

# Spatial segregation among fishing vessels in a multispecies fishery

J. J. Poos, F. J. Quirijns, and A. D. Rijnsdorp

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Individual decisions of fishers on where to fish in heterogeneous environments may shape the relation between fishing effort and fishing mortality. Fishers may be viewed as individual foragers, whose decisions are aimed at optimizing short-term gain, as in ideal free distribution (IFD) theory. Although IFD assumes all foragers to be equal, they are likely to differ in competitive abilities for different prey types or target species. Here, we present an IFD-like model of a fishing fleet consisting of two components with different competitive abilities for two target species, showing that spatial segregation can result from unequal interference competition, but also in the absence of interference competition. Differences in catch efficiency between vessels for target species in combination with differences in the spatial distribution of target species can result in spatial segregation among vessel groups. The theoretical results are used to interpret the observed spatial segregation of two components within the Dutch beam trawl fleet using observations from a vessel monitoring by satellite system. However, this study cannot pinpoint which of the processes included in the theoretical model is the prime cause of the segregation within the Dutch beam trawl fleet.

**Keywords:** competition, fleet dynamics, mixed fisheries, spatial distribution.

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## Introduction

A basic problem in fisheries research is to understand the distribution of fishing fleets, a problem closely linked to comprehending the behaviour of individual fishing vessels exploiting fish stocks (Hilborn, 1985). Based on the assumption of homogeneous mixing of fishing effort and the fish stock, a linear and constant relation between nominal fishing effort and the mortality generated by fishing is generally assumed. However, individual decisions of fishers when and where to fish may prevent homogeneous mixing, so breaking the linear relation between fishing effort and fishing mortality (Paloheimo and Dickie, 1964; Clark and Mangel, 1979; Ellis and Wang, 2007).

Fishing vessels may be viewed as individual foragers, aiming to optimize gain rates in a single currency (Krebs and Davies, 1984): in fisheries, this currency can be assumed to be short-term net revenue (Gordon, 1953; Hilborn and Kennedy, 1992). Net revenue is affected by local density and price of target species, gear efficiency, and competitive interactions among vessels, as well as fixed and variable costs (Beverton and Holt, 1957; Hilborn and Kennedy, 1992). The sum of the decisions of individual vessels results in the spatial distribution of the fishing fleet.

Behavioural ecology has a long history of studying and modelling processes affecting the spatial distribution of individual foragers. One of the most influential models is known as the ideal free distribution (IFD; Fretwell and Lucas, 1970), which has also found application in fisheries science (see Gillis, 2003, for a review). The IFD model assumes that foragers (i) are “ideal”, meaning that each individual forager chooses the habitat that maximizes its fitness, (ii) are “free”, meaning that moving between habitats is free of

costs, and (iii) are all alike, genetically and otherwise. If the relation between the gain rate and the number of foragers per patch is known, the distribution of foragers can be calculated. Interference competition, defined here as a decrease in gain rate at increasing competitor densities, not caused by decreasing local abundance of the prey, will in such a system cause the foragers to spread out over patches. Ultimately, all foragers will have equal gain rates in the equilibrium state of the process.

Interference competition may take place through direct competitive interactions among foragers (Ens and Goss-Custard, 1984), or it can be the result of prey sensing the presence of predators, and modifying their behaviour to reduce the risk of predation (Ruxton, 1995). The latter is known as prey depression. Few studies have attempted to analyse the nature of interference competition in fisheries (Abrahams and Healey, 1993). Direct interactions among vessels, reducing fishing efficiency, were suggested for the trawl fishery for silver hake (*Merluccius bilinearis*; Gillis, 1999). Prey disturbance by fishing was observed for spawning cod (*Gadus morhua*) in an otter trawl fishery by Morgan *et al.* (1997). A similar mechanism was hypothesized in the trawl fisheries for flatfish in the North Sea, causing interference competition by prey depression (Rijnsdorp *et al.*, 2000b; Poos and Rijnsdorp, 2007b).

Although the IFD assumes that foragers are equal, this may not apply in all biological systems. The effect of unequal competitors on the distribution of foragers was first examined by Sutherland and Parker (1985). Subsequent studies by van der Meer (1997), Ruxton and Humphries (1999), and Humphries *et al.* (2001) demonstrated the sensitivity of simulated forager distributions to model formulations. The models in those studies were based on

foragers exploiting a single resource species and included direct competition. Depending on the exact formulation of a mathematical model for interference competition, a truncated phenotype distribution may arise, i.e. a distribution where competitors with different competitive abilities occupy different prey patches.

Fishing vessels will differ in fishing power either through differences in vessel size or engine power (Beverton and Holt, 1957; Rijnsdorp *et al.*, 2000a), age of the vessel (Pascoe *et al.*, 2001; Rijnsdorp *et al.*, 2006), and skill of the skipper (Hilborn and Ledbetter, 1985). Fishing power of bottom trawls will be determined by (i) the swept-area of the gear, (ii) the penetration depth of the gear, and (iii) the efficiency at catching the fish in the path of the gear (Videler and Wardle, 1991; Dahm *et al.*, 2002).

An increase in engine power can be used to increase the swept-area per unit of time by increasing fishing speed, width of the fishing gear, or penetration depth of the gear. The latter is relevant to target species, such as flatfish, that bury themselves in the seabed. Fishing speed not only affects the swept-area of the gear per unit time but may also affect catch efficiency, because fish may be less able to escape from gear towed at high speed (Bublitz, 1996). Because of the proportion of fish that is accessible to the gear and the differences in fish behaviour, fishing power can differ between species.

Here, we explore the effects of unequal competitive abilities of fishing vessels in a mixed trawl fishery for two species on spatial segregation within fishing fleets. Interference competition is modelled by prey depression influencing the proportion of the population that is susceptible to the gear. The results are described in terms of the spatial distribution of the vessels, with particular emphasis on the resulting spatial segregation among fishing vessels. The model is applied to the beam trawl fishery for flatfish in the North Sea, and the predictions are compared with observations on the distribution of Dutch beam trawlers.

## Material and methods

### Model description

Spatial segregation is modelled for two uniform fleets, with 100 small and 100 large vessels that differ in engine power, and hence in their fishing power for two target species (species A and B). Difference in catch efficiency is modelled as the combination of burrowing depth of the species and penetration depth of the gear, species A being a shallow-burying species and species B a deep-burying one. The gear towed by small vessels has a shallow penetration depth and that of large vessels a deep penetration depth.

Vessels have the possibility to choose among 20 patches, which differ in the density of species A and B. Different model runs with different numbers of patches (ranging between 10 and 40) indicate that the general conclusions from the model do not depend on the number of patches. The patches are spatially segregated, but the travel cost between patches is assumed to be negligible. Interference competition is modelled by the effect of vessel density on the burying depth of the species, reducing the susceptibility for the fishing gear for higher vessel densities.

The model is used to study the effect of the following factors on the spatial segregation of small and large vessels:

- (i) differences in the spatial distribution of species A and B;
- (ii) difference in the price of species A and B;
- (iii) occurrence of interference competition.

### Distribution model without interference competition

To formulate a model without interference competition, we start with the assumption that the burrowing depth of individuals of the species A and B can be described using a normal distribution with different mean depths,  $\mu_A$ ,  $\mu_B$ , and common variance  $\sigma$ :  $\mu_B = \mu_A + \rho$ , where  $\rho$  is the difference in burrowing depth. We assume that the penetration depth  $x$  of the gear depends linearly on the engine power of the vessel type, because large vessels are capable of using more chains, providing them with greater penetration depth (Figure 1a). Gear efficiency is defined as the fraction of the population that is vulnerable given the penetration depth. This fraction can be approximated using the cumulative normal distribution function (Sokal and Rolf, 1995). The ratio of gear efficiencies for the two species is a declining function of engine power, approaching an asymptote at efficiency ratio equal to 1 (Figure 1b). The effects of engine power on the fishing speed and gear width are neglected in the model.

The densities,  $D_A$  and  $D_B$ , of the two species in each patch are linearly related as

$$D_B = \beta - rD_A. \quad (1)$$

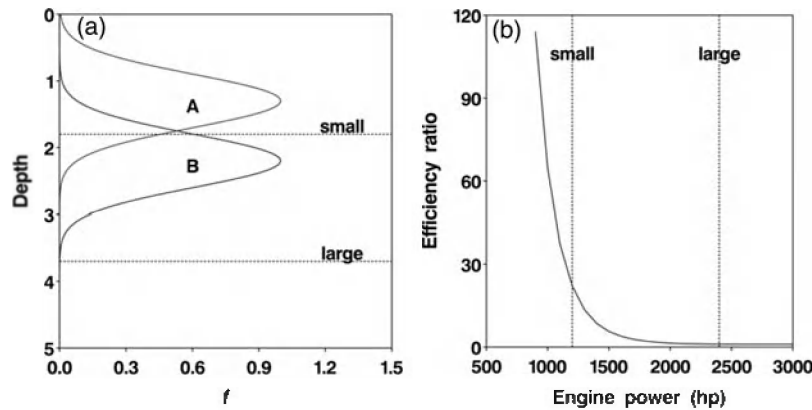
If  $r$  is positive, the densities of the two species are negatively related, but if  $r$  is negative, the species co-occur. The  $\beta$  parameter scales the overall ratio of the two densities in the system. Each of the species has a price ( $P_A$  and  $P_B$ ) when sold on the market. For simplicity, we assume that the entire catch is landed and contributes to the revenue. The costs of fishing,  $F$ , are assumed equal for all patches, and travel costs between patches are assumed to be negligible. Assuming no depletion of the resource, the net revenue  $T$  in a single unit of time in a patch for a vessel using gear with penetration depth  $x$  can be calculated as the product of gear efficiency, species density, and market price summed over the two species minus the costs of fishing:

$$T = \frac{1}{2}D_AP_A \left( 1 + \operatorname{erf} \left( \frac{-\mu_A + x}{\sqrt{2}\sigma} \right) \right) + \frac{1}{2}(\beta - rD_A)P_B \left( 1 + \operatorname{erf} \left( \frac{-\mu_A - \rho + x}{\sqrt{2}\sigma} \right) \right) - F. \quad (2)$$

Here,  $\operatorname{erf}(z)$  is the error function resulting from integrating the normal probability density function. The terms in parentheses provide an estimate of the proportion of individuals found above the gear penetration depth  $x$ . Under the assumption that fishing vessels maximize instantaneous net revenue, the optimal patch for a single vessel is the patch where net revenue  $T$ , the sum of the revenues from the catch rates of the two species minus the costs, is highest.

### Distribution model with prey depression

In a second step, interference competition through prey depression is incorporated by assuming that the average burrowing depth of a species depends on vessel density in a patch. Analogous to work by Ruxton (1995), prey can move from a vulnerable to a less vulnerable state by increasing burrowing depth by  $i$ , i.e. to  $\mu_{Av} + i$  and  $\mu_{Bv} + i$ , respectively. The proportion of prey in the different states depends non-linearly on vessel density  $v$  in the patch. The average burrowing depth of prey population A is



**Figure 1.** (a) Probability density functions of burrowing depth ( $f$ ) of species A and B. The horizontal lines indicate the penetration depth of small (1200 hp) and large (2400 hp) vessels. (b) Relation between gear efficiency ratio A:B and vessel engine power. The vertical lines indicate the hypothetical engine powers of the two vessel types.

then

$$\begin{aligned} \mu_A(v) &= \mu_{Av} \frac{1}{1 + \gamma v} + (\mu_{Av} + i) \frac{\gamma v}{1 + \gamma v} \\ &= \frac{\mu_{Av} + \gamma v(\mu_{Av} + i)}{1 + \gamma v}, \end{aligned} \quad (3)$$

and similarly for population B. The propensity  $\gamma$  of the prey to be in the less vulnerable state encompasses both the probability to enter the invulnerable state upon contact with the gear and the time spent in that state before returning to the vulnerable state again. Individuals cannot burrow deeper than  $\mu_A + i$ ,  $\mu_B + i$ , reflecting the idea that the avoidance behaviour of the prey is bounded by physiological or energetic constraints.

In the model, vessels enter the environment in a random sequence, choosing the patch with the greatest revenue, taking into account the effect of the prey and vessel densities in the patches. When all vessels have entered the environment, each vessel evaluates the environment in the random sequence again and chooses the patch with the greatest expected net revenue. This step is repeated until no vessel prefers to move. The resulting distribution of the two different types of vessel over the patches is plotted for different combinations of the parameters  $\gamma$  and  $i$ .

### Spatial segregation in the Dutch beam trawl fleet

We investigate spatial segregation in the Dutch beam trawl fleet in the North Sea. If vessels of different size select different patches, then spatial segregation of the size classes is expected based on the fact that nearest neighbours will be similar in size. Beam trawlers target the flatfish species sole (*Solea solea*) and plaice (*Pleuronectes platessa*; Daan, 1997; Gillis *et al.*, 2008). A description of the fishing practices and fishing grounds is given by Rijnsdorp *et al.* (1998). Vessels typically make trips lasting 4–5 d in the southern North Sea. Having reached the fishing grounds, the twin beam trawls are shot and fishing commences. A haul lasts approximately 2 h, and after bringing the gear in and emptying the codend, the gear is set again. Dutch beam trawlers typically visit several (neighbouring) ICES rectangles (scale >30 nautical miles), whereas the spatial patchiness of the flatfish resources occurs at a spatial scale of ~20–45 nautical miles (Poos and

Rijnsdorp, 2007a). In the beam trawl fleet, an increase in the number of chains in front of the groundrope increases the gear efficiency, especially for deeper burrowing species such as sole (Creutzberg *et al.*, 1987; Daan, 1997). The price of sole in the Netherlands is approximately four times higher than that of the shallower burrowing plaice.

Spatial distribution of beam trawlers is available from vessel monitoring by satellite (VMS) systems, mandatory onboard transmitters that send the GPS data from the vessel to the General Inspection Service. Although initially installed for inspection purposes only, high spatial (0.05') and temporal resolution (~2 h) VMS measurements are available for research purposes with the permission of vessel owners. Changes in the number of owners giving permission resulted in variable numbers of observations over time, so the period 1 January 2001 to 31 December 2001 was selected for analysis because there were a relatively large number of vessels in the sample. The 57 vessels sampled represent 38% of those active at that time.

To remove vessels that may still be searching for appropriate fishing grounds, or that are moving between ports and fishing grounds (Rijnsdorp *et al.*, 1998), only observations between Monday and Thursday were selected. To exclude observations that do not reflect fishing, observations with vessel speeds outside the fishing speed range for this fleet (5–8 knots; Piet *et al.*, 2006) were removed.

To test spatial segregation between vessels of different size, the fleet was split into two engine-power size classes. The first size class included vessels with an engine power of 300–1900 hp, and the second those >1900 hp. This boundary for the split was selected as just under 2000 hp to separate the dominant 2000 hp size class from the smaller vessels. The spatial segregation in point patterns of vessels of these two types was tested in 2-h time frames throughout the study period. Of the 57 vessels in the sample, only eight had an engine power <1900 hp. In cases where there were multiple observations of one vessel within a 2-h window, one observation was selected randomly. To prevent conclusions that would be based on very small sample sizes, we subsequently tested only those time frames where >66% of the vessels of both types present in the entire sample were fishing.

The segregation between two groups of vessels was estimated using the test statistic  $C$ , which provides an overall measure of

spatial segregation, based on the expected classification of the nearest neighbours under the null hypothesis of random labelling of observations (Dixon, 1994). Under random labelling of points,  $C$  has a  $\chi^2$  distribution with 2 degrees of freedom (d.f.), and the 2-d.f.  $\chi^2$  test is used to indicate whether the observed segregation might have arisen from random labelling of points (Dixon, 1994). All statistical testing was done using sequential Bonferroni-corrected  $\alpha$  level of 0.05 (Holm, 1979). To prevent autocorrelation of the spatial distributions between time frames affecting the estimate of  $C$ , only the time frame between 11:00 and 13:00 each day was analysed.

Data on catches made during the research period were available from EU logbooks that have mandatory catch and effort records (Rijnsdorp *et al.*, 2000a). Additional data on gear usage from the fleet were available by fishing haul from detailed logbooks voluntarily completed and submitted by a number of skippers.

## Results

### Model results without interference competition

The model outlined in Equation (2) was used to derive optimal patch choice for individual vessels of different size in a spatially heterogeneous environment ( $D_A$  varies between patches) in the absence of prey depression. Because in our model the relation between  $D_A$  and  $D_B$  is linear [Equation (1)] and the efficiency does not depend on species densities, the net revenue depends linearly on  $D_A$ . To determine whether the patch with the highest or the lowest density of A would be chosen, we consider the partial derivative of  $T$ :

$$\frac{\partial T}{\partial D_A} = \frac{1}{2} \left( P_A + P_A \operatorname{erf} \left[ \frac{-\mu_A + x}{\sqrt{2}\sigma} \right] - P_B r \left( 1 - \operatorname{erf} \left[ \frac{\mu_A + \rho - x}{\sqrt{2}\sigma} \right] \right) \right). \quad (4)$$

If this function is positive, then vessels will choose the patch with the highest density of species A. This is true if

$$r < \frac{P_A(1 + \operatorname{erf}((- \mu_A + x)/(\sqrt{2}\sigma)))}{P_B(1 + \operatorname{erf}((\mu_A - \rho + x)/(\sqrt{2}\sigma)))}. \quad (5)$$

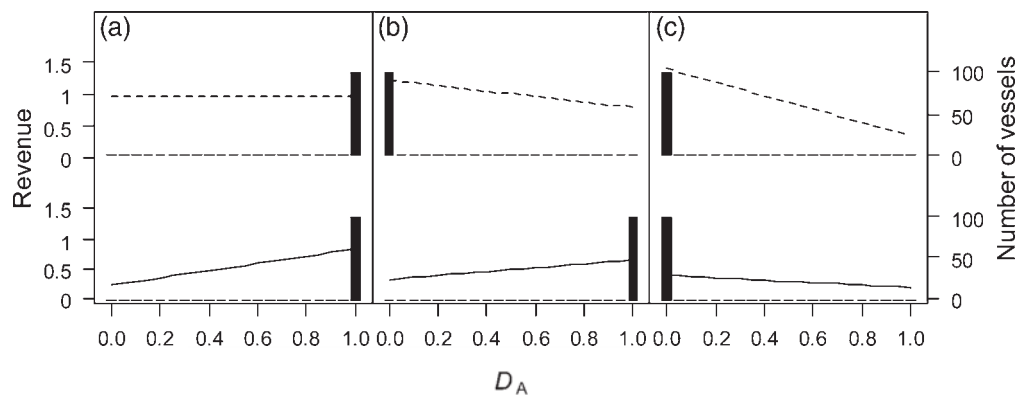
Therefore, the patch choice depends on the relation between the density of the two species  $r$ , the prices  $P_A$  and  $P_B$ , and the efficiencies.

If the two species occur in the same patches ( $r < 0$ ), then the inequality will always be true, because the right side of the inequality in Equation (5) is always positive. Hence, fishing vessels will go to those patches with the highest density of both A and B.

Alternatively, if  $r > 0$ , there is a segregation in the occurrence of the two species. Now, the patch choice depends on prices and catch efficiencies. To illustrate these effects, we describe several cases assuming  $r = 1$ . If the prices are equal ( $P_A = P_B$ ), the optimal patch for all vessel sizes is the patch with the highest density of A. The reason for this is that because  $\rho > 0$ , the efficiency for species A is by definition greater than that for species B. The numerator is hence by definition larger than the denominator, making the inequality true. Therefore, the catches of species B cannot make up for the loss in catch rates of species A when moving towards patches with greater densities of B. This situation is illustrated in Figure 2a, where both vessel types would choose the patch with the highest density of species A ( $D_A = 1$ ). If the price of species B is much higher than species A, e.g.  $P_B/P_A = 5$ , both fleets choose to fish in patches with the highest density of the deeper-burrowing species B ( $D_A = 0$  in Figure 2c). However, if the price of species B lies between the ratio of gear efficiencies A:B of the two vessel types, the maximum net revenue for the smaller vessels is found at the patch with maximum abundance of species A (Figure 2b). The increased revenue attributable to increases in species B at other patches cannot make up for losses in A because of the inaccessibility of B for those vessels. However, the larger vessels can attain higher revenues at the patches with greater abundances of B through their greater catch efficiency for B. For this reason, the larger vessels will choose the patches with maximum levels of species B ( $D_A = 0$  in Figure 2b).

### Model results with interference competition

To study the model with interference through prey depression, two distributions of the two prey species were chosen: (i) an environment where species A and B are jointly distributed over the patches, with poor patches lacking both A and B, ranging to good patches with both high densities of A and B ( $r < 0$ ), and (ii) an environment similar to the model without prey depression, with the densities of A negatively related to the abundance of B

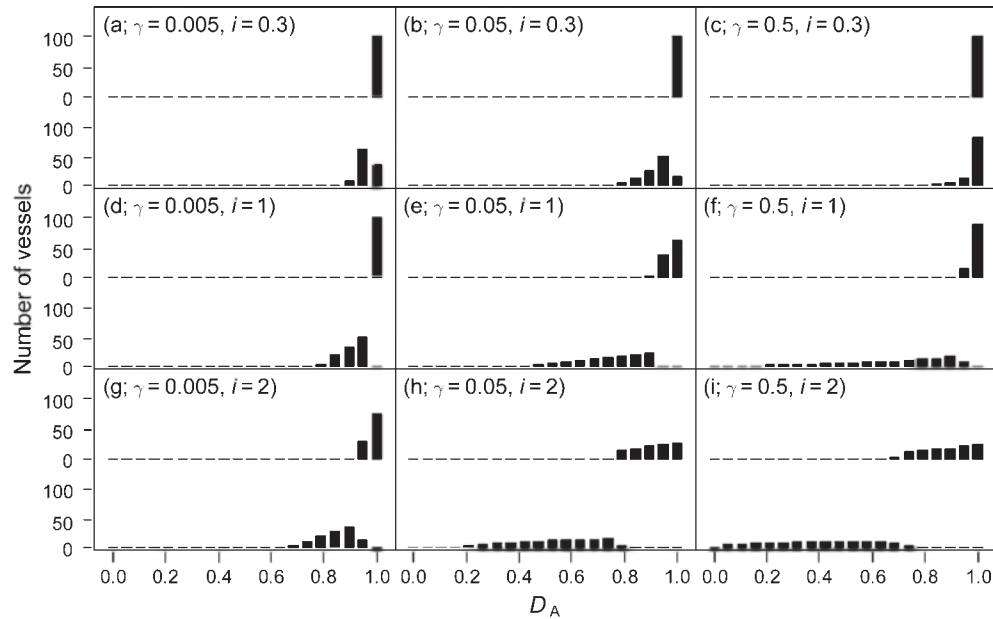


**Figure 2.** The total revenue from two species for large (dashed line) and small (complete line) vessels (left axis) from a patch, for three different price ratios: (a)  $P_B/P_A = 1$ , (b)  $P_B/P_A = 1.625$ , and (c)  $P_B/P_A = 5$ . The patches are ordered in increasing densities of species A ( $D_B = \beta - rD_A$ ,  $r = 1$ ). The resulting vessel distribution based on the revenue is represented by the bar graphs in the panels. In each panel, the distribution of the large vessels is represented by the top bar chart and that of the small vessels by the bottom bar chart.

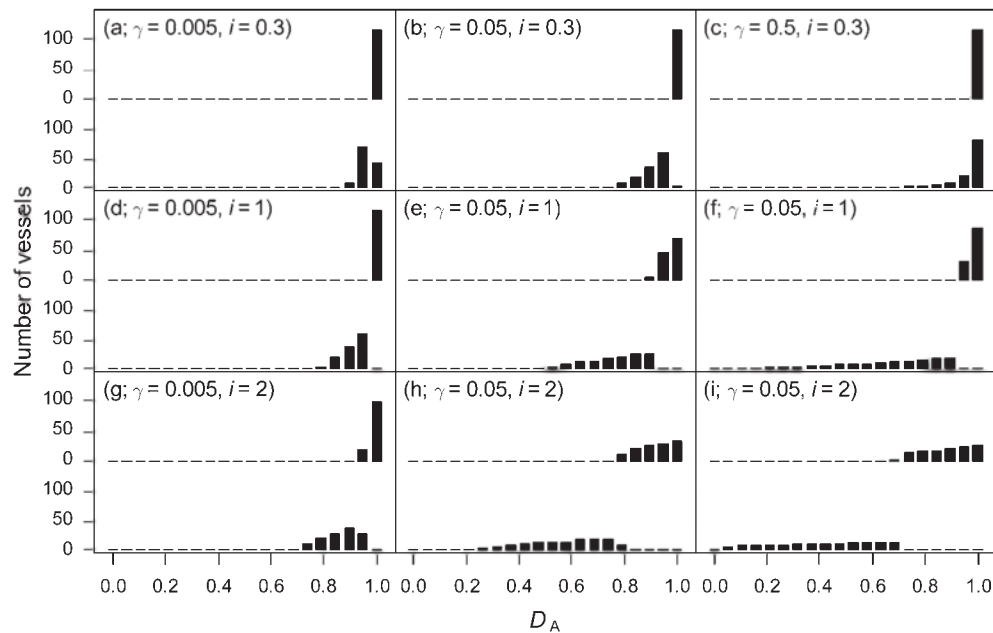
( $r > 0$ ). For the two scenarios, the effect of a price difference between the two species on net revenue is analysed.

Model results without spatial segregation of prey species ( $r = -1, \beta = 0$ ) are illustrated in Figures 3 and 4. In the absence of interference competition through prey depression, both vessel types chose the patch with the greatest abundance for both species, irrespective of price differences. If interference competition is added to the model and prices for prey species are equal, large vessels would choose the patches with the greatest

abundance of both prey species (Figure 3). If the maximum increase in burrowing depth is small, e.g.  $i = 0.3$  in Equation (3), the effect on revenue obtainable by the larger vessels in the best patch does not affect the choice made by these vessels. However, smaller vessels cannot access species A in that patch, which burrowed deeper as a consequence of the fishing activity of the larger vessels. The smaller vessels would also choose the patches with lesser abundances of A and B (Figure 3a–c). The interference competition within the group of smaller vessels



**Figure 3.** Patch choice of large and small vessels in the absence of resource segregation with equally priced species. Each of the panels represents a combination of the two parameters  $i$  and  $\gamma$  determining the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.



**Figure 4.** Distribution of large and small vessels in the absence of resource segregation with species B being 1.4 times more valuable than species A. The parameters  $i$  and  $\gamma$  determine the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.

causes their fishing activity to be spread over several of these patches. Under increasing maximum burrowing depths of the prey species (corresponding to increasing  $i$ ), the effects on revenue rates start influencing the patch choice of the larger vessels, spreading them over patches with lower prey abundances (Figure 3d–i). Because of the lower weight of the gear, smaller vessels can no longer fish in the patches occupied by large vessels, similar to the previous situation with lower maximum burrowing depths. Again, smaller vessels fish in a large number of patches with lesser abundance. Difference in prices between the two species does not substantially affect the model results (Figure 4).

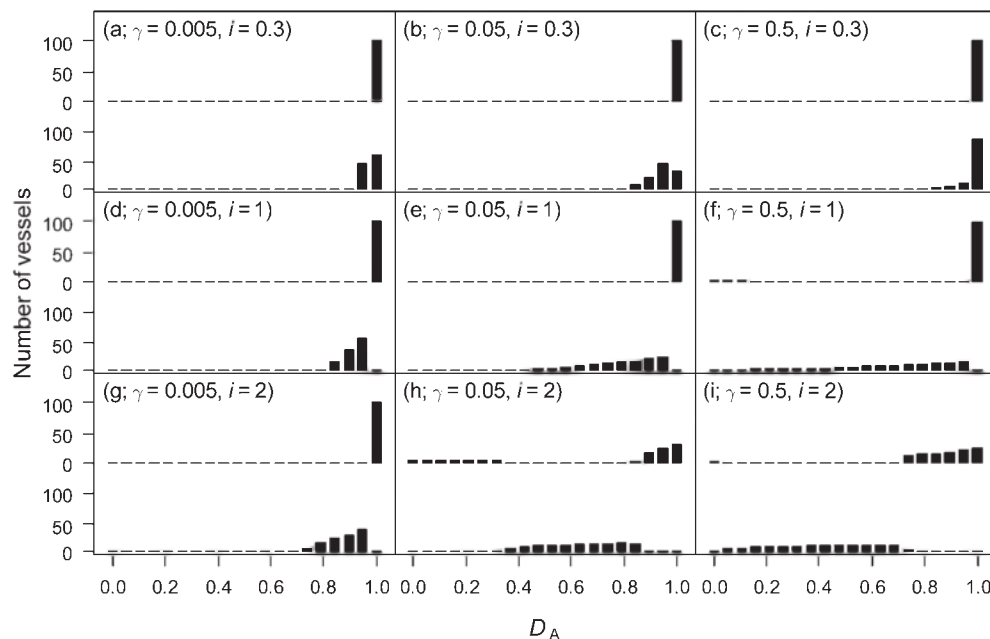
Model results with segregation of the prey species ( $r = 1$ ,  $\beta = 0$ ) are presented in Figures 5 and 6. The model without interference competition shows that both types of vessels choose the patch with the greatest abundance of A, if prices for both species are equal. Adding prey depression to the model changes the distribution of the vessels. If prey depression is small ( $i = 0.3$ ), most small vessels would still choose the patches with the greatest abundance of A and a few vessels select patches with a lesser abundance of A (Figure 5a–c). If prey depression increases, e.g.  $i = 1$ , the two types of vessel become spatially segregated. Large vessels choose the patch with the greatest abundance of A, and smaller ones the patches with lesser abundance of A, because the catch rates in the patch occupied by large vessels have decreased owing to the increase in average depth of prey species A (Figure 5d–f). Further increase of the prey depression ( $i = 2$ ) results in a spreading out of the larger vessels over the patches because the average depth of species B now exceeds the reach of the gear in heavily exploited patches (Figure 5g–i). The small vessels can only compete with the large vessels in a limited number of patches, preferring the patches with high abundance of A, because species B is not accessible to them. Depending on the strength of the prey depression, a small fraction of the large vessels may choose the

patches with low abundance of A and high abundance of B, avoiding competition in the patches with high abundance of A, and being able to catch a (limited) fraction of B. In that case, the small vessels are forced to choose the patches with intermediate abundance of either prey species (Figure 5).

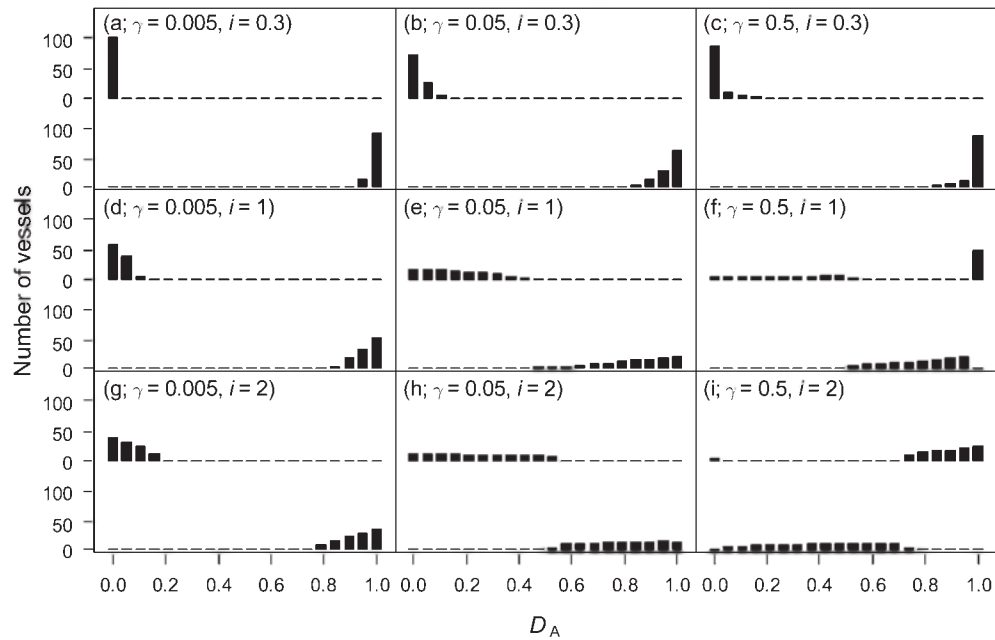
If prey species are segregated, and the deeper-burrowing species B is more valuable than species A, and the effect of interference competition through prey depression is small ( $\gamma = 0.005$ ,  $i = 0.3$ ), then there is strong spatial segregation of fishing effort (Figure 6a). The differences in gear efficiency between the prey species in interacting with the difference in price dominate the response. This result is similar to the result of the model without interference competition. However, the interference competition may spread out the two fleets at each end of the resource spectrum. For increasing prey depression, the interference competition between the two fleets results in a situation where the large vessels occupy both ends of the spectrum, leaving only the patches with moderate and more-equal quantities of the two prey species to the small vessels, which again show preference to the patches with a relatively high abundance of A. Hence, the difference in spatial distribution of the fleets that result from price differences between the two species is mitigated by strong interference competition. Therefore, the interference competition may lead to similar distributions of fleets, independent of the price of the species.

#### Spatial segregation in the Dutch beam trawl fleet

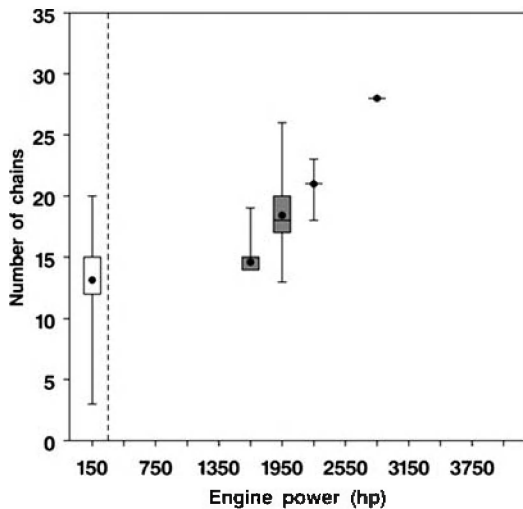
In the Dutch beam trawl fleet, the number of chains used in front of the net is positively related to the engine power of vessels  $>300$  hp (Figure 7). This observation confirms the hypothesis that the greater power in large beam trawlers is used to increase the penetration of the gear. The large number of chains in the fleet segment  $<300$  hp is linked to legislation prohibiting beam lengths  $>4.5$  m for these vessels. Therefore, those vessels are able to use more chains at lower engine power owing to the



**Figure 5.** Distribution of large and small vessels in the presence of resource segregation and equal prices. The parameters  $i$  and  $\gamma$  determine the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.



**Figure 6.** Distribution of large and small vessels in the presence of resource segregation and different prices. The parameters  $i$  and  $\gamma$  determine the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.



**Figure 7.** Box and whisker plot of the number of chains in the beam trawl gear as a function of vessel engine power. The top and bottom edges indicate the sample 25th and 75th percentiles, the horizontal line drawn within the box marks the median, and the dot marks the sample mean. The whiskers indicate the range. The dashed vertical line indicates the 300 hp limit, and shaded boxes indicate observations for vessels with engine power  $> 300$  hp. Smaller vessels have smaller beam widths by legislation, so may have more chains per horsepower than larger vessels.

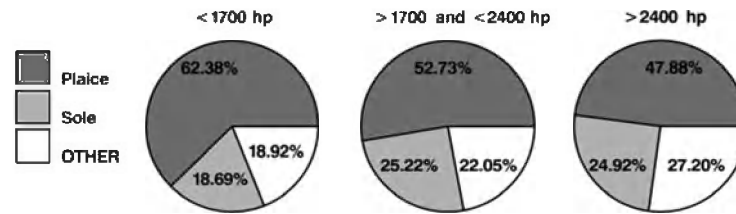
shorter lengths of the chains. For vessels  $> 300$  hp, the catch rates of the two species lie within the same order of magnitude, with plaice dominant in weight (Figure 8) and sole dominant when expressed in terms of value (not shown). Moreover, the contribution of plaice in the catches of the smaller vessels is larger than for the larger vessels, and the opposite is true for sole. As

there are no independent data available on the absolute abundances of the species in the patches visited, no conclusion can be drawn on the cause for this difference. However, possible causes could be the differences in gear efficiency or a combined effect of differences in gear efficiency and patch choice.

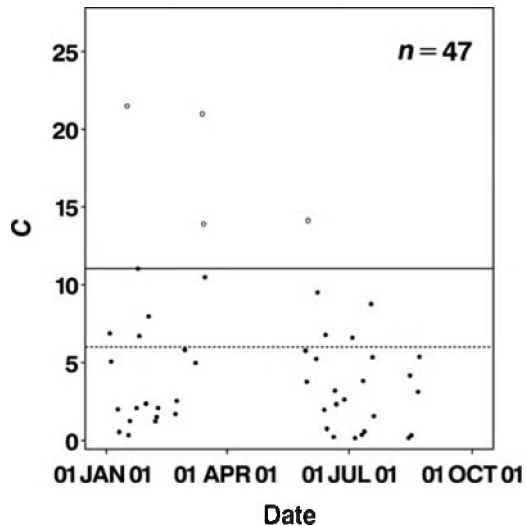
As the sample does not always meet the requirement of having  $> 66\%$  of the vessel types present in the sample at each time-step, some periods were not tested, resulting in a different number of time-steps tested for each comparison of size classes. Also, limited fishing activity in the holiday season between mid-July and mid-August results in a lack of tests in that period. In all, 47 time frames could be used for testing the  $C$  statistic. The sequential Bonferroni corrected  $\alpha = 0.05$  level for the  $C$  statistic for this number of tests was 18.1. In contrast, the uncorrected  $\alpha = 0.05$  level for the  $C$  statistic was 5.991. The tests show time-steps with significant positive  $\chi^2$  values, indicating spatial segregation between size classes (Figure 9), but only 4 of the 47 (8.5%) time-steps had significant  $C$  test statistics that exceeded the sequential Bonferroni corrected threshold.

## Discussion

We have presented and analysed a model of possible mechanisms that may result in segregation in the spatial distribution of fishing vessels operating in a multispecies flatfish fishery. The results reveal potential segregation between two fleet segments with unequal competitors through spatial segregation in prey species, price differences, and interference competition through prey depression. In the absence of interference competition, the segregation between fleets depends on differences in the distribution and prices of the prey species, combined with differences in catch efficiency. If the two species are segregated, price differences may lead to segregation in fleets with different efficiencies for the two species. In the presence of interference competition through



**Figure 8.** Landings composition by weight for three different size classes of Dutch beam trawler fishing the North Sea.



**Figure 9.** Test statistic  $C$  for spatial segregation for two size classes of Dutch beam trawl vessels, split at 1900 hp. Each dot represents a single test within a 2-h time frame at noon. Open circles indicate a statistically significant deviation from a random labelling hypothesis using sequential Bonferroni correction. The solid horizontal line indicates the corrected critical value of  $C$ , the dotted line the uncorrected critical value of  $C$ , and  $n$  is the number of tests.

prey depression, segregation can take place in the absence of price difference or segregation in the prey.

In field data, the prerequisites for segregation deriving from the multispecies nature of the fishery are met. First, the environment in which the beam trawl fleet operates creates opportunities for targeting multiple species. Our results indicate that sole and plaice indeed comprise a large part of the catch, in both weight and value, corroborating the results in Gillis *et al.* (2008). The larger vessels land more of the deeper-burrowing target species. The exploited part of those stocks is spatially segregated, at least during part of the year (Rijnsdorp *et al.*, 2006; Poos and Rijnsdorp, 2007a).

The empirical data exhibited segregation in the spatial distribution between the two size classes of beam trawlers. However, the segregation did not seem very strong, some 8% of the observations being significantly segregated. The limited number of significant cases may result from low power of the statistical test, owing to the small sample size of VMS data. Alternatively, factors not included in our model, such as incomplete information and information exchange, travel costs, and management constraints, may play a role in spatial effort allocation and influence the degree of segregation.

Within the Dutch beam trawl fleet, there is substantial variation in the engine power of fishing vessels, and a positive relation

between the engine power of vessels and the number of chains used in the fishing operation. Gear efficiency for sole and plaice depends on the number of chains used in front of the net (Creutzberg *et al.*, 1987). For sandy seabeds, the slope of this relationship for sole is estimated to be four times steeper than for plaice. Although the exact shape and form of the plaice response is not mentioned in the work of Creutzberg *et al.* (1987), the weak response can be an approximation to the asymptotic value, found for juvenile plaice < 15 cm for a 2-m beam trawl gear in the Wadden Sea (Kuipers, 1975). It should be noted that the number of chains in the experiments made by Creutzberg *et al.* (1987) was less than observed within the fleet. Finally, there is a marked difference between the prices of the two species, with the deeper-burrowing sole being approximately four times more valuable than plaice (Rijnsdorp *et al.*, 2000a). The catch composition of the vessels shows differences in the contribution of sole and plaice. As expected, sole contribute more to the catches in the large vessels than to the smaller vessels, and the reverse is true for plaice.

Spatial and ecological segregation according to efficiency for different prey has been observed in ecological studies for a wide range of species. For example, oystercatchers (*Haematopus ostralegus*) with different bill lengths specialize differently in feeding techniques and diet (Durell *et al.*, 1993). Ecological segregation can also be attributed to ontogenetic diet shifts from small to larger prey species (Daan, 1973; Aarnio *et al.*, 1996; Vinagre *et al.*, 2008).

Our study indicates that the multispecies nature of the Dutch beam trawl fishery in combination with price differences and interference competition is a plausible mechanism for spatial segregation between the two size classes of vessel. It is not possible to quantify the contribution of price differences or interference competition to spatial segregation. To disentangle the roles of spatial segregation, prices, and interference competition through prey depression, the parameters involved would have to be quantified.

In fisheries, experiments on the depression of target species generally face practical problems owing to the scale of the fishing operation and because observing the effect of the gear on the avoidance behaviour of prey is cumbersome, if not impossible. However, in general, many species exhibit quantified antipredatory behaviour (Lima and Dill, 1990). For redshanks (*Tringa totanus*) feeding on *Corophium volutator*, parameter estimates available from Goss-Custard (1970) were used in a model to show that the strength of the competition depends on the search strategy used by the forager (Stillman *et al.*, 2000). In the field, redshanks indeed used a search strategy that avoided patches used previously, sustaining high feeding rates (Yates *et al.*, 2000).

The effects of fisher behaviour following the IFD assumptions for fish stock assessments have been discussed extensively (Gillis and Peterman, 1998). Addition of the mechanisms proposed in this study may also affect the relation between nominal fishing effort and fishing mortality. A previous study has indicated



differences in fishing power and susceptibility to interference competition within the Dutch beam trawl fleet (Rijnsdorp *et al.*, 2000a). The difference in response of gear efficiency between sole and plaice was also used to explain the race for ever more powerful vessels in the 1970s and 1980s (Daan, 1997). One may expect that a fleet evolving towards ever more powerful vessels concentrates on fishing grounds with the deeper-burrowing species, resulting in strong increases in catchability for that species. Such changes have indeed been observed for the Dutch beam trawl fleet over the past five decades (Rijnsdorp *et al.*, 2008).

To conclude, weak spatial segregation between vessels of different engine size and gear efficiencies for different species have been found in the Dutch beam trawl fleet. Two alternative mechanistic hypotheses about the beam trawl fishery predict spatial segregation between size classes of vessels. One of these hypotheses depends on the difference in competitive ability between the classes, and the other depends only on the difference in catchabilities of the different target species. Several of the mechanisms involved in the two hypotheses on segregation were indeed found in the fleet studied. The extent to which each of these mechanisms plays a role in effort allocation of the fishery should be determined by carefully designed experiments. In such an experiment, differences in burrowing depth, and in the prey depression resulting from avoidance of the gear, need to be quantified.

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