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International Council for the  
Exploration of the Sea

CM 2000/N:11 Paper  
Spatial and Temporal  
Patterns in Recruitment  
Processes

## **MODELLING THE SPATIAL AND TEMPORAL STRUCTURE OF SURVIVORSHIP TO SETTLEMENT IN NORTH SEA AND WEST OF SCOTLAND HADDOCK**

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### **ABSTRACT**

Haddock spawn over a wide area of the northern North Sea and west of Scotland and the eggs and larvae experience a range of oceanographic environments during their pelagic phase. These have the potential to generate both spatial and temporal patterns in pelagic survivorship. In addition, the patterns of spawning intensity and dispersal act to precondition the population surviving to the end of the pelagic phase for competition during settlement. Settlement appears to be the main density dependent stage during the recruitment of haddock. These processes have been incorporated into a spatially resolved, individual based model of haddock early life history. Here, we present analysis of results from the model, showing the effects of spawning stock size on the spatial and temporal patterns in survivorship to various developmental stages.

### **INTRODUCTION**

Analytical relationships between spawning stock abundance and recruitment are fundamental to forecasts of the likely state of fish populations under different exploitation scenarios. These relationships are usually parameterised by statistical fitting to paired population level estimates of spawning stock abundance and recruitment from assessment time series. Typically, these models provide a rather poor fit to the data, and the large residuals lead to wide confidence intervals around forecasts. Any elaboration of either the models or the data which reduce these residuals is therefore of potential benefit. Efforts along these lines have included the incorporation of environmental data, or information on the age structure of the spawning stock where these explain a significant proportion of the residual variance (Anon, 2000; Marshall *et al.*, 1998; Marteinsdottir and Thorarinsson, 1998).

The simple equations describing the commonly applied stock-recruitment relationships belie the complexity of the underlying processes. The link between abundance of spawning fish in a population and the number of progeny which survive in a given year must involve a complex sequence of diverse physical and biological processes. Laboratory and field studies of behaviour, dispersal, growth and survival of fish eggs and larvae have exposed details of many of these processes, but integrating these across space and time to derive the whole-population response of recruitment has proven extremely difficult. Until we can find a tractable methodology for achieving this, the scope for incorporating physical and biological process knowledge into the stock assessment and forecast procedure will remain extremely limited.

An underlying assumption of most analytical stock-recruitment models is that all eggs produced by the spawning stock have an equal probability of survival. It is increasingly apparent that this assumption is at odds with our understanding of the processes contributing to the establishment of recruitment (Heath and Gallego, 1997). For example, eggs from fish of different ages and sizes, and from different parts of the spawning season vary systematically in size and viability. Spatial and temporal patterns of egg and larval development and growth also imply spatial and temporal structure in survival probability. One of the key requirements, therefore, of any new approach to relating recruitment to spawning stock abundance must be to incorporate into models some representation of the relative contributions of different spatial, temporal, and parental age and size components of the annual egg production to the surviving population of recruits.

In this paper we describe the application of an individual based modelling approach to investigating the underlying structure of the recruitment process, and ultimately deriving holistic relationships between whole-population stock and recruitment which have a sound, process orientated basis. As in a previous publication (Heath and Gallego, 1998), we have adopted a particle tracking scheme coupled to output from a hydrodynamic model to simulate the spatial and temporal patterns of dispersal and environmental conditions experienced by the eggs and larvae, and incorporated biological processes into the individual particles. The new development described here is the implementation of direct interactions between particles to simulate the density dependent survival during the transition from pelagic to demersal stages in haddock.

## MODEL DESCRIPTION

### Overview

The model comprised four components integrated into a single system:

- Egg production model
- Dispersal model
- Egg and larval development and mortality model
- Demersal carrying capacity model
- Settlement model

The egg production, dispersal, and development and mortality components have been described previously (Heath and Gallego, 1998). These aspects are only briefly described here, noting any minor variations from the published version. The settlement component is described in more detail below.

The basis of the whole system was a particle tracking scheme in which the trajectories of particles through space and time were simulated using data from a circulation model of the northeast Atlantic. Each particle represented a cluster of identical individuals, each having the same growth rate and mortality probability. Particles began their trajectories at specific locations and dates representing newly spawned eggs. During the subsequent simulated drift of the particles, the model derived the progressive development of the eggs, hatching, and growth of the larvae. At the same time, the number of individuals in each particle declined through mortality. At a defined body size, the surviving individuals began to attempt settlement, at which point there was a competition between particles for space on the seabed at their simulated locations.

The initial number of newly spawned eggs in each particle was set by the output from an egg production model, which simulated daily egg production as a function of time and space.

Egg development and larval growth were represented by temperature dependent functions, with the temporal variations in temperature along each particle track being derived from a space-time model of water temperature. Instantaneous daily mortality rate was a function of body size, so that survival over some interval of size was dependent solely on growth history.

## **Egg Production**

The egg production model was as described by Heath and Gallego (1998). The starting point for the model was the observation of Hislop (1988) that the relative fecundity (eggs  $g^{-1}$ ) of first-time spawning haddock (two years old) is approximately half that of repeat spawners (three years and older). Since a high proportion of the haddock spawning stock is composed of two year old fish, it was clearly important that any model should reflect the age structure of the stock. The spatial element of the model was derived from trawl survey data describing the relative spatial distribution of fish by age class, and stock assessment data documenting the total abundance of age classes. The temporal element was derived from a normal distribution representing the spawning fraction of female fish of each age class, parameterised from data collected during a field survey in April 1992. The magnitude of daily egg production by each age class was taken from the annual relative fecundity (Hislop, 1988), mean weight at age from stock assessment data, and an estimate of the spawning duration for individual fish. The principal assumptions of the model were that:

- all of the potential annual fecundity is realised;
- a constant fraction of the annual fecundity is spawned per day during the spawning period of individual fish;
- the proportion of spawning females of a given age class in the population can be described by a normal distribution centred on the date of peak spawning.

The spatial resolution of the egg production model was dictated by the trawl survey data which were available on a 30' latitude x 60' longitude grid (approximately 55 km x 55 km). As described by Heath and Gallego (1998), data from 1989 and 1990 were combined to define the relative spatial distributions (proportion of whole population per spatial grid cell) of 2 and 3+ year old haddock. The whole stock numbers at age were then allocated to spatial grid cells according to these relative distributions, and the time dependent egg production calculated at daily intervals from day 45 (14 February) to day 126 (6 May) for each spatial grid cell. These values were stored, and transferred to the particle tracking component of the model system.

## Particle Tracking

The particle tracking component of the system followed similar methodology to that described by Gallego *et al.* (1999a,d). The trajectories of neutrally buoyant zero drag particles held at a constant depth (30 m) was simulated using a daily sequence of flowfields for the region derived from a hydrodynamic model. In this study, no ontogenetic or temporal changes in the vertical distributions of particles were implemented, although such options are available in the model code. Particles were launched from the centres of 141 of the grid cells in the egg production model, on each day between 14 February (day 45) and 6 May (day 126). Tracking continued until day 240 (28 August) unless terminated for some reasons such as extinction through mortality (see below) or being carried out of the boundary of the model domain.

Very briefly, flowfields for the model area were generated by the Hamburg Shelf Ocean Model (HAMSOM; Backhaus and Hainbucher, 1987; Stronach *et al.*, 1993). Eight quasi-stationary seasonal flowfields (*sensu* Hainbucher and Backhaus, 1999) were used, corresponding to the winter and spring seasons and wind forcing of constant speed ( $8 \text{ m s}^{-1}$ ) and four constant directions (northwest, northeast, southeast and southwest, respectively). Daily averages of wind speed and direction, calculated from data recorded during 1996 at the Fair Isle weather station ( $59^{\circ}32'N$ ,  $1^{\circ}38'W$ ; D. Wheeler, Fair Isle, Shetland, Scotland, pers. comm.), were used to assemble a time series of individual flowfields from the hydrodynamic model (see Gallego *et al.*, 1999a). A smooth transition between consecutive wind periods was achieved by linear interpolation between seasonally interpolated flowfields over a period of 48 h.

Sea water temperature data in the surface layers (20-40 m), collected in the course of a series of surveys in the model area in 1996 were gridded and linearly interpolated within the area common to all surveys, in order to generate time-resolved (daily) temperature fields. Outside the common area, a re-parameterised warming rate regression model similar to that presented by Heath and Gallego (1997) was used. Beyond 21 June, a uniform warming rate was prescribed over the whole model domain. Temperature histories of individual particles were then estimated by projecting their geographical trajectories onto these daily temperature fields.

## Development and Mortality

Egg development rate was temperature dependent and egg mortality rate was defined as a constant, as specified by Heath and Gallego (1998). Larval growth in length was a function of age and the temperature history of the particles (Gallego *et al.*, 1999c). Larval mortality rates decreased exponentially with body weight, weight and length being linked by a constant relationship (Heath and Gallego, 1998). The number of individuals in each particle was decreased at each time step (1 h) to reflect the mortality rate appropriate to the current size of the larvae.

## Demersal carrying capacity and settlement

The settlement model was designed to represent the transition from the pelagic to demersal phase in the early life of haddock, with an associated density dependent mortality. The criteria governing the onset of settlement behaviour are not known, but body size seems to be a key factor. In this model, larvae began searching for suitable settlement conditions on the seabed on attaining a length of 35 mm.

The critical functionality of the settlement model, which introduced a density dependent mortality effect, was competition for available space on the seabed. In this version of the model, the suitability of the seabed habitat for settlement was defined solely in terms of water depth. A carrying capacity was defined for each cell in a matrix covering the model domain, with latitude and longitude resolution equal to that of the grid used in the egg production model ( $1^\circ$  longitude x  $0.5^\circ$  latitude). On this basis, three parameters were required to define the carrying capacity: maximum permissible number of settled individuals/unit area of seabed, minimum water depth for settlement, and maximum water depth for settlement. In this case, the maximum and minimum depths for settlement were set at 300 m and 5 m, based on trawl survey. The maximum permissible number per unit area was adjusted as described later to balance the survival rate during the pelagic stages of the model. Within each grid cell, the seabed area falling within the allowable depth range, and hence the maximum allowable number of settled individuals per grid cell, was estimated from a  $0.25^\circ$  longitude x  $0.125^\circ$  latitude resolution bathymetric dataset.

Once drifting particles attained the threshold body size for settlement, they were programmed to search for free carrying capacity on the seabed grid cell beneath their current location. If sufficient free capacity was found to accommodate all of the individual in all of the particles seeking to settle on a given time step, then those particles were anchored at their current locations for the remainder of the model run, and the individuals they represented continued to grow and suffer mortality. If the carrying capacity in the grid cell was zero or was already fully occupied by settled particles, then the incoming particles continued to drift. If the free capacity was sufficient to meet only part of the demands of particles seeking to settle, then the available capacity was divided up between the competing particles, and the appropriate number of individuals per particle allowed to settle. The individuals which could not be accommodated on the seabed at that time step and location were relaunched as new particles and continued attempting to settle. Particles in which the individuals attained the maximum allowable size for a pelagic stage (45 mm) without achieving settlement, were terminated.

### **Strategy For Use Of The Model**

The aim of this study was to investigate the scope for spatial and temporal patterns in survival, and in particular the sensitivity of these patterns to spawning stock abundance through the action of the density dependent survival phase. Thus, the model was used strategically, rather than in a way which could allow formal testing against observations.

The model was run with a range of different spawning stock abundances in the egg production model (10, 50, 100, 200, 400 and 600 kT), keeping all other features constant, in particular:

- Relative spatial distribution of spawning age groups from 1989/1990 trawl surveys;
- Relative fecundity and spawning time parameters as in Heath and Gallego (1998);
- Mean weight per individual of spawning age groups as in Heath and Gallego (1998);
- Total mature stock biomass of two year old fish equal to that of 3+ year old fish;
- Hydrodynamic model data, and water temperature simulation for 1996;
- Parameterisation of larval growth rates based on sampling in 1996 (Gallego *et al.*, 1999c);
- Parameterisation of size dependent mortality rate as in Heath and Gallego (1998);
- Demersal carrying capacity parameters selected as described below.

## RESULTS

### **Spatially Integrated Model Results**

Spatial integration of the simulated abundance of individuals on a particular date provided a synopsis of the year class abundance and stage composition at that time. For example, the integrated abundance of settled juveniles on the last day of the simulation (28 August) should represent an index of the simulated recruitment arising from the annual egg production, since almost all of the pelagic stage particles had either settled or died by that date. Analysis of the sensitivity of such an index to the biological parameters of the model, and to the hydrodynamic and temperature conditions, is one of the main reasons for engaging in this study. However, only a brief analysis of this sensitivity is presented here since the focus of this paper is on the simulated spatial and temporal patterns of survival.

For a given hydrodynamic, temperature and biological configuration, the model should generate an asymptotic relationship between the magnitude of annual egg production and the abundance of surviving demersal juveniles at some date as a direct consequence of the functionality built into the model. The form of this relationship should be analogous to a conventional Beverton and Holt type stock-recruitment relationship. The two descriptive parameters of such a relationship are the saturated level of recruitment at high spawning stock abundance, and the maximum rate of recruitment (recruits per egg) close to the origin where density dependence is ineffective.

The model did indeed reproduce the above form of relationship between egg production and the abundance of surviving demersal juveniles on day 240. A very brief sensitivity analysis showed that for fixed parameters of pelagic stage growth and mortality, the saturated abundance of survivors was dependent not only on the parameters of the carrying capacity model as would be expected, but also on the size interval over which settlement was permitted. Increasing this interval effectively enlarged the proportion of the total available carrying capacity in the model domain that could be exploited by the drifting particles and hence increased the spatial extent of settlement and the saturated level of survivor abundance. It would be expected that variations in hydrodynamic conditions would also affect the saturation level by the same mechanism.

The maximum rate of recruitment at low spawning abundance when density dependence was ineffective, was clearly dictated to a large extent by pelagic stage growth and mortality parameters, but also by the size at onset of settlement. The size interval for settlement was of no consequence in this case, since in the absence of competition for space, all particles were able to settle at the first opportunity.

Following this crude sensitivity analysis the maximum allowable number of settled juveniles per unit area was set at 20,000 km<sup>-2</sup>. Under these conditions, there was no competition for space in the two lowest spawning abundance simulations, and increasing competition at higher abundances. With this setting, the accessible carrying capacity of the system was never fully saturated, even at the highest simulated spawning abundance (Fig. 1). Decreasing the size interval for settlement and/or the maximum maximum allowable number of settled juveniles per unit area would have caused the relationship to saturate within the simulated range of spawning abundances.

## Spatial Distributions Of Egg Production And Survivors

The model was set up so that the relative spatial distribution of egg production (proportion of total per 1° longitude x 0.5° latitude grid cell) was constant across all simulation, although the magnitude increased in proportion to the spawning biomass. However, the relative spatial distribution of surviving juveniles on day 240 changed with spawning biomass due to the effects of the competition for settlement space (Fig. 2). At the highest spawning biomass, the distribution of settled juveniles was more diffuse than at the low biomass where there was no competition. This result is as expected from the structure of the model.

## Patterns Of Survival From Different Spawning Locations

For each spawning location, survival-to-stage was integrated over all spawning dates to investigate the spatial patterns in survival. Overall survival from location  $i$  was given by:

$$\ln \frac{\text{Spawning date 126}}{\text{Spawning date 45}} \left( \text{Abundance at stage} \right) \Big|_{\text{location } i} - \ln \frac{\text{Spawning date 126}}{\text{Spawning date 45}} \left( \text{Abundance of newly spawned eggs} \right) \Big|_{\text{location } i}$$

For all stages, pelagic stage survival was higher for spawning locations to the west of Scotland compared to those in the North Sea (Fig. 3). This was because the egg and early larval stages from these sites were exposed to higher water temperatures than those in the North Sea, exhibited higher growth rates and hence suffered lower cumulative mortality. As expected from the model structure, the spatial pattern of pelagic stage survival was independent of the initial abundance of newly spawned eggs (ie spawning stock abundance), since no density dependent process was included for stages preceding settlement. In contrast, spatial patterns of survival to demersal stages was affected by spawning stock abundance. Survival from spawning sites in the North Sea was more sensitive than that from west of Scotland spawning sites.

The intensity of the density dependent effect on survival was estimated by calculating the difference in survival to the 40 mm juvenile stage between the lowest simulated SSB (10 kT) and each of the other simulations. The greater the difference, the more intense the competition at settlement and the greater the impact of density dependence on survival. The results (Fig. 4) clearly showed that the settlement competition was more intense for progeny originating in the North Sea, compared to those from the west of Scotland. The spatial pattern of intensity was not simply related to the distribution of spawning abundance. Hence, the processes which limit overall recruitment at high spawning stock abundances, are not necessarily occurring in the main centres of egg production. Patterns of dispersal relative to the distribution of carrying capacity are presumably also very important.

## Patterns Of Survival From Different Spawning Dates

For each spawning date, survival-to-stage was integrated over all spawning locations to investigate the temporal patterns in survival. Overall survival from spawning date  $D$  was given by:

$$\ln \frac{\text{Spawning location 141}}{\text{Spawning location 1}} \left( \text{Abundance at stage} \right) \Big|_{\text{date } D} - \ln \frac{\text{Spawning location 141}}{\text{Spawning location 1}} \left( \text{Abundance of newly spawned eggs} \right) \Big|_{\text{date } D}$$

Simulated pelagic phase survival increased with spawning date due to the seasonal warming of the water and consequent increase in egg development rate and larval growth rates. In the absence of any density dependent processes in the pelagic phase, the temporal pattern of survival from different spawning dates was independent of the spawning stock abundance (Fig. 5).

At the lowest simulated spawning stock abundance, survival to demersal stages from different spawning dates paralleled that of the pelagic stages, ie increased with spawning date. However, as spawning stock abundance was increased the later spawning dates suffered decreasing survival (Fig. 5). The reason was that with increasing egg production the seabed carrying capacity was filled by the earliest spawned, fastest growing individuals in the population, and these inhibited settlement of individuals originating from later in the spawning season.

## DISCUSSION

The holistic properties of the model described here have the potential to match those of some conventional analytical stock-recruitment models, but with explicit representation of the relevant physics and biology. One of the aims of our work is to give insight into how the very simple parameters of relationships such as a Beverton and Holt, may be elaborated to include the consequences of environmental variability, variations in the spatial and temporal patterns of spawning, and the conditions governing density dependence. Sensitivity analyses similar to those described here will be an important part of this task.

Heath and Gallego (1998) described simulations of the survival of eggs and early larval stages (up to approximately 8 mm) using the model system outlined here. This earlier work was limited by the larval growth relationship, which was based on analysis of otolith microstructure data from larvae <9 mm (Campana and Hurley, 1989), and did not include any representation of density dependent effects on growth or mortality. Hence, whilst the earlier system could be used to explore spatial and temporal patterns in the survival of early pelagic stages in relation to environmental conditions, it could not provide any meaningful insight into the relationship between survival and the magnitude of annual egg production. Subsequently, the larval growth relationship was extended to approximately 50 mm body length using data from haddock larvae and pelagic juveniles collected in the North Sea (Gallego *et al.*, 1999c). Inclusion of this relationship, and a first consideration of how density dependence might operate in the system, are the major developments reported in this paper.

Density dependence is clearly a fundamental feature of survival during some stages of the early life history of fish, as evidenced by the underlying shape of relationships between recruitment and spawning stock abundance. However, despite many decades of fisheries recruitment research, the details of how and when population abundance impacts on survival are largely a matter of conjecture for the majority of species. Most research has focused on environmental factors, their effects on growth and survival, and the extent to which they may explain variability in recruitment. Whilst these are certainly important considerations, it must also be necessary to consider the circumstances which may relax or intensify density dependence because, except at low spawning stock abundances, these may be the overriding issues dictating the numbers surviving to recruitment. Extending our model system to represent the life stages at which individuals make the transition from pelagic to demersal phase, necessitated an explicit consideration of these factors, and was the key to developing a model which could have the holistic properties of an analytical stock-recruitment relationship.



There are a number of hypothetical mechanisms by which survival may be compensated by increases in spawning population abundance (Table 1), and these are neither mutually exclusive, nor necessarily always operative under all conditions for any given species. For haddock in the North Sea, the typical abundances of larvae encountered in the field seem too low to generate intra-specific competition for food, or to attract predators. Competition or predator attraction might occur at the multi-species community level, but since there is only weak spatial or temporal co-variation between species, this could not constitute density dependence at the species level. However, there is evidence of negative autocorrelation in the time series of North Sea haddock recruitment with strong year classes inhibiting the establishment of recruitment in immediately following year classes (Cook and Armstrong, 1986). The implication is that the presence of large numbers of juveniles from an earlier year inhibits the settlement of an incoming year-class. Analysis of survey abundance indices for different development stages of haddock also provides indication that the main density dependent step in the early life occurs around settlement (Heath *et al.*, 1999). Hence, we focused first on examining the dynamic consequences of incorporating a competitive exclusion process in the model.

TABLE 1

List of possible processes leading to compensatory effects on survival, together with possible schemes for their representation in an individual based model system.

Density dependent process	Manifestation and possible representation in the model
Competition for refuge or territory.	Exclusion of late arriving individuals by the presence of conspecifics in a particular habitat, and consequent mortality penalty.
Necessity to form schools for protection from predators.	School sizes increase with population abundance, such that individual members obtain less food with consequent effects on growth rates.
Competition for food. Some types of parasitism of larvae or juveniles.	Inverse relationship between local abundance of conspecifics in a given size range, and individual growth rates.
Cannibalism	Size specific mortality rate positively related to the abundance of larger conspecifics in the vicinity.
Attraction of predators to local abundances of the target species. Some types of disease.	For a given size range of individuals, size specific mortality rate positively related to the local abundance of conspecifics.

Defining the carrying capacity of the domain is critical for the performance of our model system, and is particularly problematic. Analysis of survey abundances of juvenile in relation to habitat categories does not necessarily provide information on carrying capacity since the extent to which the available capacity is occupied at each sampling location remains unknown. In the northwest Atlantic manned submersibles and remotely operated vehicles have been used to observe juvenile cod in the field and these studies seem to indicate that certain sediment types confer a camouflage refuge (Lough *et al.*, 1989), whilst others leave the fish exposed to detection by predators. Anecdotal information from these studies suggests that recently settled fish may also utilise weed mats and boulders for refuge. There seems to be no equivalent information for haddock in the North Sea, so we have

taken a very simple approach of merely setting depth limits to the settlement habitat. At present, the carrying capacity is assumed to be completely vacant at the start of a model run, but it is a trivial matter to incorporate the capacity taken up by a preceding year class, derived either from a separate simulation or from trawl survey data.

The behaviour and biology of fish during the transitions from pelagic to demersal phase is also poorly known. We have programmed our model such that pelagic stages seeking to make the transition can defer settlement if space on the seabed is already occupied. Ultimately, there is a penalty for failing to settle within a size interval. However, we simply do not know whether this is an appropriate representation of what happens in reality. An alternative, with similar holistic consequences for the model as a whole, but very different spatial dynamics might be to allow pelagic stages to settle at will, but impose a size specific mortality rate linked to the density of settled individuals. This approach should mimic the predation risk associated with insufficient refuge for the number of fish in an area. An additional issue in this area of the model is the role of active migration. At present, pelagic stages are considered to be purely passive drifters up to the point of settlement whereupon they become anchored to a grid cell ( $1^\circ$  longitude x  $0.5^\circ$  latitude) of the carrying capacity distribution. Demersal juvenile cod certainly are not anchored to their settlement location, and undertake active migrations into shallow waters for a period of time, followed by an active offshore migration. The situation seems less clear for haddock, which continue to be caught in appreciable numbers in offshore waters of the North Sea throughout the early juvenile phase. Clearly, if post-settlement migrations occur on scales larger than the carrying capacity grid cells, then their inclusion in the model could free-up carrying capacity during the simulation, with consequences for the spatial and temporal patterns of survival.

Regardless of the appropriateness of the various possibilities for including density dependence in the model, our results have suggested that the survivors to recruitment are those which achieve a balance between maximising growth rates during the pelagic phase, and minimising competition during the density dependent phase. This trade-off acts to favour different spawning dates and locations with changing spawning stock abundance. Thus, in the simulations, late spawned individuals experience warmer temperatures and hence can achieve faster growth and higher survival-to-stage. Offset against this is the higher likelihood of late spawned individuals suffering due to exclusion from settlement habitats by earlier settlers. The result of this trade-off is the dome-shaped response of survivorship to spawning date. In the past, such relationships, derived from otolith microstructure data, have been interpreted as evidence for environmental windows of survival. Our results show that this is only part of the explanation. Although the trade-off relationship emerged from the simulations based on the competitive exclusion principle, we can expect other types of density dependent process to generate essentially similar properties. We shall be testing the generality of the concept in the near future.

As presently described the model is loosely parameterised to represent North Sea and west of Scotland haddock. The next stage of our work will be to more formally parameterise the model from the historical database of stock, recruitment and spatial distributions of this species. In particular we will need to:

- refine the representation of vertical distribution of eggs and larvae;
- refine the parameterisation of the relationship between mortality rate and body size;
- reconsider the appropriateness of the larval growth model;
- review the appropriateness of the settlement model;
- review the size criteria associated with the settlement model;
- consider the inclusion of active migration behaviour post-settlement;
- attempt a more sophisticated representation of the carrying capacity.

We shall also be undertaking sensitivity analysis with respect to the effects of environmental variability on spatial and temporal patterns of survival, and the holistic performance of the model. This will follow a similar approach to that described here, except that the stock and biological configuration will be maintained as constant features, and a range of hydrodynamic and temperature conditions applied.

In summary, this strategic analysis of our model has identified the scope for intricate spatial and temporal structures to emerge from the relatively simple interaction of environmental factors and biological processes during the fish recruitment process. Most importantly, these structures responded non-linearly to spawning stock abundance, and have implications for the holistic performance of the simulated populations. Our longer term aim is to elaborate conventional analytical models of the whole population stock-recruitment relationship, to take account of these sub-grid scale processes, and produce more dynamic tools for use in stock assessment.

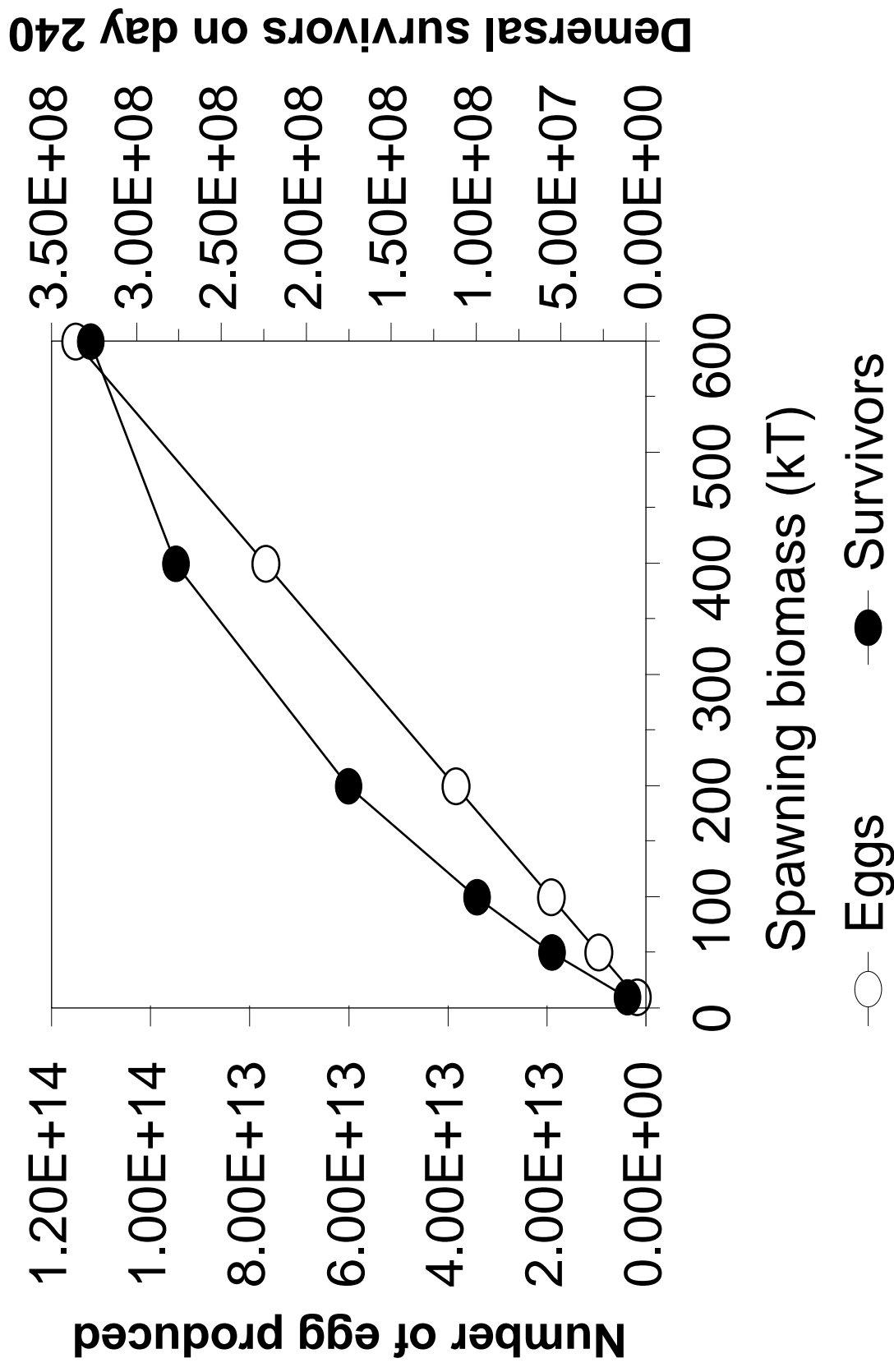
#### ACKNOWLEDGEMENTS

This work was partly supported by EU FAIR contract CT98-4122 (STEREO).

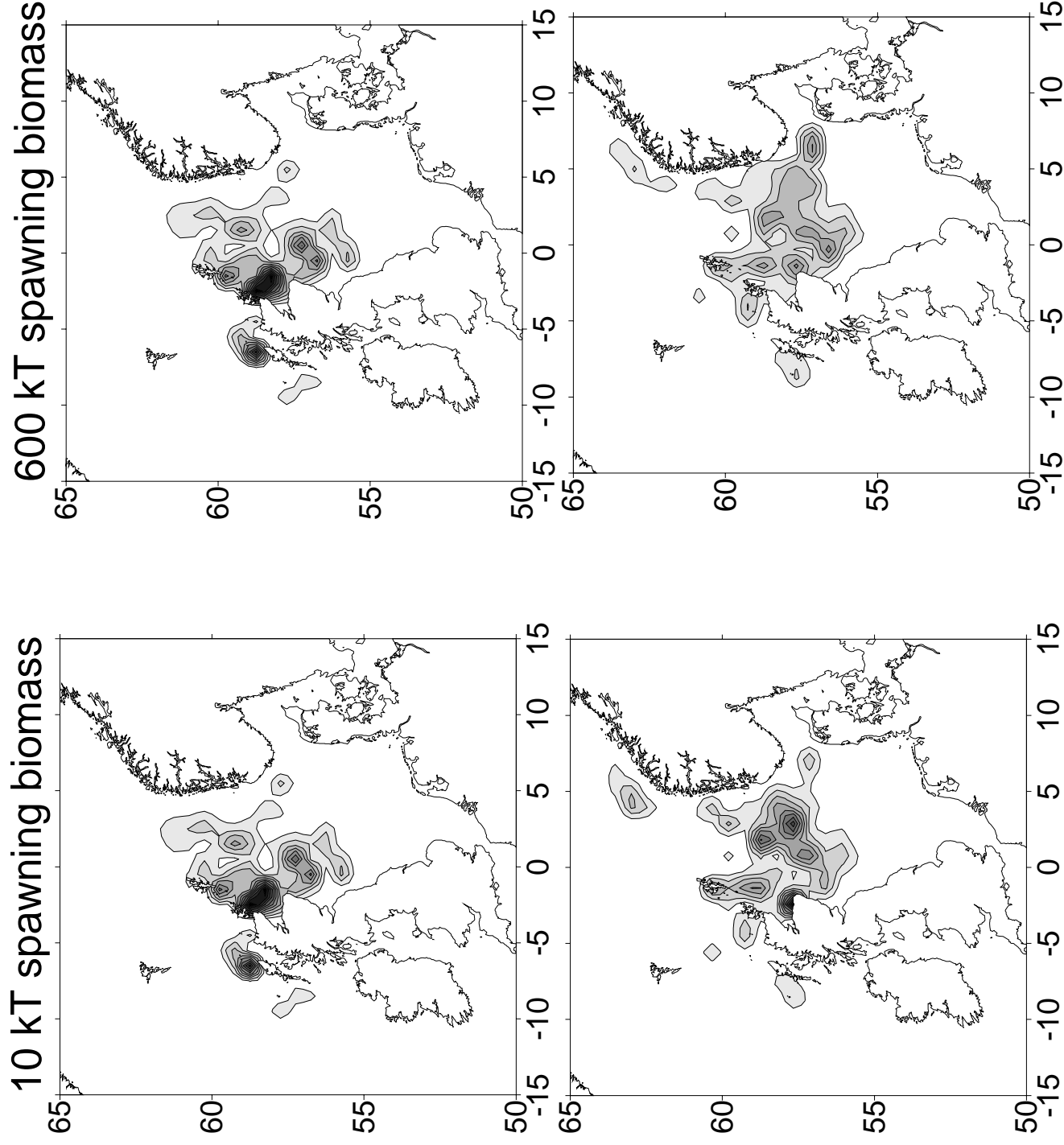
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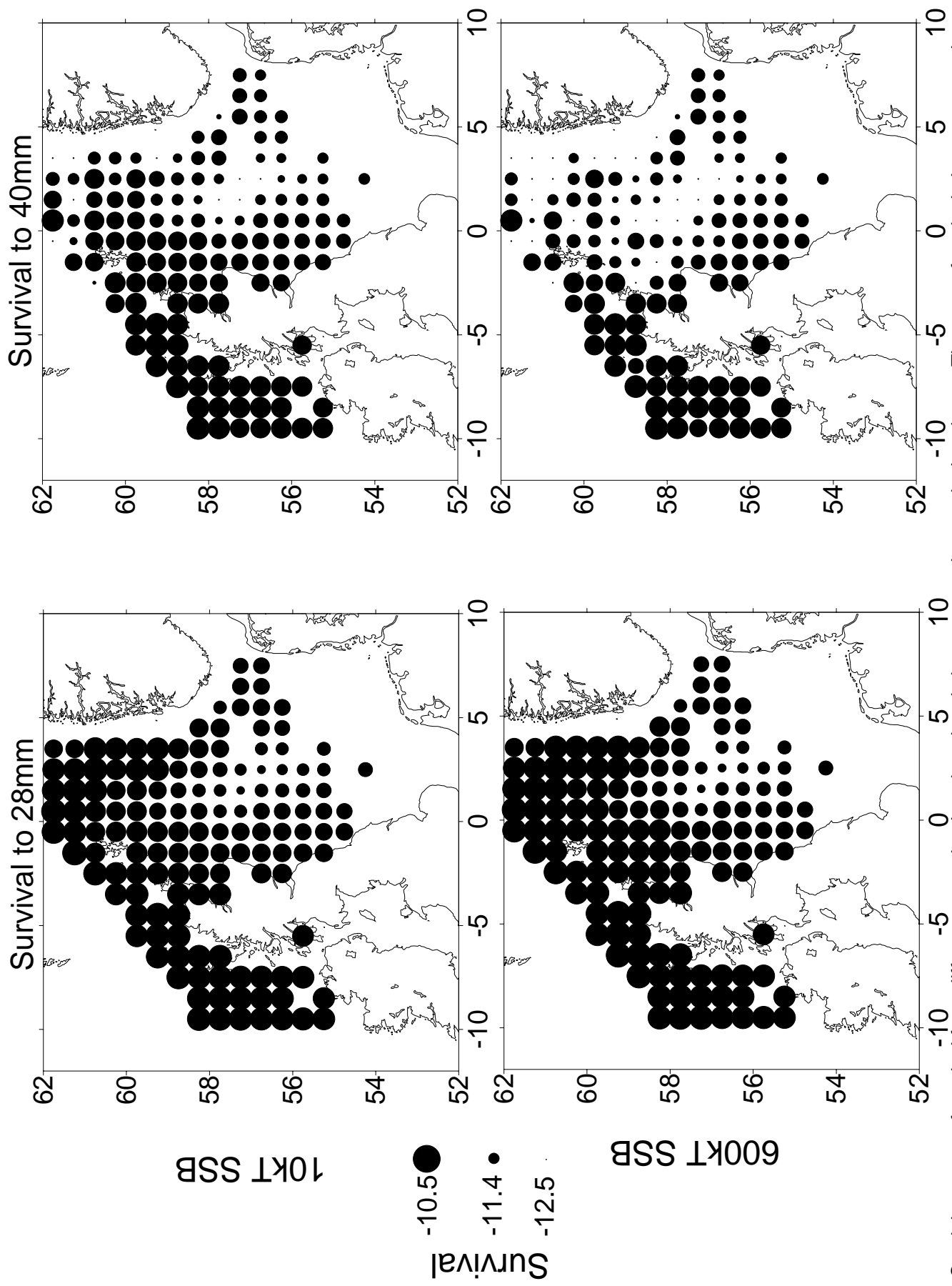
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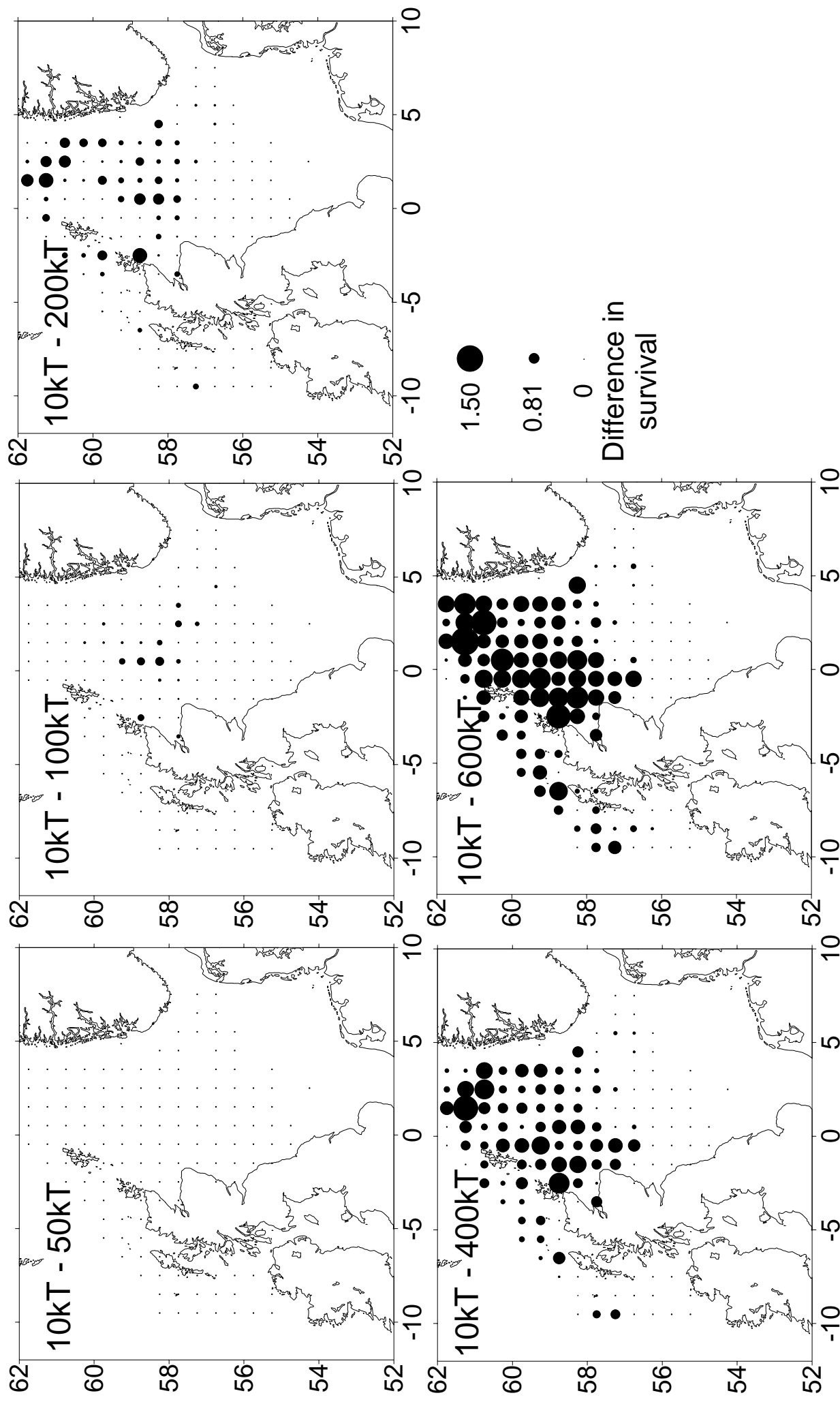
**Figure 1.** Simulated annual egg production, and number of survivors to day 240, for each spawning stock abundance scenario.



**Figure 2.** Relative spatial distributions (proportion of the spatially integrated total per  $1^\circ$  longitude  $\times$   $0.5^\circ$  latitude grid cell) of annual egg production (upper panels), and demersal juveniles on 28 August (lower panels), for the smallest (10kT) and largest (600kT) simulated spawning stock abundances. The relative spatial distributions of egg production are identical for the two simulations, but the distribution of demersal juveniles is more diffuse for the higher spawning abundance.

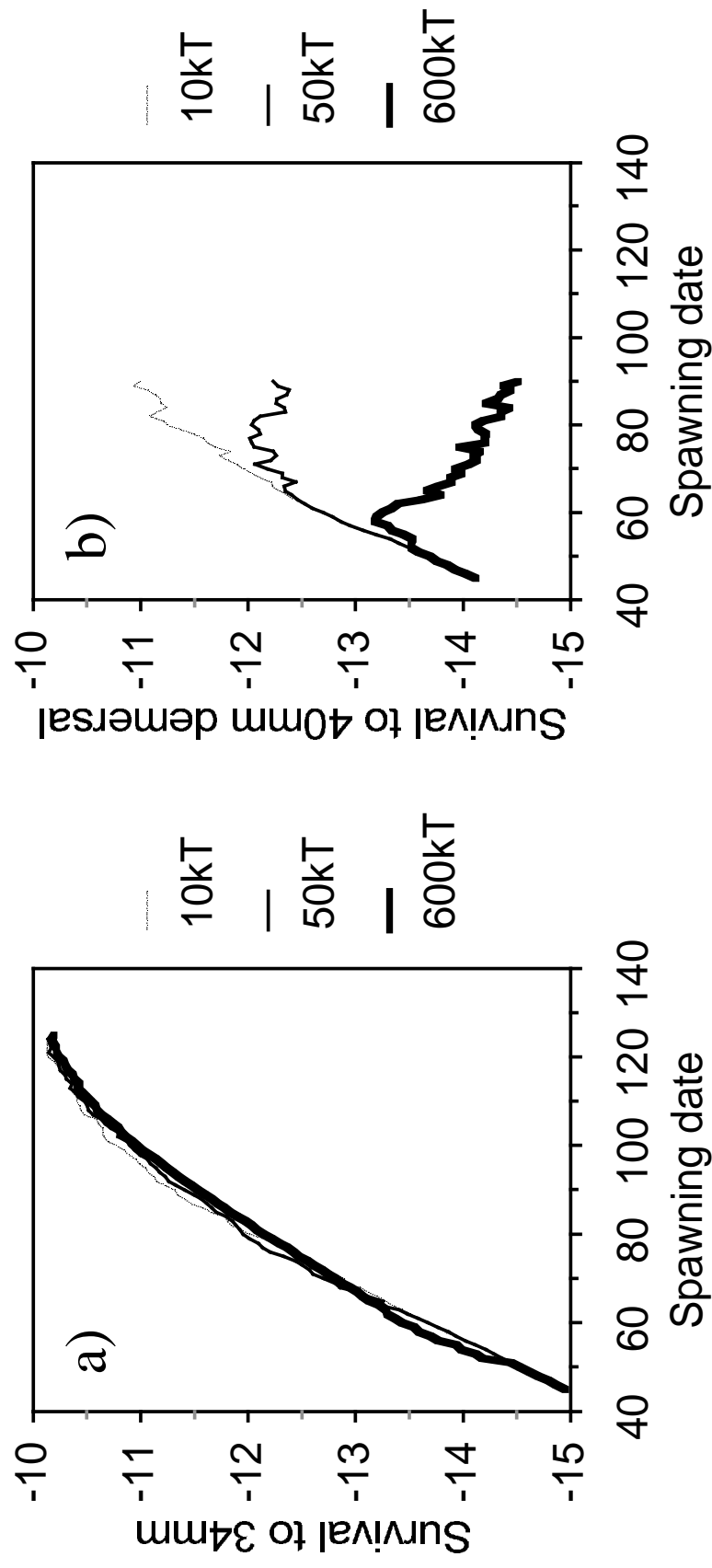


**Figure 3.** Spatial patterns of survival from different spawning locations in relation to spawning stock abundance. The area of each circle represents the annual survival from egg to 28mm pelagic stage (left panels), and egg to 40mm demersal stage (right panels), plotted at spawning locations. Upper panels show results from the lowest simulated spawning stock abundance (10kT), and lower panels show survival to the demersal stage was influenced by spawning stock abundance, but survival to pelagic stages was not.



**Figure 4.** Spatial patterns of the intensity of density dependence suffered by progeny from different spawning locations. The area of each circle represents the difference between annual survival to 40mm demersal stage for a given spawning stock abundance, and that at 10kT spawning abundance, plotted at each spawning location.





**Figure 5.** Spatially integrated survival to a) 34mm pelagic stage, and b) 40mm demersal stage, in relation to spawning date, for 3 simulated spawning stock abundance scenarios.