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Competitive interactions among beam trawlers exploiting local patches of flatfish in the North Sea

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The fishing pattern of individual beam trawl vessels comprises alternating searching and exploitation phases during a fishing trip. The searching phase is characterized by a below-average catch rate and a long distance between the midpoints of hauls. The exploitation phase is characterized by an above average-catch rate and a small inter-haul distance. During the exploitation of a local concentration of flatfish, the catch rate decreases on average by 10% over a period of 48 h. The rate of decline is a function of the engine power. Powerful vessels experience a small or no decline in catch rate, whereas less powerful vessels experience a decline of up to 16%. It is inferred that the decline in catch rate may be due to interference competition among vessels through a change in the behaviour of flatfish in response to fishing disturbance, although a reduction in local abundance may also have contributed to the decline. Areas with above-average catch rates may change on a weekly basis.

Key words: fleet dynamics, effort allocation, optimal foraging, fishing power, interference competition.

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Introduction

In the field of behavioural ecology, the foraging decisions of natural predators are analysed in terms of a trade-off between costs and benefits to maximize the net revenue (Krebs and Davies, 1978). The revenue is not only affected by the distribution and availability of prey items, but also by the presence of conspecifics. Due to competitive interactions, the capture rate may fall disproportional with density of prey (Goss-Custard, 1980; Ens and Goss-Custard, 1984; Milinski and Parker, 1991).

Competitive interactions play an important role in the understanding of the distribution of predators in relation to their prey. Without such competitive interactions, all predators gather in the best food patch, whereas in the case of interference interactions, predators will also exploit poorer food patches. In this situation, the better patches will have higher densities of predators but the prey capture rate will be similar, irrespective of the quality of the patch (Frettwel and Lucas, 1970; Sutherland, 1983; van der Meer and Ens, 1997).

This theoretical framework has been successfully applied to the study of effort allocation within fishing fleets (Hilborn, 1985; Abrahams and Healey, 1990, 1993; Gillis and Peterman, 1998). Although competitive interactions may be inferred from the distribution of fishing vessels (Hilborn and Ledbetter, 1979; Healey and Morris, 1992; Gillis *et al.*, 1993), direct evidence is scarce. In an experimental study, Abrahams and Healy (1993), manipulated vessel density of salmon trollers and found that catch rates in the low-density area were higher for chinook salmon and spiny dogfish supporting competitive interactions. However, no such effect was observed for coho salmon. Competitive interactions among beam trawlers are likely since beam trawlers exhibit a patchy distribution with more than 70% of effort concentrated in only 20% of the fished area (Rijnsdorp *et al.*, 1998). Strong support for interference interactions comes from a study that showed that individual catch rates of beam trawlers increased by 10% when vessel density was reduced to about 25% of the initial density (Rijnsdorp *et al.*, 2000). It was also demonstrated that catch rate was positively related to engine power while the increase in catch rate could only

Table 1. Summary of the data analyzed.

Set	Vessel code no.	Engine power (hp)	Year	Number of hauls	Number of trips
1	81	300	1993	567	13
2	81	300	1995	449	11
3	22	1500	1993	339	9
4	22	1500	1994	1477	35
5	83	1800	1993	1025	27
6	88	1800	1994	1079	32
7	45	1900	1993	83	17
8	45	1900	1995	1610	44
9	44	2000	1994	529	13
10	44	2000	1994	1208	30
11	44	2000	1995	1409	34
12	46	2000	1993	784	21
13	46	2000	1994	1169	33
14	46	2000	1995	327	14
15	49	2000	1994	860	26
16	49	2000	1995	615	36
17	21	2000	1993	614	14
18	21	2000	1994	1244	30
19	21	2000	1995	1484	35
20	85	2000	1995	1118	22
21	82	2000	1993	769	21
22	82	2000	1995	878	24
23	48	2200	1993	472	10
24	48	2200	1994	849	21
25	48	2200	1995	1017	27
26	89	2286	1994	1198	21
27	89	2286	1993	938	29
28	91	2364	1995	1070	29
29	86	2365	1993	727	19
30	50	3835	1994	724	17
31	50	3835	1995	1251	31
Total				27 883	745

be partly explained by the larger area swept per unit of time by the more powerful vessels, suggesting that the competitive ability increased with engine power.

Here, we focus on the dynamics of spatial fishing patterns of individual vessels to study competitive interactions within the Dutch beam trawl fleet. First, changes in fishing grounds during individual fishing trips will be analyzed in relation to the catch rate per haul in order to determine whether vessels tend to exploit local patches of flatfish. Then, changes in catch rate at such local patches will be analyzed in relation to the engine power of the fishing vessel.

Material and methods

Data

The data originate from a study of the micro-distribution of 25 beam trawl vessels using an automated device recording the position of the vessel at 6 min intervals (APR recordings) with an accuracy of ± 180 m (Rijnsdorp *et al.*, 1998). In addition to detailed data on track positions, some of the vessels provided data on the catch (kg) per haul of the target species sole (*Solea solea* (L.)) and plaice (*Pleuronectes platessa* L.) and the times of shooting and hauling of the gear.

In total 31 data sets, defined as the records from one vessel in one year, were analyzed (Table 1). Due to failure of the automatic position recording system, or gaps in the supply of additional logbook data, the number of hauls differed among sets. Of the total of 27 883 individual hauls, 26 577 valid hauls were available for analysis. The remainder were excluded because of gear damage or otherwise non-representative catch rates.

Beam trawl vessels make fishing trips lasting four to five days (Rijnsdorp *et al.*, 2000). Having reached the fishing grounds, the twin beam trawls are shot and fishing commences. One haul lasts approximately 2 h. After hauling the gear and emptying the cod end, the gear is set again. A typical 4-day fishing trip is illustrated

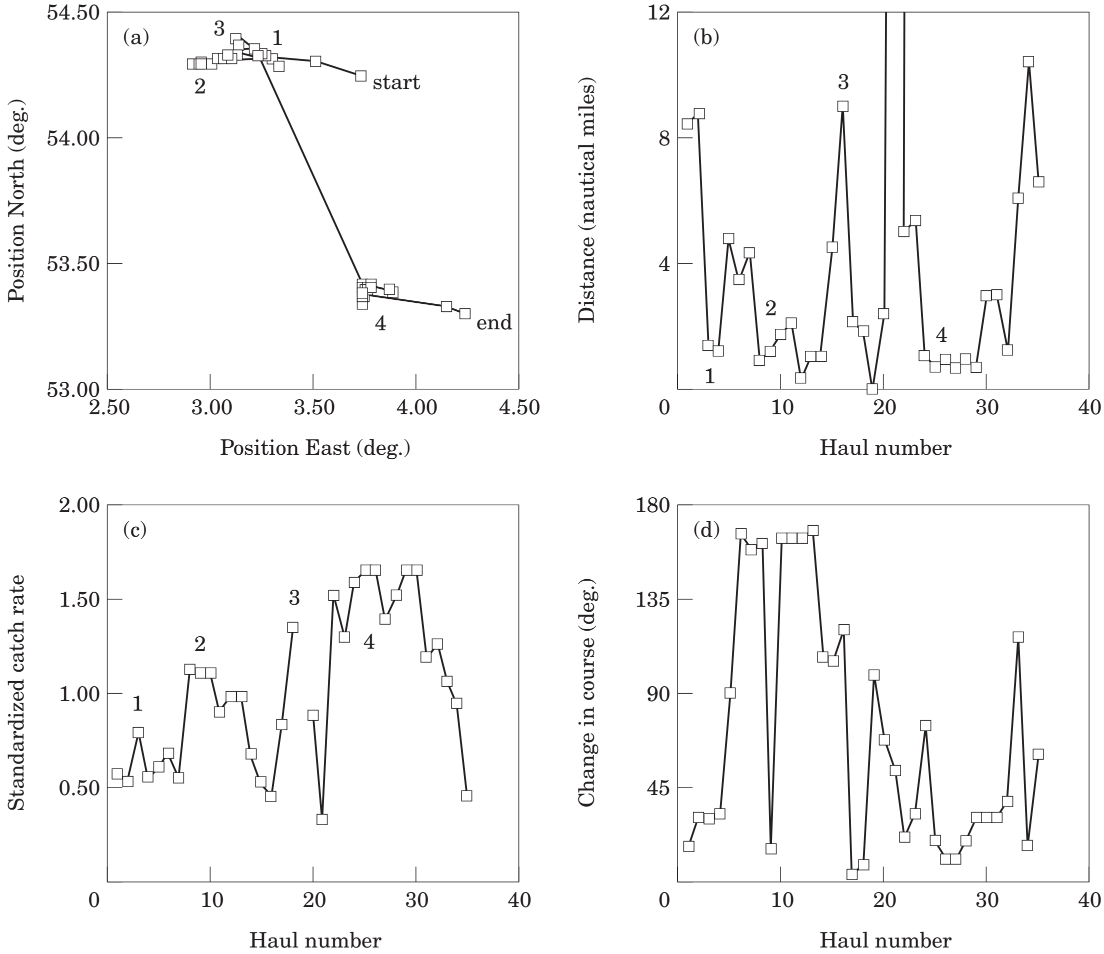

Figure 1. Dynamics of the catch rate and fishing pattern during a single fishing trip of a beam trawler fishing for sole and plaice. (a) Map of the midpoints of hauls; (b) distance (nm) between midpoint of consecutive hauls; (c) catch rate (kg h^{-1}); (d) change in course between consecutive hauls. The numbers 1–4 refer to the centres of high catch rates.

in Figure 1.[1] The geographic fishing pattern is related to the changes in catch rate during successive hauls and can be analyzed in terms of distance and change in direction between successive hauls. The fishing trip comprised 36 hauls in two groups. After 21 consecutive hauls, centred on three local concentrations (area 1, 2 and 3), the vessel steamed to another area (4), where another 15 hauls were conducted. After an initial phase of a relative low catch rate (Fig. 1C), a large inter-haul distance (Fig. 1B) and a steady course (Fig. 1D), the fishing pattern changes into one characterized by a high catch rate and short inter-haul distance. The small inter-haul distance may coincide with a more or less steady course (±30°), indicating that the vessel changed its course during the haul (area 4), or may coincide with a change in course of ±180°, indicating that the vessel was fishing along a line for 1–2 hauls and then returning over the same ground (area 2). After a period of high catch rates and low inter-haul distances, catch rate decreases and the inter-haul distance increases.

Data treatment

For each haul i, the catch rate was calculated as the revenue per unit of fishing effort: RPUEi=4 × kg (sole)+kg (plaice). The factor 4 reflects the annual difference in market value (Rijnsdorp *et al.*, 2000).

Catch rate is affected by a variety of variables, such as time of day, time of year, vessel characteristics (engine power) and fishing ground (de Groot, 1971; Rijnsdorp *et al.*, 2000). Catch rates were standardized in a two-step procedure. First, catch rates (RPUEi) were standardized to the mean catch rate in the fishing trip, to correct for the effects of the vessel and time of year:

$$Yi = RPUEi/mean(RPUE).$$

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[1] A complementary figure of fishing speed recordings at 6-min intervals of this fishing trip is given in Rijnsdorp *et al.* (1998).

In a second step, the catch rate (Yi) was corrected for the time of day (t) by dividing catch rate by predicted catch rate (Ypred) from the periodic regression:

$$\text{Ypred} = \alpha + \beta\sin(t) + \gamma\cos(t) + \text{month} + \beta'\text{month} \times \sin(t) + \gamma'\text{month} \times \cos(t) + \varepsilon$$

$$Y'i = Yi/\text{Ypred}.$$

The logbook data were linked to the APR recordings to determine the position at the start and the end of each haul as well as the mean position during the haul. For each haul, direction (degrees from north) and distance (nautical miles) between the start of the haul and the start of consecutive hauls were calculated.

Individual hauls were classified according to spatial windows of 10′ latitude and 20′ longitude (± 10 × 10 nm) based on the mean position during the haul. The number of hauls carried out in each window was calculated for each fishing trip. The 10 × 10 nm resolution is in close correspondence to the distance covered during a typical 2-h haul following a straight course and a fishing speed of 6 nm · h^{-1}.

In a second analysis, a higher spatial and temporal resolution of 1′ latitude and 2′ longitude was applied (± 1 × 1 nm). In this case, the standardized catch per haul (Y'_i) was assigned to all 1 × 1 nm squares visited. It was shown previously that beam trawling was randomly distributed within 1 × 1 nm squares (Rijnsdorp *et al.*, 1998).

In order to evaluate the possibility of depletion of a local fishing ground, the surface area of a fishing ground and the proportion swept by the gear were estimated. The surface area of the fishing grounds was estimated as the number of 1 × 1 nm squares in each 10 × 10 nm square that was fished during one trip. The area swept by the gear was calculated from (i) the number of hauls, haul duration (2 h), fishing speed (6 nm h^{-1}) and width of the gear (2 × 12 m) and (ii) the frequency of APR recordings per 1 × 1 nm square recorded by fishing trip. One APR registration (6 min) corresponds to a surface area trawled of 0.0267 km^2. At 53°N, the surface area of a square of 1′ latitude and 2′ longitude equals to 1.852 × 2 × 1852 × cos (latitude) = 4.13 km^2. Hence, at 4.13/0.0267 = 155 APR registrations at 1′ latitude and 2′ longitude window, will be trawled completely (Rijnsdorp *et al.*, 1998).

Statistical analysis

Statistical analyses were carried out employing the GENMOD routine (SAS, 1993). The assumption that the error term ε is normally distributed was tested by visual inspection of the probability ploty of the residuals.

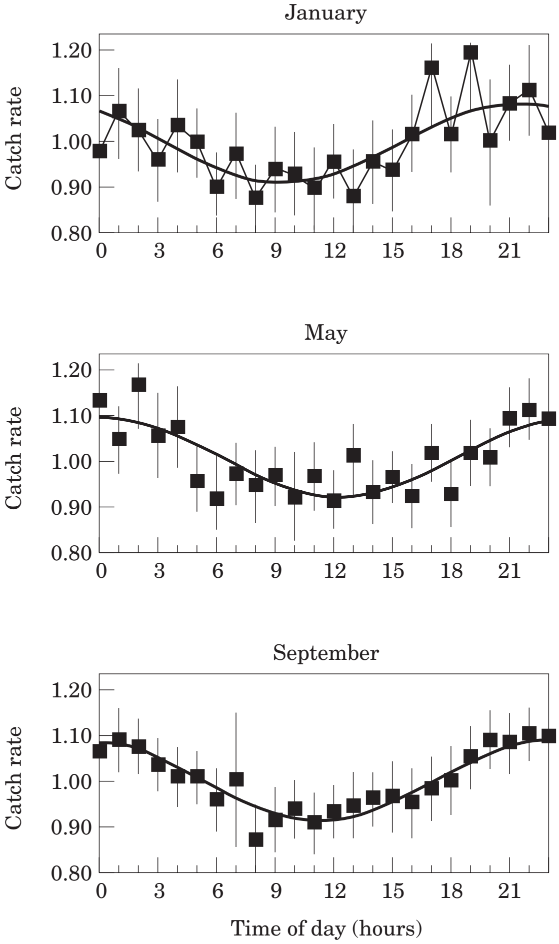

Figure 2. The mean and approximate 95% confidence interval (± 2 s.e.) of the standardized catch rate per hour of the day and the fitted periodic regression (full line) in January (a), May (b) and September (c).

Results

The catch rate showed a clear diurnal pattern throughout the year with highest catch rates at night and lowest catch rates in the day (Fig. 2). The effect of the time of day was highly significant ($F_{37,26539} = 18.29$, $p < 0.01$) and explained about 3% of the total variance (Table 2).

The mean distance between consecutive hauls decreased from about 6 nm at catch rates less than 0.5 to a distance of 1 nm or less at catch rates above 1.5 times the weekly average (Fig. 3). The frequency distribution of changes in direction between consecutive hauls showed a peak at a steady course of 0–15° irrespective of the catch rate (Fig. 4). At catch rates above two times the weekly mean, a second peak occurred at a change in course of 165–180°, reflecting a complete turn in direction. Intermediate changes in course occurred less frequently. These results indicate that vessels tended to fish

Table 2. Results of the periodic regression of the standardized catch rate of flatfish ($Yi=RPUEi/mean(RPUE)$) as a function of the time of day (t) and month (m=1 to 12) according the model: Y=intercept+sin(t)+cos(t)+month+month*sin(t)+month*cos(t).

	SS	df	MS	F	P
Full model	110.80	37	2.995	18.29	<0.01
Unexplained	4345.35	26 539	0.1637		
Total	4466.17	26 576			

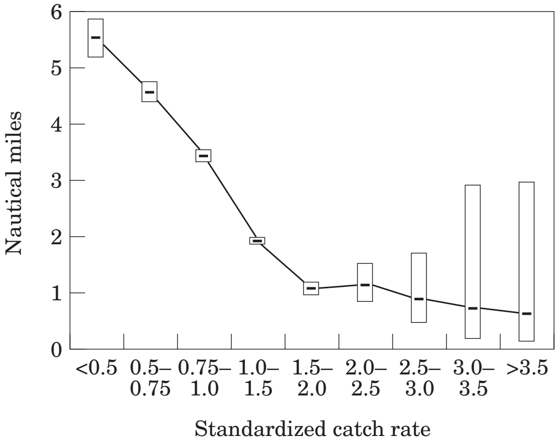

Figure 3. Mean and approximate 95% confidence interval (± 2 s.e.) of the distance (nautical mile) between the midpoints of consecutive hauls in relation to the standardized catch rate (Y'_i) in the previous haul. The distance was expressed as the distance covered during a two-hour haul.

along lines and make alternate hauls along a line when the catch rate is above average.

These results show that the fishing pattern of beam trawl vessels is composed of alternating periods of searching and exploitation. The searching phase is characterized by a relatively low catch rate, a more or less steady course and relative large distances covered between successive hauls. The exploitation phase is characterized by an above average catch rate, a small inter-haul distance and large changes in course.

To analyze the trend in catch rate during the exploitation of a local fishing ground, individual hauls were assigned to squares of 10′ longitude and 20′ latitude (± 10 × 10 nm). Catch rate showed a clear relationship with fishing intensity. In squares with 1–4 hauls, the catch rate was well below the weekly mean. In squares with more than 10 hauls, the catch rate was above the weekly mean and was independent of the number of hauls (Fig. 5). Fishing intensity varied substantially among the 10 × 10 nm squares. More than 80% of the hauls were taken in squares with more than 10 hauls during a trip (Fig. 5).

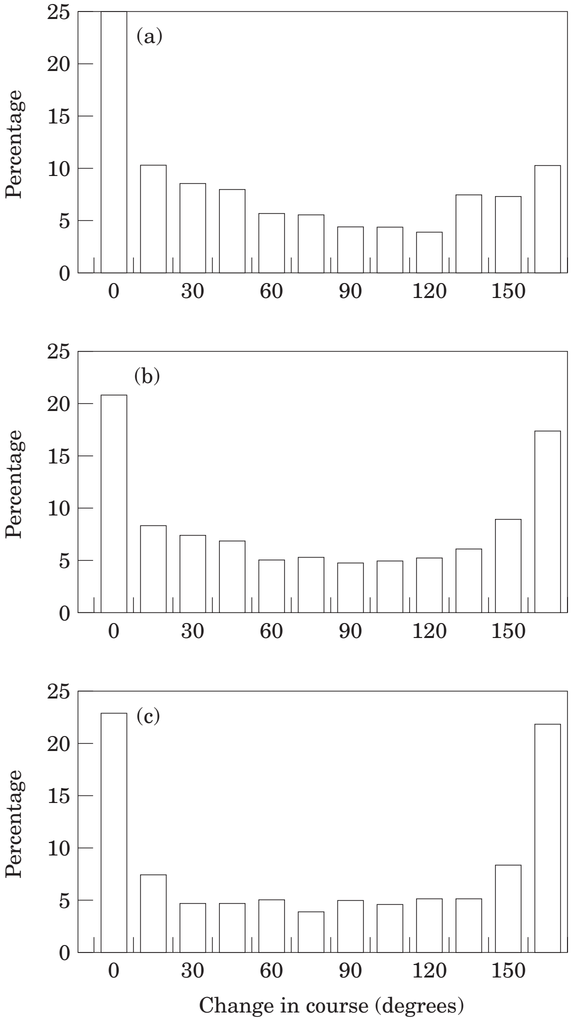

Figure 4. Changes in the fishing course (degrees) between consecutive hauls with: (a) low ($Y'_i<0.5$); (b) moderate ($1<Y'_i<1.5$) and (c) high standardized catch rate ($Y'_i>=2$). A change in course of 180° reflects that the vessel has turned around and fishes in the opposite direction over the ground fished during the previous haul.

In squares with more than 10 hauls in a fishing trip, the catch rate, calculated per 3-h period since the first haul, decreased with time elapsed since the start of fishing (Fig. 6). The decline occurred between 6–48 h of the first haul and amounted to about 10%. During the first 6 h, catch rate increased slightly. After 48 h no clear trend in catch rate was apparent. The slope in catch rate was slightly steeper in squares fished very intensively and corresponded to a higher initial catch rate (Table 3). Catch rate declined by about 4% per day in squares with 10–19 hauls, whereas in the squares with more than 30 hauls the decline was 7.5% per day. In squares with 1–4 hauls, the catch rate was well below the average weekly

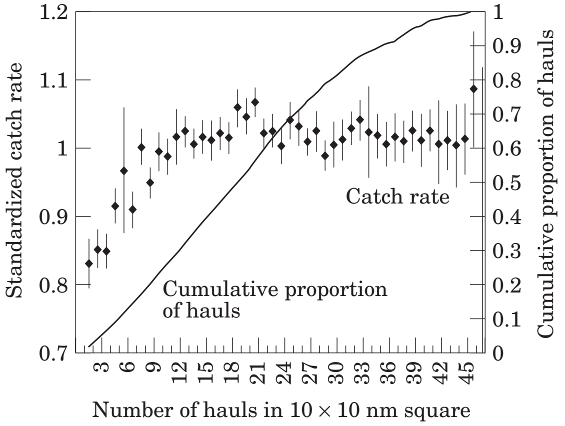

Figure 5. Relationship between the standardized catch rate (Y′$_i$) and the number of hauls taken in a 10 × 10 nm square during a trip (a) and the cumulative number of hauls (b).

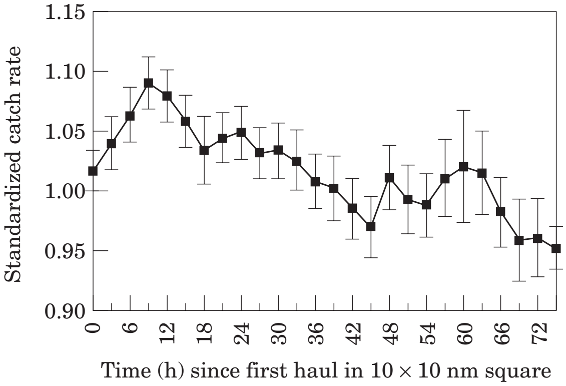

Figure 6. Mean and approximate 95% confidence interval (±2 s.e.) of the standardized catch rate (Y′$_i$) per 3-h period since the first haul in 10 × 10 nm squares which have been trawled by more than 10 hauls during a trip.

catch rate and did not show a relationship with the time elapsed since the first haul.

The decline in catch rate during exploitation of local fishing grounds differed among vessels. The decline appeared to be related to engine power. No significant decrease in catch rate was apparent in the vessels with higher engine powers, whereas the catch rate declined by up to 16% per day in the least powerful vessels (Fig. 7).

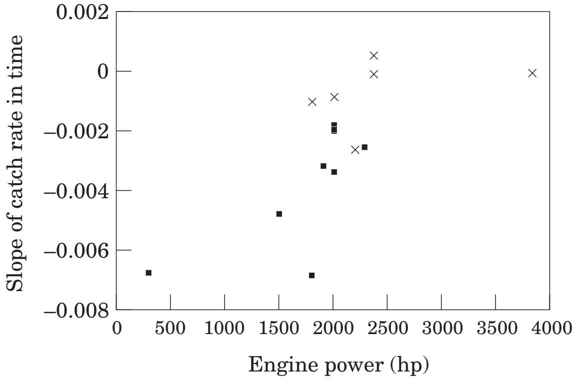

Figure 7. Scatter plot of the slope of the standardized catch rate (Y′$_i$) over time since the first haul in 10 × 10 nm squares fished with more than 10 hauls during a trip versus the engine power of individual vessels. The filled symbols represent slopes that differ significantly from zero at the 5% level.

In squares with more than 10 hauls, the size of a local fishing ground, estimated from the number of 1 × 1 nm squares fished, was on average 11.5 nm^2 (range 10–15 nm^2; Fig. 8). In squares with less than 10 hauls, the size was less than 10 nm^2. The area swept by the gear increased linearly with the number of hauls, but was considerably smaller than the size of the fishing ground (Fig. 8). For those 10 × 10 nm squares fished with more than 10 hauls, on average 2.3% of the surface area was swept.

A second approach to estimating the proportion of a local fishing ground swept was based on the relationship between the catch rate and the fishing intensity using the highest level of resolution (1 × 1 nm squares and APR recordings at 6 min intervals). Catch rate increased with fishing intensities up to 15 APR registrations. At higher fishing intensities, which only represented about 10% of all APR registrations, catch rate did not increase further

Table 3. Slopes of the linear regression of standardized catch rate (Y′$_i$) over the time (h) elapsed since the first haul for squares which are fished with a different intensity. The analysis used a time window of 6–48 h.

Number of hauls in 10 × 10 nm square	intercept	SE intercept	Slope	SE slope	r^2	n
1–4	0.933	0.0607	−0.0002	0.00202	0.000	15
5–9	1.015	0.0247	−0.0029	0.00082	0.502	15
10–19	1.066	0.0145	−0.0018	0.00049	0.517	15
20–29	1.115	0.0109	−0.0026	0.00037	0.801	15
30 plus	1.132	0.0136	−0.0032	0.00046	0.795	15

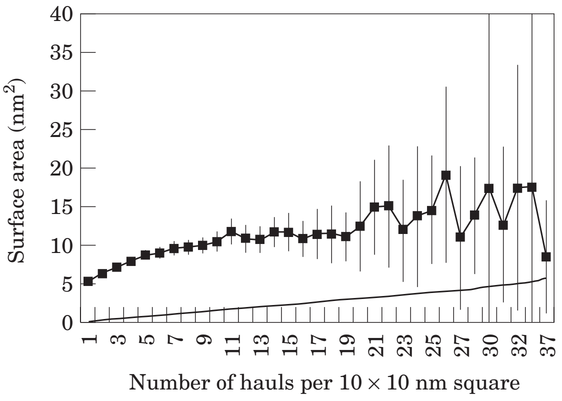

Figure 8. Size of a local fishing ground estimated as the mean number of 1 × 1 nm squares (±2 s.e.) within 10 × 10 nm squares fished in relation to the number of hauls taken during a one week fishing trip. The continuous line indicates the surface area swept by one vessel.

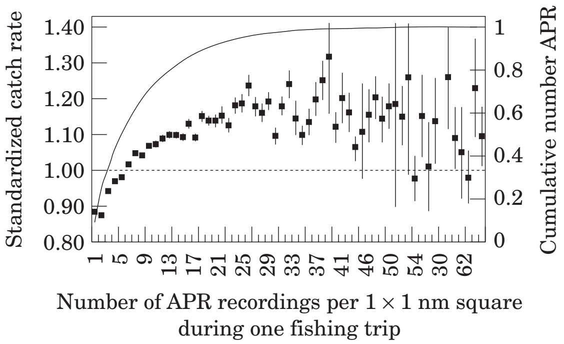

Figure 9. Standardized catch rate ($Y'_i \pm 2$ s.e.) in 1 × 1 nm squares (squares) in relation to the number of 6 min positions (APR) recordings. The full line shows the cumulative number of APR recordings.

(Fig. 9). When a local fishing ground is defined as those 1 × 1 nm squares with an above average catch rate, the average fishing intensity was 14 APR recordings. A total of 155 APR recordings (see Methods) is necessary to sweep a 1 × 1 nm square completely. Hence, only 10% of a local fishing ground will be fished by one vessel during one fishing trip (14/155).

There was a probability of 0.42 that a 10 × 10 nm square was revisited during the following week (Table 4). The probability of being revisited increased with trawling intensity in the previous week. Only 37% of the squares with 1–4 hauls during the first week were revisited during the next week, whereas 56% of the squares fished with ≥5 hauls in the first week were revisited in the subsequent week. The probability that a square is trawled with ≥10 hauls in trip i+1 increases with the trawling intensity in the previous trip.

In squares that were fished intensively in the first week (≥10 hauls) and which were revisited during the following week, the change in catch rate was analyzed over the two week period. Figure 10 shows that the catch rate declined during the first week and continued to decline, though at a slower rate, during the second week. The difference in the rate of decline seems to correspond with the difference in the number of hauls between the two consecutive weeks. If a selection is made of the squares that were trawled intensively in both weeks, a different picture emerges, indicating a recovery of the catch rate over the weekend when fishing intensity was reduced. The catch rate, however, appears to recover to a level below that of the first two days in the previous week.

Discussion

The catch rates analyzed here, which comprised an approximately equal share of sole and plaice, showed consistently higher catch rates during the night. This pattern corresponds to the diurnal activity pattern in sole and the lack of a consistent diurnal pattern in plaice (de Groot, 1971).

The fishing pattern of beam trawl skippers comprised of a searching and exploitation phase. The searching phase is in line with the concealed nature of the target flatfish species (sole and plaice) which cannot be detected

Table 4. Probabilities that a 10 × 10 nm square is being revisited in the consecutive trip (trip i+1) in relation to the number of hauls in trip in and trip i+1. The bottom row shows the proportion of occurrence of the number of hauls in trip i.

Number of hauls trip i+1	Number of hauls trip i:			
	All (>=1)	1–4	5–9	>=10
0	0.579	0.634	0.443	0.437
1–4	0.254	0.244	0.287	0.268
5–9	0.095	0.072	0.152	0.155
>=10	0.072	0.049	0.118	0.141
Sum	1.000	1.000	1.000	1.000
Proportion occurrence	1.000	0.709	0.178	0.113

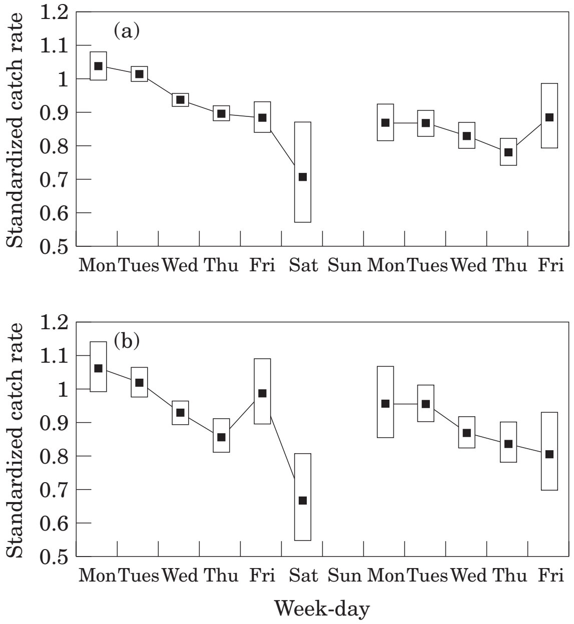

Figure 10. Mean standardized catch rate (Yí ± 2 s.e.) by week-day in squares which were fished with more than 10 hauls in the first week and which revisited during the following week (a). The same data for squares which were fished with more than 10 hauls in both consecutive weeks (b).

by echolocation because of the lack of a swimbladder and their benthic habits (Gibson, 1997; Wardle, 1986). Once a local patch of high prey density is found, the pattern switches to one where the vessel regularly changes its course during a haul or where the vessel fishes up and down a line. The exploitation phase is restricted to those areas where the catch rate is above average. When catch rate drops below the weekly mean, the fishing pattern changes to the searching phase again or the skipper may decide to stop fishing and steam to another fishing ground. The observed fishing pattern of beam trawlers, in conjunction to the decline in catch rate at a local fishing ground, is consistent with the marginal value model of Charnov (1976).

After an initial increase in catch rate during the first 12 h of exploitation of a local fishing ground, the catch rate showed a steady decline of about 10–15% over the subsequent 36 h. The initial increase in catch rate could be due to the time needed for a skipper to determine the boundaries of the local fish concentration. Another possible explanation is that fish move into recently trawled areas to feed on damaged or dead animals from the trawl track. This behaviour has been observed in a number of scavenger species such as dab and whiting, but not in plaice or sole (Kaiser and Spencer, 1996). On the other hand, the disturbance by trawling may chase away fish and dilute local fish concentrations.

The decline in catch rate may be due to depletion of a local fish concentration, interference processes, or both. In order to evaluate the possibility of depletion, we will attempt to estimate the proportion of the surface area of a local fishing ground swept during one week. This estimate is necessarily crude, as no independent information on the boundaries of the local fishing ground, the development in density of the fish, and the total fishing pressure on the local fishing ground, is available.

Assuming that local fishing grounds can be described at a spatial resolution of 1 × 1 nm squares, the percentage of a local fishing ground swept by one vessel was estimated at 2% and 10%. This assumption is supported by the observation that at this level of resolution beam trawl fishing is randomly distributed (Rijnsdorp *et al.*, 1998). As a local fishing ground will be fished by other vessels as well, the total proportion swept will be higher. Rijnsdorp *et al.* (2000) showed that ICES rectangles (30 × 30 nm) with an above average catch rate were fished on average by 10 Dutch beam trawl vessels. Under the assumption that all of these vessels exploited a local fishing ground within a 10 × 10 nm square, without an overlap in the area swept, the total proportion swept may be as high as 20% to 100%. This "worst case" scenario suggests that depletion of a local fishing ground may contribute to the observed decline in catch rate. However, it cannot explain the differences in slopes among vessels.

The steeper decline in catch rate of less powerful vessels as compared to more powerful vessels suggests that interference processes occurred among vessels. One possible mechanism may be that fish may become more alert or dig in the sediment deeper as a fishing ground is trawled intensively. As a result, fish may become less accessible to the lighter fishing gear of less powerful vessels towed at a lower speed than the heavier gear of more powerful vessels. This hypothesis is consistent with the belief held among many fishermen that a profitable fishing ground will lose its profitability when more powerful vessels join the fleet on a local fishing ground. Gillis (1999) provided evidence for interference competition among vessels through the reduction in catch efficiency of trawlers at higher vessel densities when the vessels had to alter their course more frequently to avoid collision. Such a process may occur at local fishing ground exploited by a number of vessels but cannot explain why less powerful vessels experience a faster decline in catch rate.

Whatever the mechanism of interference competition, the observed difference in the decline in catch rate at a local fishing ground in relation to the engine power provides an explanation for various observations: (i) the horse power race observed within the Dutch fleet since the re-introduction of the beam trawl in the early 1960s (Daan, 1997); (ii) the positive relationship between fishing power and horse power (Rijnsdorp *et al.*, 2000).

Further, it is consistent with the competitive interactions inferred from the observed geographical distribution of beam trawl effort (Rijnsdorp *et al.*, 2000).

The observed fishing pattern of alternating phases of searching for and exploitation of a local fish concentration will result in a concentration of vessels in local areas of high abundance of target species. In a study of the micro-scale distribution of beam trawlers, it was shown that beam trawling showed a patchy distribution with 70% of the fishing effort concentrated in only 20% of the surface area (Rijnsdorp *et al.*, 1998). On a time-scale of weeks, the heavily trawled areas may continuously change. The frequency with which 10 × 10 nm squares were revisited in successive weeks indicated that a good fishing ground in one week may not be good in the following week. The probability that a 10 × 10 nm square was fished in two consecutive trips with more than 10 hauls was 0.25 (0.141/(1–0.437) (Table 4).

The picture emerging is of a dynamic interaction between the fishery, the fish and their prey. Fish species will form local concentrations in relation to their food and local abiotic conditions (temperature). As these conditions vary in time, the fishery will have to search for local areas of high abundance continuously, reducing temporarily the local abundance of fish and also disturbing the remaining fish by their fishing activities. If conditions remain favourable, fish concentrations may rebuild after a week of exploitation and provide again profitable fishing opportunities for another week.

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