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Why is haddock overtaking cod? Comparing the effects of temperature and habitat size on both species recruitment dynamics across the N Atlantic

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ABSTRACT

Demersal fish stocks in the N Atlantic have experienced serious declines and depletions due to overfishing during the last decades. For some species, such as haddock (*Melanogrammus aeglefinus*), the situation seems to change and certain stocks are starting to recover. Other species, like cod (*Gadus morhua*), however, still remain at low levels despite restrictive management measures or even fishing closures. The main aim of our study is to investigate whether the differing responses of these species are related to differing sensitivities of their recruitment dynamics to environmental forcing, and especially temperature. Thus, we developed stock-recruit (SR) models, in a hierarchical framework, combining data across their sympatric populations. By allowing the SR parameters to depend on temperature and habitat size, it is possible to (i) determine the patterns of productivity and carrying capacity in relation to the these factors among and within species and (ii) to borrow strength and provide estimates of increased precision. Temperature during the spawning season was shown to have significant effects on the productivities of both species. Haddock, however, was found to be more resilient to warming conditions, and thus it had a higher reproductive rate than cod at increased temperature. We also found that, for both species, density-dependent regulation is determined by the available habitat size but the relationship is stronger for haddock. Synthesizing these patterns can improve our understanding of environmental impacts on key population parameter and lead to more reliable forecasts under different exploitation and temperature scenarios.

Keywords: carrying capacity, cod, climate change, habitat size, haddock, hierarchical models, productivity, temperature

INTRODUCTION

Cod and haddock are two related gadoid species, sharing various areas across the N. Atlantic and also part of their historic fluctuations, characterized by strong declines and decreased productivity for the past decades, especially at the western part of their distribution (e.g., Fogarty & Murawski 1998). Also, there is strong evidence of synchrony in their recruitment patterns among and within regions (e.g., Cohen et al. 1991; Myers et al. 1995; Fogarty et al. 2001). The two species, however, are also characterized by distinct aspects in their reproductive strategies, life-history traits and ecological responses, resulting in different exploitation resilience and recovery potential (Fogarty et al. 2001). The most recent implication involves the onset of haddock recovery, especially in the Georges Bank (Brodziak et al. 2008), while several cod stocks remain at low levels despite years of fisheries restrictions or moratoria.

Recruitment and fishing are the two factors directly influencing marine community dynamics and thus, the future of commercial fish stocks. In practice, the situation is far more complicated, since the former is highly sensitive to environmental pressure, operating through a number of mechanisms (e.g. Stenseth et al. 2002). Houde (2008) described fish early life stages as living in “a trophodynamics arena defined by physics and hydrographic features” and argued that temperature is one of the dominant mechanisms causing interannual variability in recruitment. Hence, deeper knowledge and quantification of the links between climatic factors and living resources is necessary for the accommodation of potential environmental effects in stocks management (MacKenzie & Köster 2004; Brander 2007).

The aim of the present study is to explore and compare the patterns of recruitment response to temperature among the sympatric stocks of cod and haddock. Meta-analytic methods have been recently applied by the authors to identify both the large-scale temperature effects on recruitment, and also the dependence of carrying capacity on available habitat, across the N Atlantic cod distribution (Mantzouni & MacKenzie 2008). The effects were incorporated in multi-level, hierarchical stock-recruit models, extended to allow the dependence of the parameters on these factors. Parameters were allowed to vary depending on the ecosystem-specific characteristics, temperature and area size and thus, the species levels patterns were identified. Also, by incorporating all stocks data in the model and by allowing the parameters to be estimated based on the entire dataset, the associated uncertainty was reduced, enhancing the predictive ability. The significance of temperature as an agent influencing cod maximum reproductive rate was revealed and it was also shown that the sign of the effect depended on the thermal range, with stocks closer to the lower limit being positively affected and vice versa.

In the present study, we adopt a similar hierarchical approach in order to identify potential effects of temperature, and habitat size on haddock stock-recruit dynamics. The consideration of ecosystem conditions for the derivation of the stock-recruitment models can increase our understanding on how dynamics vary geographically, over time and in relation to ecosystem properties. Also, quantifying the relationships between population parameters and biological and/or ecological factors can reduce estimation uncertainly and enhance prediction ability, especially under the light of environmental change.

MATERIALS AND METHODS

Data

We have compiled spawner stock biomass (SSB) and recruitment (R) time-series for the sympatric cod and haddock stocks (Table 1). The data were extracted from the ICES (International Council for the Exploration of the Sea) database and from NAFO (Northwest Atlantic Fisheries Organization) published reports, for the eastern and western stocks, respectively.

Following the standardization method used by Myers and colleagues in various metaanalytic studies (e.g. Myers et al. 2001), we standardized recruitment data by multiplying them with $SPR_{F=0}$ (spawners produced per recruit in absence of fishing mortality). These parameters are calculated based on natural mortality, weight at age and age at maturity (Mace 1994).

Regarding temperature (T), we used time-series of estimates at the surface layer (0-100m), during the spawning season (spring) of each stock. The length of the T time-series is analogous to the population data. For the eastern N. Atlantic the T data were assembled using the ICES oceanographic database (http://www.ices.dk/datacentre/), and the data for the western areas were compiled through the DFO (Fisheries and Oceans Canada) oceanographic databases (Gregory 2004).

We have also used habitat size estimates in order to standardize carrying capacity models for differences in region size among stocks. As in previous meta-analytic studies on cod (MacKenzie et al. 2003, Mantzouni & MacKenzie 2008), we assumed that habitat is limiting at juvenile stage (Myers & Cadigan 1993). Hence we have used the area of ocean bottom between 40-300m as representative of stock habitat, thereby excluding the upper pelagic layer.

Modelling and statistical analyses

We developed a Bayesian hierarchical Ricker stock-recruit (SR) model for the 9 haddock stocks across the N Atlantic, incorporating the effects of both habitat size and temperature on the parameters. The approach is similar to the one used in our previous study for cod (Mantzouni & MacKenzie 2008) and thus, it will be briefly outlined here. The parameters obtained by the two models for haddock (this study) and cod (Mantzouni & MacKenzie 2008) were compared between the sympatric or neighboring stocks (Table 1).

Ricker model

The linear form of the Ricker model was used:

$$\log(R_t / S_t) = \log A - BS_t + \varepsilon_t \qquad (1)$$

or to simplify notation:

$$y_{it} = \alpha_i - \beta_i^{-1} x_{it} + \varepsilon_{it} \qquad (2)$$

where $y_{it} = \log(R_{it} / S_{it})$, $x_{it} = S_{it}, \alpha_i = \log A_i$, $\beta_i = B_i^{-1}, \varepsilon_{it} \sim \mathrm{N}(0, \sigma_i^2)$ and *i* denotes the stock of a given species. It should be noted that natural logarithms are used throughout the study.

Parameter *a* (*alpha*) represents the slope of the Ricker curve near the origin and is related to the stock productivity, through the fecundity and the density independent survival rate. The spawner biomass producing maximum recruitment is given by a parameter β (*beta*), which is thus related to the density (stock)-dependent compenasatory mortality and the carrying capacity (CC).

Hierarchical modeling and ecosystem effects on the SR parameters

The stock-specific SR model in [2] can be extended to describe jointly the dynamics of species stocks, by introducing a next level of hierarchy, i.e., models on the *alpha* and *beta* parameters:

$$\alpha_i \sim \mathrm{N}(\mu_\alpha, \sigma_\alpha^2) \quad (3.1) \text{ and}$$

$$\beta_i \sim \mathrm{N}(\mu_\beta, \sigma_\beta^2) \quad (3.2)$$

where μ_α and σ_α^2 (or μ_β and σ_β^2) is the mean and the variance of the *alpha* (or *beta*) distribution describing the variability in the parameter across stocks, respectively. Thus, it is assumed that the parameters are related among the species populations and are following a normal distribution, estimated by the Bayesian model. The above models are called *stock-level* models or *priors*, describing the distribution of the parameters across stocks. These models can then be extended to account for any factors causing the variability, as it will be shown next. The parameters describing the prior distributions are called *hyper-parameters*, while the associated uncertainty is quantified by the *hyper-priors*, i.e. the priors of the hyper-parameters. Normal and uniform distributions were used as hyper-priors for the mean and the standard deviation of the stock level models, respectively, and were uninformative in all cases.

(i) Temperature

We investigate possible temperature (*T*) effects on the density-independent stock productivity, by allowing parameter *alpha* in [2] to be *T* dependent and thus time varying (α_{it}). Initially, we use a quadratic relationship, in order to allow the model reveal the functional form of the effect:

$$\alpha_{it} = c_{oi} + c_{T1i}T_{it} + c_{T2i}T_{it}^{2} \quad (4)$$

Stock-level models can be introduced on each of the above terms:

$$c_{oi} \sim \mathrm{N}(\mu_{c_o}, \sigma_{c_o}^{2}) \quad (5.1),$$

$$c_{T1i} \sim \mathrm{N}(\mu_{c_{T1}}, \sigma_{c_{T1}}^{2}) \text{ (5.2) and } c_{T2i} \sim \mathrm{N}(\mu_{c_{T2}}, \sigma_{c_{T2}}^{2}) \quad (5.3)$$

These models describe the across stocks variability either in mean productivities (5.1) or in the intensity of the temperature effect (5.2 and 5.3).

(ii) Habitat size

Parameter *beta* of the Ricker SR model is a proxy for carrying capacity and thus, it can be expected to depend on habitat size. In other words, differences in the stock-specific *H* (natural log of habitat area) can explain part of the across stocks variability in the parameter. In order to test for this possibility, the stock-level model for *beta* [3.2] can be modified to include *H* as a predictor:

$$\beta_i \sim \mathrm{N}(d_o + d_{H1}H_i + d_{H2}H_i^{2}, \sigma_{d_o}^{2}) \quad (6)$$

or $\beta_i = d_{oi} + d_{H1}H_i + d_{H2}H_i^2$ with $d_{oi} \sim \mathrm{N}(\mu_{d_o}, \sigma_{d_o}^2)$

Combining [2], [3], [4], [5] and [6], the full model becomes:

$$y_{it} = (c_{oi} + c_{T1i}T_{it} + c_{T2i}T_{it}^2) - (d_{oi} + d_{H1}H_i + d_{H2}H_i^2)^{-1}x_{it} + \varepsilon_{it} \quad (7)$$

with $c_{oi} \sim \mathrm{N}(\mu_{c_o}, \sigma_{c_o}^2)$, $c_{T1i} \sim \mathrm{N}(\mu_{c_{T1}}, \sigma_{c_{T1}}^2)$, $c_{T2i} \sim \mathrm{N}(\mu_{c_{T2}}, \sigma_{c_{T2}}^2)$ and $d_{oi} \sim \mathrm{N}(\mu_{d_o}, \sigma_{d_o}^2)$.

The final form of the model for each species was determined by testing the significance of the stock-level parameters, as previously noted.

Results and Discussion

The final hierarchical Ricker stock-recruit model for the cod stocks providing the best fit, based on the DIC (Deviance Information Criterion; Spiegelhalter et al. 2002), as estimated from the previous study (Mantzouni & MacKenzie 2008) was of the form:

$$y_{it} = (c_{oi} + c_{T1i}T_{it} + c_{T2i}T_{it}^2) - (d_{oi} + d_{H1}H_i + d_{H2}H_i^2)^{-1}x_{it} + \varepsilon_{it}$$

Thus, temperature has a significant effect on the cod maximum reproductive rate, represented by parameter alpha. This effect exhibits a dome-shaped form, being positive for relatively lower temperatures and becoming negative during warmer conditions (mainly above 6.5°C). Also, habitat size (natural log-transformed) was found to influence the parameter beta, representing density dependence.

Regarding the haddock hierarchical model, the final form was identified as:

$$y_{it} = (c_{oi} + c_{T1i}T_{it}) - (d_{oi} + d_{H1}H_i)^{-1}x_{it} + \varepsilon_{it}$$

Similarly to the cod model, parameter alpha was shown to depend on temperature. The relationship, however, was shown to be linear, and positive, across the species thermal range. The alpha-temperature relationships for the sympatric cod and haddock stocks are shown in Figure 1. It is notable that in most areas, temperature has a negative or weakly positive effect on cod, while the response of haddock productivity is positive. The increase rate of alpha is similar among most haddock stocks and slightly stronger for the Arctic, Faroe and Icelandic populations.

The species were also compared in terms of their average productivities, corresponding to the mean stock-specific temperature. The results are shown in Figure 2. It is evident that in most cases, except North Sea, cod’s average alpha is higher. This was also confirmed using the Wilcoxon signed rank test for the paired comparisons ($p=0.04$). Given the opposite temperature effects on the two species however, it is expected that the maximum reproductive rate of haddock can exceed that of cod, at increased temperature, as shown in Figure 1. Such patterns are already obvious in the W Scotland, the Faroe, and for the Brown Bank cod and Gulf of Maine/ Brown Bank haddock.

Regarding parameter beta, a significant dependence on log habitat size was found among the stocks for both species (Figure 3). When the parameters, representing SSB producing maximum replacement spawners in the absence of fishing, were compared among the sympatric stocks, it was shown to be higher for cod in all cases (Wilcoxon signed rank test, $p<0.01$; Figure 4). Thus, it seems that compensatory mortality alone is not the sole reason responsible for the lower variability in cod recruitment compared to haddock. Instead, additional factors, such as a broader spawning window and higher tolerance to ecosystem forcing, can be driving the pattern (Fogarty et al. 2001). The latter is also indicated by the comparatively higher stability of cod’s maximum reproductive rate in relation to temperature, at least among certain areas (e.g., Faroe, Scotian Shelf, Gulf of Maine and Browns Bank) shared by the two gadoids (Figure 1). Nevertheless, available space during the juvenile stage seemed to be an important factor shaping the stock-recruit dynamics and the carrying capacity of both species.

In conclusion, in this study we employed a hierarchical stock-recruit model in order to identify environmental effects on haddock recruitment dynamics, focusing especially on the response to increasing temperature. It was shown that, in comparison to sympatric cod stocks, temperature is inducing a positive effect on haddock productivity across the thermal distribution of the species. This can be partly accounting for the species higher recovery potential, since an incoming strong year-class could be a source for stock recovery, under a regime of low fisheries exploitation (Fogarty et al. 2001). Maximum reproductive capacity of various fish species has been shown to depend on life history traits, such as body size and age at maturity (Denney et al. 2002). Goodwin et al. (2006) have shown that alpha obtained from the Ricker model is inversely related to $SPR_{F=0}$. In the present study, and also in the previous study on cod (Mantzouni & MacKenzie 2008), the effect is indirectly incorporated by transforming recruits to the spawners they can produce during life time. A more explicit approach could involve modeling directly the effect of the compound parameter, and also of its possible fluctuations, on the species Ricker slope at the origin. Also, developing a hierarchical model jointly for the two species could provide additional insights, by sharing information between their stocks, while considering also their differences, and producing stock-recruit parameter estimates of greater precision.

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Table 1: Pairs of stocks compared in the analysis.

	Haddock	**Cod**
1	North Sea	North Sea
2	Arctic	Arctic
3	Faroe	Faroe
4	Iceland	Iceland
5	Rockall	W Scotland
6	W Scotland	W Scotland
7	NAFO 4TVW	NAFO 4VsW
8	Gulf of Maine/Browns Bank	Browns Bank
9	Gulf of Maine/Browns Bank	Gulf of Maine
10	Georges Bank	Georges Bank

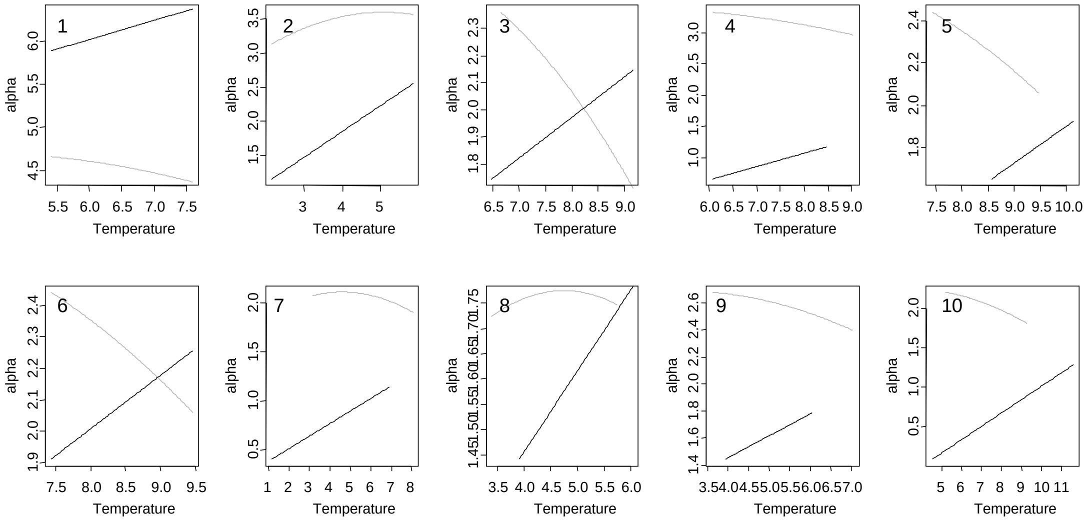

Figure 1. Alpha parameter, representing maximum reproductive rate, plotted versus temperature. The grey lines correspond to cod (estimated by Mantzouni & MacKenzie 2008) and the black lines to the haddock stocks. The pairs of stocks compared are listed in Table 1.

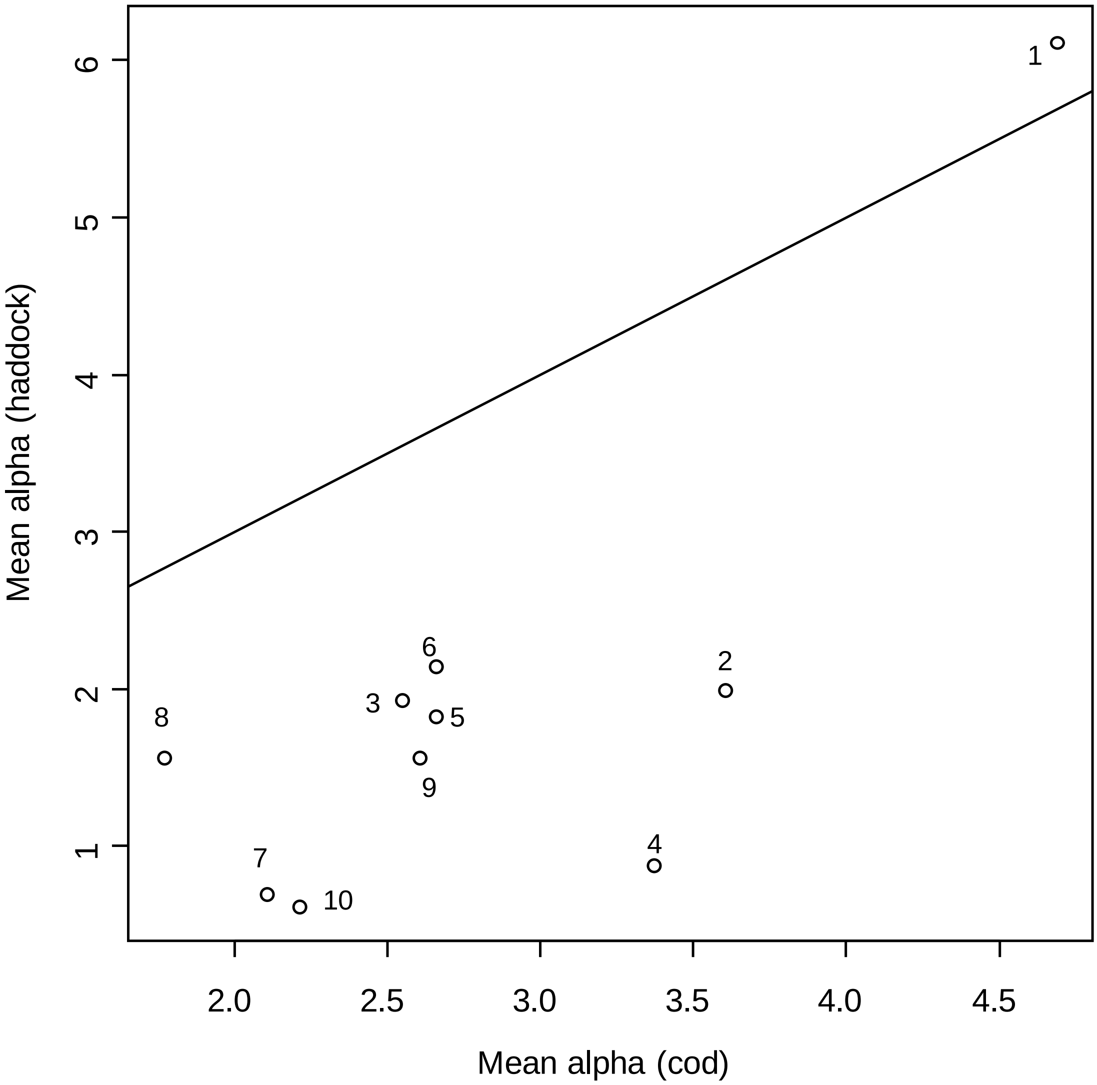

Figure 2: Alpha parameters estimated at mean stock specific temperature for haddock plotted versus the sympatric cod stocks. The stock pairs are listed in Table 1. The solid line is the 1:1 line.

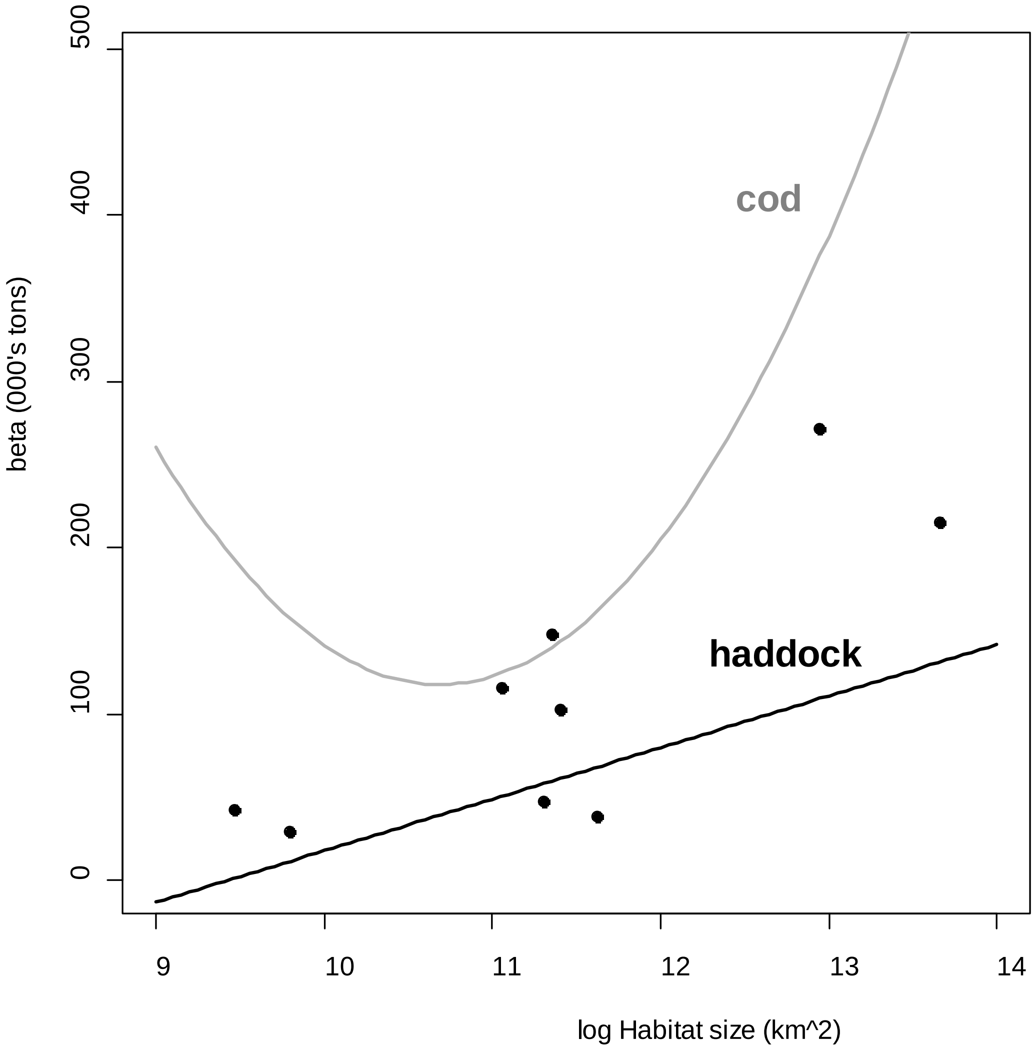

Figure 3. The stock specific beta parameters of haddock plotted versus the log of habitat size. The black solid line is the curve fitted using the hierarchical model presented in this study. The grey line represents the pattern revealed for cod using a separate Ricker hierarchical model (Mantzouni & MacKenzie 2008).

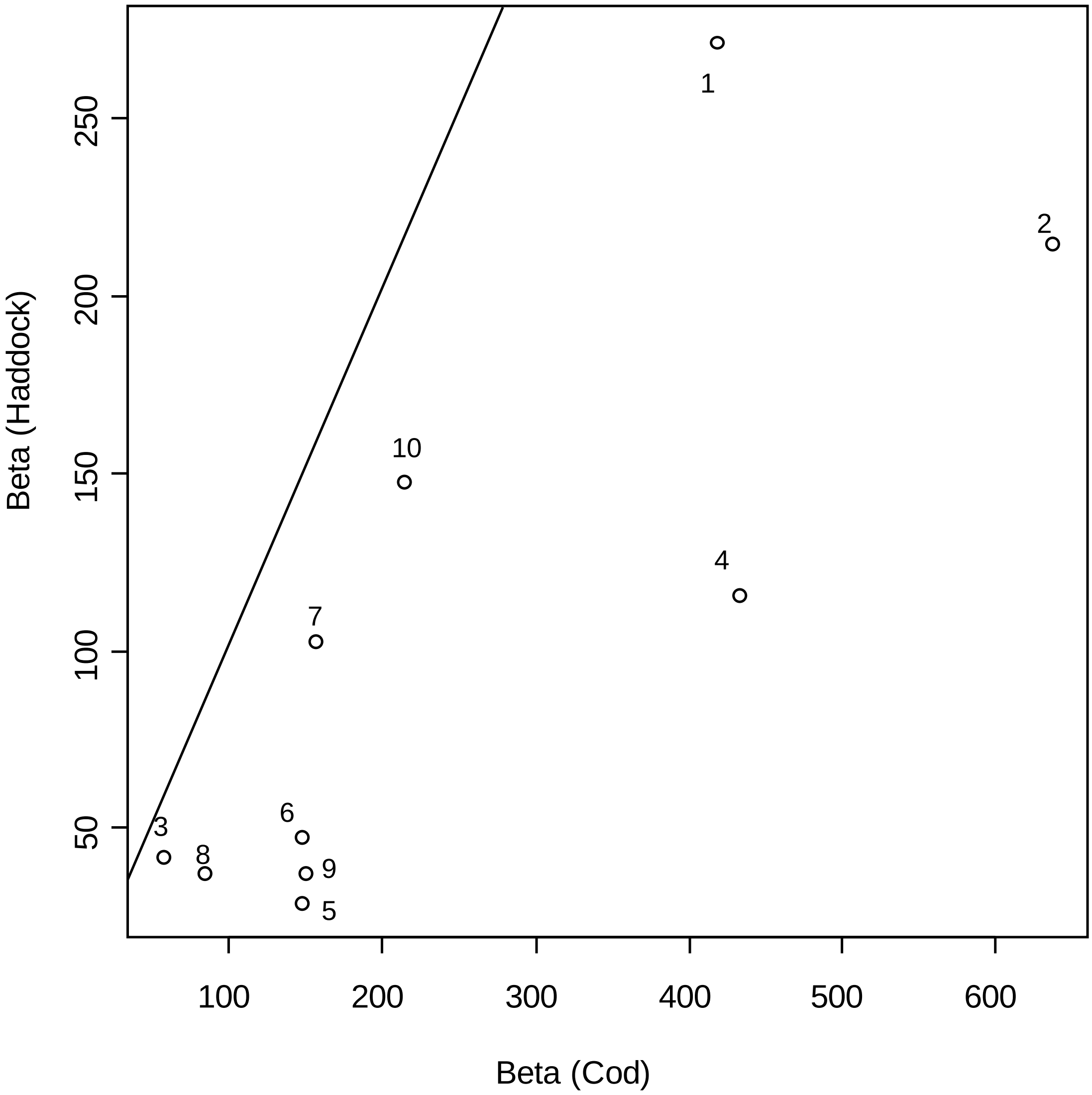

Figure 4: Beta parameters, representing SSB producing maximum replacement spawners, for haddock plotted versus the sympatric cod stocks. The stock pairs are listed in Table 1. The solid line is the 1:1 line.