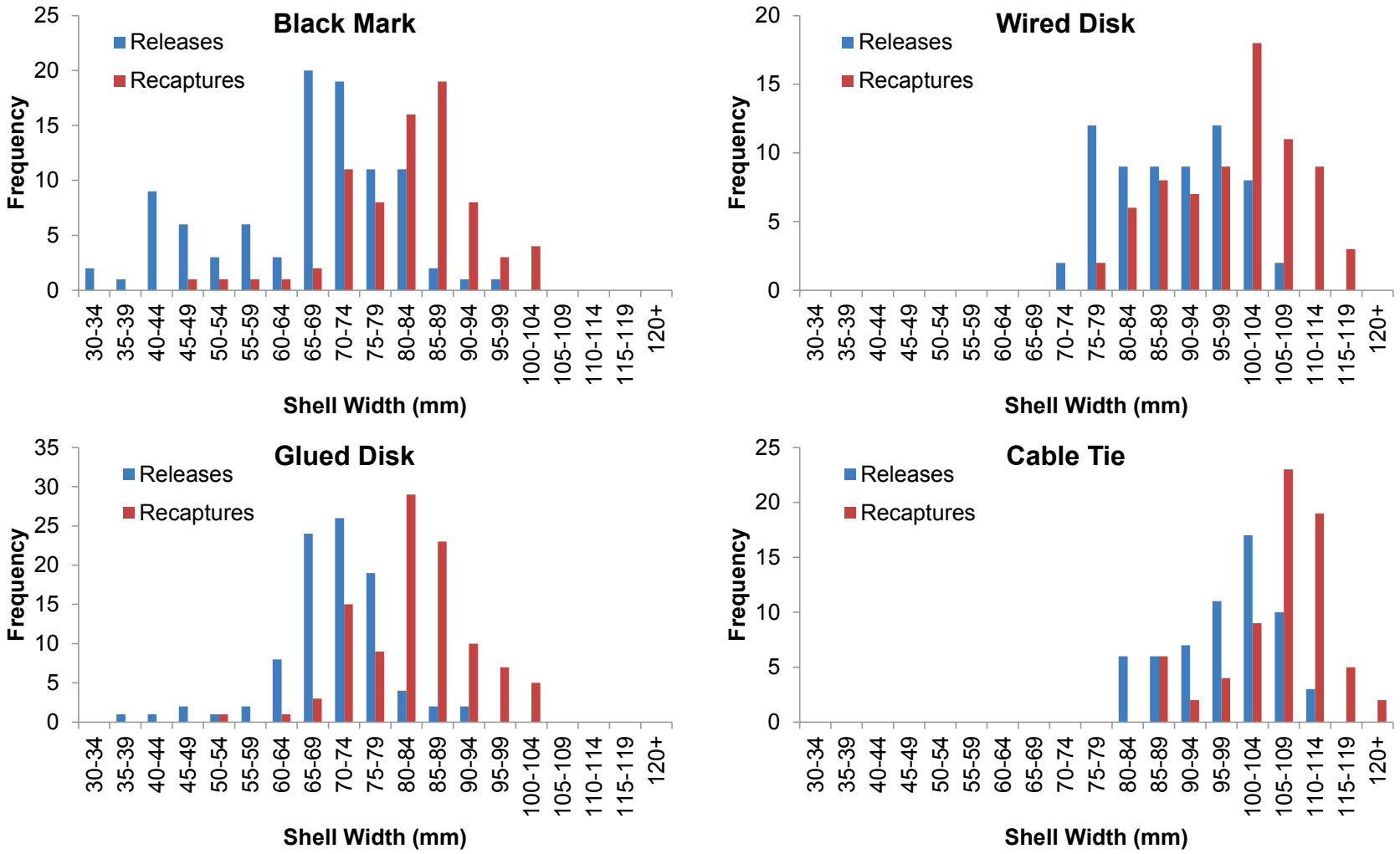

Figure 5: Size-frequency distributions of tag releases and recaptures at Wyre. Note that these data include multiple recaptures of individual tags (see Figure 6) and that growth in shell width occurs between tagging and recapture.

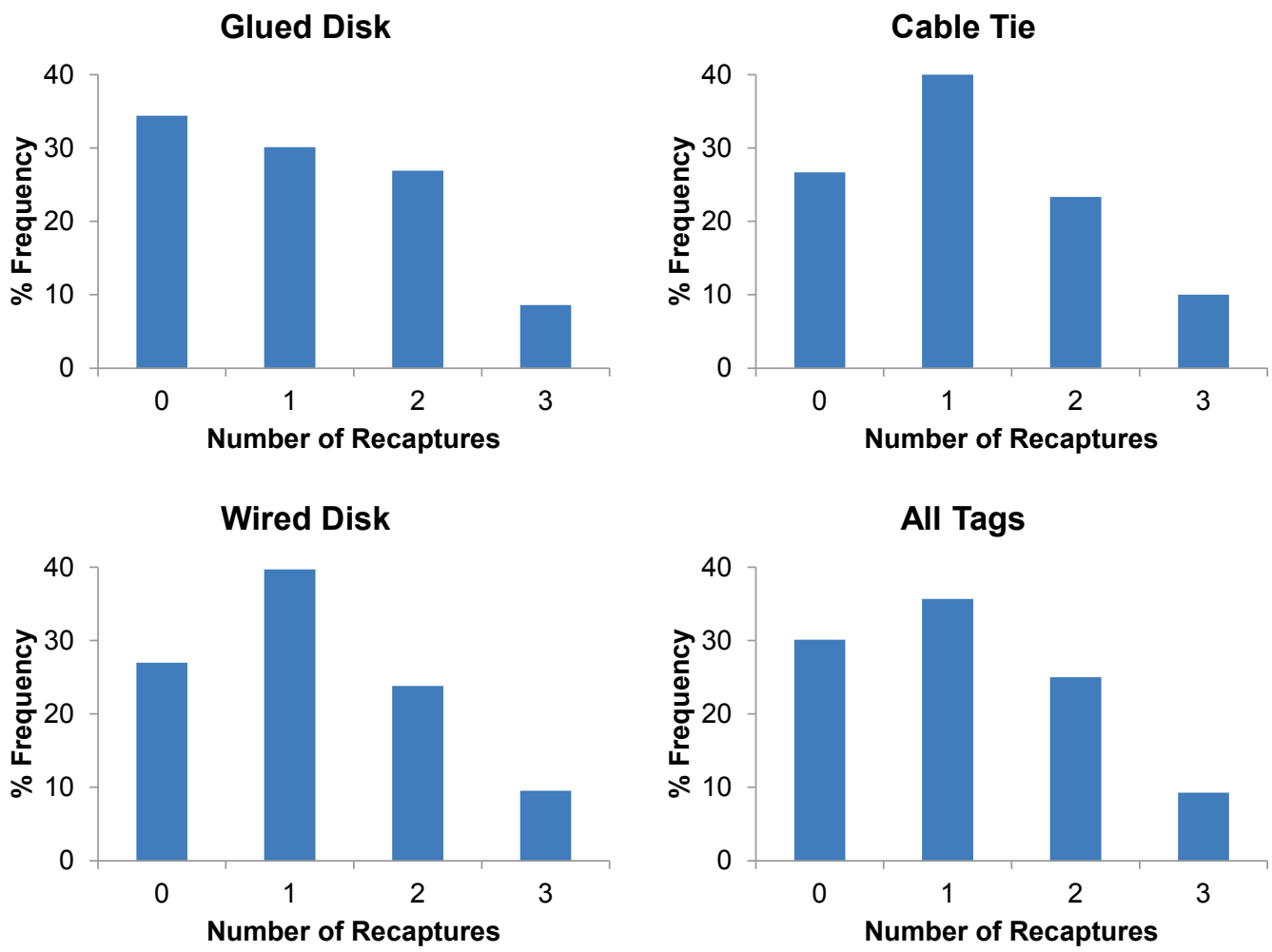

Figure 6: Recapture frequencies for tagged scallops at Wyre.

Table 2

Model selection statistics for maximum likelihood depletion models fitted to scallop catch data for the Wyre depletion site. Capture model defines constraints of capture probability between sampling occasions ('time') and shell width groups ('size'); ln *L* is the log-likelihood of the model; NP is the number of separately identifiable model parameters (before accounting for estimation of a dispersion coefficient); $QAIC_c$ is the quasi-likelihood version of the Akaike Information Criterion, adjusted for small sample size; $QAIC_c$ difference is the difference of model $QAIC_c$ from the minimum value; weight is the relative model probability. The 'best' (smallest value of $QAIC_c$) model for the data is highlighted.

Capture model	ln *L*	NP	$QAIC_c$	$QAIC_c$ difference	Weight
*time * size*	2877.92	29	-1631.70	96.20	0.000
time + size	2858.86	22	-1713.90	13.99	0.001
time	2821.36	20	-1706.53	21.37	0.000
size	**2833.34**	**18**	**-1727.90**	**0**	**0.999**
constant	2786.21	16	-1709.75	18.15	0.000

Table 3

Scallop tag recapture data for the Wyre depletion fishing site, summarised in 'reduced m-array' format. Each row of the table gives numbers from each release cohort first recaptured on each occasion. Release totals for each occasion include re-releases of previously tagged scallops recaptured on that occasion. Re-releases of scallops that had grown between size groups are included in the release totals for the recipient size group.

(a) Shell width <80 mm

		First recaptures				
Occasion	**Releases**	**August 2013**	**October 2013**	**November 2013**	**June 2014**	**Never recaptured**
June 2013	17	13	1	1	0	2
August 2013	60		34	8	0	18
October 2013	41			14	3	24
November 2013	11				0	11

(b) Shell width 80-110 mm

		First recaptures				
Occasion	**Releases**	**August 2013**	**October 2013**	**November 2013**	**June 2014**	**Never recaptured**
June 2013	38	21	5	1	0	11
August 2013	63		43	12	0	8
October 2013	99			69	2	28
November 2013	82				4	78

(c) Shell width >110 mm

Occasion	Releases	First recaptures				Never recaptured
		August 2013	October 2013	November 2013	June 2014	
June 2013	2	2	0	0	0	0
August 2013	4		3	0	0	1
October 2013	13			8	0	5
November 2013	20				1	19

Table 4

Model selection statistics for CJS-type models fitted to scallop tag recapture data for the Wyre depletion fishing site. Survival / fidelity model refers to probabilities of remaining within the survey area; recapture model refers to probability of capture on survey occasions; these probabilities are allowed to vary between occasions (*time*), shell width groups (*size*: <80 mm, 80-110 mm, >110 mm), both (*time * size*), or neither (*constant*). ln *L* is the log-likelihood kernel; NP is the number of separately identifiable model parameters; AIC_c is Akaike Information Criterion, adjusted for sample size; AIC_c difference is the difference of model AIC_c from the minimum value; weight is the relative model likelihood, used as a weight in calculating model average parameter values. The 'best' (smallest value of AIC_c) model for the data is highlighted with yellow shading. Other candidate models (AIC_c differences of around 2 or less) are shown with grey shading.

Survival / Fidelity model	Recapture model	ln *L*	NP	AIC_c	AIC_c difference	Weight
*time * size*	*time * size*	-300.90	21	645.96	10.47	0.002
*time * size*	*time*	-304.28	16	641.82	6.33	0.016
*time * size*	*size*	-303.08	15	637.27	1.78	0.157
*time * size*	*constant*	-305.05	13	636.94	1.44	0.186
time	*time * size*	-303.34	16	639.94	4.44	0.041
time	*time*	-314.19	7	642.63	7.13	0.011
time	***size***	**-310.62**	**7**	**635.49**	**0**	**0.382**
time	*constant*	-315.41	5	640.95	5.46	0.025
size	*time * size*	-305.02	15	641.15	5.66	0.023
size	*time*	-314.48	7	643.21	7.72	0.008
size	*size*	-332.23	6	676.65	41.16	0.000
size	*constant*	-335.15	4	678.39	42.90	0.000
constant	*time * size*	-305.39	13	637.62	2.12	0.132
constant	*time*	-315.74	5	641.61	6.12	0.018
constant	*size*	-334.85	4	677.79	42.30	0.000
constant	*constant*	-336.30	2	676.62	41.13	0.000

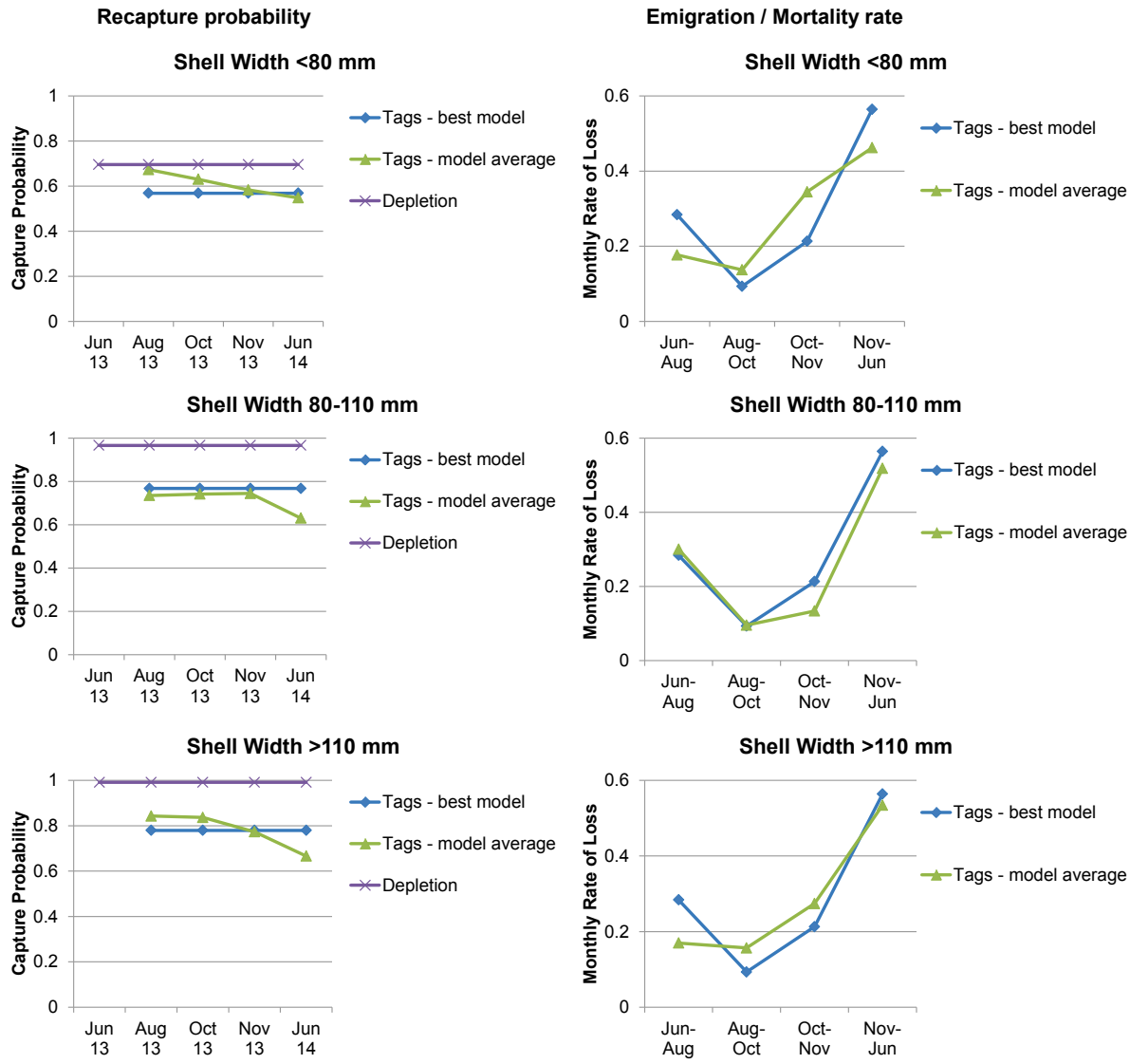

Figure 7: Recapture probabilities and loss rates of scallops at the Wyre depletion fishing site. Left-hand column shows total recapture probability on each occasion, estimated by depletion fishing and by tag recaptures. Right-hand column shows emigration/mortality rates between occasions scaled to 1 month (30 days) estimated by tag recaptures. 'Best model' estimates are from the best fitting model for tag recaptures (*time*-dependent survival/fidelity probabilities, *size*-dependent capture probabilities); 'model average' estimates are weighted averages across tag recapture models, accounting for model uncertainty.

Small Scale Spatial and Population Dynamics

As noted above, it is not possible to distinguish between permanent emigration and mortality in the tag recapture models; both processes are simply modelled (through survival/fidelity probabilities) as permanent losses to the tagged population available to be recaptured within the survey area. An instantaneous natural mortality rate of $M=0.15\ .yr^{-1}$ is assumed in stock assessments of Scottish scallops (Dobby et al., 2012). Assuming that this rate is constant through the year and that it is representative of scallops at Wyre (both are likely to be untrue to some degree, but there is no reasonable basis for alternative assumptions), we can use Eq. 4 and Eq. 5 to obtain separate estimates of emigration probabilities. As can be seen in Table 5, the loss rates modelled using tag recaptures appear to be dominated by emigration rather than mortality – compare values before and after adjustment for mortality between Table 5a and Table 5c, and between Table 5b and Table 5d. In considering small scale population dynamics no adjustment is made for mortality and it is assumed that losses not accounted by growth or fishing removals are due primarily to movements out of the survey area.

Table 5

Scallop emigration/mortality rates for the Wyre depletion fishing site, estimated from tag recaptures. Emigration is separated from mortality in (c) and (d) under an assumed instantaneous annual natural mortality rate of 0.15.

(a) Total emigration/mortality between depletion fishing occasions

	Shell Width		
Interval	**<80 mm**	**80-110 mm**	**>110 mm**
June – August 2013	0.248	0.408	0.239
August – October 2013	0.255	0.182	0.589
October – November 2013	0.447	0.182	0.361
November 2013 – June 2014	0.986	0.994	0.995

(b) Emigration/mortality scaled to monthly (30-day) rates

	Shell Width		
Interval	**<80 mm**	**80-110 mm**	**>110 mm**
June – August 2013	0.177	0.300	0.170
August – October 2013	0.137	0.096	0.157
October – November 2013	0.345	0.134	0.274
November 2013 – June 2014	0.462	0.518	0.534

(c) Assumed total emigration between depletion fishing occasions

	Shell Width		
Interval	**<80 mm**	**80-110 mm**	**>110 mm**
June – August 2013	0.234	0.397	0.225
August – October 2013	0.237	0.162	0.271
October – November 2013	0.437	0.168	0.350
November 2013 – June 2014	0.985	0.993	0.994

(d) Assumed emigration scaled to monthly (30-day) rates

	Shell Width		
Interval	**<80 mm**	**80-110 mm**	**>110 mm**
June – August 2013	0.166	0.292	0.159
August – October 2013	0.126	0.084	0.146
October – November 2013	0.337	0.123	0.265
November 2013 – June 2014	0.455	0.513	0.529

Transitions between size-groups owing to growth are estimated using Eqs. 7 and 8, based on growth between consecutive survey occasions measured in tagged scallops (Figure 8, Table 6). Collecting together these transition probabilities, loss rates between survey occasions estimated from tag recaptures (interpreted as primarily emigration) and population estimates on each survey occasion from the depletion experiments, a complete schedule of movements into and out of the survey area can be constructed based on Eqs. 6, 9, 10 & 11 (Table 7). The main point to note is that, once growth and fishing removals have been accounted for, substantial numbers of scallops are inferred to have been moving into and out of the survey area. A negative estimate of immigration for the largest size-group in October 2013 could be due to unaccounted removals, i.e. unknown fishing activities in the area during the preceding survey interval, but is more likely to be due to a lack of precision in the population dynamic process estimates rather than a process error per se. Table 8 shows a revised population dynamic schedule based on applying tag recapture estimates of capture probability to the catch numbers recorded on each occasion. This addresses the issue of incompatibility of population definition between depletion and tag recapture models. Qualitatively, the conclusions from this revised schedule are the same: substantial turnover of the scallop population at all size-groups relative to the abundance of the population in the survey area. Table 9 aggregates the movement estimates over the size-groups for both versions of the population dynamic schedule, and expresses these in terms of scallop densities.

The main difference between the two schedules is that using the larger estimates of population size from the tag recapture modelling causes estimated numbers of both movers (emigrants and immigrants) and non-movers (residents) to be increased.

Tables 7-9 provide estimates of total population fluxes between survey occasions at the Wyre site. In Tables 10 and 11 the scallop movements are expressed on monthly (30 day) basis, per unit area and per 'head' of population, for schedules based on estimates of population size from depletion modelling and tag recapture modelling respectively. This provides a more readily interpreted basis for comparisons between size groups and survey intervals. Percentages of population present are calculated based on the average of population estimates for the start and end of an interval, having first accounted for fishery removals at the beginning of the interval. Overall, immigration is greater than emigration, compensating for fishery removals. For the smallest size-group, immigration in June 2014 possibly includes a small element of recruitment; this immigration compensates for growth into the next size-group as well as for emigration, which is true also for the 80-110 mm shell width group as well. The final outcome of this analysis is that spatial turnover of scallops at the smallest spatial scale (metres to tens of metres, depending on the directionality of movements in relation to the survey strip) is estimated to have been more than a quarter of the population per month on average, varying over time from about 10-50% of the population. This is based on immigration estimates for overall population numbers estimated by depletion modelling; similar results are obtained based on population numbers estimated by tag recapture modelling, except that the upper limit of turnover is closer to 40%.

Table 6

Transfer rates between scallop size groups due to growth at the Wyre depletion fishing site.

	Shell Width Group Transition	
Interval	**<80 mm to 80-110 mm**	**80-110 mm to >110 mm**
June – August 2013	0.319	0.081
August – October 2013	0.372	0.115
October – November 2013	0.235	0.088
November 2013 – June 2014	0.724	0.253

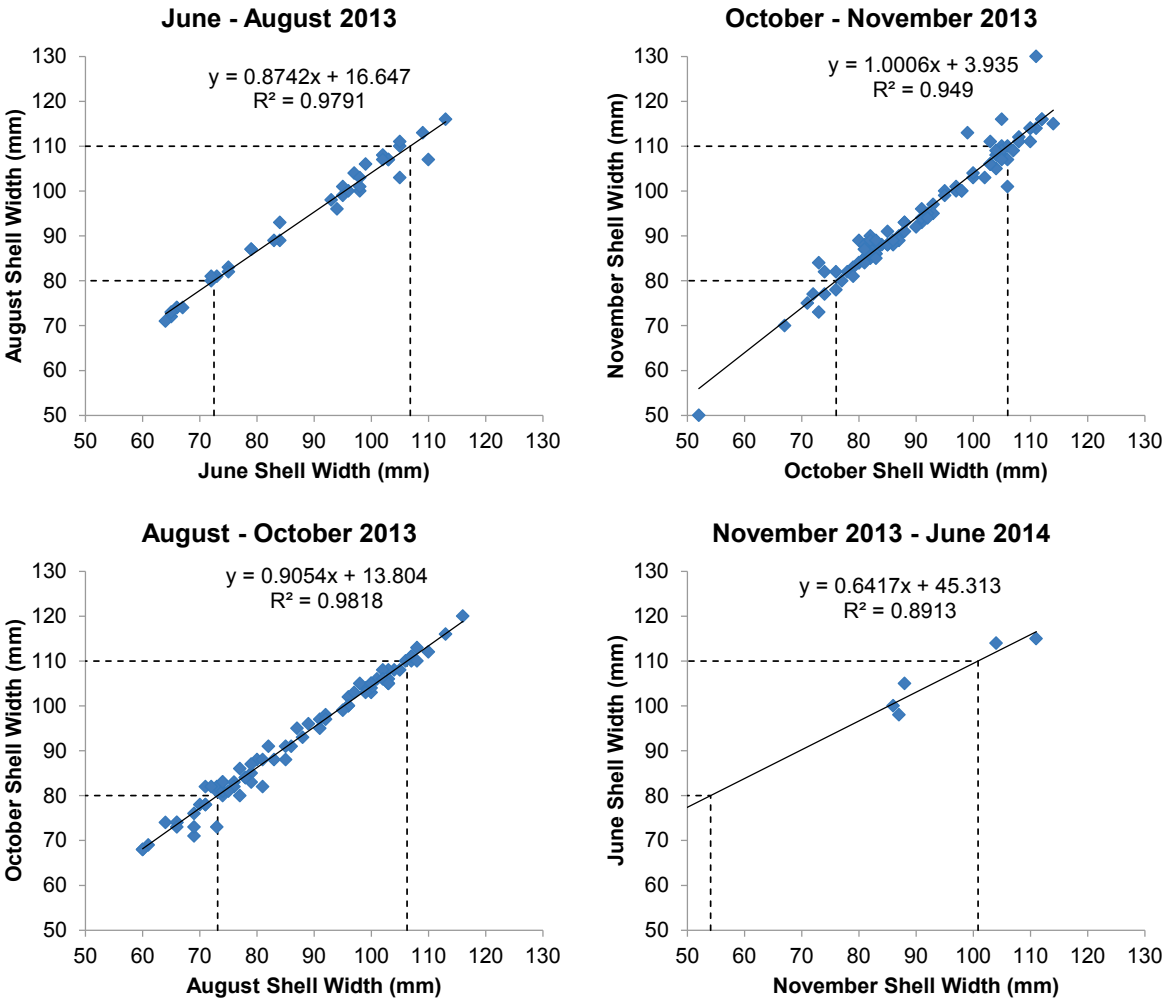

Figure 8: Growth of tagged scallops between depletion fishing occasions at Wyre: relationship of shell width at release (x-axis) and shell width at recapture (y-axis) for consecutive depletion fishing occasions. Dashed lines show the estimated sizes (y-axis) above which scallops released in one size class (<80 mm and 80-110 mm shell width) will have growth to the next size class (80-110 mm and >110 mm shell width, respectively) by the next occasion.

Table 7

Population dynamics schedule for scallops at the Wyre depletion fishing site, based on depletion fishing and tagging data. Population numbers are derived from depletion model with size-dependent recapture probabilities; emigration rates between occasions are derived from model-averaged fidelity values from CJS-type models fitted to tagging data. Note that 'emigration' includes an element of natural mortality. Note also that any apparent mismatch of totals is due to rounding of numbers to integer values.

(a) Shell width <80 mm

		Losses			Gains
Occasion	**Population**	**Emigration**	**Growth**	**Residents**	**Immigration**
June 2013	99	25	24		
August 2013	162	42	45	51	112
October 2013	116	52	15	76	40
November 2013	125	123	1	49	76
June 2014	72			0	71

(b) Shell width 80-110 mm

		Losses				Gains	
Occasion	**Population**	**Emigration**	**Growth**	**Removals**	**Residents**	**Growth**	**Immigration**
June 2013	64	23	3	8			
August 2013	81	15	8	0	31	24	26
October 2013	129	23	9	3	58	45	26
November 2013	173	161	0	11	94	15	63
June 2014	80				1	1	78

(c) Shell width >110 mm

		Losses			Gains	
Occasion	**Population**	**Emigration**	**Removals**	**Residents**	**Growth**	**Immigration**
June 2013	87	1	82			
August 2013	20	6	0	4	3	14
October 2013	17	4	5	14	8	-5
November 2013	41	20	21	8	9	25
June 2014	16			0	0	16

Table 8

Population dynamics schedule for scallops at the Wyre depletion fishing site, based on depletion fishing and tagging data. Population numbers are derived from CJS-type models fitted to tagging data. Note that 'emigration' includes an element of natural mortality. Note also that any apparent mismatch of totals is due to rounding of numbers to integer values.

(a) Shell width <80 mm

		Losses			Gains
Occasion	**Population**	**Emigration**	**Growth**	**Residents**	**Immigration**
June 2013	113	28	27		
August 2013	168	43	46	58	110
October 2013	128	57	17	78	50
November 2013	149	147	1	54	95
June 2014	91			1	91

(b) Shell width 80-110 mm

		Losses				Gains	
Occasion	**Population**	**Emigration**	**Growth**	**Removals**	**Residents**	**Growth**	**Immigration**
June 2013	87	32	4	8			
August 2013	106	19	10	0	43	27	36
October 2013	169	30	12	3	77	46	45
November 2013	224	212	0	11	123	17	84
June 2014	122				1	0	120

(c) Shell width >110 mm

		Losses			Gains	
Occasion	**Population**	**Emigration**	**Removals**	**Residents**	**Growth**	**Immigration**
June 2013	110	7	82			
August 2013	24	7	0	22	4	-2
October 2013	20	6	5	17	10	-7
November 2013	53	32	21	10	12	31
June 2014	24			0	0	23

Table 9

Population dynamic schedule for scallops at the Wyre depletion site, aggregated across size-groups and shown separately for population estimates from depletion modelling and tag recapture modelling.

(a) Numbers based on population estimates from depletion modelling

Occasion	Population	Emigration	Removals	Residents	Immigration
June 2013	250	49	90		
August 2013	263	62	0	85	152
October 2013	263	79	8	149	62
November 2013	339	304	32	151	164
June 2014	168			1	165

(b) Densities $.m^{-2}$ based on population estimates from depletion modelling

Occasion	Population	Emigration	Removals	Residents	Immigration
June 2013	0.351	0.068	0.126		
August 2013	0.370	0.087	0.000	0.119	0.213
October 2013	0.369	0.112	0.011	0.209	0.087
November 2013	0.476	0.427	0.045	0.213	0.230
June 2014	0.236			0.002	0.231

(c) Numbers based on population estimates from tag recapture modelling

Occasion	Population	Emigration	Removals	Residents	Immigration
June 2013	311	67	90		
August 2013	298	69	0	123	144
October 2013	317	93	8	172	89
November 2013	427	391	32	188	210
June 2014	237			2	234

(d) Densities .m^{-2} based on population estimates from tag recapture modelling

Occasion	Population	Emigration	Removals	Residents	Immigration
June 2013	0.436	0.094	0.126		
August 2013	0.418	0.097	0.000	0.172	0.202
October 2013	0.446	0.131	0.011	0.242	0.125
November 2013	0.599	0.549	0.045	0.264	0.295
June 2014	0.436	0.094	0.126		

Table 10

Movements of scallops into and out of the Wyre depletion fishing site, based on population estimates from depletion modelling.

(a) Monthly number of scallops emigrating per m^2

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	0.0236	0.0219	0.0011	0.0466
Aug-Oct 2013	0.0292	0.0103	0.0041	0.0436
Oct-Nov 2013	0.0522	0.0231	0.0044	0.0797
Nov-Jun 2014	0.0251	0.0327	0.0041	0.0620
Average	0.0325	0.0220	0.0034	0.0580

(b) Monthly emigration as percentage of average population present

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	12.8	22.8	6.2	15.7
Aug-Oct 2013	14.9	7.0	15.6	11.8
Oct-Nov 2013	30.8	11.0	11.7	19.1
Nov-Jun 2014	18.2	19.3	16.1	18.6
Average	19.2	15.0	12.4	16.3

(c) Monthly numbers of scallops immigrating per m^2

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	0.1073	0.0249	0.0134	0.1456
Aug-Oct 2013	0.0281	0.0183	-0.0035	0.0428
Oct-Nov 2013	0.0762	0.0632	0.0251	0.1645
Nov-Jun 2014	0.0145	0.0159	0.0033	0.0336
Average	0.0565	0.0360	0.0096	0.0966

(d) Monthly immigration as percentage of average population present

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	58.4	25.9	76.6	48.9
Aug-Oct 2013	14.3	12.4	-13.4	11.6
Oct-Nov 2013	44.9	30.1	66.7	39.4
Nov-Jun 2014	10.4	9.4	12.7	10.1
Average	32.0	19.5	35.7	27.5

Table 11

Movements of scallops into and out of the Wyre depletion fishing site, based on population estimates from tag recapture modelling.

(a) Monthly number of scallops emigrating per m^2

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	0.0269	0.0308	0.0065	0.0642
Aug-Oct 2013	0.0301	0.0136	0.0048	0.0485
Oct-Nov 2013	0.0576	0.0303	0.0056	0.0934
Nov-Jun 2014	0.0300	0.0431	0.0065	0.0796
Average	0.0362	0.0295	0.0059	0.0714

(b) Monthly emigration as percentage of average population present

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	13.6	23.7	17.7	17.6
Aug-Oct 2013	14.5	7.0	15.6	11.2
Oct-Nov 2013	29.5	11.1	11.6	18.1
Nov-Jun 2014	17.7	18.3	16.5	17.9
Average	18.8	15.0	15.4	16.2

(c) Monthly numbers of scallops immigrating per m^2

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	0.1051	0.0344	-0.0015	0.1380
Aug-Oct 2013	0.0351	0.0318	-0.0046	0.0623
Oct-Nov 2013	0.0951	0.0844	0.0314	0.2109
Nov-Jun 2014	0.0185	0.0243	0.0048	0.0476
Average	0.0635	0.0437	0.0075	0.1147

(d) Monthly immigration as percentage of average population present

Interval	<80 mm	80-110 mm	>110 mm	Total
Jun-Aug 2013	53.2	26.5	-4.1	37.9
Aug-Oct 2013	16.9	16.5	-14.9	14.4
Oct-Nov 2013	48.8	30.8	65.5	40.8
Nov-Jun 2014	10.9	10.3	12.2	10.7
Average	32.5	21.0	16.7	26.0

Discussion

It is well known that king scallops are mobile at spatial scales ranging from metres to kilometres (e.g. Baird & Gibson, 1956). In a tagging study in Irish waters, Gibson (1953) recorded movements of up to 1.6 km over a period of about 8 months, but noted that most scallops were recaptured close to their release locations. Such mobility must play an important role in determining the relationship between the stock and any fishery. For a dive fishery, such as that in Orkney waters, which targets small, discrete areas for fishing operations, movements at scales down to tens of metres will affect the likelihood of local depletion, and hence the frequency with which individual areas can be targeted.

To our knowledge, this is the first study that has described patterns of spatial turnover in a scallop population at a small spatial scale. The main finding is that turnover on a strip of ground 178 m by 4 m averaged more than 25% per month over the year, and could be up to 50% per month during the summer months. Even over winter and spring, when lower water temperatures would be expected to reduce swimming activity, turnover rates of around 10% per month were estimated. These rates are taken from estimates of the contributions of immigration to population density at any one time, hence are a fair reflection of the capacity for a ground to be re-stocked. These results suggest that, at least at this small spatial scale, it is possible for a fished ground to be restored to pre-fishing scallop population levels in under a year. This conclusion is, of course, contingent on the existence of undepleted stocks in areas adjacent to the fishing grounds, which is perhaps true only for small fishing patches in a stock which is lightly exploited overall.

Further work is needed to determine the real implications of this scale of movements on the Orkney stock. This includes analysis of data from the wider tagging study in Orkney once sufficient tag returns have been recorded, and also processing and analysis of data from the Scapa Bay and Fara depletion studies, neither of which has yet been possible within the resources available for this study. Some further model development and implementation of a fully integrated tagging and depletion model would be beneficial, although it is perhaps likely that this would not qualitatively change the nature of findings from the study reported here. Beyond these analyses, collection of more comprehensive biological sampling data for Orkney waters would allow inferences about current exploitation rates to be drawn, which would form an important context for interpreting the implications of movements for fishery sustainability.

Acknowledgements

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Appendix 1

A Simple Maximum Likelihood Model for Depletion Fishing

For repeated passes over the same plot the expected catch number on each pass $\hat{C}_i$ is a function of initial population size N and capture probabilities P_i on each occasion (i=1 to np):

$$\hat{C}_i = N\left[\prod_{j=1}^{i-1}\left(1-P_j\right)\right]P_i\,.$$

Assuming a Poisson distribution, the total log-likelihood for catches over the np passes is:

$$l = \sum_{i=1}^{np}\left(C_i \ln \hat{C}_i - \hat{C}_i\right).$$

This model has been implemented in the R statistical package (R Core Team, 2014) using the 'maxLik' library (Henningson & Toomet, 2011) for maximizing this log-likelihood and the 'numDeriv' library (Gilbert & Varadhan, 2012) to estimate numerical gradients and Hessian matrix. Initial population size and capture probabilities are constrained within feasible bounds by logarithmic and logistic transforms respectively. The next page shows an R script for fitting the model to the Wyre depletion data, with capture probability assumed to remain constant between passes. This code allows simultaneous estimation for multiple groups, with between-group constraints on capture probabilities defined through a GLM-like design matrix. Five models are shown defined in the code below:

(i) unconstrained estimation of model parameters separately for each group;

(ii) capture probability constrained to be an additive logistic function of size-group and fishing occasion effects;

(iii) capture probability constrained to be the same in each size-group but differing between occasions;

(iv) capture probability constrained to be the same on each occasion, but differing between size-groups; and

(v) capture probability constrained to be constant across occasions and size-groups.

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R Script for Defining and Fitting Maximum Likelihood Depletion Models

```
##-----------------------------------------------------------------
## MAXIMUM-LIKELIHOOD DEPLETION MODEL
##-----------------------------------------------------------------

require(MASS)     ## for generalized inverse function, ginv()
require(Matrix)   ## for rankMatrix() function
require(maxLik)   ## maximum likelihood estimation
require(numDeriv) ## numerical derivatives for gradient & Hessian
## N.B. numDeriv must be loaded AFTER maxLik so that hessian
## function from maxLik is masked by that from numDeriv rather
## than vice versa

##-----------------------------------------------------------------
## POISSON LOG-LIKELIHOOD FUNCTION FOR A DEPLETION MODEL
##   p[npp+ng] is the estimated parameter vector
##   C[nr] is the catch vector
##   Pdesign[nr,npp] is the design matrix for P parameters
##   gt[nr,2] gives group and time qualifiers
##   npp is the number of P parameters in the estimated vector
##   nr is the number of data rows
##   ng is the number of groups (populations)
##   ntmax is the maximum number of passes for any population
##-----------------------------------------------------------------
loglikDeplete<-function(p,C,Pdesign,gt,npp,nr,ng,ntmax)
{
  ##Extract P from estimated parameters
  P<-matrix(nrow=ng,ncol=ntmax)
  for(i in 1:nr) {
    g<-gt[i,1]
    t<-gt[i,2]
    P[g,t]<-0
    for(j in 1:npp) {
      P[g,t]<-P[g,t]+Pdesign[i,j]*p[j]
    }
    P[g,t]<-1/(1+exp(-P[g,t]))
  }

  ## Extract N from estimated parameters
  N<-vector(length=ng)
  for(i in 1:ng) {
    N[i]<-exp(p[npp+i])
  }

  ## form log-likelihood
  LL<-0
  for(i in 1:nr) {
    g<-gt[i,1]
    t<-gt[i,2]
    nj<-t-1
    Pprod<-1
    if(nj>0){
      for(j in 1:nj) {
        Pprod<-Pprod*(1-P[g,j])
      }
    }
    Cfit<-N[g]*Pprod*P[g,t]
    LL<-LL+C[i]*log(Cfit)-Cfit
  }
```

```
  return(LL)
}

##-----------------------------------------------------------------
## CALCULATE FITTED VALUES
##   Same calculations as loglikDeplete, but returns fitted
##   values of catch numbers rather than log-likelihood
##-----------------------------------------------------------------
calcFit<-function(p,C,Pdesign,gt,npp,nr,ng,ntmax)
{
  ##Extract P from estimated parameters
  P<-matrix(nrow=ng,ncol=ntmax)
  for(i in 1:nr) {
    g<-gt[i,1]
    t<-gt[i,2]
    P[g,t]<-0
    for(j in 1:npp) {
      P[g,t]<-P[g,t]+Pdesign[i,j]*p[j]
    }
    P[g,t]<-1/(1+exp(-P[g,t]))
  }

  ## Extract N from estimated parameters
  N<-vector(length=ng)
  for(i in 1:ng) {
    N[i]<-exp(p[npp+i])
  }

  ## form log-likelihood
  Cfit<-vector(length=nr)
  for(i in 1:nr) {
    g<-gt[i,1]
    t<-gt[i,2]
    nj<-t-1
    Pprod<-1
    if(nj>0){
      for(j in 1:nj) {
        Pprod<-Pprod*(1-P[g,j])
      }
    }
    Cfit[i]<-N[g]*Pprod*P[g,t]
  }
  return(Cfit)
}

##-----------------------------------------------------------------
## NUMERICAL GRADIENT OF THE LOG-LIKELIHOOD
##-----------------------------------------------------------------
gradDeplete<-function(p,C,Pdesign,gt,npp,nr,ng,ntmax)
{
  g<-grad(loglikDeplete,p,C=C,Pdesign=Pdesign,gt=gt,npp=npp,
                          nr=nr,ng=ng,ntmax=ntmax)
  return(g)
}

##-----------------------------------------------------------------
## NUMERICAL HESSIAN OF THE LOG-LIKELIHOOD
##-----------------------------------------------------------------
hessDeplete<-function(p,C,Pdesign,gt,npp,nr,ng,ntmax)
{
  h<-hessian(loglikDeplete,p,C=C,Pdesign=Pdesign,gt=gt,npp=npp,
```

```
                          nr=nr,ng=ng,ntmax=ntmax)
  return(h)
}

##-----------------------------------------------------------------
## FIT THE DEPLETION MODEL BY MAXIMUM LIKELIHOOD
##   Returns dmod as object of class maxLike (estimated parameters
##                          are returned as component dmod$estimate)
##   Returns var as covariance matrix
##   Returns se as vector of standard errors for model parameters
##   Returns NP as number of identifiable model parameters
##   Returns AIC as Akaike Information Criterion
##   Returns AICc as small sample AIC
##-----------------------------------------------------------------
FitDeplete<-function(p,C,Pdesign,gt,npp,nr,ng,ntmax)
{
  ## Fit the model
  dmod<-maxLik(loglikDeplete,grad=gradDeplete,hess=hessDeplete,
               start=p,method="BFGS",
               C=C,Pdesign=Pdesign,gt=gt,npp=npp,nr=nr,ng=ng,
               ntmax=ntmax)

  ## Get model fit statistics
  var<-ginv(-dmod$hessian)
  se<-sqrt(diag(var))
  NP<-rankMatrix(dmod$hessian,method="maybeGrad")
  attributes(NP)<-NULL ## strip the object down to a value
  AIC<-(-2*dmod$maximum)+2*NP
  AICc<-AIC+2*NP*(NP+1)/(length(C)-NP-1)

  ## Extract logit(P) estimates and SEs
  logitP<-vector(length=nr)
  SElogitP<-vector(length=nr)
  for(i in 1:nr) {
    g<-gt[i,1]
    t<-gt[i,2]
    logitP[i]<-0
    SElogitP[i]<-0
    for(j in 1:npp) {
      logitP[i]<-logitP[i]+Pdesign[i,j]*dmod$estimate[j]
      for(k in 1:npp) {
        SElogitP[i]<-SElogitP[i]+Pdesign[i,j]*Pdesign[i,k]*var[j,k]
      }
    }
    SElogitP[i]<-sqrt(SElogitP[i])
  }

  ## Extract log(N) estimates and SEs
  logN<-vector(length=ng)
  SElogN<-vector(length=ng)
  for(i in 1:ng) {
    logN[i]<-dmod$estimate[npp+i]
    SElogN[i]<-se[npp+i]
  }

  ## Get the model deviance
  LLsaturated<-0
  for(i in 1:nr) {
    if(C[i]>0) {
      LLsaturated<-LLsaturated+C[i]*log(C[i])-C[i]
    }
```

```
  }
  deviance<-2*LLsaturated-2*dmod$maximum

  ## Get the model fit
  Cfit<-vector(length=nr)
  Cfit<-calcFit(p=dmod$estimate,C=C,Pdesign=Pdesign,gt=gt,npp=npp,
                nr=nr,ng=ng,ntmax=ntmax)

  return(list(dmod=dmod,var=var,se=se,logitP=logitP,
              SElogitP=SElogitP,logN=logN,SElogN=SElogN,
              NP=NP,AIC=AIC,AICc=AICc,deviance=deviance,
              Cfit=Cfit))
}

##-----------------------------------------------------------------
## DATA FOR WYRE EXPERIMENT

ng<-15   ## 5 occasions x 3 size groups
nr<-45   ## 15 groups x 3 passes per group
ntmax<-3 ## maximum of 3 passes

## Catch vector
C<-as.vector(c(41,15,13,
               56,6,0,
               76,6,4,
               47,32,34,
               53,15,10,
               8,12,0,
               57,21,3,
               94,27,4,
               11,5,1,
               32,30,25,
               112,43,12,
               39,1,1,
               10,31,9,
               43,22,12,
               12,2,2),
               mode="numeric")
## Group and time qualifiers
gt<-matrix(c(1,1,
             1,2,
             1,3,
             2,1,
             2,2,
             2,3,
             3,1,
             3,2,
             3,3,
             4,1,
             4,2,
             4,3,
             5,1,
             5,2,
             5,3,
             6,1,
             6,2,
             6,3,
             7,1,
             7,2,
             7,3,
             8,1,
```

```
              8,2,
              8,3,
              9,1,
              9,2,
              9,3,
              10,1,
              10,2,
              10,3,
              11,1,
              11,2,
              11,3,
              12,1,
              12,2,
              12,3,
              13,1,
              13,2,
              13,3,
              14,1,
              14,2,
              14,3,
              15,1,
              15,2,
              15,3),
            nrow=nr,ncol=2,byrow=TRUE)

##-------------------------------------------------------------------
## SET UP MODEL STRUCTURES - Size Group * Occasion

npp=15 ## P parameters for 15 populations

## Initial values for parameter estimates
##   first 15 are logit(P), next 15 are log(N)
p<-as.vector(c(rep(0,15),rep(4,15)))

## Design matrix mapping estimated to structural parameters
Pdesign<-matrix(c(1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
                  1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
                  1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
                  0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,
                  0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,
                  0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,
                  0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,
                  0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,
                  0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,
                  0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,
                  0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,
                  0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,
                  0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,
                  0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,
                  0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,
                  0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,
                  0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,
                  0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,
                  0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,
                  0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,
                  0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,
                  0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,
                  0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,
                  0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,
                  0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,
                  0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,
                  0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,
                  0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,
                  0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,
                  0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,
                  0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,
                  0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,
                  0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,
                  0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,
                  0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,
                  0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,
                  0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,
                  0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,
                  0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,
                  0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,
                  0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,
                  0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,
                  0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
                  0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
                  0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
```

```
                    0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,
                    0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,
                    0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,
                    0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,
                    0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,
                    0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,
                    0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,
                    0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,
                    0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,
                    0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,
                    0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,
                    0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,
                    0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,
                    0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,
                    0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,
                    0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
                    0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
                    0,0,0,0,0,0,0,0,0,0,0,0,0,0,1),
                nrow=nr,ncol=npp,byrow=TRUE)

##-------------------------------------------------------------------
## RUN THE MODEL - Size Group * Occasion
DM1<-FitDeplete(p,C,Pdesign,gt,npp,nr,ng,ntmax)

##-------------------------------------------------------------------
## SET UP MODEL STRUCTURES - Size Group + Occasion

npp=7 ## P parameters

## Initial values for parameter estimates
##   first 7 are logit(P), next 15 are log(N)
p<-as.vector(c(rep(0,7),rep(4,15)))

## Design matrix mapping estimated to structural parameters

Pdesign<-matrix(c(1,0,0,0,0,0,0,
                  1,0,0,0,0,0,0,
                  1,0,0,0,0,0,0,
                  1,0,0,0,0,1,0,
                  1,0,0,0,0,1,0,
                  1,0,0,0,0,1,0,
                  1,0,0,0,0,0,1,
                  1,0,0,0,0,0,1,
                  1,0,0,0,0,0,1,
                  0,1,0,0,0,0,0,
                  0,1,0,0,0,0,0,
                  0,1,0,0,0,0,0,
                  0,1,0,0,0,1,0,
                  0,1,0,0,0,1,0,
                  0,1,0,0,0,1,0,
                  0,1,0,0,0,0,1,
                  0,1,0,0,0,0,1,
                  0,1,0,0,0,0,1,
                  0,0,1,0,0,0,0,
                  0,0,1,0,0,0,0,
                  0,0,1,0,0,0,0,
                  0,0,1,0,0,1,0,
                  0,0,1,0,0,1,0,
                  0,0,1,0,0,1,0,
                  0,0,1,0,0,0,1,
```

```
                    0,0,1,0,0,0,1,
                    0,0,1,0,0,0,1,
                    0,0,0,1,0,0,0,
                    0,0,0,1,0,0,0,
                    0,0,0,1,0,0,0,
                    0,0,0,1,0,1,0,
                    0,0,0,1,0,1,0,
                    0,0,0,1,0,1,0,
                    0,0,0,1,0,0,1,
                    0,0,0,1,0,0,1,
                    0,0,0,1,0,0,1,
                    0,0,0,0,1,0,0,
                    0,0,0,0,1,0,0,
                    0,0,0,0,1,0,0,
                    0,0,0,0,1,1,0,
                    0,0,0,0,1,1,0,
                    0,0,0,0,1,1,0,
                    0,0,0,0,1,0,1,
                    0,0,0,0,1,0,1,
                    0,0,0,0,1,0,1),
                nrow=nr,ncol=npp,byrow=TRUE)

##-------------------------------------------------------------------
## RUN THE MODEL - Size Group + Occasion
DM2<-FitDeplete(p,C,Pdesign,gt,npp,nr,ng,ntmax)

##-------------------------------------------------------------------
## SET UP MODEL STRUCTURES - Occasion

npp=5 ## P parameters

## Initial values for parameter estimates
##   first 5 are logit(P), next 15 are log(N)
p<-as.vector(c(rep(0,5),rep(4,15)))

## Design matrix mapping estimated to structural parameters

Pdesign<-matrix(c(1,0,0,0,0,
                  1,0,0,0,0,
                  1,0,0,0,0,
                  1,0,0,0,0,
                  1,0,0,0,0,
                  1,0,0,0,0,
                  1,0,0,0,0,
                  1,0,0,0,0,
                  0,1,0,0,0,
                  0,1,0,0,0,
                  0,1,0,0,0,
                  0,1,0,0,0,
                  0,1,0,0,0,
                  0,1,0,0,0,
                  0,1,0,0,0,
                  0,1,0,0,0,
                  0,0,1,0,0,
                  0,0,1,0,0,
                  0,0,1,0,0,
                  0,0,1,0,0,
                  0,0,1,0,0,
                  0,0,1,0,0,
```

```
                    0,0,1,0,0,
                    0,0,1,0,0,
                    0,0,1,0,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,1,0,
                    0,0,0,0,1,
                    0,0,0,0,1,
                    0,0,0,0,1,
                    0,0,0,0,1,
                    0,0,0,0,1,
                    0,0,0,0,1,
                    0,0,0,0,1,
                    0,0,0,0,1),
                nrow=nr,ncol=npp,byrow=TRUE)

##------------------------------------------------------------------
## RUN THE MODEL - Occasion
DM3<-FitDeplete(p,C,Pdesign,gt,npp,nr,ng,ntmax)

##------------------------------------------------------------------
## SET UP MODEL STRUCTURES - Size Group

npp=3 ## P parameters

## Initial values for parameter estimates
##   first 3 are logit(P), next 15 are log(N)
p<-as.vector(c(rep(0,3),rep(4,15)))

## Design matrix mapping estimated to structural parameters

Pdesign<-matrix(c(1,0,0,
                  1,0,0,
                  1,0,0,
                  0,1,0,
                  0,1,0,
                  0,1,0,
                  0,0,1,
                  0,0,1,
                  0,0,1,
                  1,0,0,
                  1,0,0,
                  1,0,0,
                  0,1,0,
                  0,1,0,
                  0,1,0,
                  0,0,1,
                  0,0,1,
                  0,0,1,
                  1,0,0,
                  1,0,0,
                  1,0,0,
                  0,1,0,
                  0,1,0,
```

```
                   0,1,0,
                   0,0,1,
                   0,0,1,
                   0,0,1,
                   1,0,0,
                   1,0,0,
                   1,0,0,
                   0,1,0,
                   0,1,0,
                   0,1,0,
                   0,0,1,
                   0,0,1,
                   0,0,1,
                   1,0,0,
                   1,0,0,
                   1,0,0,
                   0,1,0,
                   0,1,0,
                   0,1,0,
                   0,0,1,
                   0,0,1,
                   0,0,1),
                 nrow=nr,ncol=npp,byrow=TRUE)

##------------------------------------------------------------------
## RUN THE MODEL - Size Group
DM4<-FitDeplete(p,C,Pdesign,gt,npp,nr,ng,ntmax)

##------------------------------------------------------------------
## SET UP MODEL STRUCTURES - Constant P

npp=1 ## P parameters

## Initial values for parameter estimates
##   first 1 is logit(P), next 15 are log(N)
p<-as.vector(c(0,rep(4,15)))

## Design matrix mapping estimated to structural parameters

Pdesign<-matrix(c(rep(1,45)),
                nrow=nr,ncol=npp,byrow=TRUE)

##------------------------------------------------------------------
## RUN THE MODEL - Constant P
DM5<-FitDeplete(p,C,Pdesign,gt,npp,nr,ng,ntmax)
```

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