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Original Article

Competitive interactions between two fishing fleets in the North Sea

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We examine whether the landing rates of Belgian beam trawlers in the Southern Bight of the North Sea were affected through competitive interactions with the Dutch beam trawler fleet and whether the development of a pulse trawler fleet has altered competitive interactions between both fleets. Effects of competition were investigated through a natural experiment based on the different weekly exploitation patterns of both fleets. Logbook data were used to fit a generalized additive mixed model for the daily landing rates of the target species sole (*Solea solea*) and plaice (*Pleuronectes platessa*). Results showed that landing rates of sole by the Belgian beam trawlers (>221 kW) from 2006 to 2013 were lower during weekdays than during weekends when the Dutch trawler fleet is in harbour, while no such effect was found for plaice. After the development of a pulse trawler fleet in 2011, the negative weekday effect in the sole landing rates was much more pronounced in 2012 and 2013. This increased loss of efficiency during weekdays, as a result of increased competition with the Dutch trawler fleet, coincided with a reallocation of fishing effort by the Belgian beam trawler fleet.

Keywords: fleet dynamics, interference competition, landings per unit effort, pulse trawling.

Introduction

Commercial fishers constantly innovate to remain economically competitive and to increase the value of their catch, reduce operational costs, aid navigation, and improve safety at sea (Valdemarsen, 2001; Eigaard *et al.*, 2014). Such innovations may occur suddenly, as was observed when beam trawls were introduced in the Dutch flatfish fishery in the early 1960s. In <10 years, the demersal fishery changed from an otter trawl fishery to a beam trawl fishery (Rijnsdorp *et al.*, 2008). The innovations often cause an increase in the catchabilities of fish species and could arguably be one of the main reasons that many of the world's fisheries are suffering from declining resources (Eigaard *et al.*, 2014).

The social and economic dynamics of uptake of new technologies are complex (Eigaard, 2009), and we often observe that the speed of uptake is heterogeneous in fisheries. In the transition period, where some parts of fishing fleets adopt new technologies while others remain unchanged, the competitive dynamics among fleets change. This change can cause knock-on effects in the fishery, such as changes in fishing effort allocation.

In the North Sea, we have observed a sudden change in fishing technology in one of the major demersal fisheries: the Dutch demersal flatfish fishery. As a result of the increased pressure on the beam trawler fishery (Soetaert *et al.*, 2015), the EU in 2009 allowed the use of the pulse trawl gear for part of the beam trawlers active in the North Sea (EU, 2009). The major difference is that heavy tickler chains are substituted by electrodes producing electric stimuli. This results in a weight reduction and decline in fuel usage of ca. 50% compared with beam trawling (van Marlen *et al.*, 2014). Until 2013, the transition to pulse trawling occurred mainly in the Dutch beam trawler fleet.

The development of a pulse trawler fleet is expected to alter fishing tactics in the Dutch trawler fleet (Batsleer *et al.*, 2016), potentially resulting in increased spatial overlap with the beam trawler fleet of neighbouring Belgium. In this paper, we examine the occurrence of competition between both fleets and whether this changed since the development of the Dutch pulse trawler fleet. We also study how the change in competitive interactions has altered fishing behaviour in the Belgium fleet as a knock-on effect of the changes in the Dutch fleet.

Competitive interactions affect the relationship between fish abundance and catch per unit effort (cpue) and thus the allocation of fishing effort (Gillis and Peterman, 1998; Gillis, 2003; Poos and Rijnsdorp, 2007; Girardin *et al.*, 2015). Competition among fishing vessels is a result of (i) direct interactions among fishing vessels (interference competition), e.g. through increased risk of net-loss or inducing a change in fish behaviour and/or (ii) through local depletion of the resource (exploitation competition). Knowledge about the mechanistic processes causing interference competition and about the fine-scale dynamics in fish abundance is required to distinguish interference competition from exploitation competition. However, interference competition results typically in a direct and negative response in catch rates towards an increase in vessel density, while we expect exploitation competition to result in a gradual response in catch rates to changes in vessel density.

Empirical research to quantify the effects of competition on catch rates is difficult because of practical constraints. First, biotic factors affecting the distribution of fish species are difficult to control when carrying out field experiments (Abrahams and Healey, 1993). Second, setting up experiments with fishing vessels is hampered by high financial costs. To our knowledge, only one experiment was conducted in which vessel density was directly manipulated (Abrahams and Healey, 1993). In this study, increased vessel density in the British Columbia salmon troll fleet had negative, positive, and no effect on catch rates, depending on the fish species. In studies by Rijnsdorp *et al.* (2000a) and Poos and Rijnsdorp (2007), competitive interactions among Dutch beam trawlers were quantified based on "experimental" periods with (i) low vessel density during a week of "prayer" and (ii) high vessel density due to a temporal area closure.

To study the competitive interactions between the Belgium and Dutch fleets, we use a cultural difference between the fleets as a natural experiment. While Dutch vessels tend to stay in port over the weekend, Belgium vessels fish irrespective of the weekday. This weekly, cyclic change in vessel density puts us in a unique position to analyse the effects of competition between both fleets.

By assessing the effects of competitive interactions among fishing fleets as a result of different uptake speed of fisheries technologies and the adaptive response of fishers, this paper aims to gain more insights into the underlying mechanisms of fleet dynamics. This may reduce the uncertainty generated through unintended behaviour of fishers and increase the effectiveness of fisheries management in achieving its ecological and socio-economic goals.

Material and methods

Development of the flatfish fishery in the Southern Bight

During the study period (2006–2013), the flatfish fishery in the Southern Bight targeted a wide range of demersal fish species, with sole (*Solea solea*) and plaice (*Pleuronectes platessa*) being the dominant species landed (Rijnsdorp *et al.*, 1998). The fishery is dominated by beam trawlers fishing under the Belgian or Dutch flag. Because the nominal value of sole (10 € kg^{-1}) is ca. 7.5-fold higher than the nominal value of plaice (1.3 € kg^{-1}), sole accounts for >60% of the landed value of the Belgian beam trawl fishery in the Southern Bight. Hence, sole is the main target species in terms of revenue.

Before 2011, Dutch beam trawlers were generally equipped with chains in the net opening penetrating the seabed (Creutzberg *et al.*, 1987; Eigaard *et al.*, 2015). Depending on seabed characteristics, two configurations of chains were used: (i) V-shaped tickler chains or (ii) chain mats (Fonteyne and Polet, 1995; Eigaard *et al.*, 2015). V-shaped tickler chains are used on fishing grounds with smooth surfaces, such as sandy sediments (Rijnsdorp *et al.*, 2008). On rough fishing grounds, a matrix design of the tickler chains called chain mats is used. While most Dutch beam trawlers traditionally used the V-shaped tickler chain configuration, the Belgian beam trawlers typically used chain mats (Fonteyne and Polet, 1995; Rijnsdorp *et al.*, 2008). Hence, rocky fishing grounds were mainly exploited by Belgian beam trawlers, whereas smooth fishing grounds were mainly trawled by Dutch vessels. Consequently, Belgian and Dutch beam trawl fleets were spatially segregated (Figure 1). Vessels from other countries were less numerous and mainly exploited other fishing grounds; therefore, they are not taken into account in this study.

In pulse trawls, the mechanic stimulus of fish by chains is replaced by electric stimuli of electrodes rigged in the net opening (Soetaert *et al.*, 2015). These electrodes cause muscle contractions in fish, decreasing their ability to swim away or dive under the net opening. The relatively light design of the pulse trawl allows operation on a wider range of sediments (Rasenberg *et al.*, 2013). Additionally, catch composition of pulse trawlers differs compared with beam trawling (van Marlen *et al.*, 2014). The change in catch composition affects the relative profitability of the various fishing grounds because of the mixed nature of the flatfish fishery where different fish species are caught simultaneously. As a result, the development of the commercial Dutch pulse trawler fleet caused a reallocation of fishing effort (Batsleer *et al.*, 2016).

Data

In this study, we focus on the Belgian beam trawler segment with engine powers >221 kW. These vessels are obliged to fish outside the 12-mile coastal zone. More than 80% of the fishing effort by the Belgian study fleet in the Southern Bight was concentrated in four ICES statistical rectangles (1° longitude × 0.5° latitude, ca. 30 × 30 nautical miles): 32F1, 32F2, 33F2, 34F2 (Figure 1). Other statistical rectangles were incidentally fished, but not retained for analysis.

Mandatory logbook data for 2006–2013 were used for statistical analysis. In these logbooks, fishers report fishing activity daily by specifying fishing location (by ICES statistical rectangle), fishing gear, mesh size, and estimated weight of landings by species. In addition, vessel information (reference number, length, motor engine, and gross tonnage) was available for analysis. No data on discarding were available. Hence, the analysis is restricted to the landings per unit effort (lpue), which is the portion of the daily catch commercialized. Logbook records for the Belgium fleet (>221 kW) fishing in the study area are summarized in Table 1. Fine-scale spatial distribution of the Dutch and Belgium fleet is obtained using the VMS data (Hintzen *et al.*, 2012).

Analysis of competition in a natural experiment

Competition was analysed using the different weekly exploitation patterns of Belgian and Dutch fishers. Dutch fishers typically make fishing trips of 4 d duration starting on Monday morning and ending on Thursday (Rijnsdorp *et al.*, 2000a). Consequently, fishing activity by the Dutch beam trawlers is much lower from Friday until Sunday (Table 2). In contrast, the Belgian beam trawlers

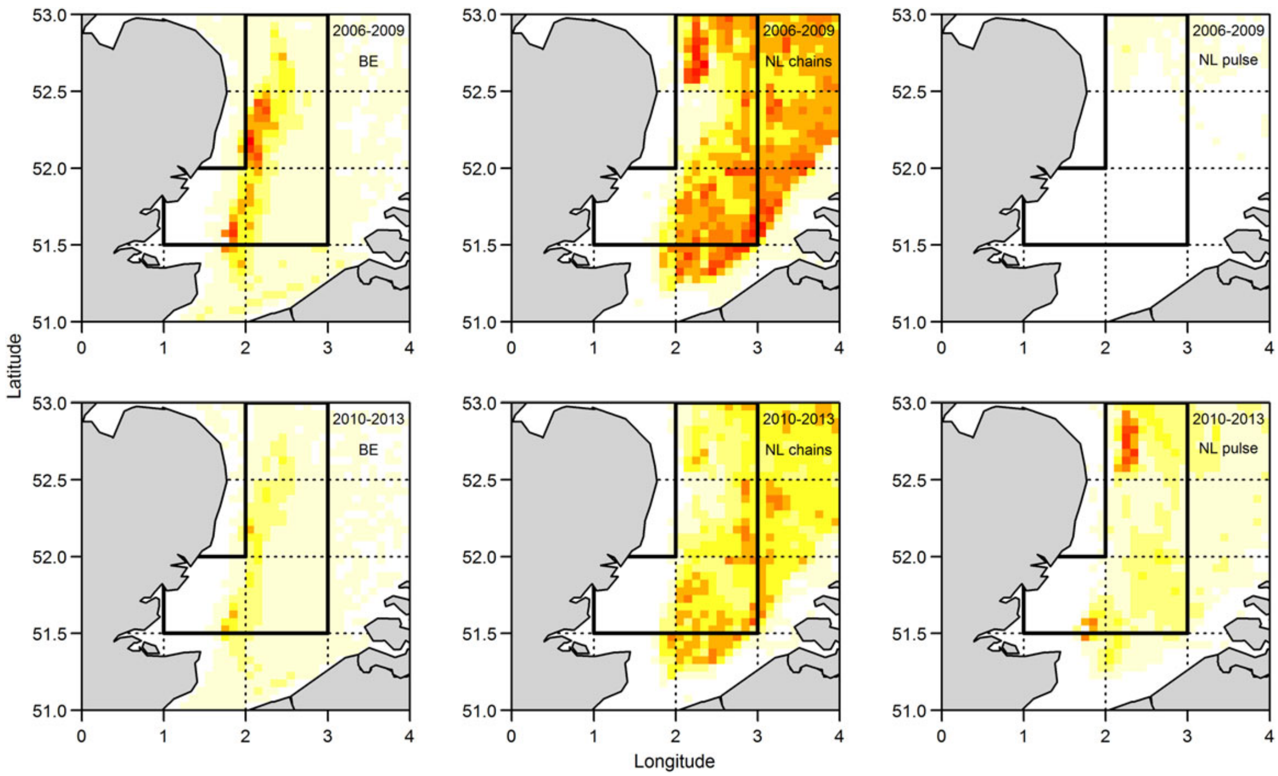

Figure 1. Spatial distribution of fishing effort of the Belgian beam trawlers (>221 kW) (left panels), Dutch beam trawlers with tickler chains (middle panels), and Dutch pulse trawlers (right panels) in the Southern Bight during the period 2006–2009 and 2010–2013, as recorded by satellite-based vessel monitoring systems (VMS). The four ICES statistical rectangles comprising the study area are enclosed by the black frame. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Table 1. Annual number of fishing trips and summary statistics of the dataset used for analysis grouped by year and weekday or weekend. The number of logbook events and different vessels that were active in the study area, the average engine power (kW), and daily landings (kg) of sole and plaice. In total, there are 5063 logbook events recorded during weekdays and 3767 recorded during weekends.

			Weekdays (n = 5 063)				Weekends (n = 3 767)			
Year	No. of vessels	No. of trips	Logbook events	Engine power	Sole landings	Plaice landings	Logbook events	Engine power	Sole landings	Plaice landings
2006	48	341	880	810	247	220	688	806	266	229
2007	42	236	566	775	302	264	437	774	315	246
2008	46	335	966	877	363	249	741	878	395	268
2009	41	370	1 056	910	335	311	773	907	335	269
2010	30	280	801	899	358	523	519	885	363	481
2011	27	150	352	868	390	484	248	858	373	587
2012	23	91	181	859	300	450	131	824	349	485
2013	21	101	261	780	427	650	230	779	503	621

Table 2. Daily distribution of the effort (time present) in the study area (expressed as percentages) based on the logbooks of the Belgian and Dutch beam trawler fleet (engine power >221 kW).

	Belgium							The Netherlands						
Year	Mon	Tue	Wed	Thu	Fri	Sat	Sun	Mon	Tue	Wed	Thu	Fri	Sat	Sun
2006	14	14	13	14	15	16	15	19	24	24	23	7	1	1
2007	13	15	14	14	14	16	14	19	25	25	23	6	1	1
2008	14	14	14	14	14	16	15	20	24	25	23	6	1	1
2009	15	15	15	14	13	15	14	20	25	24	23	5	1	1
2010	14	16	16	14	13	13	13	20	25	24	22	6	1	1
2011	14	14	15	15	15	15	12	21	24	24	22	6	2	1
2012	16	16	13	11	13	17	14	22	25	24	19	6	2	2
2013	12	11	12	14	16	19	16	21	24	24	20	7	3	2

have no fixed weekly exploitation patterns. Most fishing trips have a duration of 8–10 d, and fishing effort is spread equally throughout the week.

As a result of these different weekly fishing patterns, the probability of a Belgian fishing vessel encountering other vessels is much higher Monday–Thursday than Friday–Sunday. Consequently, effects of competition should be higher during weekdays than weekends.

Competition was examined by analysing the daily landing rates (lpue) of the target species sole and plaice. To investigate both linear and non-linear relationships between the landing rates per unit effort (kg) and the explanatory variables, a generalized additive mixed model (GAMM) was fitted. The vessel reference number was included as a random effect (μ) to correct for vessel effects. Such vessel effects include skipper effects and physical characteristics of vessels that are not recorded in the data. The temporal patterns of the dependent variables were compared in different regression models. The null model [Equation (1)] includes the annual and seasonal temporal trends, a vessels' engine power, and an intra-trip effect:

$$\log(\text{lpue}) = \beta_0 + \beta_{1_i}\text{year} + \beta_2 \log(\text{engine power}) + f\,(\text{month})_{\text{rect}} + f\,(tripday) + \varepsilon + \mu. \quad (1)$$

The model is fitted to both species separately. In the null model, β_0 represents the intercept. A categorical variable (year) was used to capture the annual variation in landing rates. The first year of the analysis, 2006, was the reference year and is included in the intercept. Therefore, β_{1_i} represents the year effect of each year i ($i \in 2007, \ldots,$ 2013) relative to 2006. The coefficient β_2 is the slope of the log-linear relationship between engine power (log(engine power)) of a vessel and landing rates (Rijnsdorp *et al.*, 2000a). The intra-annual variation caused by seasonal migration of adult sole and plaice (Rijnsdorp *et al.*, 1998) was captured by a seasonal term of the catch month for each ICES statistical rectangle [$f(\text{month})_{\text{rect}}$]. This term is smoothed to the data using regression splines (Wood, 2004). Because a seasonal trend is assumed, cyclic cubic splines were used to avoid discontinuity at the endpoints (Wood, 2006). To examine intra-trip variation in the landing rates, a tripday effect was included. This variable represents the number of days left before the end of the trip; hence, the day of arrival in a harbour is 0. Since there is no *a priori* knowledge about the underlying pattern, the intra-trip variation was included as a non-parametric effect and smoothed to the data. To allow overdispersion and 0 catches, a logarithmic link function between the linear predictor and the mean was specified with a negative binomial distribution of the error term (ε).

To investigate the reduction in landings during weekdays resulting from competition, the null model was extended to include a weekday effect without [Equation (2)] and with [Equation (3)] interaction with the annual effect:

$$\log(\text{lpue}) = null\ model + \beta_4\ \text{weekday}, \quad (2)$$

$$\log(\text{lpue}) = null\ model + \beta_{4_i}\ \text{weekday} \times \text{year}. \quad (3)$$

In the first model [Equation (2)], a categorical weekday effect (weekday) was added to the null model. The weekday variable was assigned a value of 0 for weekdays (Monday–Thursday) and a value of 1 for weekends (Friday–Sunday). Therefore, β_4 represents the effect of the weekend compared with weekdays. In the second model [Equation (3)], the categorical weekday effect is included as an interaction term with the categorical year variable (weekday $\times$ year). Hence, β_{4_i} represents the change in the dependent variable in weekends relative to weekdays for each year i ($i \in 2007, \ldots,$ 2013) of the study period.

Finally, to gain insight in the type of competition, we analysed whether landing rates during weekdays and weekends showed a negative or positive slope, which could indicate the occurrence of competition through local depletion of fish stocks (exploitation competition):

$$\log(\text{lpue}) = \text{null model} + \beta_{5_j}\text{day} \times \text{weekday}. \quad (4)$$

Therefore, the null model was extended with an interaction term between the numeric day effect (day) (Monday = 1, . . ., Sunday = 7) and the categorical weekday effect (weekday) [Equation (4)]. Hence, the coefficient of β_{5_j} represents the slope of the landing rates during weekdays and weekends.

The open-source software platform R (version 3.1.3; R Core Team, 2015) was used for analyses. Logbook data were used and processed following the workflow as described in the *vmstools* R-package (Hintzen *et al.*, 2012) and time–date conversions were carried out with the *lubridate* R-package (Grolemund and Wickham, 2011). The R-package *mgcv* was used to fit the GAMM models (Wood, 2004).

Results

During the study period, the number of Belgian beam trawlers participating in the flatfish fishery in the Southern Bight declined, and the fishery reallocated fishing effort. This resulted in a decline in fishing effort in the Southern Bight (Figure 2). The number of vessels showed a decline during the study period (Table 1). Fishing effort allocation was characterized by a more complex pattern. After an increase in 2008 and 2009, fishing effort in the Southern Bight strongly decreased. The steepest decline occurred from 2010 to 2012, when a reduction of 76% was observed. In 2013, fishing effort increased again. Nevertheless, fishing effort allocation in the Southern Bight in 2013 was still more than 50% lower than in 2006–2010.

Apart from spatial effort reallocation, a shift occurred in the weekly exploitation patterns of the Belgian beam trawlers fishing in the Southern Bight. Most vessels land their fish in a Belgian harbour the day before the auction to sell their landings. Auctions

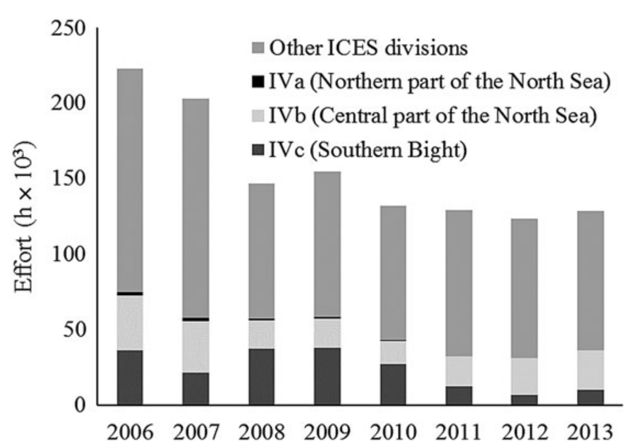

Figure 2. Fishing effort allocation per ICES Division of the Belgian beam trawler fleet (>221 kW).

occur weekly on Monday, Wednesday, and Friday; hence, most fishing trips end on Sunday, Tuesday, and Thursday (Table 3). During 2006–2011, >50% of the fishing trips of the study fleet ended on Tuesday or Thursday, while less trips ended on Sunday, except in 2007. In contrast, a shift occurred in 2012 and 2013, with a larger proportion of trips ending at the end of the weekend on Sunday or just after the weekend on Monday.

All parametric effects of the null model were significant at the 0.05 level for both sole and plaice (Table 4). There was a positive log-linear relationship with vessel engine power, indicating that more powerful vessels have higher landing rates. Similar intra-trip patterns were found in the landing rates of both species (Figure 3). At the start of a trip, lpue values for both species show increasing trends with wide confidence interval bounds. Between 10 and 3 d before the end of a trip, landing rates are rather stable and decline again towards the end of the trip. The slopes of the increase and decrease at, respectively, the start and end of a trip are steeper for sole lpue than for plaice lpue. Seasonal variation in sole lpue differed between ICES statistical rectangle 32F1 and the other ICES statistical rectangles of the study area (Figure 4). The seasonal pattern in rectangle 32F1 was characterized by two peaks, one in spring and one in autumn, while sole lpue in the other rectangles had a single peak in autumn. In contrast, the seasonal variation in plaice lpue showed similar patterns in each of the four ICES statistical rectangles of analysis, with low values in spring and a strong increase in summer, after which the landing rate of plaice remained equal until the end of the year (Figure 5).

Table 3. Weekly distribution of Belgian beam trawlers (<221 kW) (expressed as percentages) embarking in a Belgian harbour after a fishing trip in the Southern Bight (source: logbook data).

Year	Mon	Tue	Wed	Thu	Fri	Sat	Sun
2006	6	29	5	24	6	10	20
2007	3	28	6	25	1	7	30
2008	3	32	3	27	4	7	24
2009	3	30	4	24	7	8	25
2010	2	28	3	31	7	8	21
2011	3	31	2	30	7	7	21
2012	5	21	7	25	4	4	33
2013	15	19	5	25	4	4	29

The null models were extended with a weekday effect with (weekday × year) and without (weekday) interaction with the year effect. A weekday effect was found significant (t-value = 2.33; p-value = 0.02) in sole lpue during 2006–2013. Landing rates of sole ($\beta = 0.036$; s.e. = 0.016) were 4% higher from Friday to Sunday compared with weekdays (Monday–Thursday). In contrast, no overall weekday effect was found at the 0.05 level in the landing rates of plaice.

Including the weekday effect as interaction effect with the year effect resulted in significant (p-value < 0.05) weekday effects in the landing rates of sole in 2008 and 2013 (Figure 6). In 2006 (t-value = 1.85; p-value = 0.07) and 2012 (t-value = 1.84; p-value = 0.07), weekday effects showed a similar trend. In all of these years, the effect was positive, indicating that sole landings were depressed during weekdays. In 2006 and 2008, daily sole landings were, respectively, 7% ($\beta = 0.068$; s.e. = 0.037) and 9% ($\beta = 0.085$; s.e. = 0.036) lower during weekdays compared with weekends, whereas in 2012 (16%) ($\beta = 0.149$; s.e. = 0.081) and 2013 (13%) ($\beta = 0.125$; s.e. = 0.063), the magnitude of the weekday effect was considerably higher. The landing rates of plaice were only characterized by a positive weekend effect in 2011 (t-value = 1.803; p-value = 0.07) during which plaice landings were ca. 19% higher in weekends (Friday–Sunday).

Analysis of landing rates during weekdays and weekends showed a negative trend in lpue for sole during weekdays, whereas no pattern was found in the landing rates of plaice during weekdays. During Monday–Thursday, landing rates of sole declined with 4% ($\beta = -0.014$; s.e. = 0.006; t-value = −2.345; p-value = 0.02). The landing rates of both species during weekends did not show a decreasing or increasing trend.

Discussion

Patterns in lpue of sole and plaice

The landing rates of the target species sole and plaice of Belgian beam trawlers using chain mats are positively related to a vessel's engine power, similar to other trawl fisheries (Rijnsdorp *et al.*,

Table 4. Estimated coefficients (β) and standard error (s.e.), and t-value (right side of F/t-value columns) of the parametric effects and ANOVA output, with the degrees of freedom (d.f.) and F-value (left side of F/t-value columns) per variable of the null model of sole and plaice lpue.

	lpue sole				lpue plaice			
Parameter	β (s.e.)	d.f.	F/t-value	p-value	β (s.e.)	d.f.	F/t-value	p-value
Intercept	2.09 (0.82)	–	2.55	0.01	0.16 (1.32)	–	0.13	0.90
Year	–	7	20.7	<0.01	–	7	55.2	<0.01
2006	–	–	–	–	–	–	–	–
2007	0.17 (0.03)	–	5.70	<0.01	0.17 (0.05)	–	3.22	<0.01
2008	0.20 (0.03)	–	7.34	<0.01	0.08 (0.05)	–	1.81	0.07
2009	0.13 (0.03)	–	4.85	<0.01	0.21 (0.04)	–	4.70	<0.01
2010	0.19 (0.03)	–	6.43	<0.01	0.61 (0.05)	–	12.61	<0.01
2011	0.24 (0.04)	–	6.63	<0.01	0.77 (0.06)	–	13.17	<0.01
2012	0.12 (0.05)	–	2.57	0.01	0.60 (0.08)	–	7.91	<0.01
2013	0.46 (0.05)	–	10.95	<0.01	0.84 (0.07)	–	12.34	<0.01
log(engine power)	0.48 (0.12)	1	4.03	<0.01	0.77 (0.19)	1	3.94	<0.01
f(tripday)	–	3.92	97.9	<0.01	–	3.58	22.1	<0.01
$f(\text{month})_{32F1}$	–	2.90	11.2	<0.01	–	2.96	153.6	<0.01
$f(\text{month})_{32F2}$	–	0.76	0.4	0.22	–	2.96	113.3	<0.01
$f(\text{month})_{33F2}$	–	2.63	26.0	<0.01	–	2.98	115.8	<0.01
$f(\text{month})_{34F2}$	–	2.41	16.7	<0.01	–	2.90	28.2	<0.01

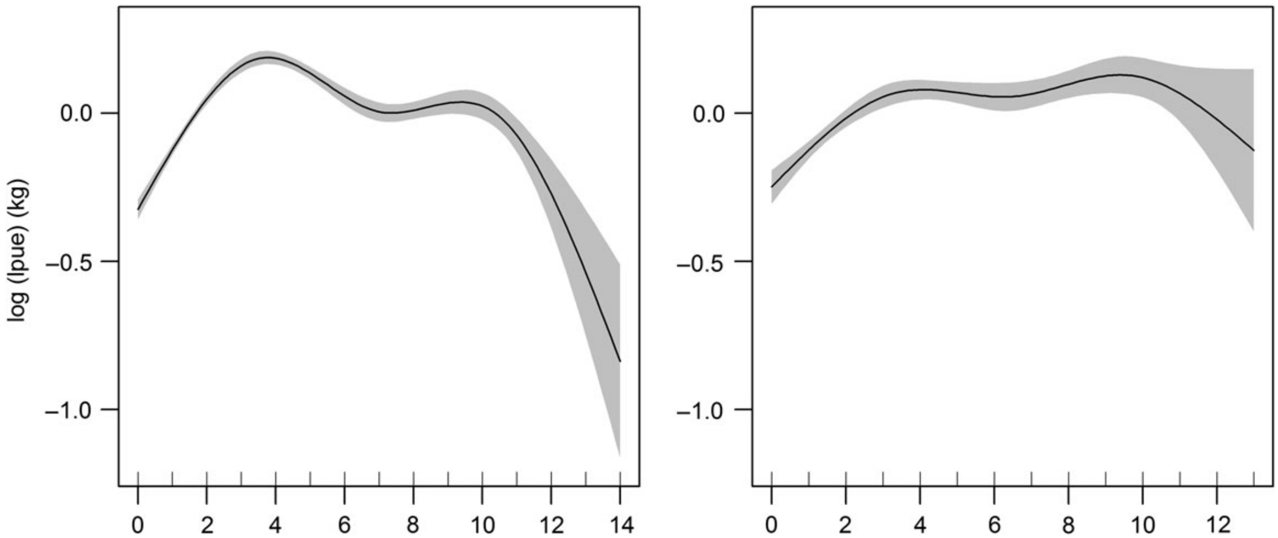

Figure 3. Plot of the non-parametric intra-trip effect [*f*(tripday)] of the null model. The *x*-axis represents the number of days before the end of the trip, while the *y*-axis is the marginal response in sole lpue (left panel) and plaice lpue (right panel). The grey shade represents the 95% confidence interval.

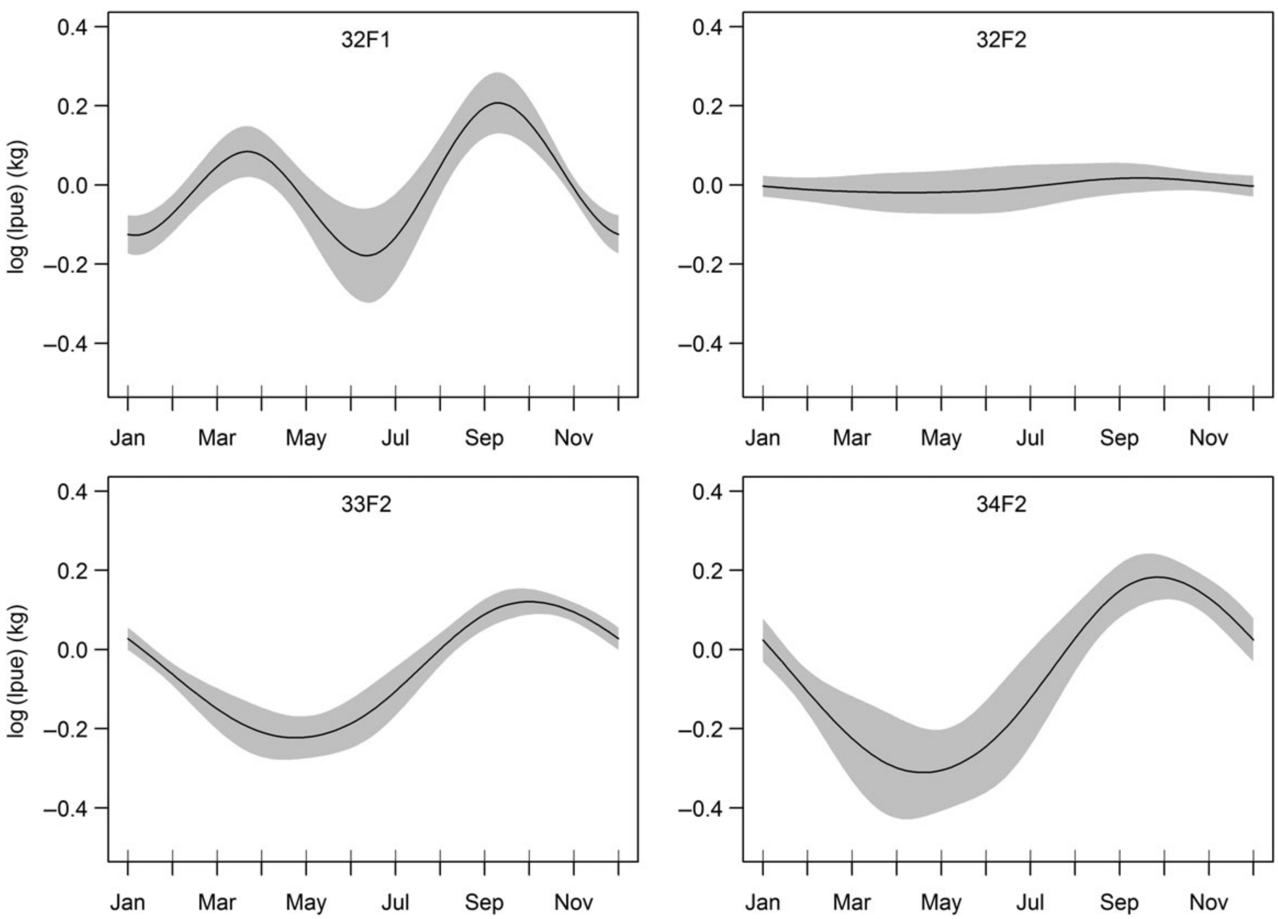

Figure 4. Plot of the non-parametric seasonal effect [*f*(month)rect] of the null model of sole lpue. The grey shade represents the 95% confidence interval.

2000a; Eigaard and Munch-Petersen, 2010). More powerful vessels are able to tow faster and use heavier fishing gear with more chains in the net-opening, and the increased penetration depth of the fishing gear results in higher catchability.

The null model reveals a strong effect of tripday on catch rate showing similar patterns with the exploitation dynamics found in the Dutch beam trawler fishery (Rijnsdorp *et al.*, 2000b, 2011). Following Rijnsdorp *et al.* (2000b), we hypothesize that at the

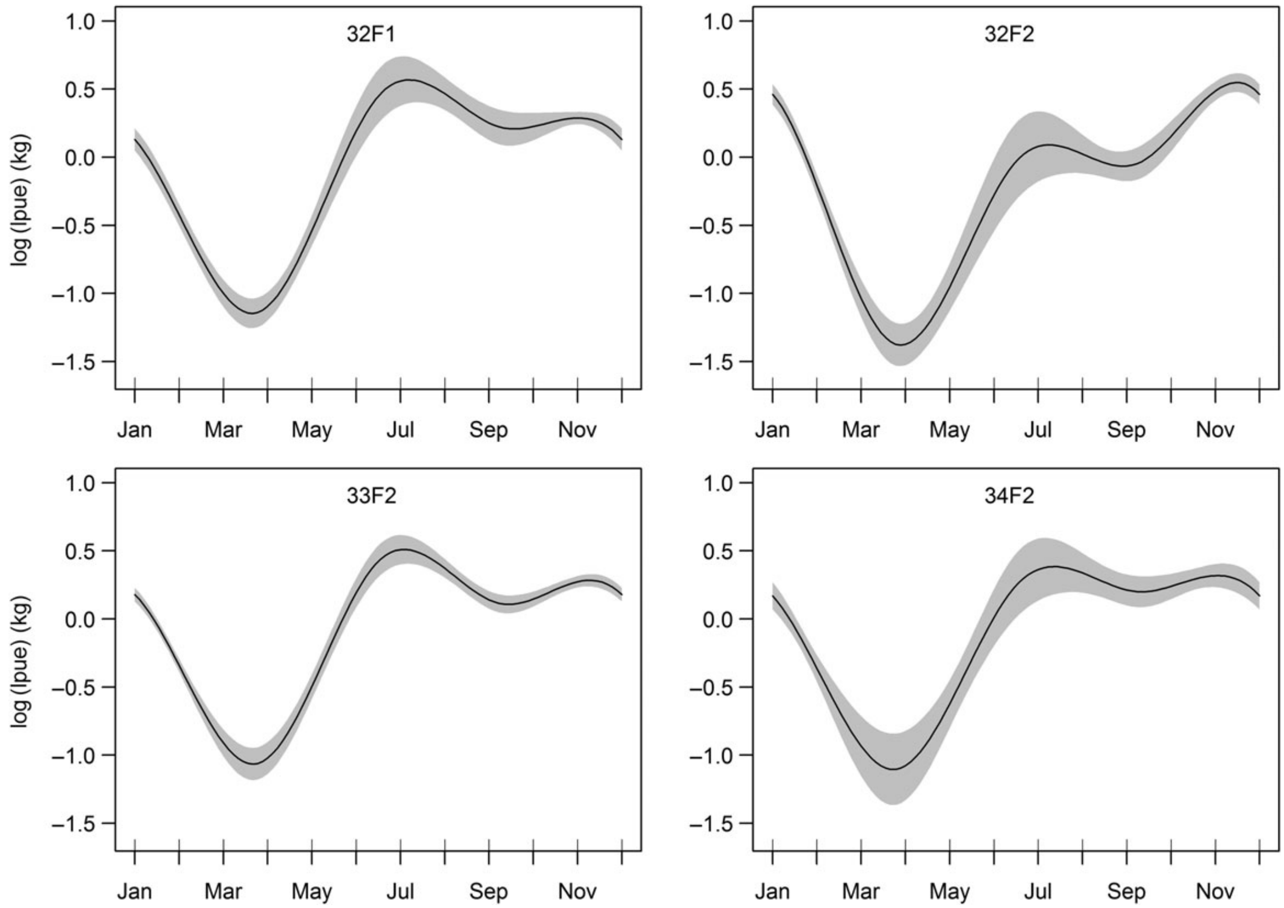

Figure 5. Plot of the non-parametric seasonal effect [f(month)rect] of the null model of plaice lpue. The grey shade represents the 95% confidence interval.

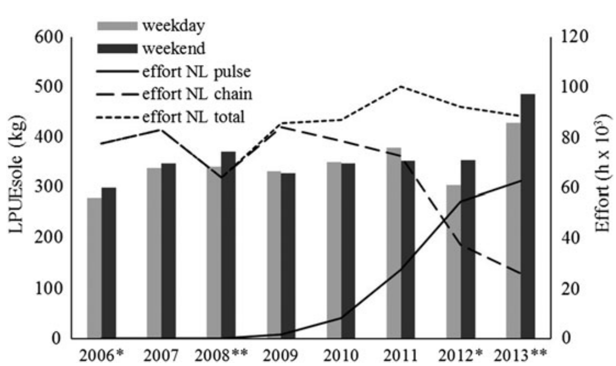

Figure 6. Bar plot of the fitted values [Equation (3)] of sole lpue in weekdays and weekends (engine power = 900 kW; month = January; ICES rectangle = 32F1; tripday = 3). Years with a difference between landing rates in weekdays and weekends are indicated with * (p-value < 0.1) and ** (p-value < 0.05). Line plot of the annual effort of the Dutch beam trawler fleet (pulse, chain, and total trawler fleet).

beginning of a trip, skippers search for local high densities of fish, which explains the increasing trend in lpue. Once skippers have located local hotspots of fish, an exploitation phase follows, during which lpue is high. At the end of a trip, lpue tends to decrease again, which may be a consequence of a local depletion of the resources.

Seasonal patterns in sole and plaice lpue are related to the spawning–feeding migrations of both species. Sole migrate in spring to spawning grounds in shallow coastal waters (Rijnsdorp *et al.*, 1992). One of these spawning grounds, the Thames estuary, is partially located within our study area (ICES rectangle 32F1), which explains the occurrence of a peak in sole lpue in April in this ICES rectangle. In autumn, sole leaves the coastal areas and migrates to warmer, offshore waters, coinciding with a peak in sole landing rates in October. Compared with sole, the migration of plaice to and from spawning areas occurs over longer distances, resulting in stronger seasonal variation in landing rates (Poos and Rijnsdorp, 2007). Mature plaice migrate between spawning grounds in the south in winter and feeding grounds in the north in summer and autumn (Houghton and Harding, 1976). This migratory behaviour of plaice does not correspond to the high landing rates of plaice observed in summer. A possible explanation for the strong increase in plaice lpue in July is the allocation of the national quota which is distributed several times a year to individual vessels. Until June, Belgian beam trawlers have a limited plaice quota in the North Sea. In July, quota is redistributed, whereby the individual plaice quota strongly increases. We hypothesize that this affects the targeting and discard behaviour, which, in turn, affects the observed seasonal lpue levels.

Competition

The weekday effect found in sole lpue suggests that competition is related to the fishing activity of the Dutch trawler fleet. When

Dutch trawlers fish from Monday to Thursday, sole landings of Belgian beam trawlers are lower, while the opposite occurs when the Dutch beam trawler activity drops from Friday to Sunday. Since we did not examine the underlying mechanisms, there is no unequivocal explanation for the occurrence of this weekday effect. Nevertheless, the direct and reversible response of landing rates to a change in fishing activity of the Dutch beam trawlers suggests the occurrence of interference competition. However, the decreasing trend from Monday to Thursday in the landing rates of sole, which was also found in the Dutch beam trawler fleet (Rijnsdorp *et al.*, 2000b), suggests that local depletion of the sole fishing grounds occurs as well (exploitative competition).

Inspection of the interaction effect of weekday and year did not suggest a clear relationship between the development of the Dutch pulse fleet and the reduction in lpue during weekdays in the Belgian fleet. This could be the result of several confounding effects that were not tested. Interannual variation in the distribution of sole and plaice may alter the exploitation dynamics of both fleets and their spatial overlap and thus competitive interactions between the different years of analysis. Additionally, changes in external factors such as fuel prices may affect fishing tactics and spatial interactions between fishing vessels. Poos *et al.* (2012) showed that Dutch beam trawlers fished closer to harbours in response to high fuel prices in 2008. Additionally, the number of vessels participating in the fishery may have affected the level of competition between both fleets. Despite the development of the pulse trawl fleet in 2009, no weekday effects were observed in 2009–2011. During these years, nominal fishing effort of the pulse trawler fleet was much smaller (Figure 6); moreover, fishers learned about optimal use of fishing gear and characteristics of new fishing grounds, which may explain the absence of the weekday effect (Rasenberg *et al.*, 2013).

Landing rates of plaice were not characterized by a weekday effect over the entire study period. This suggests no clear relationship between landing rates of plaice and exploitation patterns of the Dutch beam trawlers nor with the development of the pulse trawler fleet.

Differences in the response of catchability of different fish species to vessel density were also found in the experiment of Abrahams and Healey (1993). Additional research about the underlying mechanistic processes of interference competition, e.g. through experiments with tagged fish species, potentially provides insights about the observed differences in the response of sole and plaice catchability to vessel density.

Since sole is the most important species, in terms of revenue in this fishery, the absence of a weekday effect in plaice lpue may be related to the fleet's targeting behaviour for sole. Another possible suggestion is that pulse trawlers catch less plaice than beam trawlers (van Marlen *et al.*, 2014), owing to a different response to the pulses (Breen *et al.*, 2011). This different response of both species might induce a different level of interference competition and might explain why plaice lpue is not affected by a change in vessel density.

The design of our study did not allow us to quantify the relationship between vessel density and interference competition. Despite this limitation, the relative decline in revenue per unit effort (rpue) towards an increase in fishing effort during weekdays measured in our study is similar to the decline in rpue found in studies by Rijnsdorp *et al.* (2000a) and Poos and Rijnsdorp (2007). In those studies, rpue, based on landings of the target species sole and plaice, for a vessel with engine power of 2000 HP (ca. 1491 kW) dropped by, respectively, 10 and 14% when vessel density increased. In our study, in which sole accounts for 67% of the total landed value, rpue declined by 11% (2012) and 9% (2013) for a vessel of 1200 kW. Despite the different set up in the vessel density experiment in all of these studies, a similar response in revenue rates in response to a change of vessel density was measured.

Spatio-temporal effort allocation of the Belgian beam trawlers

Fishing effort allocation in the Belgian beam trawler fleet (>221 kW) in the Southern Bight showed strong variation during the study period. The high effort allocation in the Southern Bight in 2008 and 2009 is strongly related to the fuel price crisis at the end of 2008. Fishers adapted their fishing strategies by reallocating fishing effort closer to harbours to reduce steaming costs (Poos *et al.*, 2012; Bastardie *et al.*, 2013). After the fuel price crisis, fishing effort in the Southern Bight declined again. The Belgian beam trawlers reallocated fishing effort to grounds outside the North Sea and in the central part of the North Sea (ICES Division IVb). Effort reduction in the Southern Bight occurred simultaneously with the development of the Dutch pulse trawlers in 2011. We hypothesize that increased competition between both fleets was an important driver of this effort reallocation.

Apart from spatial effort reallocation, a shift occurred in the weekly exploitation patterns of the Belgian beam trawlers. Since sole lpue was reduced during weekdays in 2012 and 2013, a larger proportion of the fishing trips in the Southern Bight ended on Sunday and Monday, while the share of fishing trips ending on Friday and Saturday decreased. This shift can be understood from the viewpoint of increased competition: the drop in sole lpue through increased interference competition on Monday would force more fishers to leave fishing grounds in the Southern Bight and return to the harbour on Monday, while ending fishing trips on Friday or Saturday would be less likely due to the higher landing rates of sole on weekends, creating an incentive to continue fishing.

Management implications

Competitive differences may have important consequences for both the short- and long-term dynamics of the beam trawler fleet in the North Sea. The occurrence of spatial segregation as a result of different competitive abilities of fishing vessels was observed in the Dutch beam trawler fleet and the French demersal fleet. In studies by Rijnsdorp *et al.* (2000a), Poos *et al.* (2010), and Girardin *et al.* (2015), the occurrence of segregation among vessels was shown, with higher prevalence of more powerful vessels on the best fishing grounds. In contrast, less powerful vessels lost efficiency in the presence of stronger vessels and were more prevalent on poorer fishing grounds (Rijnsdorp *et al.*, 2000a, b). Because no Belgian trawlers used the pulse during the study period, we could not analyse competitive differences between beam and pulse trawlers.

This study provides an example of how different uptake of new technologies in fisheries can affect the performance of a fleet through changes in lpue as a result of competitive interactions. Disregarding this may lead to misinterpretation of cpue trends and bias stock estimates. Additionally, different adaptation speed of fishing fleets towards new technologies can force fishers to adapt fishing strategies and undermine effective fisheries management when not expected.

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