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Improving the interpretation of fishing effort and pressures in mixed fisheries using spatial overlap metrics

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Abstract :

Managing mixed fisheries requires understanding fishers' behaviour to allow predicting future fisheries distribution and impact on marine ecosystems. A new approach was developed to compare fine scale fishing effort distribution of Eastern English Channel (EEC) bottom trawlers, to the monthly- and spatially-resolved abundance distributions of commercial species. First, the added-value of using species-specific spatial overlap metric to quantify effective fishing effort and improve the relationship between fishing effort and fishing mortality was assessed. Second, based on the Ideal Free Distribution (IFD) theory, the species-specific weights given by fishers to different species were estimated by maximizing the overlap between target species assemblage and effort distributions in October. At a seasonal scale our results emphasized the importance of cuttlefish and red mullet for the global distribution of EEC bottom trawlers. In October, cuttlefish and red mullet were clearly more determining fishers' location choice than historically harvested species, and also than the overall expected revenue. This is likely due to external constraints such as low cod quota, causing IFD assumptions violated. This study evidenced the importance of getting good insights into spatio-temporal distributions of stocks and fleets to understand fishers' behaviour and improve mixed fisheries management advice

Keywords : fishing effort, seasonality, target species assemblages, Eastern English Channel

1. Introduction

The implementation of Ecosystem-Based Fisheries Management (EBFM) entails new methods to assess and manage exploited marine ecosystems (FAO 2001; Pikitch *et al*. 2004; Long *et al.* 2015). Successfully implementing the EBFM requires a thorough understanding of the mechanisms inherent in fishers' behaviour and particularly their relation with targeted stock assemblages (Fulton *et al*. 2011; Marchal *et al*. 2013; van Putten *et al*. 2013).

Understanding the relation between fishers and stocks' distributions is particularly challenging when it comes to (demersal) mixed fisheries. Mixed fisheries simultaneously harvest several species, the composition of which may change according to seasons (Poos *et al*. 2010), with a target-bycatch dichotomy (i.e. landing are composed by both target species and non-target but still valuable bycatch species; Wilson and Jacobsen 2009) associated with a poor selectivity (Marchal 2008). Fishing fleets and gears operating in such fisheries interact technically (Ulrich *et al*. 2012; Cardoso *et al*. 2015), and are prone to high discard rates (Catchpole *et al*. 2005; Johnsen and Eliasen 2011), particularly of undersized and/or over-quota fish catches (Andersen *et al*. 2010; Fernandes and Cook 2013). These technical interactions make fisheries management challenging, and especially where species/stocks are managed individually.

To address this challenge and improve mixed fisheries management, numerous research studies have been carried out (i) to better quantify fishing effort and, (ii) to anticipate the dynamics of fishers' behaviour and its impact on the several species targeted or caught as bycatch when fishing patterns are changing.

With regards (i), a number of fishing effort analyses have focused on the identification of manageable fishing units (Laurec *et al.* 1991; Marchal 2008; Ulrich *et al*. 2012). Other fishing effort studies have focused on the quantification of fishing power and/or of the relationship between fishing effort and fishing mortality, with a focus on technical development (Kirkley *et* *al.* 2004; Marchal *et al.* 2007; Eigaard *et al*. 2014) and tactical adaptations (Hilborn 1985; Rose and Kulka 1999; Salthaug and Aanes 2003). The metrics considered in these studies were used to standardise nominal fishing effort and calculate an effective fishing effort, thereby improving the estimation of the actual fishing pressure exerted on fish stocks. Such metrics, however, were derived from vessels, gears and/or skippers' characteristics only, and hence not explicitly considering the relative availability of the different targeted species. In our study, we calculate effective fishing effort including fish availability and fishers' ability to target and catch fish, which we quantify by the overlap between stocks and fishers' spatial distributions.

The first objective of this study will then be to quantify the effective fishing effort in a mixed fishery's context, and *in fine* improve the relationship between fishing effort and fishing mortality (Gascuel *et al.* 1993; Winker *et al.* 2013; García-Carreras *et al.* 2015), using a combination of vessel characteristics and species-specific spatial overlap metrics.

With regards (ii), fleet dynamics has been subject to considerable attention in the past decades (see Van Putten *et al*. 2012 for a review), a process largely supported by fine-scale and georeferenced data becoming increasingly available (e.g., Bastardie *et al.* 2010; Hintzen *et al.* 2012). Different theories have been proposed to explain the mechanisms of fishers' behaviour. The Ideal Free Distribution (IFD, Fretwell and Lucas 1970; Fretwell 1972) is one of the most widespread conceptual approaches that has been applied to predict the distribution of foragers (here fishers) in relation to available resources (Kacelnik *et al.* 1992; Kennedy and Grey 1993). The IFD states in particular that the number of foragers that will aggregate in various areas is proportional to the amount of resources these may supply. In a fisheries context, the spatial distribution of nominal fishing effort and of their harvested resource would then overlap (Abrahams and Healey 1993; Gillis *et al.* 1993; Rijnsdorp *et al*. 2000). In mixed fisheries, where several fish species are harvested together, the amount of resources has often been translated into aggregated economic revenue metric like the value per unit of effort (VPUE) (e.g. Rijnsdorp *et al.* 2000; Abernethy *et al.* 2007; Gillis and van der Lee 2012), making the hypothesis that fishers would try to maximize their expected revenue more than the volume of species they could catch.

Applying the IFD results in fishers' behaviour being fully driven by short-term economic consideration: the species with the largest expected return is the most targeted.

However, many studies have shown that species targeting could also be driven by other factors including regulations as well as longer-term economic and social considerations. For instance, valuable species may be avoided, when fishers do not have a sufficient quota provision to harvest them (e.g., choke species; Schrope 2010; Ulrich *et al.* 2011; Baudron and Fernandes 2014), or because they do not have a market channel to sell them (Marchal *et al.* 2009), or because targeting these species is not part of their habit (Vermard *et al.* 2008; Marchal *et al*. 2009; Girardin *et al*. 2017), thereby inducing deviations from the basic IFD predictions. These results suggested in particular that the relative interest fishers give to the different species they harvest is not entirely reflected by their landed value.

The second objective of this study is then to quantify, using a novel method, the relative value fishers assign to their different targets, and to link it with current knowledge of their ecological, economic and regulatory environment.

The research pertaining the two objectives of this study will be evaluated for a typical EU mixed fishery, consisting of French otter trawlers harvesting demersal species in the Eastern English Channel.

2. Material and methods

2.1. Study area and fleet characteristics

The Eastern English Channel (EEC; ICES Division 27.7.d) is delineated by latitudes 49.3°N and 51°N and longitudes 2°W and 2°E (Figure 1). This shallow area constitutes a corridor between the northeast Atlantic Ocean and the North Sea, and is home to intense and diversified human activities including fishing, shipping, wind farms, aggregate extraction (Ulrich *et al.* 2002; Dauvin 2012). This area is also important for several commercially important migratory species, e.g., red mullet (*Mullus surmuletus*) (Mahé *et al*. 2005), mackerel (*Scomber scombrus*) (Eltink *et al*. 1986), herring (*Clupea harengus*) (ICES 2015), European seabass (*Dicentrarchus labrax*) (Pawson *et al*. 2007) and cuttlefish (*Sepia officinalis*) (Boucaud-Camou and Boismery 1991). The current study focuses on French exclusive (i.e. using the same gear throughout the year) bottom otter trawlers (OTB), of length above 18m and using a mesh size above 80mm. This fleet category is an archetype of mixed fisheries and is studied here for three reasons. First, this fleet category gets the bulk of yearly French bottom otter trawlers catches for the main demersal species in the EEC (Table S1). Second, as non-exclusive OTB are usually smaller than exclusive ones, they mostly operate in coastal areas close to their home harbor thus their spatial distribution is limited and only covers a limited portion of the EEC. Finally, exclusive otter trawlers above 18m generally use the same gear (with a mesh size above 80mm) all year round, making the exploration of their dynamics more tractable. Mesh sizes below 80mm are rarely used by this fleet (for only 5% of their landings in average, see Table S1), and only when targeting a reduced list of species (EC 1998).

2.2. Data

This study requires spatial distributions of otter trawlers' nominal fishing effort and of the abundance of the main EEC stocks they harvest in terms of tonnage and revenue (Table 1). To estimate species distribution, both in time and space, we used the delta-GLM (Generalized

Linear Model) approach described by Bourdaud *et al*. (2017) that is applied separately to survey and commercial data.

The input data sources for this delta-GLM are the Channel Ground Fish Survey (CGFS) for the fisheries independent data and on-board commercial fisheries observation (hereby named as OBSMER) data for the fisheries dependent information. These data sources are complementary, with CGFS data providing insights into inter-annual patterns (only in October, when the survey is operated), and OBSMER data being fit to investigate seasonal variability. Spatial distribution of species abundances are computed for each species above a length threshold (L_s; Ravard *et al*. 2014), where individuals are considered to be well sampled. For species with a minimum landing size (MLS) in the EEC, L_s was assigned to that MLS. For others, L_s was approximately set for each species at the length of the highest mode of the length-frequency of combined catches from the different gears (Table 1). The delta-GLM applied to OBSMER data contains a maximum of six explanatory variables:

$$logit\left(\mathrm{p}^{>0}_{\mathrm{v,i,m,y}}\right) = \beta_i \delta_m + \lambda_y + \omega_g l \ + \vartheta_s \qquad (1)$$

$$\log\left(IA^{>0}_{v,i,m,y}\right) = \beta_i \delta_m + \lambda_y + \omega_g l \ + \vartheta_s + \varepsilon_{v,i,m,y} \quad (2)$$

where $p^{>0}_{v,i,m,y}$ is the mean presence probability and $IA^{>0}_{v,i,m,y}$ the CPUE of a species caught by vessel v of length l rigged with gear g (e.g. bottom otter trawl, trammel net), fishing in (0.3° x 0.3°) area i, year y and month m. β_i is the area effect of the fishing operation (treated as factor), δ_m is the month effect of the fishing operation, λ_y is the annual effect, ω_g is the gear effect, ϑ_s is a sediment effect, which accounts for small scale habitat variability and is decomposed into five categories s: mud, fine sand, coarse sand, gravel and pebble, based on a sediment map of EEC from Larsonneur *et al*. (1982), and $\varepsilon_{v,i,m,y}$ a term of residual error.

Sediments proved to have the strongest influence on the distribution of species in the shallow EEC, compared to, e.g., depth, temperature and salinity (see Carpentier *et al*. 2009). For complete justifications about the choices of the models parameterization, see Bourdaud *et al*. (2017).

The final predicted abundance values $IA_{v,i,m,y}$ from commercial data are obtained by the product of presence probabilities $p^{>0}_{v,i,m,y}$ and CPUE for positive values $IA^{>0}_{v,i,m,y}$.

CGFS survey data are always collected in October (i.e. no month effect) with the same research vessel (i.e. no vessel or gear effects), hence the previous formula was reduced to the following, with a maximum of three explanatory variables:

$$logit\left(\mathrm{p}^{>0}_{\mathrm{i,y}}\right) = \beta_i + \lambda_y + \vartheta_s \quad (3)$$

$$\log\left(IA^{>0}_{i,y}\right) = \beta_i + \lambda_y + \vartheta_s + \varepsilon_{i,y} \qquad (4)$$

The final predicted abundance values $IA_{i,y}$ from survey data are obtained by the product of presence probabilities $p^{>0}_{i,y}$ and CPUE for positive values $IA^{>0}_{i,y}$.

In the delta-GLM applied to commercial CPUEs, every parameters were kept, except the sediment parameter in the presence/absence model of cuttlefish (Table S2). In the delta-GLM applied to survey CPUEs, the parameters selection was case-dependent (Table S3).

Access to all fishing effort information was provided by the French Directorate for Sea Fisheries and Aquaculture (DPMA). Nominal fishing effort is derived from the Vessel Monitoring System (VMS) and is here defined as an amount of fishing time for each month in a 0.3° x 0.3° area, a scale chosen to match the scale of the species abundance distributions computed above, and corresponding to a trade-off between the amount of data required and a sufficient level of precision (Bourdaud *et al*. 2017).

To validate our results, we used monthly landings derived from combined logbooks and sales slips record (SACROIS) over the period 2008-2014. Landings data extracted from SACROIS were available by vessel, fishing trip, ICES rectangle and gear used. Activity calendars, collected directly from fishers on a regular basis by Ifremer, provided fishers' targeting intention, i.e. species assemblage targeted during each fishing operation. These assemblages were chosen to be the closest to the studied species (Table 1). For French exclusive OTB operating in the EEC during the period 2008-2014, 70% of the target assemblages in the calendars were classified as 'fishes (miscellaneous)', indicating no specific target. Among the remaining records, 79% mentioned targets corresponding to one of the species studied here. Numbers of fishing days are summed by month for each target species and were scaled to the year in order to obtain a monthly relative distribution of fishing time targeting this species.

2.3. From nominal fishing effort to spatially-derived species-specific fishing pressure

As defined by Mahévas *et al*. (2004) and Bordalo-Machado (2006), the effective fishing effort (*fe*) measures the real pressure exerted by fishers on a stock during a time unit. It can be defined as the product of the nominal fishing effort (*fn*) and a global fishing power, i.e., the ability of a fisher to catch available fish. The global fishing power combines the capacity of fishers to find the targeted fish (targeting capacity), and the catching capacity inferred from vessels' physical attributes, e.g., vessel length (physical capacity).

Physical capacity Pc is assumed to correspond to the $\omega_g l$ term for OTB gear in the delta-GLM equations 1 and 2 applied to commercial data, and characterizes the impact of vessel length and the gear effect on fish catchability. This parameter is used to weight nominal fishing effort per spatial unit by the length category of each vessel:

$$If_{k,i,m,y} = \sum_v fn_{v,i,m,y} \times Pc_{l,k} \qquad (5)$$

Where $If_{k,i,m,y}$ is the integrated nominal fishing effort in area *i* for species *k* fished by a vessel *v* of length *l* during the month *m* and year *y*.

Targeting capacity is then measured for each species *k* as the similarity between the distributions of integrated nominal fishing effort and of harvested fish, using the spatial overlap index LIC (Local Index of Collocation, Woillez *et al*. 2009):

$$LIC_{m,y} = \frac{\sum_i If_{i,m,y} \times IA_{i,m,y}}{\sqrt{\sum_i If_{i,m,y}{}^2 \times \sum_i IA_{i,m,y}{}^2}} \qquad (6)$$

Noting $IA_{i,m,y}$ the abundance of the species concerned in area *i* during month *m* of year *y*, estimated from on-board commercial data. The LIC was computed using R package {RGeostats} (Renard *et al.* 2014),

it ranges between 0, showing absolutely no match between the two spatial distributions, and 1, demonstrating a perfect match between them.

Finally the monthly relative fishing effort of each year (i.e. between 0 and 1, with the sum of fishing effort in each year = 1, see Figure 2) is weighted by the monthly LIC:

$$fe_{m,y} = \frac{LIC_{m,y} \times \sum_v \sum_i fn_{v,i,m,y}}{\sum_m \left(LIC_{m,y} \times \sum_v \sum_i fn_{v,i,m,y}\right)} \qquad (7)$$

In order to evaluate the respective merits of *fe* and *fn*, in reflecting actual fishing pressure, both effort values were compared with available surrogates of fishing pressure: 2008-2014 averaged monthly landings (as extracted from SACROIS) and fishers' intentions (expressed for each month as the number of days targeting a given species, as extracted from activity calendars). We computed the residual sum of squares (RSSQ) between the monthly resolved time series of, (1) nominal fishing effort (*fn*) and landings, (2) effective fishing effort (fe) and landings, (3) nominal fishing effort and fishers' intention and, (4) effective fishing effort and fishers' intention. Should the effective fishing effort we processed in this study reflect actual fishing pressure better than nominal fishing effort, we could then expect that *fe* would track monthly variations of both landings and fishers' intentions more closely than *fn*, for those species being targeted by otter trawlers. This improvement would also result in the RSSQ derived from (2) (respectively (4)) being lower than the RSSQ derived from (1) (respectively (3)).

2.4. Defining species targeting factors for mixed fisheries from spatial overlap metrics

While the monthly species-specific effective effort computed previously aims at better apprehending the variations of the fishing pressure exerted on each single species, it does not allow evaluating how variable the effort allocated to each species targeting is relative to the others. A combined-species approach is thus required to get better insights into the full dynamics of species targeting in a mixed fisheries context, including swaps from one target to another and their determinism. Combined-species targets were computed building on the maximization of the spatial overlap, measured with the LIC metric, between the distributions of fishing effort and of weighted combined-species abundances. Such approach requires a comprehensive and consistent spatial coverage across all species being considered, and therefore could only be realized for October, the only month covered by a scientific survey over the entire EEC, limiting the results to reflect inter-annual variations with no exploration of seasonal patterns. In order to maximize the LIC, each of the (k) species relative spatial distributions (i.e. scaled between 0 and 1) is multiplied by a combined-species targeting coefficient, β, which is bounded between 0 and 1 using the transformation:

$$\beta_k = \frac{e^{\alpha_k}}{\sum_k e^{\alpha_k}} \quad (8)$$

Where α is the unconstrained coefficient to be optimized, using the 'optim' function of the R package {stats} (R Core Team 2013) and the L-BFGS-B method. Using relative spatial distributions allows to combine the different species even if their catchabilities vary. The objective function to be maximized with respect to α may then be formulated as:

$$\frac{\sum_i\left[fe_i\times\sum_k\left[\left(\frac{e^{\alpha_k}}{\sum_k e^{\alpha_k}}\right)\times\left(\frac{IA_{k,i}}{\sum_i IA_{k,i}}\right)\right]\right]}{\sqrt{\sum_i fe_i^{\,2}\times\sum_i\left[\sum_k\left[\left(\frac{e^{\alpha_k}}{\sum_k e^{\alpha_k}}\right)\times\left(\frac{IA_{k,i}}{\sum_i IA_{k,i}}\right)\right]^2\right]}} \qquad (9)$$

If fishers' foraging pattern was in consistency with IFD predictions, one could assume that fishing effort distribution would match EEC wealth distribution. The amount of available revenue *W* generated by each area *i* in year *y* may be computed by:

$$W_{i,y} = \sum_k (IA_{k,i,y} \times Price_{k,y}) \qquad (10)$$

knowing the abundance of species *k* in the area obtained from CGFS data and the mean price of the species in October in year *y* (Table S4). We consider here that differences in the catchability between the main species caught during the survey and the commercial trawls would be in the same order of magnitude, so equation 10 may be used to infer and compare the fishers' revenues operating in an area relative to the other.

The LIC values obtained from maximizing (9) are then compared to the LIC obtained from the comparison between fishing effort and available wealth in the EEC, one of the main hypothesis of fishing location driver (van Putten *et al*. 2012).

3. Results

3.1. Seasonal fishing pressure exerted on each commercial species

The seasonal variation of effective fishing effort is shown for each species separately in Figure 2. Fishing pressures (estimated from effective fishing efforts, *fe*) exerted on cuttlefish and seabass have the most pronounced pattern, with peaks reached in autumn for the former, and spring and autumn for the latter. Fishing pressure exerted on other species (see for example plaice or squids) exhibited a smoother seasonal pattern, with a peak in winter. Fishing pressure and landing seasonal patterns match for some species (cod, cuttlefish, plaice, red mullet, squids), but not for others (mackerel, seabass, whiting).

Fishers' intention from activity calendars were strongly related to the landings, except for cod, red mullet, plaice and black seabream, but were subject to wider inter-annual fluctuations (Figure 3). There is a good match between fishing pressure and fishers' intention for cuttlefish and seabass except in autumn, but not for the other species under consideration.

Considering monthly *fe* instead of *fn* improves substantially the correlation between fishing effort and landings for two species: red mullet and cuttlefish (Figure 4A). At the same time, substituting nominal by effective effort does not improve the correlation between effort and landings, and even deters it for mackerel, whiting, and seabass. Almost similar average results are obtained when investigating the effects of substituting nominal by effective fishing effort on the correlation with the species-targeted numbers of fishing days derived from activity calendars, but these were subject to large inter-annual fluctuations (Figure 4B).

3.2. Combined-species targeting

The relative target factors obtained by maximizing the (β-weighted) LIC are presented in Figure 5 for the six main October commercial species: cod, cuttlefish, mackerel, red mullet, squids and whiting. In October, the two main target species of French exclusive OTB are cuttlefish (44% of the annually averaged sum of target, with a peak of 78% in 2012), and secondly red mullet (22% on average, peaking to 59% in 2009). It is worth noting that the inter-annual variability can be very high for these species. For instance, the targeting factor for cuttlefish goes from 0% in 2009 to 78% in 2012, while the red mullet factor goes from 0% in 2012 to 59% in 2009. The targeting factors of mackerel, cod and squids are less variable over the years, and fluctuate between 0% and 29%. Finally, whiting never appears to be targeted.

The maximized (β-weighted) LIC value was compared with the revenue-based LIC value, i.e., reflecting the overlap between fishers' distribution and the potential revenue W (Table 2). Every year the LIC value obtained by maximization was higher than the revenue-based LIC by at least 0.10, even reaching 0.22 in 2014. The range of maximized LIC is of 0.57-0.81, while the range of revenue-based LIC values is of 0.46-0.63, almost always below the 0.60 threshold below which spatial overlap is not meaningful (Scrimgeour and Winterbourn 1987). This represents a substantial deviation from the IFD predictions.

3.3. Species targeting fluctuations and external factors

Cuttlefish abundance and economic attractiveness is highly fluctuating during the period, with peaks in 2010 and 2012 (Figure 6A). Cuttlefish targeting intensity follows economic attractiveness well, except for 2009 where there is no targeting. The correlation is particularly visible in the 2010-2014 fluctuations. Cod abundance and economic attractiveness show a clear decrease from 2008 to 2010, and then remain constant, while remaining quota shows at the same time an increase before being constant (Figure 6B). Cod targeting intensity increases from 6 to 15% between 2008 and 2010, when abundance and economic attractiveness both decrease. From 2010 onwards, the cod targeting factor is consistently above 10%, except in 2012. No clear pattern in abundance, attractiveness or remaining quota can be related to the low 2012 targeting. However, it may be noted that during 2012 the targeted species were dominated by cuttlefish (see Figure 5).

4. Discussion

4.1. An improved quantification of fishing pressure

Adjusting nominal fishing effort using the species-specific LIC improved our understanding of seasonal fishing pressure (here measured by relative landings and species targeting expressed by fishers) exerted by French otter trawlers on EEC cuttlefish and red mullet. These results have direct operational implications, as such effective fishing effort could be used to remove the seasonal effect in catch rates series used to calibrate cuttlefish and red mullet stock assessments. Such an improvement in the relationship between seasonal fishing pressure and fishing effort could not be observed for the other species under investigation, and particularly cod and whiting, which used to be traditional target species for French otter trawlers. Several reasons could explain a lack of improvement (or even a deterioration) in the relationship between fishing effort and estimated fishing pressure: i) high discards rate, which is not accounted for in landings data, ii) high spatial patchiness for some species, which increases landings variability, iii) high monthly fluctuation in biomass, which is not taken into account in landings data (e.g. migration from or to the EEC) and finally, iv) limited spatial coverage of abundance indices derived from fisheries-dependent OBSMER data (Bourdaud *et al*. 2017).

In their study, Sagarese *et al*. (2015) also quantified the overlap between fish distribution from survey data and fishing effort, in order to quantify the availability of spiny dogfish to sink gillnetters and otter trawlers. However, their approach was designed in a binary fashion (i.e. presence/absence), compared to ours, as they compared the number of cells with fishing effort and the number of cells with presence of spiny dogfish *Squalus acanthias*. Note that we assumed here a linear relationship between fishing pressure and our LIC spatial overlap index. Such a linear relationship is, however, a first proxy, and more work could be dedicated to finding either refined spatial overlap indices, or more realistic relationships relating the LIC to the real fishing pressure exerted on the different fish species.

Previous studies have been able to quantify other impacting factors on catchability, such as technical effects (Rijnsdorp *et al.* 2006; Marchal *et al.* 2007; Mahévas *et al*. 2011), individual vessel effects (Tidd 2013; Thorson and Ward 2014) or vessel competition (Gillis and van der Lee 2012). The effects of technological creep could in principal enhance the perception of fishing pressure we obtained. In our case study, technological differences among vessels and among years are, however, expected to be relatively limited, as we only focus on one single fleet category, the French OTB >= 18m, and on a relatively short period of time (seven years).

4.2. Fishers' intentions and the IFD

The IFD theory builds on several key assumptions: i) interference competition among vessels exists in proportion to their local density, ii) fishers have equal competitive abilities, iii) no restrictions exist for effort allocation and iv) ideal knowledge of fishing grounds' local density (Gillis 2003). We consider in this study that a poor spatial overlap between the distributions of fishing effort and of available wealth results from one or several of IFD assumptions being at fault. Deviations from IFD predictions are then related to factors that could potentially compromise the validity of these base assumptions. In doing so, we particularly considered assumption (iii), since additionally to external economic factors such as fuel costs (Poos *et al.* 2010; 2013) or spatial competition, fishing access to several of the EEC species being investigated (and hence effort allocation) has been restricted by Total Allowable Catches, direct effort (number of days at sea) limits, and minimum mesh size regulations. This is particularly true for cod, for which a recovery plan has been implemented since 2002 in the North Sea and the EEC. Departs from assumptions (ii) and (iv) are considered more limited, since we consider vessels belonging to one fleet category and no individual quotas are presently set for these boats (ii), and because the EEC is a small and shallow maritime domain, so we can reasonably assume that fishers have a good knowledge of their fishing grounds (iv). Although the legitimacy of assumption (i) is difficult to evaluate, previous studies did evidence that interference competition occurs between EEC fishing fleets (Girardin *et al.* 2015; Tidd *et al.* 2015).

Mixed fisheries in the Eastern English Channel target an assemblage of different species (Marchal 2008, Girardin *et al*. 2015, ICES 2017), and our study proposed a novel approach, building on the optimization of a spatial species abundance / fishing effort overlap metric, to identify their key targets, and hence fishers' intentions. This approach was applied only in October as it required a good spatial coverage of both fishing effort and species distributions. Although Quirijns *et al*. (2008) also determined an explicit index for the targeting behaviour in a mixed fisheries context involving two species (i.e. sole and plaice in the North Sea), our approach is different as it explores fishers' intentions using fishery-independent data, and in an optimization fashion.

Our results evidenced that cuttlefish and red mullet have been the primary target species of the French EEC bottom trawlers over the period 2008-2014, which confirmed the strong fishing pressure exerted on both species in October (Figures 2 and 3). It is informative that cuttlefish and red mullet, the catch of which is not limited by quotas, are much more targeted than cod, whiting and mackerel, three species managed by TAC (Total Allowable Catches). This could result from an adaptation of fishers to increasingly restrictive TAC limitations, and more particularly in the context of the North Sea recovery plan (Horwood *et al*. 2006), thereby confirming the decline of traditional targets and the emergence of valuable and poorly regulated species such as red mullet (Mahé *et al*. 2005) and cuttlefish (Gras *et al*. 2014). Concerning cuttlefish this can also be an adaptation to a gain in economic attractiveness during the same period (Figure S1).

It is noteworthy that mackerel has a significant target factor value every year in October. This could be seen as a surprise, as pelagic species such as mackerel are not usually targeted by bottom trawlers. This could be due to the nature of the EEC, a shallow sea (< 50m), with strong mixing and benthic-pelagic coupling processes (Giraldo *et al.* 2017). The substantial mackerel targeting contrasts, however, with the weak (and even negative) effect of the LIC on the computed fishing pressure exerted on this species. This contrast may be explained by the larger intra- and inter-annual abundance fluctuations pelagic species are subject to, compared to the other species we considered.

The optimized spatial overlap between the distributions of fishing effort and the combined-species resource was achieved with species-specific weightings differing substantially from the available revenue coefficients used to derive VPUE as the aggregated resource metric. This difference measures the deviation between the actual spatial distribution of fishing effort and the one predicted under the IFD. In previous studies, the IFD provided a useful conceptual framework to predict fishing effort distribution patterns (e.g. Gillis and Frank 2001; Swain and Wade 2003). In several studies, however, the IFD did not predict fishing effort distribution well, which was interpreted as limited knowledge of fishing grounds, or external foraging constraints (Pet-Soede *et al*. 2001; Abernethy *et al*. 2007).

In our study, and without excluding other possible causes, we interpret here the deviation between observed and predicted effort patterns as IFD assumption (iii) (unrestricted access to the different EEC fishing grounds) being at fault and this for several reasons. First, while the large trawlers investigated here have the capacity to cover all the EEC, they might limit their visits to the closest fishing grounds to save fuel and time at sea costs. Second, weather and especially wind conditions could be poor in the EEC, and could influence the choice of fishing grounds (Wilen *et al.* 2002; Respondek *et al*. 2014). Third, fishing habits may be more influential than economic opportunism in choosing fishing grounds (Salas and Gaertner 2004; Holland 2008; Girardin *et al.* 2017), although these may be highly correlated (Van Putten *et al.* 2012). Fourth, the EEC is a particularly congested sea, where fisheries may compete for space with other fisheries, or other maritime activities (e.g., shipping, aggregate extractions), which could occasionally restrict their activities (Girardin *et al.* 2015; Tidd *et al.* 2015).

Finally, management is an obvious cause of restricted access to fishing grounds. This has been evidenced extensively in the case of Marine Protected Areas (e.g. Stelzenmüller *et al*. 2008; Dowling *et al*. 2012), although the fleet investigated in our study is only subject to limited spatial management measures within the 12 nautical miles coastal areas (EC 1998). TAC management may also affect the spatial distribution of fishing effort (Batsleer *et al.* 2013; Baudron and Fernandes 2014), particularly when the TAC for a species is so low that this species becomes a choke species. This is an issue that we have investigated more thoroughly here, as cod has become a choke species in the EEC following the 2002 implementation of the North Sea cod recovery plan (Horwood *et al.* 2006), with an impact on the spatial distribution of EEC bottom trawlers and their cod targeting.

4.3. Influence of external factors on species targeting fluctuations

The interpretation of cod targeting fluctuations is not straightforward. Thus, it seems at first glance difficult to capture why cod targeting increases over 2008-2010, while stock abundance reflected by CGFS decreases during the same time period. The rationale underlying these contrasted trends becomes, however, clearer when one considers the drastic increase in the unutilized cod quota, from 0 tons in 2008 to 817 tons available in October 2010. With cod quota becoming somehow less restrictive, it is not surprising that cod targeting increased somewhat. The 2011-2014 fluctuations in cod targeting, and the drop observed in 2012, are difficult to explain without considering the other species' targeting factors. Thus cuttlefish targeting, not restricted by quotas, varied synchronously with economic attractiveness, over 2008-2014, with a 2012 maximum corresponding to the sharp decrease in cod targeting concomitantly with a high economic attractiveness for cuttlefish during that year. Another illustration of the combined-species targeting complexity is the decline of red mullet targeting between 2008-2009 and 2010-2014. This could be due to increased spatial and market competition with Dutch fly-shooters, which targeted red mullet in the EEC from 2010 onwards (Marchal *et al*. 2014). The low red mullet targeting observed in 2012-2013 could also be related to the low abundance and economic attractiveness for this species during that year (Figure S2).

Future work could be dedicated to identifying groups of fishers according to their targeting patterns, leading to a more precise definition of métiers, and also to evaluate whether habits could be detected in these patterns. We also made a number of simplifications, which could be revisited. Thus, we neglected fishers' home harbour, although this has implications on travel costs, fishing grounds location, and hence the validity of IFD-based effort predictions (Gordon 1953; see also Gillis 2003 for a review). Furthermore, in combination with spatio-temporal distributions of species abundance and fish prices fluctuations, geographical features can induce traditional fishing patterns only revealed by fishers' interviews (Christensen and Raakjær 2006; Boonstra and Hentati-Sundberg 2014).

The method developed in this study is not aimed at forecasting fishers' intentions, as past choices are not causal (Van Putten *et al.* 2013). However, it could be included in individual-based models (IBM), which are considered particularly well-adapted for forecasting, especially in changing management regimes (Ulrich *et al*. 2012; Van Putten *et al*. 2012). Our approach could thus be combined to a number of existing integrated ecological-economic fisheries models (see Nielsen *et al*. 2017 for a review), by supplying knowledge on real fishers' intentions, which may contrast with preliminary modelling assumptions and choices.

A future development of this study could also be to consider extensions from the IFD conceptual framework, such as isodars (for 'iso-Darwin'; Morris 1988, 2003). Isodars build on an ecological theory, predicting numbers in one area knowing numbers in another area and explicit expressions of local density-dependent per capita fitness. Isodars have been applied to fleet dynamics by Gillis and van der Lee (2012) and even proved to predict observations better than discrete choice models (van der Lee *et al*. 2014). If determination of the nature of factors in isodars may not be easily interpretable, a challenge could be to develop the approach at a more disaggregated level (e.g. by home port) so to, (i) gain better knowledge of the basic desirability level of the different fishing areas at fine scale, in relation to associated operational costs and tradition aspects and, (ii) improve the estimation of species target factors, by including those area desirability factors identified in (i).

This study used spatial distributions collocations to improve the definition of fishing effort and our understanding of its determinism. Our results at seasonal scale emphasized the importance of cuttlefish and red mullet in determining the global distribution of Eastern English Channel bottom trawlers. These results have clear management benefits, in improving the definition of catchability, effective fishing effort, and how these relate to fishing mortality for red mullet and cuttlefish. We also used a metric measuring the optimized spatial overlap between fishing effort and combined-species abundances. It revealed the importance of cuttlefish, red mullet and, to some extent, mackerel targeting relative to the other species in October, which was in contrast with IFD predictions, probably owing to external factors including limiting quota, travelling costs, or competition with other sectors of activity. Our results could be validated by available fishers' knowledge (e.g. Neis *et al.* 1999; McCluskey and Lewison 2008; Hind 2015).

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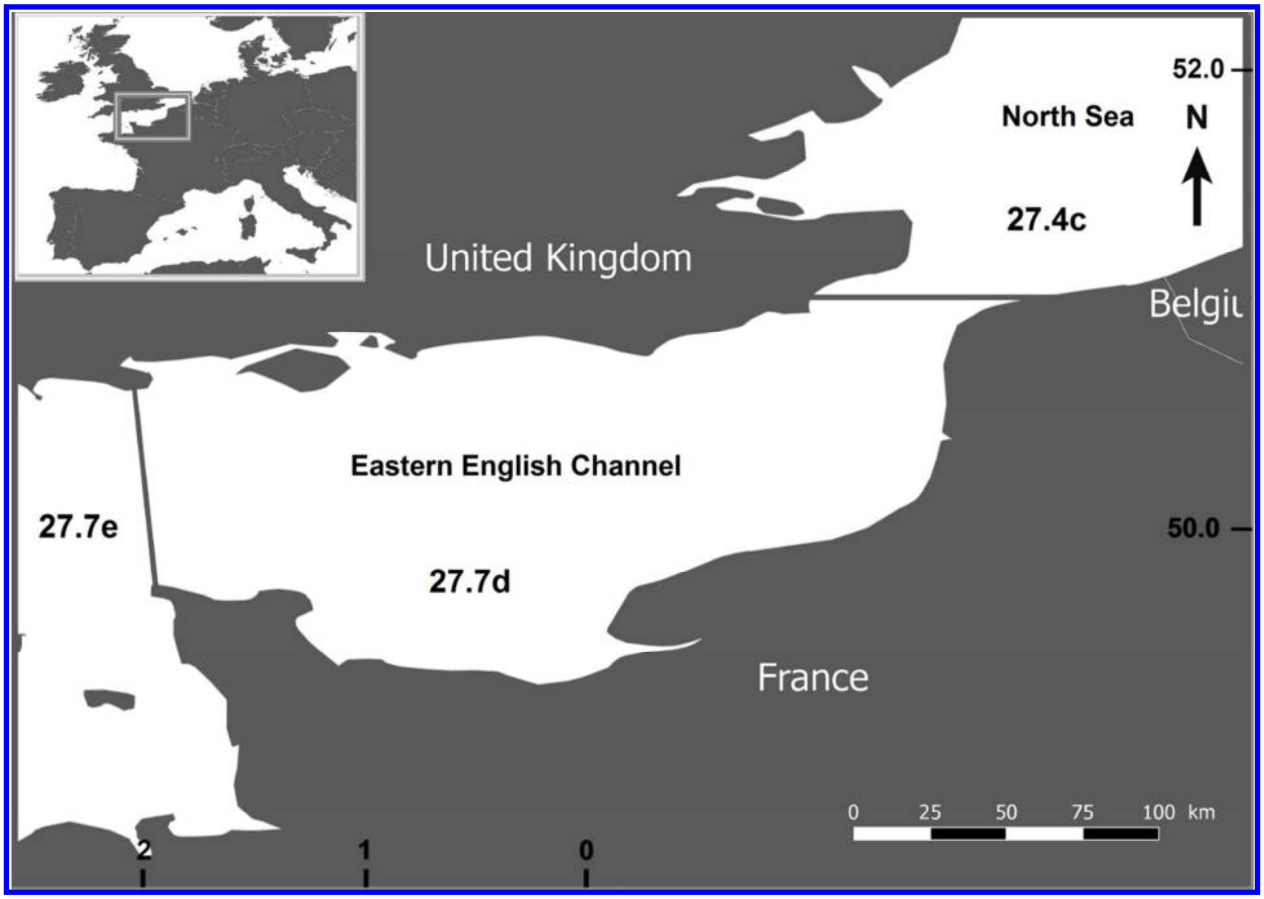

Figure 1. Study area of the Eastern English Channel, corresponding to the ICES Division 27.7d.

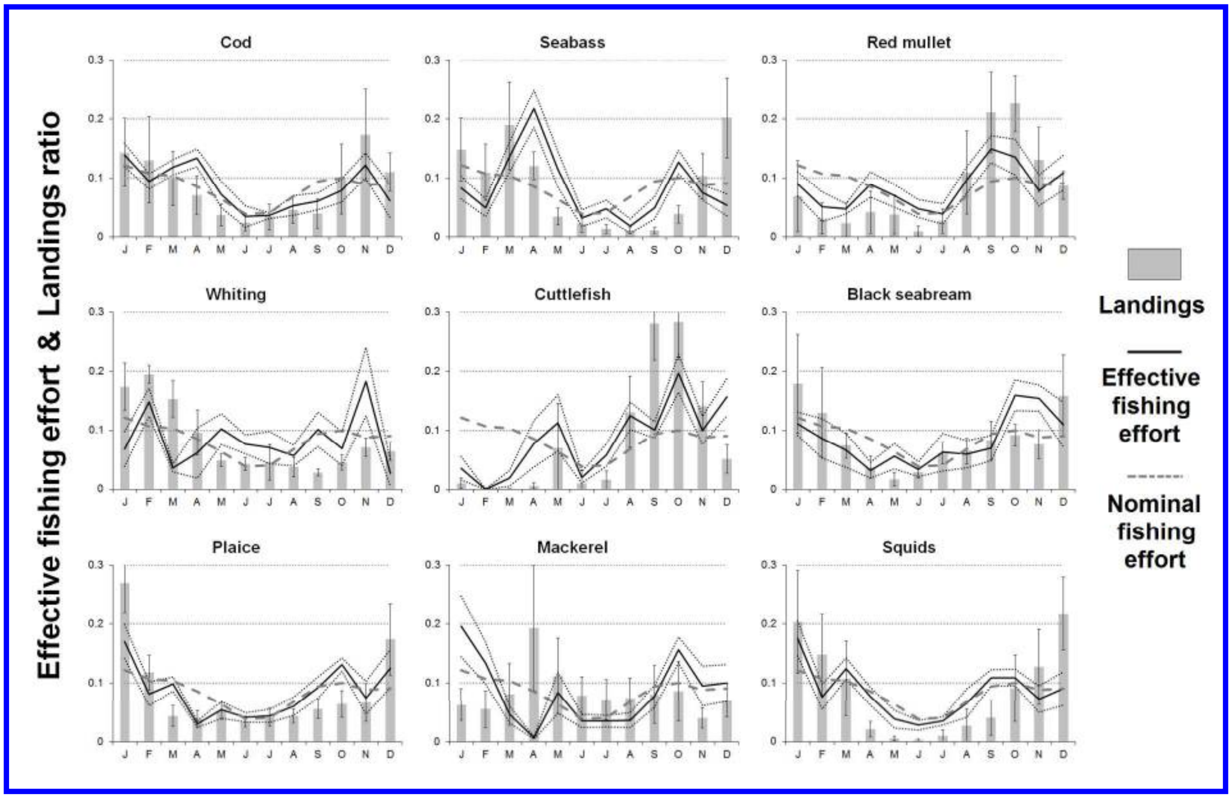

Figure 2. Average monthly nominal fishing effort, effective fishing effort and yearly standardized landings of exclusive bottom otter trawlers for nine main commercial species of the Eastern English Channel. Dotted lines and error bars indicate inter-annual variability over the period 2008-2014.

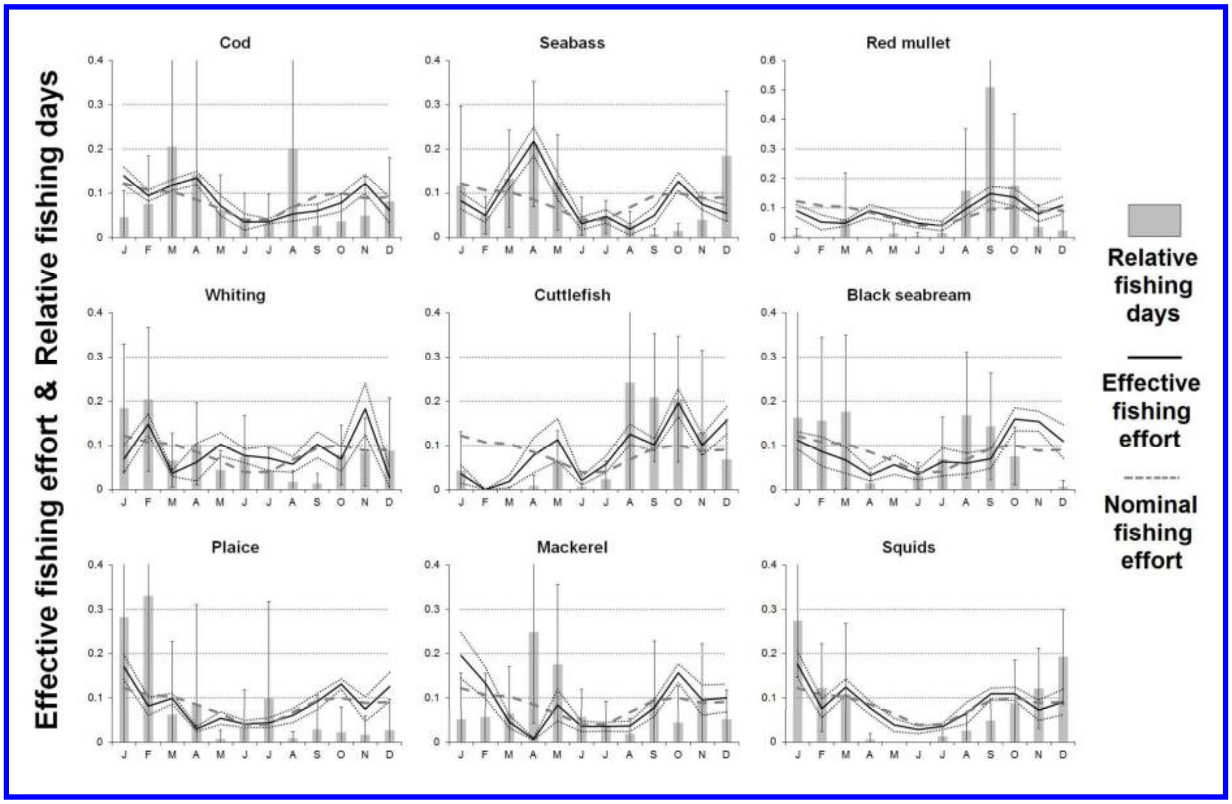

Figure 3. Average monthly nominal fishing effort, effective fishing effort and yearly standardized number of fishing days from activity calendars of exclusive bottom otter trawlers for nine main commercial species of the Eastern English Channel. Dotted lines and error bars indicate inter-annual variability over the period 2008-2014.

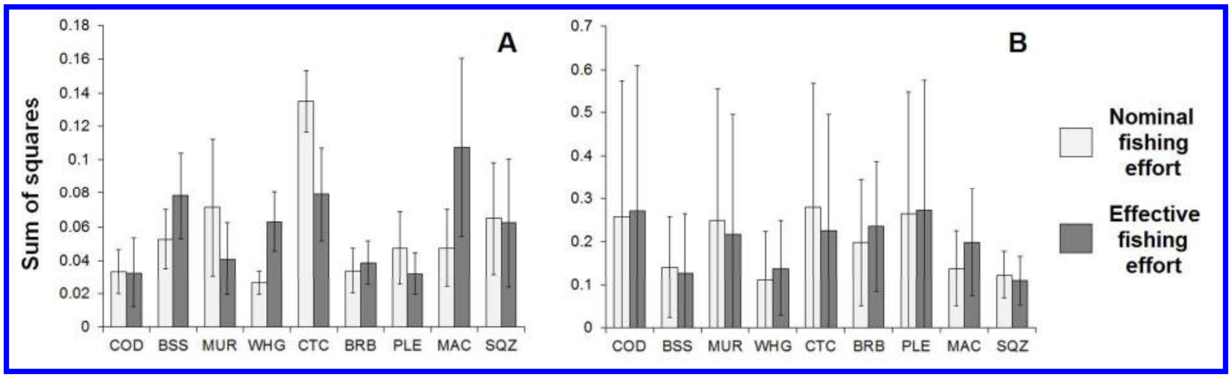

Figure 4. RSSQ between the monthly-resolved time series of (A) (i) nominal fishing effort and landings, (ii) effective fishing effort and landings; (B) (iii) nominal fishing effort and fishers' intention, (iv) effective fishing effort and fishers' intention; for nine key commercial species caught by exclusive bottom otter trawlers operating in the Eastern English Channel. Error bars indicate inter-annual variability over the period 2008-2014. COD: cod. BSS: Seabass. MUR: red mullet. WHG: whiting. CTC: cuttlefish. BRB: black seabream. PLE: plaice. MAC: mackerel. SQZ: squids.

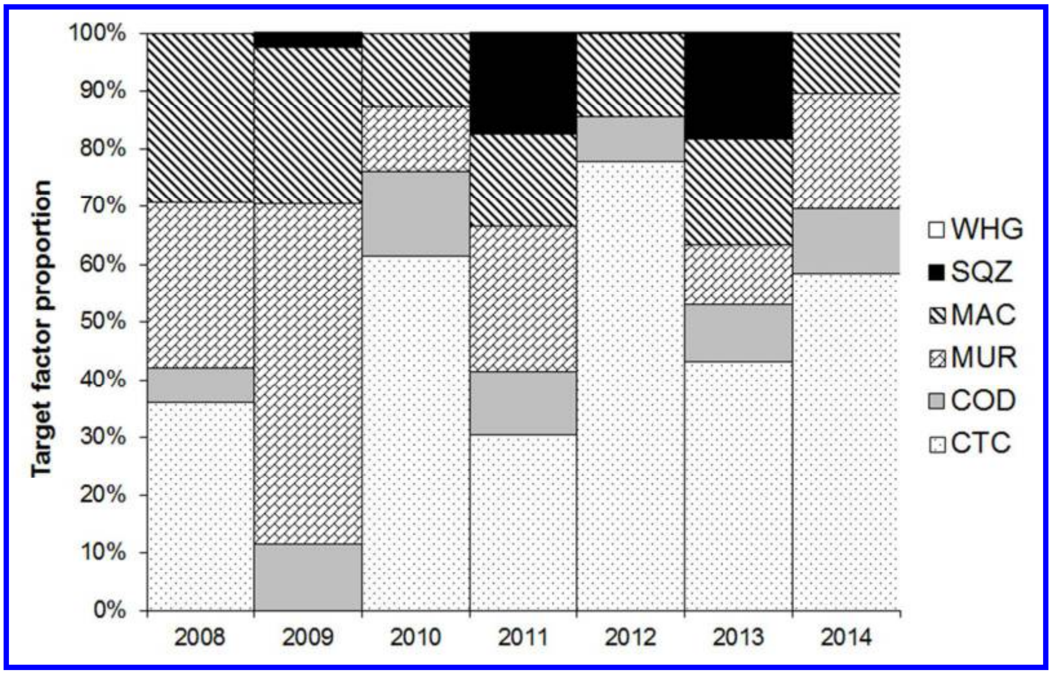

Figure 5. Relative target factor in October for whiting (WHG), squids (SQZ), mackerel (MAC), red mullet (MUR), cod (COD) and cuttlefish (CTC) for exclusive bottom otter trawlers in October over the period 2008-2014 in the Eastern English Channel, estimated by maximizing the Local Index of Collocation.

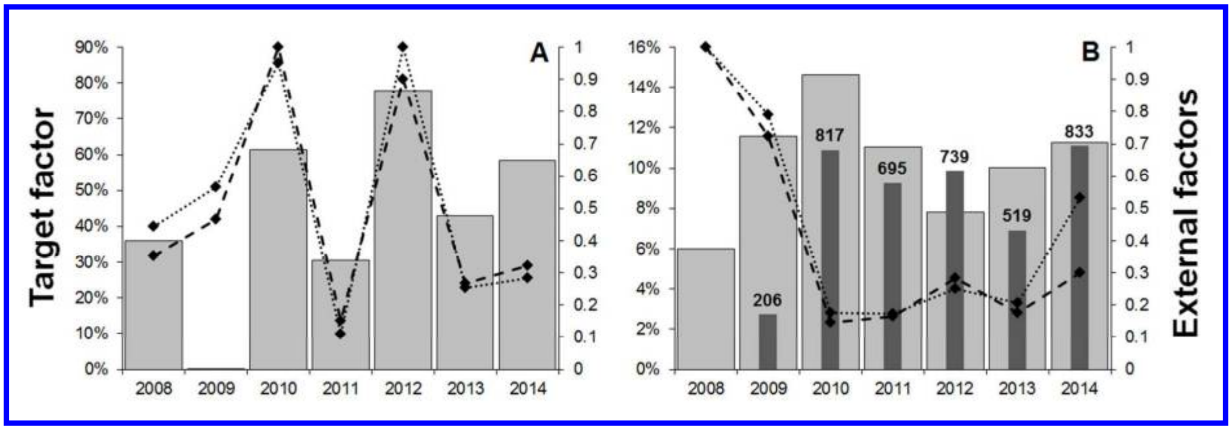

Figure 6. Relative A) cuttlefish and B) cod targeting factors in October, over the period 2008-2014 (light grey bars), compared to their relative abundances (dotted lines), relative economic attractiveness's (abundance x price; dashed lines) and remaining French quota in tons for cod (dark grey bars).

Table 1. List of Eastern English Channel species considered in this study, with their Minimum Landing Size (MLS, in cm) when existing, the minimum total length L_s (cm) above which individuals are considered to be equally selected by survey and commercial gears, and their closest code in commercial activity calendars.

Common name	**Scientific name**	**MLS (cm)**	**L_s (cm)**	**Activity calendars code**
European seabass	*Dicentrarchus labrax*	36	36	Bass (miscellaneous)
Atlantic cod	*Gadus morhua*	35	35	Cod
Squids	*Loligo* spp.	-	14*	Squids (miscellaneous)
Whiting	*Merlangius merlangus*	27	27	Whiting
Red mullet	*Mullus surmuletus*	-	15	Red mullet (miscellaneous)
European plaice	*Pleuronectes platessa*	27	27	Flatfishes (miscellaneous)
Atlantic mackerel	*Scomber scombrus*	20	20	Mackerel (miscellaneous)
Common cuttlefish	*Sepia officinalis*	-	13*	Cuttlefish, sepia (miscellaneous)
Black seabream	*Spondyliosoma cantharus*	-	17	Sparidae (seabream, dentex, sargo, …)

*mantle length

Table 2. Overlapping LIC values between the distribution of fishing effort and the distribution of potential revenue (revenue-based LIC) or the combined distributions of species (maximized LIC). The difference between both metrics measures the deviation between actual fishing effort distribution and that predicted by IFD.

	Revenue-based LIC	**Maximized LIC**	**Difference**
2008	0.63	0.81	+ 0.18
2009	0.59	0.74	+ 0.15
2010	0.46	0.64	+ 0.18
2011	0.57	0.70	+ 0.13
2012	0.52	0.74	+ 0.22
2013	0.46	0.57	+ 0.11
2014	0.51	0.73	+ 0.22