ICES Journal of Marine Science, 2022, **79**, 2093–2106
DOI: 10.1093/icesjms/fsac142
Advance access publication date: 12 August 2022
Original Article

Fishing tactics and the effect of resource depletion and interference during the exploitation of local patches of flatfish

A. D. Rijnsdorp [1,*], G. Aarts[1], N. T. Hintzen [1,2], J. C. van Rijssel[1], A. M. Winter[1] and J. J. Poos [1,2]

[1]Wageningen Marine Research, Wageningen University and Research, Haringkade 1, 1976 CP IJmuiden, Netherlands
[2]Aquaculture and Fisheries Group, Wageningen University, 6700 AH Wageningen, Netherlands

* *Corresponding author: tel: +31 317487191;* e-mail: adriaan.rijnsdorp@wur.nl

The fine-scale exploitation pattern of fishers and the interactions among fishing vessels determine their impact on exploited populations, habitats, and ecosystems. This study used a unique combination of high resolution data of fishing tracks (positions recorded at 1 and 6 min intervals) and catch rates of sole (*Solea solea*) and plaice (*Pleuronectes platessa*) per tow, to study how pulse trawl (PUL) and tickler chain beam trawl (TBT) fishers exploit patches of concealed flatfish. PUL and TBT fishers had similar tactics. Effort was concentrated in the core of the patch. PUL fishers trawled in a systematic manner with successive tows segments placed parallel to each other at a median distance of ∼200 m. In 45% of the cores, simultaneous trawling by multiple PUL vessels occurred. A total of 40% of the cores were revisited in the following week, of which 50% were re-exploited. Catch rate in the core was ∼50% higher than the background catch rate and decreased over time due to resource depletion and interference related to the response of flatfish to the fishing activities. Interference contributed up to 67% to the decline in catch rate and was larger in TBT than in PUL.

Keywords: area restricted search, beam trawl, competition, effort allocation, fishing behaviour, fishing grounds, fleet dynamics, North Sea, pulse trawl, sole.

Introduction

The study of the behaviour of fishers forms an integral part of fisheries science. The understanding and the ability to predict fishers behaviour is important for sustainable fisheries management (Hilborn, 1985; Salas and Gaertner, 2004; Fulton *et al.*, 2011; van Putten *et al.*, 2012) as well as marine spatial planning (Janßen *et al.*, 2018). Where to fish is one of the key elements in fishing behaviour (Hilborn, 1985; van Putten *et al.*, 2012) and has been studied using a variety of approaches. Most studies used statistical models to explore how the observed distribution of fishing vessels in space and time could be explained. Such studies generally showed the importance of previous catch rate and seasonal patterns in resource distribution as well as fishing cost and the safety of fishing operations (review in Girardin *et al.*, 2017). Other, more mechanistic studies have focused on the behaviour of individual fishers and modelled the consequences of behavioural rules or management constraints on effort distribution (Dreyfus-Leon, 1999; Dorn, 2001; Babcock and Pikitch, 2000; Poos *et al.*, 2010; Batsleer *et al.*, 2016). For these behavioural models to be effective, a mechanistic understanding of the search and exploitation behaviour in relation to resource hotspots is needed. Due to the absence of high-resolution (minutes) location data in combination with success in catch rates, such information was currently lacking.

The location choice of fishers will largely depend on the distribution of the fisheries resource that is often patchy. The precise locations of high-density patches of the target species are unknown, although the approximate location may be inferred from previous experience or from knowledge on the seasonal migration patterns of the resource (Poos and Rijnsdorp, 2007a; Santa Cruz *et al.*, 2018). For example, the occurrence and predictability of resource patches may be related to various biological mechanisms such as (pre-) spawning aggregations (Corten, 2002; van Overzee and Rijnsdorp, 2015; de Mitcheson, 2016), or winter aggregations (Horwood and Millner, 1998; Poos and Rijnsdorp, 2007a). Resource patches that are related to high density of suitable food for fish will be less predictable and may last for up to a few weeks as fish will gradually deplete their local food resource (Fiedler and Bernard, 1987; Shucksmith *et al.*, 2006; Temming *et al.*, 2007). High-density patches of the target species, therefore, have to be located by searching in potential profitable areas. Some target species, such as pelagic fish schools, can be detected using acoustic fish finders, while other more cryptic species, like those living in or on the seafloor, in particular those that lack a swim bladder that cannot be detected by an echosounder, have to the found by exploratory searching and exploitation.

Indeed, studies focusing on movement dynamics of fishers confirmed periods of long steps and strong directional movements alternated with periods of short steps, frequent turns, and large turning angles, which reflected the activity modes of searching and exploitation, respectively (Rijnsdorp *et al.*, 2000b; Mills *et al.*, 2007; Vermard *et al.*, 2010; Sys, 2018). Such two-scale searching strategies are highly efficient and even outperform scale-free ones (Benhamou and Collet, 2015), like the Levy flight movement (Viswanathan *et al.*, 1999; Bertrand *et al.*, 2005; Marchal *et al.*, 2007). The studies that were able to link movement pattern to catch rate corroborated the expectation that the exploitation mode characterized by area restricted search coincided with above average catch rates and resulted in an aggregation of fishing activities

Received: March 27, 2022. **Revised:** July 19, 2022. **Accepted:** July 20, 2022

Table 1. Size of the Dutch beam trawl fleet of large (>221 kW) pulse trawlers (PUL) and tickler chain beam trawlers (TBT) in two study periods, and the number of fishing vessels, trips, and tows sampled for the catch and automated position recordings (APR).

Data set	Gear	Period	Time interval of APR registrations	Fleet size	Sample size		
				Vessels	Vessels	Trips	Tows
PUL.APR	PUL	2018–2019	1 min	56	19	407	17 453
TBT.APR	TBT	1994–2000	6 min	190	22	1 199	48 182

in local resource patches (Rijnsdorp *et al.*, 2000b; Gillis and Showell, 2002; Rijnsdorp *et al.*, 2011; Zhang *et al.*, 2021).

Local resource patches are the fundamental unit where fishing vessels interact with their target species, impact ecosystems and seafloor habitats, and interact with other fishing vessels. The time required to find such a local patch, the density of the resource, the crowding of vessels therein, and the impact of the fishing activity on the resource determine the efficiency of the fishing operations. Analysis of the catch per unit effort (CPUE), recorded by onboard observers on fishing vessels, showed that repetitive fishing of the same locations for 2 d resulted in a mean depletion by 4–10% for Patagonian toothfish and around 20% for icefish and marbled notothen (Bez *et al.*, 2006). In the flatfish beam trawl fishery, the decline in CPUE on local fisheries patches was estimated at 20% per day (Rijnsdorp *et al.*, 2011). This decline in catch rate on a fisheries patch may be due to local depletion of the resource but may also be related to interference. Interference may occur if fishing vessels are hampered by each other, or when fishing operations trigger an avoidance response of the target species which results in an apparent prey depression (Gillis, 1999, 2003).

Disentangling the role of these two processes, depletion and interference, is important because they play a crucial role in understanding the spatial distributions of foragers. For example, one central model to describe the equilibrium distribution of competitors over habitat patches, is the Ideal Free Distribution (IFD) theory. The IFD, which was developed in the field of behavioural ecology to describe the equilibrium distribution of competitors over habitat patches (Fretwell and Lucas, 1969; Kacelnik *et al.*, 1992), has been successfully applied in both animal and fisheries studies (review in Gillis, 2003). Under the IFD, animals (or fishers) are assumed to select the resource patch of the highest quality. However, once the patch is used, patch quality is reduced, making it less attractive for others. If resource patch quality declines linearly with the amount used, fishers will be distributed in proportion to resource abundance, and all will achieve equal catch rate irrespective of the quality of the fishing ground. This is the (implicit) null-model for most species habitat-association models (Matthiopoulous *et al.*, 2020). However, when both depletion and interference play a role, this linear relationship between patch quality and patch use is no longer guaranteed. In addition, depletion and interference are important because they can influence the relationship between fishing effort and fishing mortality and decouple CPUE from population abundance (Paloheimo and Dickie, 1964; Gillis and Peterman, 1998; Branch and Hilborn, 2008; Dowling *et al.*, 2017).

Despite the importance of interference competition in theoretical and empirical studies on species distributions (Kacelnik *et al.*, 1992; Gillis and Peterman, 1998; Dowling *et al.*, 2017), only few studies have attempted to simultaneously investigate the role of resource depletion and interference empirically. Most papers inferred the importance of interference by studying the relationship between catch rate and vessel density (Gillis *et al.*, 1993; Rijnsdorp *et al.*, 2000a; Gillis and Frank, 2001; Branch and Hilborn, 2008). Fewer studies have experimentally manipulated vessel density. Abrahams and Healey (1993) manipulated the density of salmon trollers. They found variable effects on the catch rate of three species and concluded that variation in vessel density may exert a substantial influence on catch rates. Empirical evidence for interference has been provided by analysing the effect of sudden changes in vessel density due to management regulations or social habits (Rijnsdorp *et al.*, 2000b; Poos and Rijnsdorp, 2007b; Sys *et al.*, 2017; Santa Cruz *et al.*, 2018).

Here, we study beam trawl fishers targeting sole (*Solea solea*) and plaice (*Pleuronectes platessa*) in the North Sea using tow-by-tow catch records and corresponding automated positions recordings (APR) collected at ≤6 min time intervals. We study how flatfish fishers find and exploit their main target species at a tow-by-tow resolution, quantify the size of exploitation patches and the resource distribution within these patches, and estimate the decrease in catch rate during the exploitation process. We estimate the relative contribution of resource depletion and interference to the observed decrease in catch rate by comparing the decrease in catch rate of two types of beam trawls (tickler chain beam trawls TBT, pulse trawls PUL; Rijnsdorp *et al.*, 2020) that differ in their catch efficiency for sole and plaice (Poos *et al.*, 2020).

Material and methods

Case study description

We study the flatfish beam trawl fishery by Dutch vessels (>221 kW) using two 12 m wide tickler chain beam trawls (TBT) and a 80 mm cod-end mesh size in the North Sea, south of the 55°N, west of 5°E, and 56°N east of 5°E (Gillis *et al.*, 2008; Rijnsdorp *et al.*, 2008, 2020). Part of the fleet temporarily switched to electrical stimulation using the pulse trawl (PUL) between 2009 and 2020 (Poos *et al.*, 2020; Rijnsdorp *et al.*, 2020). The PUL is towed at a 23% lower speed (PUL = 5 nm·h^{-1}; TBT = 6.4 nm·h^{-1}) and was shown to be more efficient per unit area swept in catching sole and less efficient in catching plaice than the TBT (Poos *et al.*, 2020). Both TBT and PUL vessels typically make trips of 4–5 d leaving port on Monday morning and returning on Thursday or Friday. Tow duration is ~2 h for both gears.

Data sources

In a dedicated monitoring program, a representative sample of the Dutch beam trawl fishers recorded data on the catch of sole and plaice (kg), and the time and position of the start and end of individual tows, while the vessel position was recorded by an automated position recorder (APR) system at 6 (TBT.APR) and 1 min (PUL.APR) intervals (Table 1). The TBT.APR data set comprised data of 1199 fishing trips and

Table 2. Glossary of terms used to describe the fishing pattern.

Term	Definition
Fishing trip	The journey and fishing activities of a trawler between the departure from, and return to harbour
Tow	Fishing activities between the shooting and hauling of the gear
Tow track	All automated fishing positions (APR) during a tow recorded with 1 of 6 min time interval
Tow segment	Sequence of ≥10 fishing positions (APR) of a single tow where the change in bearing between successive positions did not exceed 5°
Exploitation patch	Area in which fishing positions by tow are clustered during a fishing trip. Spatially defined by a polygon (concave hull) around the APR of the three or more tows clustered with a distance criterion of $h = 3$ nm.
Core of patch	Concave hull around the fishing positions of the tows clustered with a distance criterion of $h = 0.5$ nm.
Peels of exploitation patch	Discrete delineation of an exploitation patch in successive parts from the core to the edge. Peel 1 is the core of the patch. Peel 2 is the concave hull of tows clustered at $h = 1$ nm that does not fall in peel 1, and so on.
Exploitation event	Serie of tows in an exploitation patch
Revisit event	Series of tows in an exploitation patch in a subsequent week
Re-sampling event	Revisit event with ≤2 tows in the following week
Re-exploitation event	Revisit event with ≥3 tows in the following week
Exploitation mode	The behaviour of a fisher when trawling an exploitation patch with ≥3 tows clustered at a distance criterion of 3 nm
Exploration mode	The behaviour of a fisher when searching for a local aggregation of the resource comprising ≤2 tows clustered at a distance criterion of 3 nm
Catch rate (CR)	Catch per tow expressed in $kg \cdot h^{-1}$
Relative catch rate (RCR)	Catch rate per tow standardized to the mean CR of all tows during a trip
Catch ratio (R)	Ratio of the CR in an exploitation patch between successive trips

48 thousand tows from 22 vessels in the period 1994–2000 (Rijnsdorp *et al.*, 1998, 2000b). PUL.APR data set comprised data of 407 fishing trips and 17 thousand tows from 19 vessels in the period 2018–2019.

Catch and effort data of the total Dutch beam trawl fleet, collected at a lower spatial and temporal resolution, were available from the Vessel Monitoring by Satellite (VMS) and logbook datasets. The VMS data contained information on the location, speed, and bearing recorded at intervals between 60 and 120 min for the period 2018–2019. The logbook data set comprised the recordings of the marketable catch, gear type, mesh size, and fishing location (ICES rectangle of 0.5° latitude × 1° longitude) per day for the period 2018–2019 and the period 1994–2000.

Methods

Fishing pattern and tactics

The fishing pattern of beam trawlers was analysed for separate fishing trips elaborating the approach of Rijnsdorp *et al.* (2011). This approach is based on a cluster analysis of tow positions and enables the distinction of the two different modes of trawling behaviour, exploitation and exploration, as well as the definition of exploitation patches as aggregated fishing activities within a fishing trip. Tows are clustered by single linkage clustering based on the inter-tow distance matrix between each tow pair using function *hclust* of R library *stats* version 3.6.1. The inter-tow distance matrix between each tow pair was estimated as the average of the minimum distances (D) between the APR recordings of each tow pair: $D = (\boldsymbol{D}_{1,2} + \boldsymbol{D}_{2,1})/2$, where $\boldsymbol{D}_{1,2}$ is the vector of minimum distances between each APR position of tow X1 to the APR positions of tow X2, and $\boldsymbol{D}_{2,1}$ is the vector of minimum distances of each APR position of tow X2 to the APR positions of tow X1. Distances were determined using the function *rdist* from the R library *fields*.

Single linkage clustering is an agglomerative clustering process. It starts with individual tows that are sequentially clustered based on the shortest distance to another tow. The clusters are then combined into larger clusters by increasing the distance threshold. By setting a distance criterion, tows are classified as either exploitation or exploration tows, while the clusters of exploitation tows reveal the local exploitation patches during the trip. Table 2 provides a glossary of terms used in this paper.

We used a distance criterion of $h = 3$ nm. This choice is based on the distance criterion of $h = 4$ nm used previously for the TBT fishery taking account of the 23% lower towing speed of the PUL (Poos *et al.*, 2020). At this threshold, the difference in catch rate between exploitation and exploration tows was maximised (Rijnsdorp *et al.*, 2011).

Exploration tows were defined as unclustered tows, or tows clustered with one other tow. During exploration tows a vessel generally followed a more or less steady course. Exploitation tows, defined as tows that were clustered with ≥3 tows, were placed close to each other by towing parallel to a previous tow (Rijnsdorp *et al.*, 2000b), or by folding a tow track into two or more linear segments (see Supplementary Material SM1). Linear tow segments were defined as a sequence of ≥10 fishing positions (APR) of a single tow where the change in bearing between successive positions did not exceed 5°. The distance between parallel tow tracks, or parallel tow segments, was estimated for PUL by selecting tow segments within an exploitation patch for which the difference in bearing was less than 10°. The distance between parallel tow segments was then estimated by selecting the segment for which the mean distance was smallest (see Supplementary Material SM2).

Exploitation patches

An exploitation patch was defined as a cluster of exploitation tows. The size of each exploitation patch was estimated as the surface area (function *gArea* from the R library *rgeos*) of the spatial polygon around the APR position recordings of clustered tows (function *concaveman* from the R library *concaveman)*. The rationale for using a concave hull rather than a convex hull used previously (Rijnsdorp *et al.*, 2011) is that the concave hull follows the bended shape of the clustered tows more closely than the previously used convex hull and hereby accounts for the heterogeneity in the seafloor landscape that is often closely followed by bottom trawlers (van der Reijden *et al.*, 2018).

The geometry of an exploitation patch was described by successive peels from the core to the edge of the patch. Tows clustered at a distance threshold of $h = 0.5$ nm represent the core of the patch (peel 1: 0–0.5 nm). Tows added when using $h = 1$ nm represent the second peel (peel 2: 0.5–1 nm), tows added when using $h = 1.5$ represent the third peel (peel 3: 1–1.5 nm), and so on. In this study, the exploitation patch is limited to the boundary of the sixth peel, corresponding to $h = 3$ nm.

The pattern of fishing effort (surface area swept, km^2) and catch rate (*CR)* within an exploitation patch was estimated for the core and successive peels by fishing trip. To be able to compare *CR* across fishing trips, we calculated the relative catch rate (RCR_{ij}): $RCR_{ij} = CR_{ij} / \sum_{i=1}^{n} \frac{CR_{ij}}{n}$, where CR_{ij} is the catch per unit of effort (kg·h^{-1}) in tow *i* and fishing trip *j*, and *n* is the number of tows of fishing trip *j*. Other metrics estimated were the time between the start of the first tow and the end of the last tow in the exploitation patch and the proportion of the surface area swept within each peel. The latter was defined as the surface area swept (fishing track length × beam width) in each peel, divided by the surface area of each peel.

The estimated size and shape of the exploitation patches will be sensitive to the time interval between the APR recordings. Supplementary Material SM3 compares the estimated metrics of the patch geometry by sub-sampling the 1 min PUL data set to subsets corresponding to a 6, 30, 60, and 120 min registration intervals. A comparison of the PUL results based on 1 min data and 6 min subset showed relatively little differences. Data sets subsampled to larger registration interval ($\geq$60 min) resulted in increasingly different surface area estimates for the different peels, with a serious underestimate of the size of the core of the patch and an overestimate of the proportion of the patches that is swept. Hence, such larger registration intervals are less useful to determine the structure of the patches (see Supplementary Material SM3). Nevertheless, patches can be estimated using data sets with larger polling intervals as long as the distance criterion used is not set too low ($h \geq 2$ nm; see Supplementary Figure SM3.1).

Recurrent exploitation of patches during successive trips

Fishers may revisit an exploitation patch in successive trips. As the fish density in an exploitation patch may have changed, a fisher may re-sample or re-exploit the patch. We defined a revisit as a re-sampling event when the exploitation patch overlapped with APR recordings of exploration tows in the successive trip. A revisit was defined as a re-exploitation event when the exploitation patch of the first trip overlapped with an exploitation patch in the successive trip. Because the fishing effort in an exploitation patch was highly aggregated in the core peel (see below), the analysis was carried out for the core peel of the exploitation patch. The overlap was determined using the function *over* from the *sp* library in R-3.6.1. The analysis was carried out for the PUL fishery. For the TBT fishery, the recurrent exploitation of patches was analysed in Rijnsdorp *et al.* (2000b).

We studied the effect of the time interval between trips (*delta_t)* and the fishing effort in the patch in the reference trip (*f*) on the probability (*P*) to revisit, or re-exploit, the core peel by fitting the following *glm* model:

$$P \sim Bin\,(1, p)\,; Logit\,(p) = \log_e\,(delta\_t) + f + f : \log_e\,(delta\_t)\,. \tag{1}$$

The changes in catch ratio (*R*) between successive trips ($R = CR_{w+dt}/CR_w$) was studied in relation to *delta_t* and *f* by fitting a *glm* model:

$$\log_e R \sim N(\mu, \sigma);\, \mu = \log_e\,(delta\_t) + f + f : \log_e\,(delta\_t)\,. \tag{2}$$

Crowding of multiple vessels on an exploitation patch

Exploitation patches were defined for individual (reference) vessels but may also be trawled by other vessels. For PUL vessels, we estimated the effort of other PUL vessels in the exploitation patch of the reference vessel using the VMS data set of the total PUL fleet. VMS fishing recordings of the PUL fleet were selected that fell within the core peel of the exploitation patch and between the start and end of the exploitation phase by the reference vessel. Effort (km^2) was estimated as the sum of the registration interval of the VMS recordings that represented fishing activities (Hintzen *et al.*, 2012), times the average towing speed of pulse vessels and width of their gear.

For the TBT study period, no VMS recordings were available to estimate the crowding in exploitation patches. Difference in crowding between the TBT and PUL, therefore, was estimated as the number of vessels fishing in the ICES rectangle (n_{ices}) of the reference exploitation patch during the same week.

Catch rate and location during the exploitation of a patch

We studied how the relative catch rate [$log_e(RCR)$] experienced by the fisher evolved during an exploitation event and how this was related to the location in the exploitation patch. The tow location was measured as the probability (*P*[core]) that the tow was located in the core peel of the exploitation patch. The response variables were analysed as a function of the serial number of the tow (*I*) and the total number of tows on the patch (*J*) by fitting a *gam* model where *s*(*I*), *s*(*J*), and *s*(*I*, *J*) are smooth functions based on a tensor product smoother (Zuur, 2012)

$$\log_e\,(RCR) \sim N(\mu, \sigma);\, \mu = s\,(I) + s\,(J) + s\,(I, J)\,, \tag{3}$$

$$P\,[core] \sim Bin\,(1, p)\,; Logit\,(p) = s\,(I) + s\,(J) + s\,(I, J)\,. \tag{4}$$

Decline in catch rate during the exploitation of a patch

The decline in CR during the exploitation of a resource patch will not only be related to a decline in the resource abundance but also by the location of the tows within the patch. To study the decline in CR, we therefore restricted the analysis to tows taken in the core peel of the patch. The decline in catch rate was estimated using a negative binomial mixed effects model (equation 5). The catch was collapsed into bins of 5 kg for sole and 10 kg for plaice, reflecting the dominant unit used by fishers in their logbooks. The response variable was represented by the bin number. Log tow duration (*TD*, hour) was included as an offset which allowed us to use the discrete catch (C) as the response variable for catch rate.

$$C = NB\left(\mu, k\right)$$
$$E\left(C\right) = \mu \text{ and } \mathrm{var}\left(C\right) = \mu + \frac{\mu^2}{k}$$
$$\log_e\left(\mu\right) = \beta \boldsymbol{X} + r_1 + r_2 + TD$$
$$r_1 \sim N\left(0, \sigma^2_{vessel}\right)$$
$$r_2 \sim N\left(0, \sigma^2_{fg}\right). \tag{5}$$

The term r_1 was a random intercept representing a normally distributed vessel effect with mean 0 and variance σ^2_{vessel}. Likewise, r_2 was a random intercept representing the normally distributed patch effect (*fg*) with mean 0 and variance σ^2_{fg}. *TD* represents the tow duration (included as offset) and ***X*** represents the matrix of fixed effects.

Three models of increasing complexity of the fixed effects were run to investigate how catch rate was related to the cumulative proportion surface area of the patch swept (*S*) and how this relationship was affected by the number of vessels fishing in the area (n_{ices}) and the interaction between n_{ices} and *S*. The term *d* represents the diurnal periodicity $d = \sin(\text{time}) + \cos(\text{time})$ observed in the catch rate of sole and plaice (Rijnsdorp *et al.*, 2011).

$$m1 : \log\left(\mu\right) \sim \beta_0 + \beta_s * S + \beta_d * d + r_1 + r_2 + TD, \tag{6}$$

$$m2 : \log\left(\mu\right) \sim \beta_0 + \beta_s * S + \beta_n * n_{ices} + \beta_d * d + r_1 + r_2 + TD, \tag{7}$$

$$m3 : \log\left(\mu\right) \sim \beta_0 + \beta_s * S + \beta_n * n_{ices}\beta_{ns} * + n_{ices} : S + \beta_d * d + r_1 + r_2 + TD. \tag{8}$$

The analysis was carried out with the *glmer* function of the lme4 library in the R package. Model selection was based on the Akaike Information Criterion (AIC). The model with fewer predicting variables was selected when ΔAIC <2 (Burnham and Anderson, 2002).

Disentangling the role of exploitation and interference

Catch Rate (*CR*) in a patch will be a function of gear efficiency (*E*), cumulative proportion of the surface area swept (*S*), and interference (F): $CR_s = CR_0\exp(-E \times F \times S)$. Assuming that the resource distribution is always uniform within a peel (instant redistribution), the term $E \times S$ represents the rate of decline due to resource depletion, whereas the term *F* represents how the rate of decline is modulated by interference. CR_0 is the catch rate at the start of the exploitation event and was set at 1. The decline in catch rate estimated with model *m1* includes both the effects of resource depletion and interference. To disentangle the contribution of both, we estimated the contribution of interference by subtracting the observed decline in *CR* from model *m1* with the expected decline in *CR* due to resource depletion only.

The decline in *CR* due to resource depletion was simulated to take account of the differences in fishing effort in the PUL and TBT study periods and the differences in gear efficiency of the PUL and TBT gear types (Table 3). For each gear × species combination mean *CR* was simulated for a random sample of exploitation events for a range of values of *S*. For each exploitation event, the fishing effort of other vessels was estimated by sampling the observed frequency distribution of the number of vessels fishing simultaneously in the same ICES rectangle in the PUL (low vessel density) and the TBT (high vessel density) study periods. Gear efficiency was based on Poos *et al.* (2020), who showed that PUL caught 52% more sole and 12% less plaice than TBT per unit area swept. Assuming a gear efficiency $E = 1$ for the PUL-sole and TBT-plaice, the efficiency of PUL-plaice will be 0.88 (1–0.12) and the efficiency of TBT-sole will be 0.66 (1/1.52). The simulated decline in CR due to resource depletion (*CRsim)* was compared to the observed decline in *CR (CRobs)* estimated from a random sample of the fixed effect coefficient $\beta_s = N(\mu,\sigma)$ of model *m1*. The relative contribution of resource depletion and interference was estimated for each simulation *i* as $Depletion_i = log_e\left(CRsim_i\right)/log_e(CRobs_i)$ and $Interference_i = 1 - Depletion_i$, and calculating the mean and 95% prediction interval of the depletion and interference. Further details of the simulation are given in the Supplementary Material SM4.

Table 3. Relative gear efficiencies (*E*) of PUL and TBT gear for sole and plaice and the vessel density scenario to estimate the contribution of resource depletion in the decline in catch rate (*CR*).

Species	Gear	Gear efficiency (*E*)	Vessel density
Sole	PUL	1	Low
Plaice	PUL	0.88	Low
Sole	TBT	0.66	High
Plaice	TBT	1	High

Results

Fishing pattern and tactics

During a trip, fishers spent about 10% of their tows exploring and spent about 90% of their tows exploiting. On average 2.4 (2.5% quantile = 1; 97.5% quantile = 5; PUL) and 2.5 (2.5% quantile = 1; 97.5% quantile = 5; TBT) exploitation patches are visited during a fishing trip. The percentage of searching tows was unrelated to the season (results not shown).

Pulse trawl fishers swept an exploitation patch in a systematic manner and avoided overlapping trawl tracks as illustrated in Figure 1. The fishing pattern showed the typical alteration between closely packed parallel tow trajectories with sharp turns and more dispersed tracks. The closely packed trajectories (coloured lines) represent the exploitation tows that are clustered with a distance threshold of $h = 3$ nm. The pale red polygons show the concave hull around all 1 min APR positions of the clustered tows that represent the exploitation patches. The blue polygons show the core peel of the tows clustered with a distance criterion $h = 0.5$ nm. More dispersed tracks (grey lines) reflect exploration activities of tows that are not clustered or clustered with only one other tow.

Figure 1 shows that fishers may fold a tow tracks in linear segments that are placed parallel to each other. The tow segments had a median length of 17 APR recordings (2.5% quantile–10 APR; 97.5% quantile–56 APR). For most vessels the distance between parallel tow segments ranged between about 50 and 500 m. The overall median distance was estimated at 193 m (2.5% quantile = 75 m; 97.5% quantile = 879 m) (Figure 2). The frequency distributions of the change in bearing between successive tows and tow segments is presented in Supplementary Material SM1.

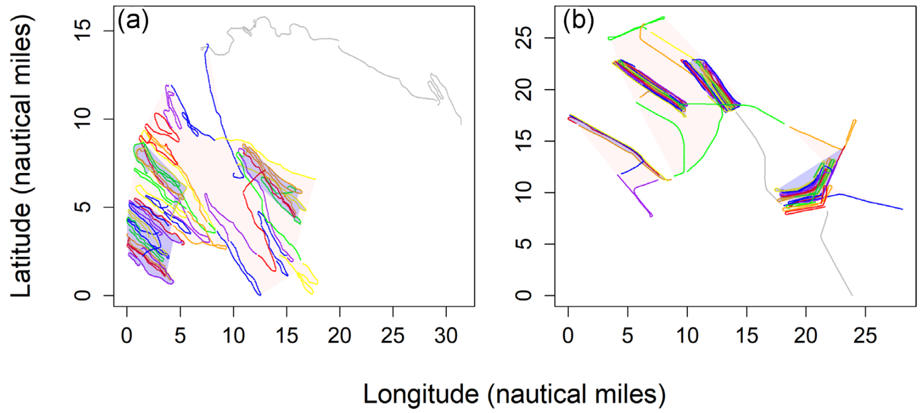

Figure 1. PT: trawling trajectories of two fishing trips showing 1 min APR of the exploration (grey lines) and exploitation tows (coloured lines). Panel (a) shows one exploitation patch (red shaded polygon) with three core peels (blue shaded polygons). Panel (b) shows three exploitation patches with one core peel (left and right) and one exploitation patch with two core peels (centre). Exploitation tows were distinguished by colouring them consecutive blue, yellow, green, orange, red, purple, blue, etc. To comply with the confidentiality agreement, fishing positions were expressed relative to the minimum and maximum longitude and latitude during each trip.

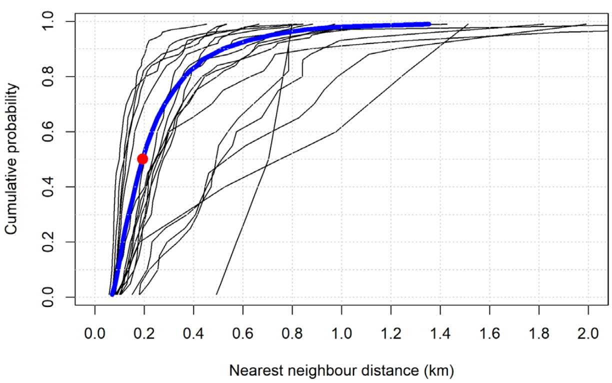

Figure 2. PT: cumulative probability of the distance (km) between parallel trawl segments of 19 individual pulse trawlers (black lines) and the overall relationship estimated with the pooled data (blue line). The red dot indicates the median distance between parallel trawl segments of all vessels.

Exploitation patches

The size of exploitation patches was quite variable and tends to be slightly smaller in PUL (mean = 251 km^2) than in TBT (mean = 303 km^2). The size of the core was estimated at 24 km^2 (PT) and 34.0 km^2 (TBT). The time period between the start of the first tow and the end of the last tow of the exploitation patch varied around a median value of 1.45 d for both gears. For the core, the median time between the first and the last tow was just over half a day for both gears.

The characteristics of an exploitation patch were furthermore described by the distribution of the catch rate, fishing effort, and the surface area of the different peels. Results show a large similarity between PUL (Figure 3a–e) and TBT (Figure 3f–j). The relative catch rate (RCR) in the core was about 50% higher than the background RCR outside the exploitation patch. The RCR reduced in successive peels to the background level (dashed line in Figure 3a, b, f, and g), except for plaice in the PUL where the RCR was relatively high in all peels of the exploitation patch. Variability in RCR increased from the core to the peripheral peels. In the core, the lowest observed RCR exceeded the mean RCR in the peripheral peels. Although in peripheral peels the highest observed RCR is similar to the highest RCR observed in the core, the lowest RCR decreased strongly from the core to the peripheral peels. Fishing effort, estimated as the surface area swept (km^2), is concentrated in the core peels and quickly dropped in more peripheral peels (Figure 3c and h). The surface area of the peels exploited during a fishing trip gradually increased from the core peel to the outermost peel (Figure 3d and i). The proportion of the surface area of a peel swept during a fishing trip decreased quickly from around 0.20 in the core peel to about 0.05 in peel $h = 1$ nm and ≤ 0.03 in peels $h > 1$ nm (Figure 3e and j).

Recurrent exploitation of patches during successive trips

The fishing effort in the core peel ranged between 3 and 60 h and did not show a clear relationship with fishing effort in that area during the successive trip (Figure 4a). Fishing effort in the core peel in the successive trip was generally less than in the reference trip (Figure 4b). The average catch ratio of sole [$log_e R = log_e(CR_{ref+1}/CR_{ref})$] when revisiting the core peel was well below the catch rate in the reference week. In only 20% of the cases did the fisher experience the same or a higher CR ($log_e R \geq 0$) when revisiting the core peel (Figure 4c).

The effect of the time interval between trips (*delta_t*) and fishing effort (*f*) on the probability (*P*) to revisit, or re-exploit, the core peel was studied by fitting *glm* models. Results of the selected models are shown in Figure 5. Details on the model selection are presented in Supplementary Table SM5.1. The probability to revisit the core peel decreased from 0.4 in week 1 to about 0.25 in week 8 after the exploitation event. The re-exploitation probability decreased from about 0.2 in week 1 to 0.1 in week 8 (Figure 5a). The probabilities were significantly affected by fishing effort in the core peel during the reference trip. The probability to revisit or re-exploit a core peel increased with the effort in the core peel during the reference trip (Figure 5a). The probability to revisit the core peel increased from about 0.27 when the reference effort was low (2.5% percentile) to almost 0.6, when the reference effort was high (97.5% percentile). The probability to re-exploit a core peel increased from 0.18 when the reference effort was low

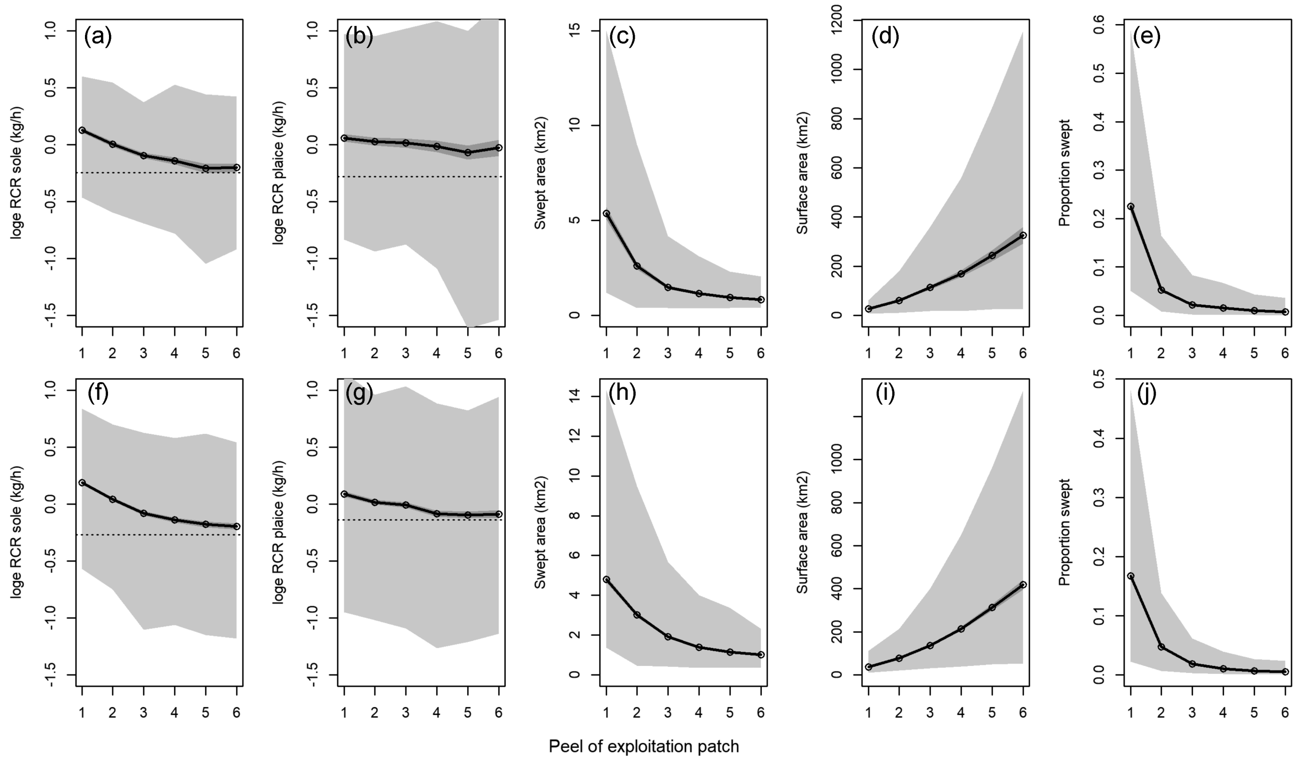

Figure 3. Characteristics of exploitation patches of PUL (top panels) and TBT (bottom panels) showing the distribution of the relative catch rate RCR ($kg{\cdot}h^{-1}$) of sole (a, f) and plaice (b, g), fishing effort (km^2) over the different peels of exploitation patches (c, h), surface area (km^2) of the peels (d, i), and the proportion of the surface area of the peel swept (e, j). Symbols show the mean values. Dark grey polygons show the 95% *CL* of the mean. Light grey polygons show the 95% range of individual estimates per exploitation patch. The horizontal dashed line in (a) and (b) shows the mean RCR outside the exploitation patch.

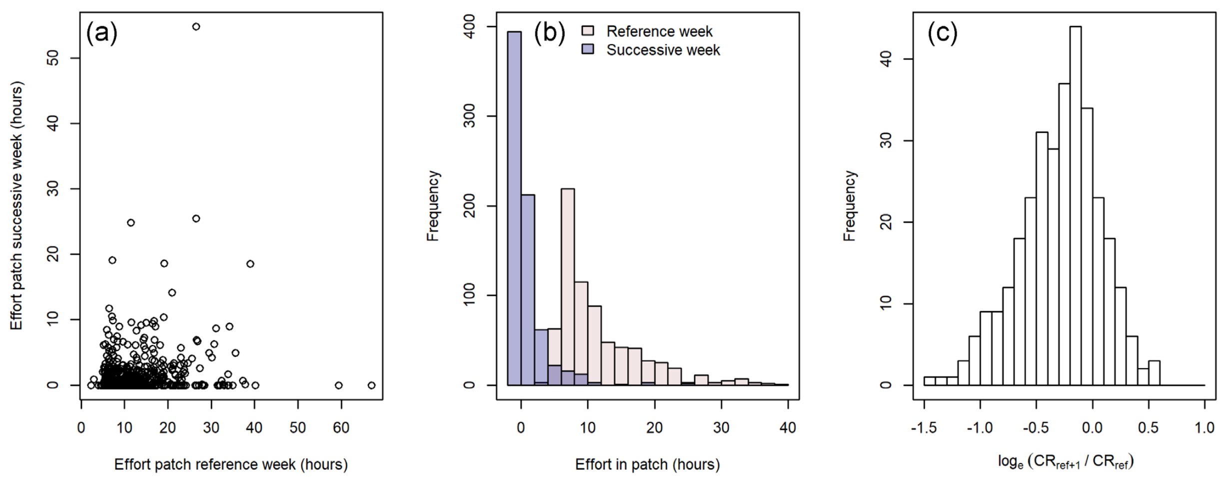

Figure 4. PUL: (a) Relationship between the fishing effort (hours) in the core peel of an exploitation patch in the reference and successive week; (b) frequency distribution of the fishing effort in the core peel in the reference week and successive week; (c) frequency distribution of the ratio of the relative catch rate of sole [log_e (CR_{ref+1}/CR_{ref})], during a revisit of the core peel in the subsequent week and the reference catch rate.

(2.5% percentile) to over 0.25 when the reference effort was high (97.5% percentile).

The CR during a revisit or a re-exploitation event was independent of the time interval since the reference trip and was not affected by the fishing effort during the reference exploitation event (Figure 5b). Revisiting a core peel resulted in a 25% lower CR [exp(−0.289) = 0.749] compared to the CR of the preceding exploitation event. During a re-exploitation event when the fisher continued trawling in the core peel for three or more tows, the CR was on average 16% lower [exp(−0.174) = 0.840].

Crowding of multiple vessels on an exploitation patch

About 36% of the core peels were fished simultaneously by two or more PUL vessels (Figure 6a). Most were fished by one other vessel and 5% were fished by more than two vessels.

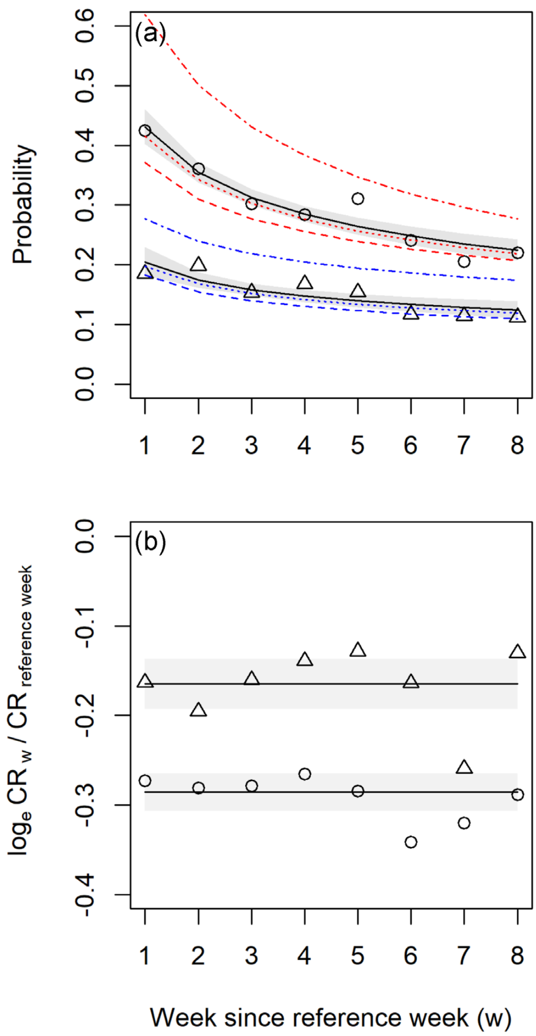

Figure 5. PUL: (a) probability to revisit () or re-exploit (Δ) the reference core peel of an exploitation patch (week = 0) in successive weeks (solid lines) for different levels of fishing effort in week = 0 (red: revisit; blue: re-exploit; dashed–5 percentile; dotted—median, dotted-dashed–95 percentile); (b) relative catch rate of sole (RCR) during a revisit of the core peel relative to the catch rate in week = 0 (= revisit; Δ = re-exploitation event) in successive weeks. Shaded areas show the 95% *CI*. Symbols show the observed mean probabilities.

The fishing effort in the core peels that were simultaneously trawled by other vessels, was quite variable. The scatter plot of the swept area of other vessels and the swept area of the reference vessel showed that the fishing effort of other vessels was generally less than the fishing effort of the reference vessel (Figure 6b).

Temporal pattern in catch rate and location during exploitation of a patch

The development of RCR experienced by the fisher and the probability that a tow is located in the core peel during an exploitation event is shown in Figure 7 for exploitation events of variable duration. RCR showed an initial increase at the beginning and decreased towards the end of the exploitation event. The dome-shaped pattern in RCR coincided with a similar pattern in the trawling location within the exploitation patch. The maximum RCR increased with the duration of the exploitation event. The pattern in RCR matched the pattern in the probability to trawl in the core peel of the exploitation patch. Details of the model selection and model fit are presented in Supplementary Table SM6.1.

The analysis showed that during the exploitation event PUL and TBT trawlers climbed the prey field landscape and reached the core fishing ground where they continued fishing for some time. After the catch rate started to decline, the trawlers gradually moved away from the core and finally left the exploitation patch. The catch rate at the end of an exploitation event is generally well below the mean RCR [ln(RCR) = 0] during the trip (Figure 7b and d). For PUL trawlers, the RCR at the end of an exploitation event increased with the number of tows during an exploitation event. For TBT trawlers an opposite pattern was found.

Decline in catch rate during the exploitation of a patch

The decrease in *CR* of PUL-sole was proportional to the cumulative proportion swept as the 95% *CI* of the estimated coefficient of model *m1* included −1 ($\beta_s = -1.116$, lwr = −0.977, upr = −1.255), but declined almost twice as fast for PUL-plaice ($\beta_s = -1.613$, lwr = −1.393, upr = −1.835) and more than twice as fast for TBT-sole ($\beta_s = -2.488$, lwr = −2.359, upr = −2.617) and TBT-plaice ($\beta_s = -2.781$, lwr = −2.034, upr = −3.528). The rate of decline also differed between gears. TBT had a faster rate of decline than PUL for both species. Given the mean *S* observed (PUL = 0.22; TBT = 0.18; Figure 3e and 3j), a PUL and TBT fisher experienced, during an average exploitation event, a decline in CR of sole of 22% exp(−0.22 × 1.116) and 36% exp(−0.18 × 2.488), respectively.

Model comparison showed that the model with the lowest AIC for PUL-sole (*m3*) included the cumulative proportion swept (*S*) as well as the number of vessels (n_{ices}) fishing in the ICES rectangle of the exploitation patch and their interaction (n_{ices}*: S*) (Table 4). The selected model for PUL-plaice only included *S* (*m1*), whereas in selected model for TBT included *S* and n_{ices}, but not their interaction (*m2*). The coefficients of the fixed effects of the selected models are presented in Table 5. In PUL-sole, the rate of decline became steeper with the number of vessels ($\beta n_{\text{ices}}{:}S = -0.064$; se = 0.017) and was close to proportional with *S* for $n_{\text{ices}} = 4$. The analysis further showed that the number of vessels positively affected the CR ($\beta n_{\text{ices}} > 1$) except for PUL-plaice.

Disentangling the role of exploitation and interference

For PUL-PLE, TBT-SOL, and TBT-PLE the observed decline in catch rate (*CRobs)* was much faster than the simulated decline due to resource depletion (*CRsim)* while taking account of the number of vessels (n_{ices}) in the study period. For PUL-SOL the observed decline was very close to the simulated decline (see Supplementary Figure SM4.3). Comparison of the simulated with the observed decline provided an estimate of the relative contribution resource depletion and interference. It was shown that resource depletion contributed between 33 and 55%, and interference contributed between 45 and 67% to *CRobs* (Figure 8). Only for PUL-SOL did resource depletion fully explained *CRobs*. For PUL, the contribution of resource depletion exceeded the contribution of interference, while for TBT the contribution of interference was stronger than the contribution of resource depletion.

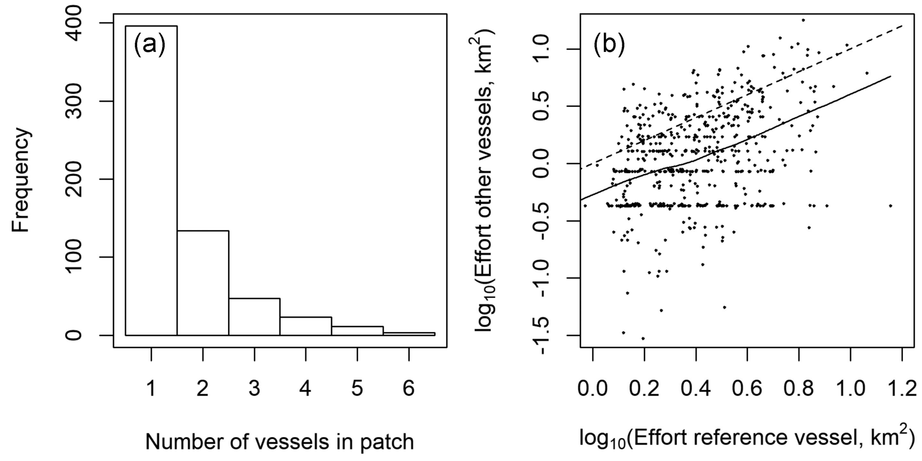

Figure 6. PUL: (a) Frequency distribution of the number of PUL vessels fishing simultaneously in the core peel of the exploitation patch; (b) scatter plot and loess smoother (solid line) of the swept area (km^2) of other vessels and the reference PT vessel in shared core peel. The dashed line shows the proportional relation.

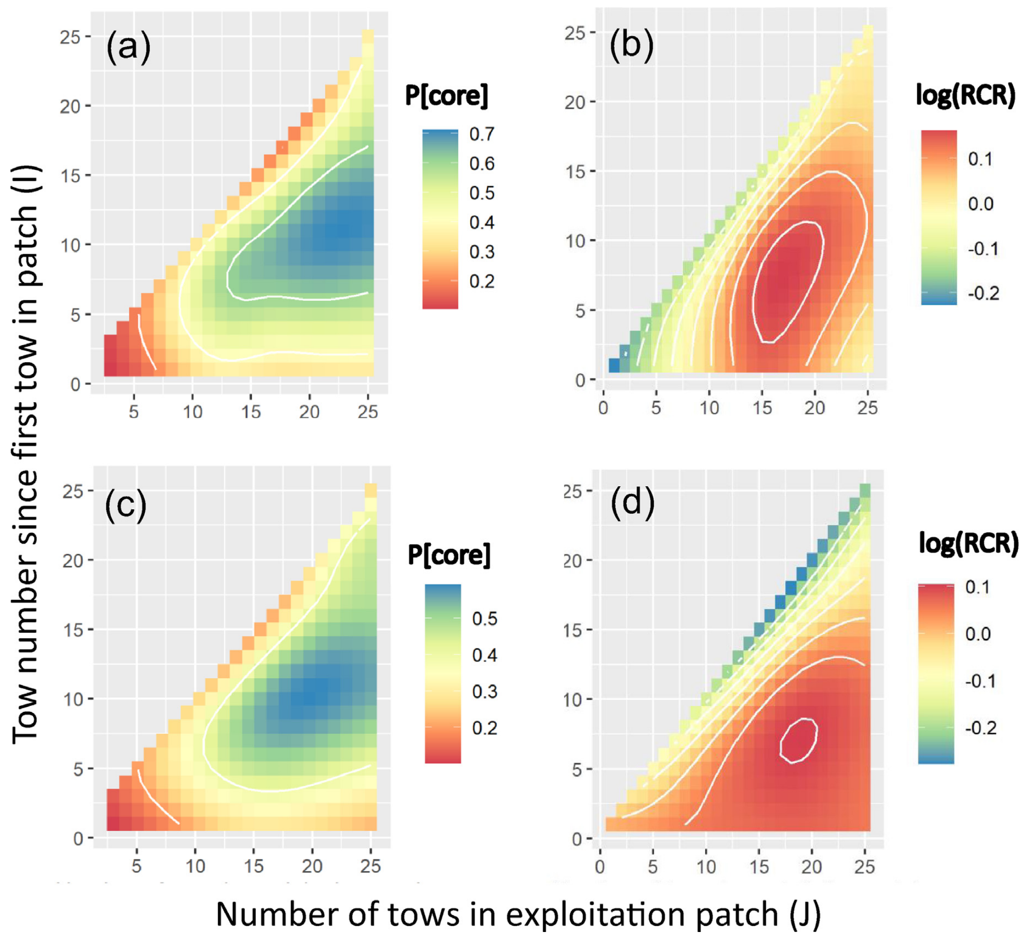

Figure 7. Tow location (P[core] = probability to be located in the core peel of an exploitation patch) (a, c) and mean relative catch rate (log$_e$ RCR) of sole (b, d) during exploitation events with a duration up-to 25 tows. Top panels (a, b) show results for the PUL. Bottom panels (c, d) show results for TBT. The tow location is expressed as the mean peel number ranging between the core (1) and edge (6) of the exploitation patch. Clusters with 1 or 2 tows in panel (b) and (d) represent exploration tows outside the patch.

Discussion

Fishing pattern and tactics

Our study showed that beam trawl fishers concentrated their fishing activities in the core peel of exploitation patches where they achieved catch rates that were about 50% above the background level outside of the patch. The movement pattern of vessels comprised of series of tows in the same direction, coinciding with relative low catch rates (exploration phase),

Table 4. Model selection of mixed effect models of the catch rate of sole and plaice in the core peel of an exploitation patch for the pulse trawl (PUL) and tickler chain beam trawl (TBT).

Mo-del	Covariates fixed effects				df	AIC-PUL ($n = 7100$)		AIC-TBT ($n = 15\,969$)	
	d	S	n_{ices}	$n_{\text{ices}}:S$		Sole	Plaice	Sole	Plaice
m1	x	x			7	38 077.51	**32 981.05**	82 656.65	83 865.50
m2	x	x	x		8	38 065.51	32 982.95	**82 614.56**	**83 854.22**
m3	x	x	x	x	9	**38 055.57**	32 983.46	82 616.21	83 855.17

Covariates included as fixed effects are: diurnal periodicity [$d = \sin(\text{hour})+\cos(\text{hour})$], number of vessels ($n_{\text{ices}}$), and the proportion surface area of the core peel swept (S). Selected models with lowest AIC are indicated in bold.

Table 5. Coefficients of the fixed effects of the selected model of the catch rate as a function of the cumulative proportion of the core area swept (S), the number of vessel recorded in the ICES rectangle (n_{ices}), the diurnal periodicity [sin(hour) + cos(hour)], and the interaction between n_{ices}: S.

	Sole			Plaice		
	Estimate	Std. error	Pr(>|z|)	Estimate	Std. error	Pr(>|z|)
Pulse trawl (PUL)						
$\beta 0$	0.383	0.056	<0.0001	− 0.488	0.103	<0.0001
βs	− 0.722	0.116	<0.0001	− 1.613	0.110	<0.0001
βn_{ices}	0.014	0.003	<0.0001	–	–	–
$\beta n_{\text{ices}}:S$	− 0.064	0.017	0.0001	–	–	–
sin(hour)	− 0.009	0.005	0.089	− 0.036	0.008	<0.0001
cos(hour)	0.059	0.005	<0.0001	− 0.014	0.008	0.076
Beam trawl (TBT)						
$\beta 0$	0.123	0.154	0.424	0.118	0.159	0.459
βs	− 2.497	0.066	<0.0001	− 2.795	0.075	<0.0001
βn_{ices}	0.011	0.002	<0.0001	0.008	0.002	<0.001
sin(hour)	− 0.021	0.004	<0.0001	− 0.033	0.004	<0.0001
cos(hour)	0.064	0.004	<0.0001	0.024	0.004	<0.0001

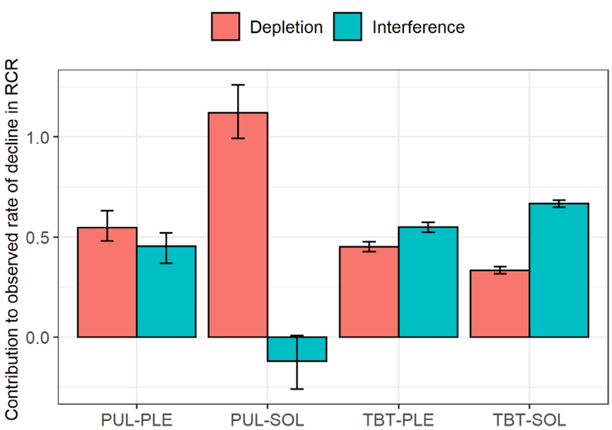

Figure 8. Simulated contribution of resource depletion and interference to the observed rate of decline in catch rate (CR) of sole (SOL) and plaice (PLE) in the pulse trawl (PUL) and tickler chain trawl (TBT).

alternated with series of closely packed tows coinciding with high catch rates (exploitation phase). The exploration phase ended when the catch rate increased and the fisher made a U-turn and located the next tow parallel to the previous one. The exploitation phase ended after a few tows with a relative low catch rate. This fishing tactic enabled a fisher to climb up the unknown density landscape of the target species.

Local patches were exploited in a systematic manner by sweeping the sea bed in predominantly parallel tow tracks that are regularly spaced. By systematic trawling, fishers obtain information on the distribution of their target species. By folding tow tracks during the exploitation of a patch, fishers can more precisely allocate their fishing effort and trawl the surface area of patches more or less uniformly, avoiding covering the same parts twice.

With the median distance of 200 m between parallel tow tracks ∼12% of the seabed of a core patch will be trawled, roughly comparable to the estimated proportion swept of 20%. The bearing of the parallel tow tracks on a local fishing ground may be related to the seabed topography which is comprised of areas of sandbanks and troughs. The seascape in the southern North Sea is a well-structured relief at a scale of 5–10 km caused by tidal ridges (Koop *et al.*, 2019; van der Reijden *et al.*, 2019). Hotspots of the beam trawl fishery for sole, determined over longer time periods, were located in depressions with high bottom tidal shear stress values and low wave action (van der Reijden *et al.*, 2018; Hintzen *et al.*, 2021). These troughs are associated with higher benthic species abundance (Baptist *et al.*, 2006; van Dijk *et al.*, 2012; Damveld *et al.*, 2018). The homogeneous bearing of tow tracks on a fishing ground may also reflect the borders of closed areas, such as the 12 mile zone or the Plaice Box, or the safety zones around wind farms and oil and gas platforms, or may be related to the prevailing direction of the wind and tide during fishing.

Exploitation patches were found by sampling areas that were profitable in the past. The location choice of beam trawl fishers may be supported by information on the suitability of seabed for the target species, e.g. the type of seabed and the bathymetric profile (Able and Fodrie, 2015; van der Reijden *et al.*, 2018) that can be obtained from echosounders, and by real time information on movements of other vessels tracked using radar or AIS (Vignaux, 1996). In only 20% of the exploitation patches analysed, the catch rate remained high when the core peel was exploited again in successive weeks. In the other cases, the fisher moved-on after one or two tows as the catch rate was well below the catch rate in the previous week.

Hence, local patches are ephemeral phenomena that may last for a few days to up to a few weeks (Poos and Rijnsdorp, 2007a). The results clearly show that skippers rely heavily on information from previous trips as they only visit two to three exploitation patches during a one-week fishing trip and hence do not randomly sample the seafloor (Able and Fodrie, 2015; van der Reijden *et al.*, 2018).

The fishing tactics of beam trawlers targeting flatfish is comparable to the foraging behaviour of natural predators using patchy distributed food resources (Stephens and Krebs, 1986). After each tow, a fisher decides whether to stay put by locating the next tow close to the previous ones, or resume searching for another local aggregation of the resource by trawling away. The alternation between exploration and exploitation tows resembles a two-scale searching strategy that is highly efficient even when prey are scarce and cryptic (Benhamou and Collet, 2015), which outperforms scale-free ones, like the Levy flight movement (Viswanathan *et al.*, 1999; Bertrand *et al.*, 2005; Marchal *et al.*, 2007) or the Brownian motion.

Optimal foraging theory predicts that a fisher should leave a patch when the marginal catch rate at time of leaving equals the long-term average, the residence time increases with the quality of a hotspot, and the catch rate of different quality patches will be reduced to a similar level before leaving (Charnov, 1976; Stephens and Krebs, 1986; Wajnberg *et al.*, 2000). Our results are in broad agreement with these predictions. The RCR at the end of an exploitation event is below the mean RCR during the trip and the maximum RCR increases with the number of tows on an exploitation patch. In a more detailed analysis of TBT data, it was shown that deviations from the predictions may occur (Rijnsdorp *et al.*, 2011). Their analysis of giving-up catch rates (GUP) at the end of an exploitation event, showed that TBT fishers left the patches too early as GUP was on average 9% above the predicted optimal rate. The deviation could be explained by the management constraints which created an incentive for beam trawl fishers to leave a rich exploitation patch when the available individual quota for the target species was insufficient. Fishers may also stop fishing at the end of the week to return home and land their fish for the auction on Friday or Monday.

Comparing fishing tactics of PUL and TBT fishers

The similarity in tactics of PUL and TBT is expected as it were the same fishers exploiting the same resource with a different gear. Irrespective of the gear, beam trawl fishers used 10% of their tows searching for a local aggregation of their resource as could be expected. The main difference between PUL and TBT gear is that the TBT fisher make longer tow tracks, hence gather information at a coarser resolution than the PUL fisher. The difference is due to the faster towing speed of the TBT vessels (PUL = 5 $nm \cdot h^{-1}$; TBT = 6.4 $nm \cdot h^{-1}$) and about equal tow duration. Given these typical towing speeds, tow duration (2 h), and gear width (2 × 12 m), the length of a tow track of a PUL fisher is 10 nm, as compared to 13 nm for a TBT fisher. The longer tow tracks of the TBT fishers may also explain the larger size estimates of the patch size of the TBT.

Resource depletion and interference

Although the number of vessels fishing in the same area significantly affected the rate of decline in CR of sole in PUL, this effect can be caused by the additional resource depletion or interference, or both. However, the comparison of the observed rate of decline in catch rate with the simulated rate of decline due to resource depletion, which took account of the fishing effort of other vessels, provided strong evidence for the importance of interference. The estimated importance of resource depletion and interference competition is conditional on the assumptions made to estimate the expected rate of decline due to resource depletion. Evaluating these assumptions indicated that we may have under-estimated the role of interference competition. First, the gear efficiencies used are relative values assuming that the PUL gear catches all sole and the TBT gear catches all plaice that occur in the path of their trawl. As it seems unlikely that a trawl is 100% efficient, the contribution of resource depletion will be over-estimated and the contribution of interference will be under-estimated. Second, we assumed that the resource was uniformly distributed and instantaneously redistributes itself over the patch. Given the average size of the core peel (about 30 km^2) and average duration of an exploitation event of the core peel (about 0.5 d), the instantaneous redistribution seems unlikely. If the resource only partly redistributes itself during the exploitation event, we expect the catch rate to decline at a slower rate. Since PUL trawlers were shown to systematically trawl the surface area of the core peel, we may even expect that the catch rate would remain stable. Redistribution could be enhanced if the resource are attracted to the previously trawled seabed as observed for scavengers, but this behaviour has not been observed for sole (Groenewold and Fonds, 2000). Third, the results will be affected by the accuracy at which the rate of decline was estimated. In some cases, the concave hull did not tightly enclose the APR fishing positions of the clustered tows, which will have resulted in a slight overestimation of the surface area of the core peel and hence in an overestimation of the CR (resource depletion + interference).

One possible mechanism that could cause interference is the response of fish to the trawling activities by swimming away from the source of disturbance, or by burying deeper in the sediment. There is some support that bottom trawling may chase away fish (Morgan *et al.*, 1997; De Robertis and Handegard, 2012). Direct observations in the mouth of the trawl showed that flatfish may already move away from the approaching trawl before they make physical contact with the gear (Bublitz, 1996). Albert *et al.* (2003) collected video recordings of the behaviour of halibut in the mouth of an otter trawl, showing that the highest number of halibut were observed in the first 200 m of the trawl tracks. This suggests that halibut already moved away from the gear before entering the mouth of the trawl. Kuipers (1975) showed in a comparative trawling experiment that young plaice were less efficiently caught when the beam trawl was towed directly behind the boat as compared to beam trawls that were towed at some distance at the side of the boat. The response to trawl disturbance may also explain why fishers place the tow tracks at some distance from each other as they believe that their catch rate would be reduced due to the disturbance of the fish if they would tow closer to the previous tow track (P. Molenaar, personal communication). The estimated 200 m distance between parallel tow tracks corresponds to the distance at which the structure of cod shoals changed in response to a trawling disturbance (Morgan *et al.*, 1997). Consistent with the interpretation that the CR in an exploitation patch is influenced by interference, we observed that in about 20% of the cases that a core peel was revisited in the subsequent week the CR had recovered to, or even above, the level observed in the reference week ($log_e R \geq 0$).

Interference competition may also occur if the trawling operations are hampered by the presence of other vessels (Gillis, 1999). We consider this mechanism to play at most a modest role, because simultaneous trawling of two or more trawlers occurred in only 36% of the core patches of PUL trawlers studied.

The response of fish to trawling activities is an important mechanism that drive competitive interactions among vessels aggregated on local concentrations of fish. Due to an arms race among fishers using the same gear, catchabilities of the fleet more than doubled in a ten year time-period (Rijnsdorp *et al*., 2008) while the change to PUL negatively affected Belgian beam trawlers when trawling in the same area (Sys *et al*., 2016). The results of the present study are consistent with the results of earlier vessel density manipulation studies which showed a drop in catch rate at higher vessel density (Rijnsdorp *et al*., 2000b; Poos and Rijnsdorp, 2007b; Sys *et al*., 2017). The stronger inference in TBT as compared to PUL is likely due to the stronger disturbance (noise, sediment plume) of the TBT gear due to the deployment of tickler chains and the higher towing speed. The reduced disturbance of sole by PUL could explain the falling catch rates of gillnet fishers during the transition from TBT to PUL, which was unlikely due to the depletion of sole on the coastal fishing grounds of the gillnetters (Rijnsdorp *et al*., 2018). Vessel interactions due to interference have important consequences for fisheries management as it will affect the relationship between catch rate and resource abundance (Gillis and Peterman, 1998). Changes in fleet capacity, for instance due to a vessel buyback scheme, resulted in a discontinuity in the relationship between catch rate and resource abundance (Dowling *et al*., 2017).

Because high resolution monitoring of fishing effort and catches became technically feasible, fisheries scientist are now able to collect and analyse data sets at the temporal and spatial scale at which the fishery interact with its resource and at which fishing vessels interact. These data contain a wealth of information to advance our knowledge for instance to assess the impacts of bottom trawling on exploited populations, marine habitats and the ecosystem, and to study the importance of competition among fishers, for instance in relation to the rapid decline in available fishing area due to offshore windfarm development and development of MPAs.

Conclusion

We showed that beam trawl fishers concentrated their effort in local patches where they obtained a ~50% higher catch rate compared to peripheral areas. Local patches are the fundamental unit where fishing vessels interact with their target species, impact ecosystems and seafloor habitats, and interact with other fishing vessels. Local patches were trawled in a systematic manner with successive tows segments placed parallel to each other avoiding overlap of trawl tracks. When exploiting a local patch, we inferred that flatfish responded to trawling activities by avoiding being caught as reflected by the catch rate that decreased at a faster rate than could be expected based on cumulative proportion of the core that was swept and the catch efficiency of the gear. The response of fish to trawling activities will affect the catchability of a fishery, will shape the relationship between catch rate and abundance, and drive competitive interactions among fishing vessels and among different fishing gears.

Data availability statement

APR data and catch data per tow of the TBT and PUL trawlers, as well as the primary VMS-data, are subject to confidential agreements. One should contact Sieto Verver, Head of the Centre for Fisheries Research (sieto.verver@wur.nl) for permission using these data.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Funding

The TBT data were collected within the F-project (3.24.12470.02). The PUL data collection and the analysis was funded by the Ministry of Economic Affairs for the purposes of Policy Support Research Theme BO Nature inclusive Fisheries (project no. BO-43–023.02–004).

Author contributions statement

Conceptualization: ADR and JJP; design and methodology: ADR, NTH, GA, JCR, JJP, and AMW; data curation: JCR, ADR, JJP, and NTH; analysis of the findings: ADR, NTH, GA, and JJP; funding acquisition: ADR; drafting manuscript: ADR; revising: ADR, JCR, NTH, GA, JJP, and AMW.

Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgements

The contribution of Wouter van Broekhoven and David Ras (Visned), Brita Trapman, and Emma de Boer (Nederlandse Vissersbond) in the data collection of PUL logbooks is gratefully acknowledged. Harmen Klein Woolthuis (HFK engineering) supported the extraction of the data logger information. The study would not have been possible without the contribution of all participating fishers. The comments of two anonymous reviewers is greatly acknowledged.

References

Able, K. W., and Fodrie, F. J. 2015. Distribution and dynamics of habitat use by juvenile and adult flatfishes. *In* Flatfishes: Biology and Exploitation. pp. 242–282. Ed. by R. N. Gibson, A. J. Geffen, R. D. M. Nashand and H. W. van der Veer. Blackwell Science Ltd, Oxford.

Abrahams, M. V., and Healey, M. C. 1993. Some consequences of variation in vessel density: a manipulative field experiment. Fisheries Research, 15: 315–322.

Albert, O. T., Harbitz, A., and Hoines, A. S.. 2003. Greenland halibut observed by video in front of survey trawl: behaviour, escapement, and spatial pattern. Journal of Sea Research, 50: 117–127.

Babcock, E. A. and Pikitch, E. K. 2000. A dynamic programming model of fishing strategy choice in a multispeices trawl fishery with trip limits. Canadian Journal of Fisheries and Aquatic Sciences, 57: 357–370.

Baptist, M. J., van Dalfsen, J., Weber, A., Passchier, S., and van Heteren, S. 2006. The distribution of macrozoobenthos in the southern North Sea in relation to meso-scale bedforms. Estuarine Coastal Shelf Science, 68: 538–546.

Batsleer, J. Rijnsdorp, A. D. Hamon, K. G. van Overzee, H. M. J. and Poos, J. J. 2016. Mixed fisheries management: Is the ban on discarding likely to promote more selective and fuel efficient fishing in the Dutch flatfish fishery?. Fisheries Research, 174: 118–128.

Benhamou, S., and Collet, J. 2015. Ultimate failure of the lévy foraging hypothesis: two-scale searching strategies outperform scale-free ones even when prey are scarce and cryptic. Journal of Theoretical Biology, 387: 221–227.

Bertrand, S., Burgos, J. M., Gerlotto, F., and Atiquipa, J. 2005. Levy trajectories of peruvian purse-seiners as an indicator of the spatial distribution of anchovy (*Engraulis ringens*). ICES Journal of Marine Science, 62: 477–482.

Bez, N., De Oliveira, E., and Duhamel, G. 2006. Repetitive fishing, local depletion, and fishing efficiencies in the Kerguelen Islands fisheries. ICES Journal of Marine Science, 63: 532–542.

Branch, T. A., and Hilborn, R. 2008. Matching catches to quotas in a multispecies trawl fishery: targeting and avoidance behavior under individual transferable quotas. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1435–1446.

Bublitz, C. G. 1996. Quantitative evaluation of flatfish behavior during capture by trawl gear. Fisheries Research, 25: 293–304.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information—Theoretic Approach, 2nd edn. Springer-Verlag, New York (NY).

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology, 9: 129–136.

Corten, A. 2002. The role of “conservatism”in herring migrations. Reviews in Fish Biology and Fisheries, 11: 339–361.

Damveld, J. H., van der Reijden, K. J., Cheng, C., Koop, L., Haaksma, L. R., Walsh, C. A. J., Soetaert, K. *et al.* 2018. Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. Geophysical Research Letters, 45: 11837–11846.

de Mitcheson, Y. S. 2016. Mainstreaming fish spawning aggregations into fishery management calls for a precautionary approach. Bioscience, 66: 295–306.

De Robertis, A., and Handegard, N. O. 2012. Fish avoidance of research vessels and the efficacy of noise-reduced vessels: a review. ICES Journal of Marine Science, 70: 34–45.

Dorn, M. W. 2001. Fishing behavior of factory trawlers: a hierarchical model of information processing and decision-making. ICES Journal of Marine Science, 58: 238–252.

Dowling, N. A., Mangel, M., and Haddon, M. 2017. Quantifying the effect of vessel interference on catch rates: a theoretical approach. Ecological Modelling, 359: 293–300.

Dreyfus-Leon, M. J. 1999. Individual-based modelling of fishermen search behaviour with neural networks and reinforcement learning. Ecological Modelling, 120: 287–297.

Fiedler, P. C., and Bernard, H. J. 1987. Tuna aggregation and feeding near fronts observed in satellite imagery. Continental Shelf Research, 7: 871–881.

Fretwell, S. D., and Lucas, H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica, 19: 16–36.

Fulton, E. A., Smith, A. D. M., Smith, D. C., and van Putten, I. E. 2011. Human behaviour: the key source of uncertainty in fisheries management. Fish and Fisheries, 12: 2–17.

Gillis, D. M. 1999. Behavioral inferences from regulatory observer data: catch rate variation in the Scotian Shelf silver hake (*Merluccius bilinearis*) fishery. Canadian Journal of Fisheries and Aquatic Sciences, 56: 288–296.

Gillis, D. M. 2003. Ideal free distributions in fleet dynamics: a behavioral perspective on vessel movement in fisheries analysis. Canadian Journal of Zoology, 81: 177–187.

Gillis, D. M., and Frank, K. T. 2001. Influence of environment and fleet dynamics on catch rates of eastern Scotian Shelf cod through the early 1980s. ICES Journal of Marine Science, 58: 61–69.

Gillis, D. M., and Peterman, R. M. 1998. Implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. Canadian Journal of Fisheries and Aquatic Sciences, 55: 37–46.

Gillis, D. M., Peterman, R. M., and Tyler, A. V. 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. Canadian Journal of Fisheries and Aquatic Sciences, 50: 323–333.

Gillis, D. M., Rijnsdorp, A. D., and Poos, J. J. 2008. Behavioral inferences from the statistical distribution of commercial catch: patterns of targeting in the landings of the Dutch beam trawler fleet. Canadian Journal of Fisheries and Aquatic Sciences, 65: 27–37.

Gillis, D. M., and Showell, M. A. 2002. Risk and information use in two competing fleets: Russian and Cuban exploitation of silver hake (*Merluccius bilinearis*). Canadian Journal of Fisheries and Aquatic Sciences, 59: 1275–1286.

Girardin, R. G., Hamon, K., Pinnegar, J., Poos, J. J., Thébaud, O., Tidd, A., Vermard, Y. *et al.* 2017. Thirty years of fleet dynamics modelling using discrete-choice models: What have we learned?. Fish and Fisheries, 18: 638–655.

Groenewold, S., and Fonds, M. 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES Journal of Marine Science, 57: 1395–1406.

Hilborn, R. 1985. Fleet dynamics and individual variation—why some people catch more fish than others. Canadian Journal of Fisheries and Aquatic Sciences, 42: 2–13.

Hintzen, N. T., Aarts, G., Poos, J. J., Van der Reijden, K. J., and Rijnsdorp, A. D. 2021. Quantifying habitat preference of bottom trawling gear. ICES Journal of Marine Science, 78: 172–184.

Hintzen, N. T., Bastardie, F., Beare, D., Piet, G. J., Ulrich, C., Deporte, N., Egekvist, J. *et al.* 2012. VMStools: open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. Fisheries Research, 115–116: 31–43.

Horwood, J. W., and Millner, R. S. 1998. Cold induced abnormal catches of sole. Journal of the Marine Biological Association of the United Kingdom, 78: 345–347.

Janßen, H., Bastardie, F., Eero, M., Hamon, K. G., Hinrichsen, H.-H., Marchal, P., Nielsen, J. R. *et al.* 2018. Integration of fisheries into marine spatial planning: Quo vadis? Estuarine, Coastal and Shelf Science, 201: 105–113.

Kacelnik, A., Krebs, J. R., and Bernstein, C. 1992. The ideal free distribution and predator–prey populations. Trends in Ecology & Evolution, 7: 50–55.

Koop, L., Amiri-Simkooei, A. J., van der Reijden, K., O’Flynn, S., Snellen, M. G., and Simons, D. 2019. Seafloor classification in a sand wave environment on the Dutch continental shelf using multibeam echosounder backscatter data. Geosciences 2019, 9: 142.

Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). Netherlands Journal of Sea Research, 9: 69–85.

Marchal, P., Poos, J. J., and Quirijns, F. 2007. Linkage between fishers’ foraging, market and fish stocks density: examples from some North Sea fisheries. Fisheries Research, 83: 33–43.

Matthiopoulos, Jason, Fieberg, John R, and Aarts, Geert. 2020. Species-Habitat Associations: Spatial Data, Predictive Models, and Ecological Insights. University of Minnesota Libraries Publishing, Minneapolis, MN.

Mills, C. M., Townsend, S. E., Jennings, S., Eastwood, P. D., and Houghton, C. A. 2007. Estimating high resolution trawl fishing effort from satellite-based vessel monitoring system data. ICES Journal of Marine Science, 64: 248–255.

Morgan, M. J., DeBlois, E. M., and Rose, G. A. 1997. An observation on the reaction of Atlantic cod (*Gadus morhua*) in a spawning shoal to bottom trawling. Canadian Journal of Fisheries and Aquatic Sciences, 54: 217–223.

Paloheimo, J. E., and Dickie, L. M. 1964. Abundance and fishing success. Rapports et Procès-Verbaux des Réunions Conseil International pour l’Exploration de la Mer, 155: 152–162.

Poos, J. J. Bogaards, J. A. Quirijns, F. J. Gillis, D. M. and Rijnsdorp, A. D. 2010. Individual quotas, fishing effort allocation and over-quota

discarding in mixed fisheries. ICES Journal of Marine Science, 67: 323–333.
Poos, J. J., Hintzen, N. T., van Rijssel, J., and Rijnsdorp, A. D. 2020. Efficiency changes in bottom trawling for flatfish species as a result of the replacement of mechanical stimulation by electric stimulation. ICES Journal of Marine Science, 77: 2635–2645
Poos, J. J., and Rijnsdorp, A. D. 2007a. The dynamics of small-scale patchiness of plaice and sole as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the fleet dynamics. Journal of Sea Research, 58: 100–112.
Poos, J. J., and Rijnsdorp, A. D. 2007b. An "experiment" on effort allocation of fishing vessels: the role of interference competition and area specialization. Canadian Journal of Fisheries and Aquatic Sciences, 64: 304–313.
Rijnsdorp, A. D., Buys, A. M., Storbeck, F., and Visser, E. G. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES Journal of Marine Science, 55: 403–419.
Rijnsdorp, A. D., Depestele, J., Eigaard, O. R., Hintzen, N. T., Ivanovic, A., Molenaar, P., O'Neill, F. G. *et al.* 2020. Mitigating seafloor disturbance of bottom trawl fisheries for North Sea sole *Solea solea* by replacing mechanical with electrical stimulation. PloS One 8: e61357.
Rijnsdorp, A. D., Dol, W., Hoyer, M., and Pastoors, M. A. 2000a. Effects of fishing power and competitive interactions among vessels on the effort allocation on the trip level of the Dutch beam trawl fleet. ICES Journal of Marine Science, 57: 927–937.
Rijnsdorp, A. D., Poos, J. J., and Quirijns, F. J. 2011. Spatial dimension and exploitation dynamics of local fishing grounds by fishers targeting several flatfish species. Canadian Journal of Fisheries and Aquatic Sciences, 68: 1064–1076.
Rijnsdorp, A. D., Poos, J. J., Quirijns, F. J., HilleRisLambers, R., de Wilde, J. W., and Den Heijer, W. M. 2008. The arms race between fishers. Journal of Sea Research, 60: 126–138.
Rijnsdorp, A. D., van Maurik Broekman, P. L., and Visser, E. G. 2000b. Competitive interactions among beam trawlers exploiting local patches of flatfish in the North Sea. ICES Journal of Marine Science, 57: 894–902.
Rijnsdorp, A.D., van Rijssel, J., and Hintzen, N.T. 2018. Declining catch rates of small scale fishers in the southern North Sea in relation to the pulse transition in the beam trawl fleet Wageningen Marine Research report C051/18 Wageningen Marine Research, IJmuiden.
Salas, S., and Gaertner, D. 2004. The behavioural dynamics of fishers: management implications. Fish and Fisheries, 5: 153–167.
Santa Cruz, F., Ernst, B., Arata, J. A., and Parada, C. 2018. Spatial and temporal dynamics of the Antarctic krill fishery in fishing hotspots in the Bransfield Strait and south Shetland Islands. Fisheries Research, 208: 157–166.
Shucksmith, R., Hinz, H., Bergmann, M., and Kaiser, M. J. 2006. Evaluation of habitat use by adult plaice (*Pleuronectes platessa* L.) using underwater video survey techniques. Journal of Sea Research, 56: 317–328.
Stephens, D. W., and Krebs, J. R. 1986. Foraging Theory. Princeton University Press, Princeton, NJ. 247pp.
Sys, K. 2018. Exploitation dynamics of the Belgian beam trawl fleet targeting hotspots of flatfish. PhD thesis, Faculty of Bioscience Engineering, Ghent University, Ghent. 129pp.
Sys, K., Poos, J. J., Van Meensel, J., Polet, H., and Buysse, J. 2016. Competitive interactions between two fishing fleets in the North Sea. ICES Journal of Marine Science, 73: 1485–1493.
Sys, K., Van Meensel, J., Polet, H., and Buysse, J. 2017. A temporal race-for-fish: the interplay between local hotspots of flatfish and exploitation competition between beam trawlers after a seasonal spawning closure. Fisheries Research, 193: 21–32.
Temming, A., Floeter, J., and Ehrich, S. 2007. Predation hot spots: large scale impact of local aggregations. Ecosystems, 10: 865–876.
van der Reijden, K. J., Hintzen, N. T., Govers, L. L., Rijnsdorp, A. D., and Olff, H. 2018. North Sea demersal fisheries prefer specific benthic habitats. PloS One, 13: e0208338.
van der Reijden, K. J., Koop, L., O'Flynn, S., Garcia, S., Bos, O., van Sluis, C., Maaholm, D. J. *et al.*. 2019. Discovery of *Sabellaria spinulosa* reefs in an intensively fished area of the Dutch continental shelf, North Sea. Journal of Sea Research, 144: 85–94.
van Dijk, T. A. G. P., van Dalfsen, J. A., Van Lancker, V., van Overmeeren, R. A., van Heteren, S., Doornenbal, P. J., Harris, P. T., *et al.*. 2012. 13—benthic habitat variations over tidal ridges, North Sea, the Netherlands. *In* Seafloor Geomorphology as Benthic Habitat, pp. 241–249. Ed. by P. T. Harrisand and E. K Baker. Elsevier, London.
van Overzee, H. M., and Rijnsdorp, A. D. 2015. Effects of fishing during the spawning period: implications for sustainable management. Reviews in Fish Biology and Fisheries, 25: 65–83.
van Putten, I. E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K. G., Hutton, T., and Pascoe, S. 2012. Theories and behavioural drivers underlying fleet dynamics models. Fish and Fisheries, 13: 216–235.
Vermard, Y., Rivot, E., Mahévas, S., Marchal, P., and Gascuel, D. 2010. Identifying fishing trip behaviour and estimating fishing effort from VMS data using Bayesian Hidden Markov models. Ecological Modelling, 221: 1757–1769.
Vignaux, M. 1996. Analysis of spatial structure in fish distribution using commercial catch and effort data from the New Zealand hoki fishery. Canadian Journal of Fisheries and Aquatic Sciences, 53: 963–973.
Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P., and Stanley, H. E. 1999. Optimizing the success of random searches. Nature, 401: 911–914.
Wajnberg, E., Fauvergue, X., and Pons, O. 2000. Patch leaving decision rules and the marginal value theorem: an experimental analysis and a simulation model. Behavioral Ecology, 11: 577–586.
Zhang, H., Yang, S.-L., Fan, W., Shi, H.-M., and Yuan, S.-L. 2021. Spatial analysis of the fishing behaviour of tuna purse seiners in the western and central Pacific based on vessel trajectory data. Journal of Marine Science and Engineering, 9: 322.
Zuur, A. F. 2012. A beginners guide to generalized additive models with R, Highland Statistics Ltd, UK.

Handling Editor: Pamela Woods