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Hake catchability by the French trawler fleet in the Bay of Biscay: estimating technical and biological components

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Several factors affect trawl catchability: (i) gear and vessel technical characteristics, (ii) anthropogenic factors, and (iii) biological factors. The objectives of this study were to assess the relative contribution of each factor to variations in hake (*Merluccius merluccius*) landings by the French trawler fleet operating on the shelf of the northern Bay of Biscay (ICES Subdivision VIIIa). Using generalized linear models, the impact of technical and anthropogenic factors was evaluated using landings per unit effort (lpue) obtained from logbooks. Variations in hake lpue were explained primarily by anthropogenic factors. For studying the biological components of catchability, the results of a scientific trawl survey in July 2006 involving three similar trawlers of the French trawler fleet were used. Daytime accessibility to large hake was lower than at night, and about zero for small hake (<19 cm). Estimates of spatial variation made using generalized linear mixed models showed a patchy fine-scale spatial distribution, but a random larger-scale distribution of hake over the area surveyed.

Keywords: accessibility, beam trawl, catchability, fishing power, GLMM, spatial distribution.

Introduction

Catch rates resulting from commercial fishing activities or from designed fishing experiments are linked to fish abundance by a factor referred to as catchability. Catch rates are affected by two types of processes: (i) those linked to the technical characteristics of the fishing gear and the vessel and anthropogenic factors such as skipper experience or strategy (Hilborn and Ledbetter, 1985; Goñi *et al*., 1999; Mahévas *et al*., 2004), and (ii) factors linked to the biology of the exploited resources, e.g. variations in spatial distribution or diel availability (Casey and Myers, 1998). Spatial and temporal variability in these factors can affect the relationship between observed catch rates and true stock abundance.

Evaluating the combined effects of fishery characteristics and biology requires that catch-rate data be collected along with fishery and biological covariables at an appropriate spatio-temporal scale. However, linking both types of information to catches remains a challenge. Many studies have considered the separate influences on commercial catch rates of technical and anthropogenic factors on the one hand (Hilborn and Ledbetter, 1985; Robins *et al*., 1998; Goñi *et al*., 1999) and the effects of fish behavioural patterns mainly for trawl-survey catches on the other (Engås and Godø, 1986; Walsh, 1991; Engås and Soldal, 1992; Michalsen *et al*., 1996; Aglen *et al*., 1999; Petrakis *et al*., 2001). Few studies have evaluated the magnitude of both classes of factor together. However, because several factors interact, even clear biological signals such as the diel behavioural patterns might not be detectable in commercial catch rates (Trenkel *et al*., 2008). The objective of this study is to quantify the respective effects of anthropogenic and technical components and biological features of hake on French trawler fleet catches of hake (*Merluccius merluccius*) in the Bay of Biscay.

We first studied the relationship between catch rates (landings per unit effort, lpue) and technical (e.g. vessel tonnage, length) and anthropogenic factors. Variations in catch rates not explained by technical vessel characteristics were interpreted as the result of a vessel or "skipper" effect (*sensu* Hilborn, 1985; Hilborn and Ledbetter, 1985; Squires and Kirkley, 1999). A significant skipper effect means that the skill and experience of the skipper and crew contribute significantly to a vessel having a better catch rate than its competitors. Variations in catch rate can be due to fishing tactics (Marchal *et al*., 2006) or to the local knowledge of the skipper and crew (Hilborn and Ledbetter, 1985). Commonly confused with the skipper's strategy, this effect is brought about essentially by the choice of fishing location and the choices of target species for specific times of the year (Hilborn and Ledbetter, 1985).

It has been argued that to evaluate the impact of a given fishing fleet on a particular resource reliably, one must take into account the spatial and seasonal characteristics of fishing activities (Booth, 2000). A clear seasonal pattern, with better catch rates in summer, is common in the Bay of Biscay bottom-trawl hake fishery (Poulard, 2001). To address the spatio-temporal variation in lpue analyses, we here connect catch rates with a location (the ICES rectangle in the logbook data) and with a métier variable (the combination of a gear, a set of target species, and a season; ICES, 2004) accepted as a basic feature of fishing activities.

After assessing the effects of technical and anthropogenic factors on variability in trawler lpue, we tested the influence of hake behaviour and small-scale spatio-temporal distribution on the remaining variability in the catch rates. For example, hake,

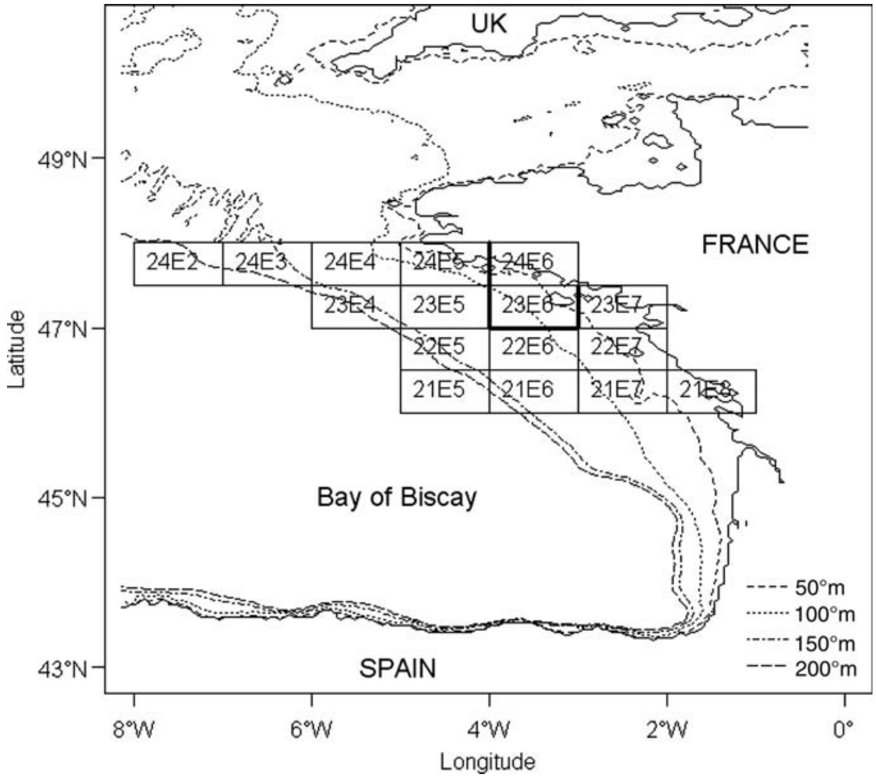

Figure 1. Map showing ICES Area VIIIa, including ICES rectangles 23E6 and 24E6 (within dark lines) in which the scientific trawl survey took place.

especially juveniles, undertake nocturnal vertical migration (Bozzano *et al*., 2005), which can affect the lpue. To investigate the behavioural component of catchability, we carried out a scientific trawl survey involving three French vessels of similar size belonging to the same fleet (trawlers catching hake in the Bay of Biscay). The trawlers simultaneously performed standardized parallel trawls in the same area of the northern part of the Bay of Biscay. The survey design minimized inter-vessel technical and anthropogenic differences so as to isolate the biological factors and make it easier to identify those that accounted for a significant amount of the variability in trawler lpue.

Material and methods

Lpue, vessel, and gear characteristics

Logbook information on fishing effort and landings by fishing sequence was extracted from the Harmonie database (Ifremer's national French fisheries database) for the French trawler fleet exploiting hake in ICES Subdivision VIIIa over the period 1999–2003 (Figure 1). A fishing sequence is defined as consecutive hauls taking place in the same ICES statistical rectangle with the same fishing gear during a single fishing trip. The fleet consists of 311 trawlers between 12 and 24 m long. For each vessel trip (1457 over the period 1999–2003), total trawling time and hake landings were available per statistical rectangle (the lpue database in Table 1). Corresponding technical information on vessel or gear or both was missing often. Therefore, we compiled two additional datasets, one including the information on lpue and technical vessel characteristics (lpue and techvess) and one with lpue and gear characteristics (lpue and techgear; Table 1). The available technical characteristics for each vessel were length, tonnage, year of acquisition, engine power (number of revolutions per minute), hull material (wood, steel, or plastic), the presence of a variable pitch propeller, the presence of a bulbous bow (a rounded feature to reduce turbulence), the number of drums, and the number of echosounders. In terms of gear characteristics, the data available included the type of groundrope (single or double rig, rockhopper), the number of panels, the number of warps, the weight of the otter boards, and the headline length. The lpue and techvess and the lpue and techgear databases contain data for 52 and 38 vessels, respectively, out of the 311 vessels in the fleet. Figure 2 shows the activities of these vessels.

Table 1. Description of datasets for lpue, technical vessel characteristics (techvess), and gear type (techgear) for French trawlers operating in the northern Bay of Biscay (ICES Area VIIIa) from 1999 to 2003 (extracted from the HARMONIE database).

Parameter	Lpue	Lpue and techvess	Lpue and techgear
Number of vessels	311	52	38
Number of fishing trips	1 457	692	577
Number of fishing sequences	8 114	1 511	1 078
Mean vessel length (m)	17.2	17.31	18.24
Mean vessel tonnage (grt)	4 756	4 831	5 447
Average hake lpue (kg h^{-1})	0.08	0.1	0.09

One of two métiers was attributed to each fishing sequence based on the species composition in its landings, following the

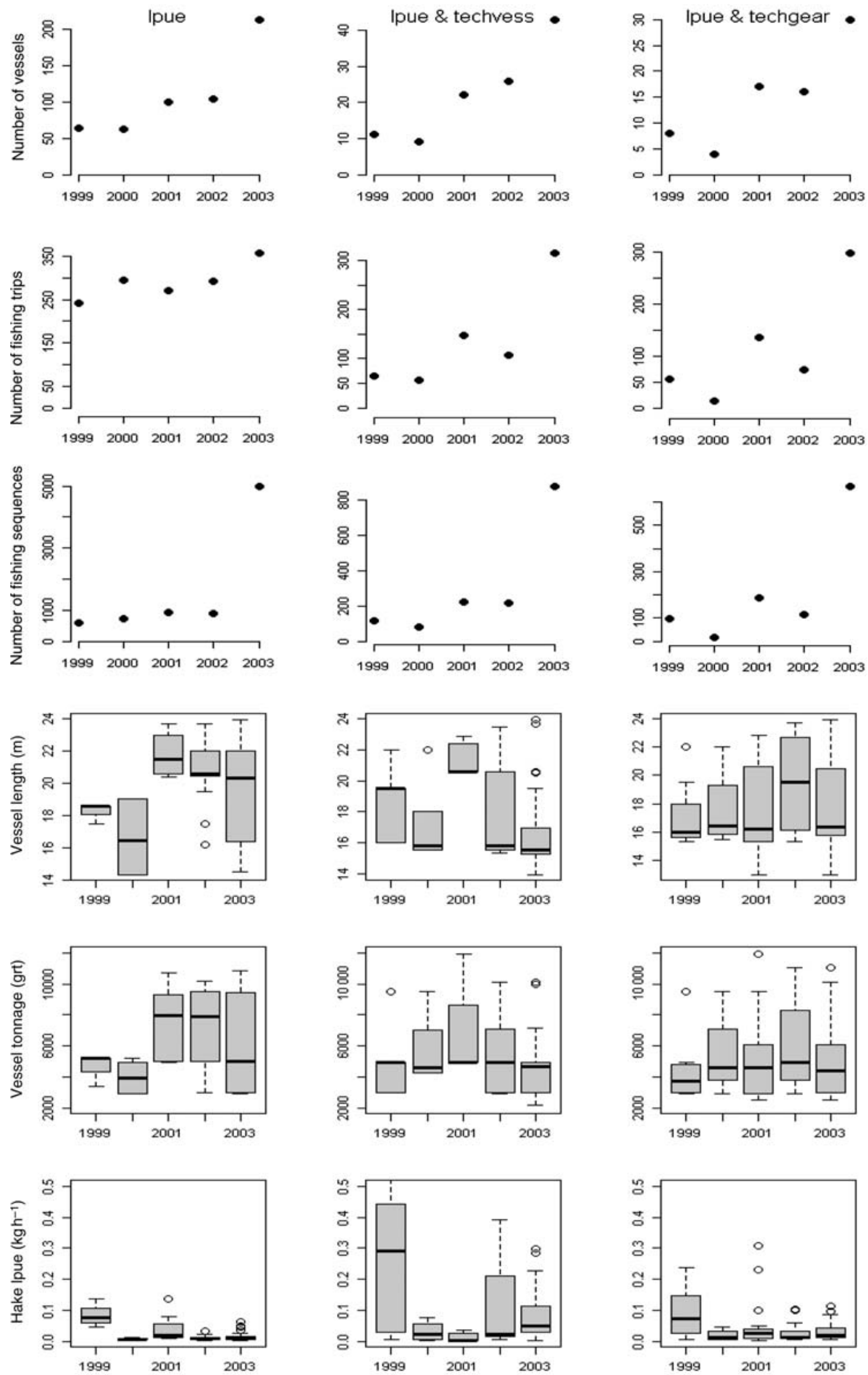

Figure 2. Comparison of the interannual distribution of lpue, technical vessel characteristics (techvess) and gear type (techgear) for French trawlers operating in the northern Bay of Biscay (ICES Area VIIIa) from 1999 to 2003 (extracted from the HARMONIE database) from the three available datasets supporting diagnostics of representivity of techvess and techgear in fleet samples: number of vessels, number of fishing trips, number of fishing sequences, vessel length, vessel gross registered tonnage, and hake lpue.

method outlined in Mahévas *et al*. (2004). Fishing sequences with a total catch of >40% cod (*Gadus morhua*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), and ling (*Molva molva*) belonged to the "demersal" métier, and the "*Nephrops*" métier included all fishing sequences with at least 10% Norway lobster (*Nephrops norvegicus*).

To isolate variations in catching power, we removed the potentially confusing effect of variations in hake abundance on lpue by dividing hake landings by a survey index of hake abundance, as in Mahévas *et al*. (2004). The survey index was calculated based on the survey data collected in autumn every year using a GOV bottom trawl; the survey covers the whole of the Bay of Biscay from 30 to 600 m deep, so encompasses the spatial distribution of the fleet studied. In this context, the index of abundance is computed to describe interannual variations in population abundance. As the scientific survey catches mainly juveniles, this index is an estimate of prerecruits. Consequently, the index derived from the survey in year t is used to standardize the lpue in year $t+1$. The spatial distribution of the study fleet is fully covered by the survey. Values of lpue were obtained by dividing the corrected hake catch (weight) by the total fishing effort (hours fished) for each fishing sequence. To make these results comparable with the second part of the study, the lpues were standardized to 30 min.

The scientific survey

The survey was conducted in the northern part of the Bay of Biscay (the dark box in Figure 1) in July 2006 using three chartered commercial trawlers, FV "Davidson", FV "Hebeilan", and FV "Océanie", belonging to the fleet studied previously. Ideally, hauls would have been conducted randomly within ICES Area VIIIa. For practical reasons, the survey was restricted to a small homogeneous area (Figure 1) with depths between 90 and 100 m and a sandy or muddy seabed.

The three vessels were similar in length, tonnage, and gear characteristics, and they all used their own professional four-panel pelagic trawls. They always fished simultaneously side by side, with the vessel order kept constant throughout the survey: "Hebeilan" in the middle, "Océanie" to its port, and "Davidson" on its starboard side, each at a distance of 200 m (Figure 3). Haul duration was 30 min from the moment the net stabilized on the seabed. Trawling speed was 4 knots, but varied slightly because of the currents. The actual trawling speed was recorded using SCANMAR sensors for "Hebeilan" and "Océanie", along with vertical and horizontal net opening. Fishing depth and trawl geometry were recorded every 5 min. Average horizontal and vertical trawl opening was 40 and 20 m, respectively. The groundline was kept ~0.5 m off the seabed. The geographic position of the three vessels was recorded with the vessels GPS.

The whole catch was sorted, and all or a subset of fish were measured to the nearest cm. The number of hake caught, their length, and the sampling rates were recorded electronically (Battaglia *et al*., 2006). In all, 84 hauls were carried out (at least 28 per vessel). Series of five hauls per vessel were conducted successively along a transect line and by day and night.

The number of hake caught of each length class and the sampling rates were used to calculate the total catch in numbers by haul and vessel. Individual weight (kg) was obtained using a published length–weight relationship (ICES, 2008). The SCANMAR information was used to select hake catches (kg) made during fishing hauls for which trawl geometry was stable (82 hauls). Hauls carried out between 23:30 and 05:30 (European summertime) were treated as night-time hauls (12 hauls) and those between 10:00 and 22:00 as daylight hauls (15 hauls).

Acoustic data were also collected during and between fishing stations using a Simrad ER60 echosounder connected to a

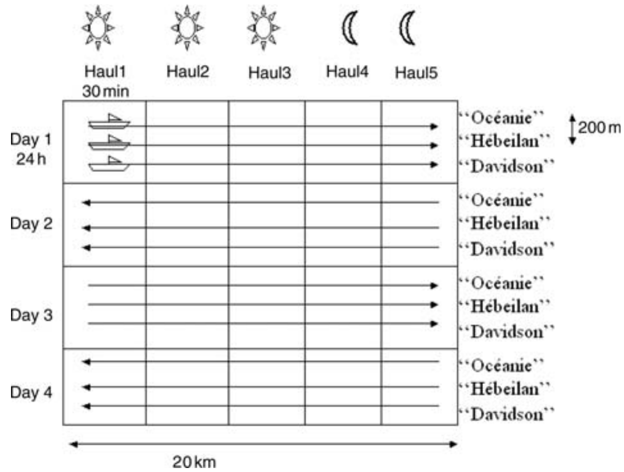

Figure 3. Experimental design of the Chapauv'06 scientific survey, which operated three commercial trawlers for 4 d.

transducer in a paravane ~2 m below the surface on the port side of the vessel. Acoustic data were replayed with Movies+ software (Weill *et al*., 1993) and archived in the international hydroacoustic data format (HAC; Simard *et al*., 1997) at a threshold of −80 db. A specific study is dedicated to the analysis of these acoustic data (Doray *et al*., 2010).

Defining catchability

There are several definitions of catchability in the literature. Seber (1982) defined it as the probability of a fish being caught by a standardized unit of effort. This assumes that nominal fishing effort (classically, fishing time for trawlers) can be translated into effective fishing effort. Probably more commonly, catchability is defined as the probability of a fish being caught by a haul (Beverton and Holt, 1957; Hilborn and Walters, 1992). Using the latter definition, catchability q is the multiplicative coefficient in the relationship between instantaneous fishing mortality rate F for species i and nominal fishing effort E for vessels j:

$$F_i = \sum_j F_{ij} = \sum_j q_{ij} E_i. \quad (1)$$

Catchability q can be analysed into several coefficients depending on species characteristics, vessel characteristics, or both:

$$q_{ij} = a_i v_{ij} s_{ij} p_j, \quad (2)$$

where a_i is how the accessibility of species i varies according to its horizontal and vertical distribution, v_{ij} defines how the vulnerability of species i depends on its reaction to the fishing gear of vessel j, s_{ij} is the selectivity of the gear of vessel j for species i, and p_j shows how the catching power of vessel j depends on vessel and gear characteristics as well as on crew and skipper skills.

Using the Baranov catch equation, the lpue of species i of vessel j can be approximated by the product of catchability and species abundance N:

$$\text{lpue}_{ij} = \frac{\text{Landings}_i}{\text{Nominal fishing effort}_j} = \frac{F_{ij} N_i}{\text{Nominal fishing effort}_j} = q_{ij} N_i. \quad (3)$$

Table 2. Description of covariables for French trawlers operating in the northern Bay of Biscay (ICES Area VIIIa) from 1999 to 2003 (extracted from the HARMONIE database) included in statistical models.

Variable	Unit	Number of levels/ continuous
Vessel	Vessel identifier	Model 1, 311 Model 2a, 52 Model 3a, 38
Area	ICES rectangle	16
Month	From 1 to 12	12
Year	From 1999 to 2003	5
Date of acquisition	Integer number, from 1970 to 2000	Continuous
Hull material	Wood ($W = 1$); Steel ($S = 2$); GRP ($G = 4 =$ plastic)	3
Bulbous bow	Yes/no	2
Number of echosounders	Integer number (0, 1, or 2)	3
Engine rotations per minute	rpm	Continuous
Variable pitch propeller	Yes/no	2
Number of net drums	Integer number (from 1 to 4)	4
Length	m	Continuous
Tonnage	grt	Continuous
Number of warps	2 or 3	2
Number of panels (or not applicable if not a trawl)	2 or 4	2
Length of headline	m	Continuous
Type of groundrope	Diabolo,1; rockhopper, 2; chains, 3; metallic spheres, 4; rubber, 5; plain wire, 6	6
Weight of otter board	kg	Continuous

Therefore, two vessels operating simultaneously in a given area with the same nominal fishing effort could have different catch levels as a consequence of differences in catchability and/or spatial variation in fish density.

Here, we focus first on hake-trawl catching power p_j disentangling skipper skill, technical vessel characteristics, and gear characteristics. In a second step, we assess the spatial variation in hake accessibility a_i.

Assessing the impact of vessel and gear characteristics on lpue

Exploratory analysis was conducted to identify the main trends in the data and the relevant explanatory variables (Table 2). Then, the respective effects of area (ICES rectangles; Figure 1), temporal factors (month, year), and technical vessel and gear characteristics in explaining the variability in catch rates between fishing sequences were assessed using generalized linear models (GLMs; McCullagh and Nelder, 1989), with a gamma error distribution and a log-link function. Spatial fishing effects are taken into account in the model in both the vessel and the area effect. The area effect includes spatial variations in abundance and fleet distribution at the scale of the ICES rectangle, and the vessel effect includes the skipper's skill at locating fish within a rectangle. The type (continuous/categorical) of each explanatory variable included in statistical models is driven by the nature of the variable (continuous/discrete) in the databases. Therefore, all continuous variables were treated as continuous regressors, whereas discrete and non-numerical variables were treated as categorical factors (Table 2). The choice of variable type for discrete and numerical variables was determined according to the number of levels induced by the range of variation in the variable and the expected effect of this variable (linear/non linear) on the results of the exploratory analysis.

The number of echosounders per vessel in the fleet varies from 0 to 2 and the number of net drums from 1 to 4, and no strong relationship can be shown. On the other hand, the vessels' dates of acquisition vary from 1969 to 2000, and the lpue appears on average to be negatively linearly correlated with this variable. Consequently, the date of acquisition was introduced in statistical models as a regressor, whereas the numbers of drums and echosounders were treated as factors. The best models were selected using Akaike's information criterion (AIC; Anderson *et al.*, 2000), the levels of deviance explained, and visual diagnostics of the residuals (normality and homoscedasticity). Three sets of model (Table 3) were fitted to the three datasets described (see also Tables 1 and 2). For all explanatory variables, the main effects and the first-order interactions were tested.

Model 1 (Table 3) is meant to assess the relative contribution of vessel effect to lpue variability for the whole fleet over the study period. Models 2a and 3a (Table 3) provide the same information, but for the subsample of vessels contained in the techvess and techgear databases. Assuming that both vessel samples are representative of the fleet studied, the vessel effects are expected to have the same order of magnitude in all models.

The vessel effect (in models 1, 2a, and 3a; Table 3) characterizes the part of lpue variability that can be linked to the vessel, not distinguishing between human skill and technical efficiency. A better understanding of this effect can be achieved by disentangling the anthropogenic contribution from the technical contribution. This can be achieved by removing the vessel factor from the model, and adding some technical factors (such as VC and GC in models 2b, 2c, 3b, and 3c; Table 3). In these models, the VC and GC effects are expected to assess the contribution of technical characteristics to fishing efficiency.

For the models including vessel characteristics (dataset lpue and techvess), the relative contribution of each characteristic was assessed using single-variable models (model 2b; Table 3). Again the AIC was used to select the most distinguishing vessel characteristics. To compare the capacity of vessel characteristics to explain differences in vessel catching power, we designed a model with a

Table 3. GLMs fitted to the three datasets (Table 1), lpue, lpue and techvess, and lpue and techgear.

Dataset	Model
Lpue	1: lpue = vessel + area + month + year + métier + interactions
Lpue and techvess	2a: lpue = vessel + area + month + year + métier + interactions
Lpue and techvess	2b: lpue = area + month + year + métier + VC + interactions
Lpue and techvess	2c: lpue = area + month + year + métier + selected VC + interactions
Lpue and techgear	3a: lpue = vessel + area + month + year + métier + interactions
Lpue and techgear	3b: lpue = area + month + year + métier + GC + interactions
Lpue and techgear	3c: lpue = area + month + year + métier + selected GC + interactions

Interactions are first-order interactions between all explanatory variables. VC, discriminant vessel technical characteristics (hull material, year of acquisition, and vessel length). GC, discriminant gear technical characteristics (type of groundrope, number of panels, number of warps, and weight of otter boards).

Table 4. Meaning of the variables used to explain the variability in catch rates during the scientific trawl survey carried out in the northern Bay of Biscay.

Variable	Meaning
Haul	Small temporal (h) and spatial (intra-transect) variation in distribution
Day (date of survey)	Daily spatio-temporal effects
Day/night	Changes between day and night, with size-specific distribution in the water column
Vessel	Small spatial variation (≤200 m)

Table 5. Linear models (LMs) and linear mixed models (LMMs) fitted to hake cpue (kg 0.5 h^{-1}) from the scientific survey assuming a Gaussian distribution for the residuals, and a GLM fitted to the hake cpue (*n* per 30 min) from the scientific survey assuming a Poisson distribution for residuals and a log-link function.

Model	Description
LM1	cpue = vessel × day + vessel × day/night + $\varepsilon \sim N(O, \sigma)$
LM2	cpue = day × vessel + day × day/night + $\varepsilon \sim N(O, \sigma)$
LM3	cpue = haul + $\varepsilon \sim N(O, \sigma)$
LM4	cpue = day/night × vessel + day/night × day + $\varepsilon \sim N(O, \sigma)$
LMM1	cpue = day/night + random effect(vessel) $\sim N(O, \psi_v)$ + $\varepsilon \sim N(O, \sigma_v)$
LMM2	cpue = day/night + random effect(haul) $\sim N(O, \psi_h)$ + $\varepsilon \sim N(O, \sigma_h)$
LMM3	cpue = day/night + random effect(day) $\sim N(O, \psi_d)$ + $\varepsilon \sim N(O, \sigma_d)$
GLM	$cpue_n$ = day/night|haul + $\varepsilon \sim p(\lambda)$

ε, residuals' random distribution; $N(\cdot,\cdot)$, Gaussian distribution; σ, standard deviation of the residuals; ψ, standard deviation of the random-effect variable; the indices denote the scale of the catchability variability: v for inter-vessel, h for inter-haul, and d for day.

fixed vessel effect (model 2a; Table 3) along with a model without the vessel effect but with all other distinguishing vessel characteristics (model 2c; Table 3). The same approach was used to assess the role of gear characteristics (models 3; Table 3). The diagnosis of goodness-of-fit using AIC makes it possible to classify models according to their respective ability to capture the variability in lpue. Therefore, for nested models fitted to the same dataset (e.g. models 2a and 2c or models 3a and 3c), a goodness-of-fit diagnosis can be used also to compare how much fishing power is affected by technical characteristics and by vessel effect.

Assessing the impact of biological factors on catch rates

The survey was designed to explore the influence of factors linked to small spatial and temporal scales, but blocking out the effects of inter-vessel variability caused by differences in vessel and gear characteristics. Variations in catchability caused by diel behavioural patterns (e.g. position in the water column) can be investigated by considering the differences between day and night catches. Similarly, the inter-vessel differences for the same haul number should show the effects of small-scale spatial variability of the resource, whereas the differences between hauls and between days for the same vessel should show the effects at somewhat broader spatio-temporal scales (Table 4).

We used GLMs and generalized linear mixed models (GLMMs; Pinheiro and Bates, 2000; Venables and Dichmont, 2004) to assess how spatio-temporal variations in the targeted resource could affect the catch rates of hake. Again the best models were selected using AIC, the deviance explained, and visual diagnostics of the residuals (normality and homoscedasticity). We first explored the relative magnitude of each effect by testing the effects associated with the categorical variables [haul number (haul), vessel, day, and day/night (DN)] using linear models (Table 5). Because the haul number is nested within vessel, day, and day/night factors, it cannot be introduced jointly with other factors in the model.

We then explored the between-factor and within-factor variability for each explanatory factor (vessel, haul, and day) using random effects. In the absence of a vessel effect (discerned by standardizing the fishing method of each of the three vessels), the three fishing hauls (one for each vessel) for any given haul number can be treated as repeated measures. The same assumption can be made for hauls and days. The variability in catches can therefore be estimated between vessels (for each haul) to approach instantaneous spatial variation in hake distribution, and within vessels (between hauls of each vessel) to approach the spatio-temporal variation in hake distribution. For this, we fitted three separate

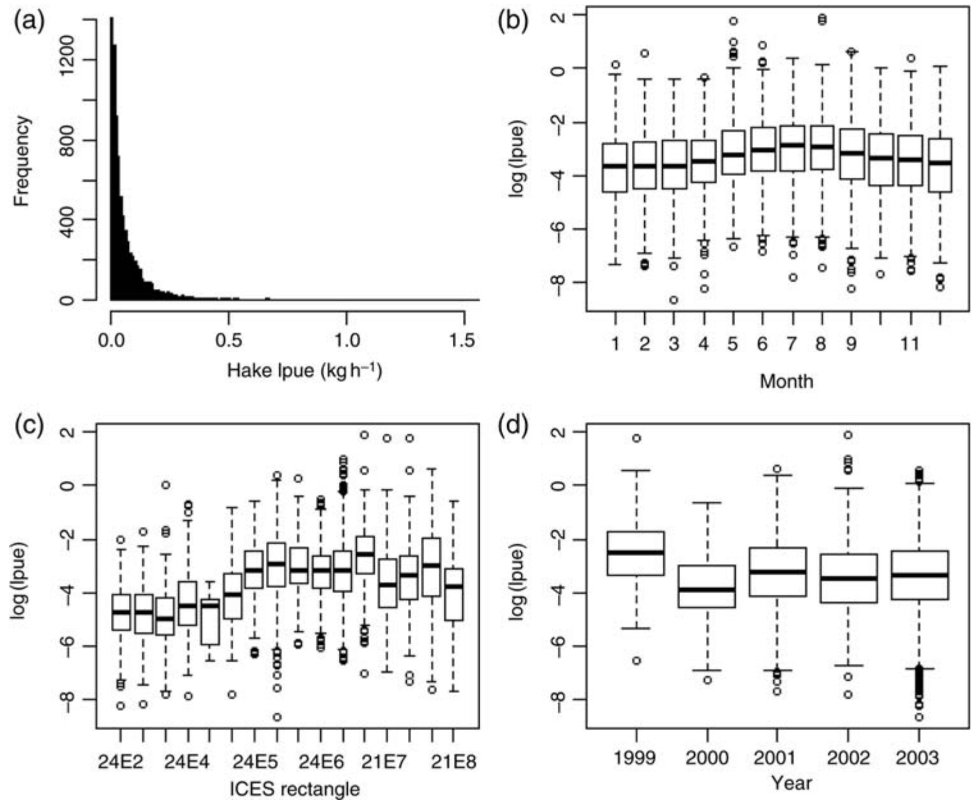

Figure 4. (a) Histogram of hake lpue, and plots of log(lpue) against the explanatory variables (b) month, (c) fishing area (ICES rectangle), and (d) year.

GLMMs with DN as fixed effect and either vessel, haul, or day as random effect (Table 4). Normal error distributions were assumed for all models. Using the mixed-model formulation, ψ denotes the standard deviation of the random-effect variable and σ the standard deviation of the residuals; ψ estimates the random-factor standard deviation (Pinheiro and Bates, 2000). Therefore, ψ_v estimates the variability in catchability for the inter-vessel scale (and similarly ψ_h for the inter-haul scale, and ψ_h and ψ_d for the inter-day scale). Given that vessels were separated by 200 m during the survey, we associated ψ_v in model LMM1 (Table 5) with a very small spatial scale variability (<200 m) averaged over the survey period. On the other hand, the ψ_h and the ψ_d in models LMM2 and LMM3 (Table 5) measure the spatio-temporal variability in catchability, respectively, at the scale of hauls (3 km per 0.5 h) and days (tens of kilometres per 24 h).

Finally, using catch in numbers per haul, we tested whether hake were randomly distributed over the survey area, fitting a GLM to hake catches in numbers assuming a Poisson distribution (Table 5).

Results

Impact of vessel and gear characteristics on commercial catch rates

The exploratory analysis clarified the role of each of several potential explanatory variables for hake lpue. It was best described by a Gamma distribution (Figure 4a), varying between statistical rectangles, with an increasing trend in lpue along a southeast–northwest direction (Figure 4c). A seasonal effect was present, with the highest value of hake lpue in spring and summer (Figure 4b). There was little variation in lpue between years, although the values in 2000 were lower than in the other years (Figure 4d). That was the year with the fewest recorded fishing sequences. *Nephrops* was the most represented métier, and it was also the métier with the highest lpue, whereas there were few fishing sequences for the demersal métier. Recently, acquired vessels seemed to have a lower and more variable lpue than vessels acquired some time ago (Figure 5). Finally, there was little variation in lpue relative to any of the vessel or gear characteristics, but differences in lpue were noticed relative to the engine's number of revolutions per minute (rpm; Figure 5).

The GLM fitted to the lpue dataset indicated that the vessel effect explained the largest amount of difference in hake lpue, followed by month, year, area, and métier (Table 6). We fitted the models using the variables in this order and also tested for possible interactions between variables. The best model (lowest AIC) included an interaction term for vessel and métier (vessel:métier in Table 6). This interaction revealed that vessel effects differed by métier (one-third of the fleet practiced two métiers), i.e. the same vessel had a different catching power depending on the métier it carried out. As our factorial design is unbalanced, the orthogonality property of the main effects and the interactions among them applicable to balanced data are no longer valid (Montgomery, 2005). This means that changing the order of the factors in the model could lead to differences in the estimated effects. Fortunately in our case, the imbalance did not affect the results of the model.

For the datasets with technical information on either vessels or gear characteristics, the best fitting models were obtained by including a vessel factor rather than technical characteristics of vessels or

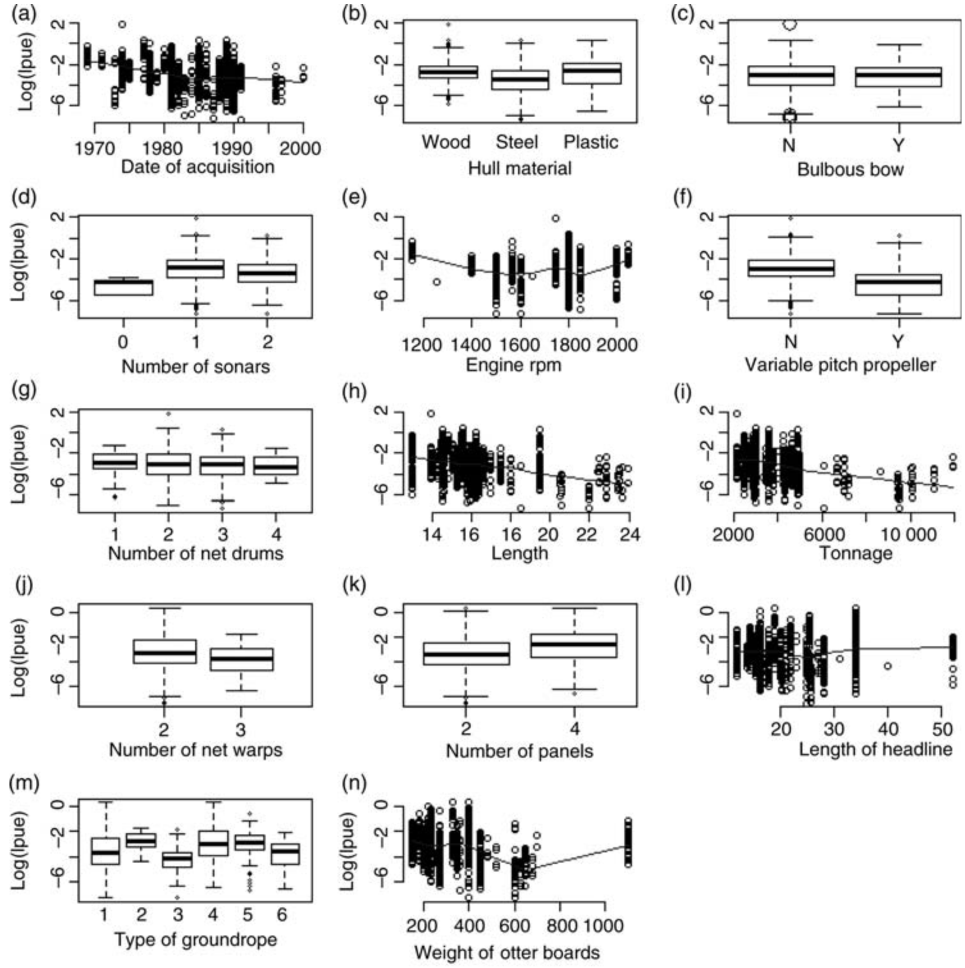

Figure 5. Plots of log(lpue) against explanatory variables: (a) date of acquisition; (b) hull material; (c) presence/absence of bulbous bow; (d) number of sonars; (e) engine rpm; (f) presence/absence of a variable pitch propeller; (g) number of net drums; (h) length (m); (i) tonnage (grt); (j) number of warps; (k) number of panels; (l) length of headline (m); (m) type of groundrope (1, diabolo; 2, rockhopper; 3, chains; 4, metallic spheres; 5, rubber; 6, plain wire); (n) weight of otter boards.

Table 6. Analysis of deviance for model 1 (Table 2) for commercial catch rates (dataset lpue; Table 1), AIC, and the % deviance explained for nested models.

Parameter	d.f.	Deviance	Residual d.f.	Residual deviance	*F*	Probability (>*F*)	AIC	% deviance explained
Null	–	–	8 113	13 583.8	–	–	−25 144	–
Vessel	310	7 114.9	7 803	6 468.9	20.8	<0.001	−31 609	52.4
Area	15	98.1	7 788	6 370.8	5.9	<0.001	−31 609	53.1
Month	11	276.4	7 777	6 094.5	22.8	<0.001	−31 719	55.1
Year	4	168.2	7 773	5 926.2	38.1	<0.001	−32 346	56.4
Métier	1	72.7	7 772	5 853.5	65.9	<0.001	−32 456	56.9
Vessel:métier	100	363.8	7 672	5 489.8	3.6	<0.001	−32 835	59.6

gears. When only the vessel characteristics were included in the model, area, month, and year made a similar contribution, and métier still contributed to reducing the residual deviance (results not shown). The explanatory power of gear characteristics was weak. Only the hull material (MAT), year of acquisition (YOA), and vessel length were significant. The next significant factor (next lowest AIC value) was the engine power, but the *p*-value of the Fisher test was too large. The diagnostic plot of these models revealed no violation of the hypothesis of normality and homoscedasticity. For the model including only gear characteristics, the type of groundrope, the number of panels, the number of warps, and the weight of the otter boards were the only significant variables. However, the AIC showed that variability in lpue was explained less by gear characteristics than by a vessel effect (AIC of −6330 for model 3a and 6048 for model 3c), as was true for vessel characteristics.

Impact of biological factors on the catch rates

The exploratory analysis of the scientific survey data revealed systematic differences in catch per unit effort (cpue) according to all

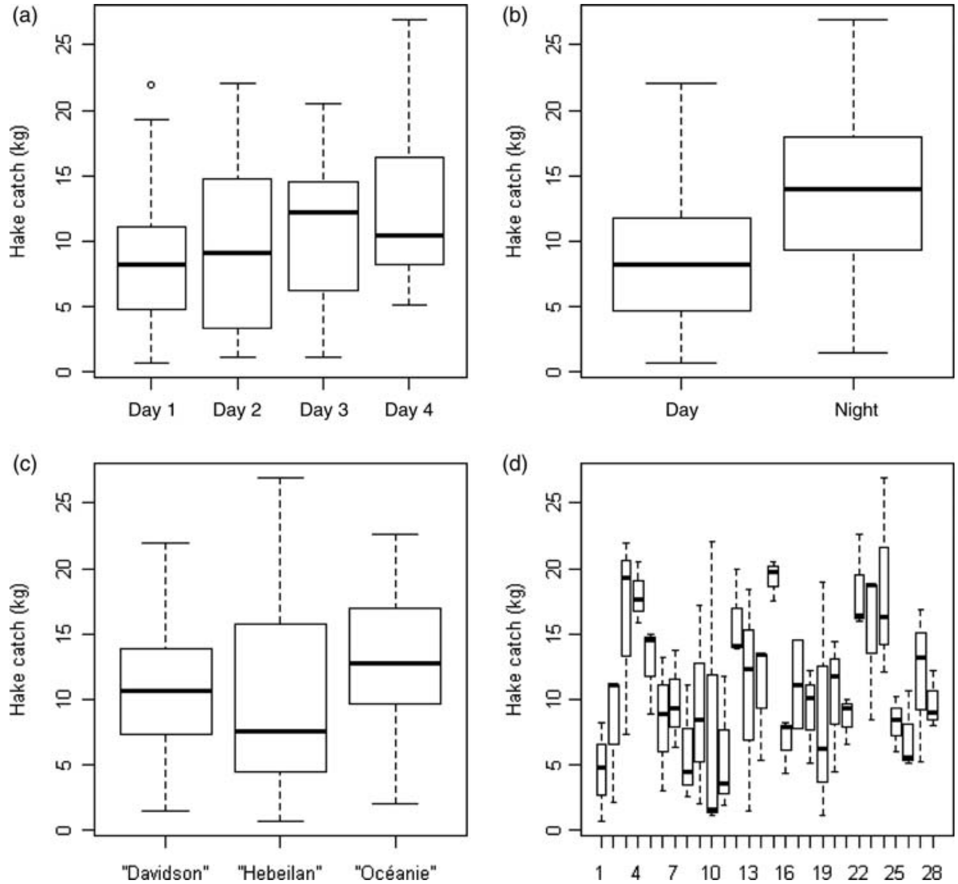

Figure 6. Boxplots of hake catch (kg) per vessel per haul by (a) sampling date, (b) day or night, (c) vessel, and (d) haul number.

Table 7. Analysis of deviance for single-variable models fitted to scientific survey hake cpue, with the models as defined in Table 5.

Model	d.f.	Residual deviance	Residual d.f.	Deviance	F	Probability (>F)	AIC
Vessel	2	136 016 005	80	2 932 214 513	1.8555	–	1 686
Date	3	90 355 870	79	2 977 874 649	0.799	–	1 689
Haul number	27	1 433 170 215	55	1 635 060 304	1.7855	*	1 688
Day/night	1	529 412 705	81	2 538 817 814	16.891	***	1 672

***$p < 0.001$, *$0.01 < p < 0.05$.

explanatory factors but also generally great variability (Figure 6). As expected based on the standardization procedure of the survey (similar vessel and gear characteristics), there were no systematic differences in hake catches by the three vessels ($p = 0.2$ for testing the difference between the means). However, the gear-geometry data (SCANMAR) showed a significant difference in the mean water volume sampled by two vessels because of a significant difference in the trawl-opening area (830 m^2 for "Océanie", 730 m^2 for "Hebeilan"). The fact that the trawl-opening area did not have a significant effect is consistent with the fact (reported above) that headline length also failed to have a significant effect on lpue.

GLMs with just one explanatory variable indicated that there was no significant vessel or date effect (Table 7), confirming that the standardization process applied in the scientific survey had been successful: all three vessels had the same catching power. The single most significant factor (lowest AIC) was a systematic day–night difference ($p \leq 0.001$), followed by haul ($p \leq 0.05$). This day/night effect was linked to a change in vertical hake distribution caused by diurnal behaviour of the fish: catches in number were larger by night, and no small hake (<19 cm) were caught by day (Figure 7). This reveals a lower catchability of large hake and a zero catchability of small hake by day for the trawl gear studied. As the bottom of the trawl was held 50 cm from the seabed, the most probable explanation for this is that hake are distributed close to the seabed by day, but move up in the water column at night.

The three random-effect models revealed that inter-vessel and inter-haul variability in catches were similar. They explained 21 and 24%, respectively, of the total variance (Table 8). In contrast, inter-date variability might be negligible (point estimate 3%), but the large confidence intervals caused by the small sample size (4) indicate that this was unreliably estimated. Hence, the spatial distribution of hake was probably patchy at a small scale, but patches were randomly distributed over the survey spatio-temporal scale. The GLM fitted to catch numbers per haul confirmed the latter hypothesis. Using a Poisson distribution and a fixed-haul effect, it explained 65% of deviance. Residual plots were used to check model assumptions, and no structure in the residuals could be detected.

Discussion

The results of our study indicate that the vessel effect contributes most to explaining differences in the fishing power of French commercial trawlers fishing in the northern part of the Bay of Biscay. This vessel effect explained the greatest percentage of deviance, whereas the other significant variables (geographic area, month, and métier) explained just a small part of the deviance. To explore further the effects of technical variables in fishing power, we fitted models with technical variables, characteristic either of the vessel or of the gear. The explanatory power of these factors was marginal, pointing towards the importance of a skipper effect in explaining the catching-power differences between vessels in the French trawler fleet exploiting hake.

The effects of several technical variables were nevertheless revealed. When we considered vessel characteristics (the lpue and techvess dataset), the most important variable was month, but both the date of acquisition and the hull material made notable contributions, and both were significant. The significance of month confirms the seasonality in hake accessibility, which had already been noted by Poulard (2001). The significance of area goes against the assumptions of homogeneous fishing power and hake accessibility overfishing areas, but it does confirm the explanation advanced by Hilborn (1985) that local knowledge impacts catching power. Similar results were found for bottom trawlers targeting anglerfish (*Lophius* spp.) in the Bay of Biscay (Mahévas *et al.*, 2004). The fact that the date of acquisition was the most significant variable might offer a partial explanation for the skipper effect. The date of acquisition indicates the length of time each vessel has been owned by its present skipper, so it shows a skipper's familiarity with his vessel and perhaps also the fishing grounds. Spatial variability in catching power was interpreted by Hilborn (1985) as indicating that the skippers are specialists in certain areas. Finally, for this fishery, vessels made of wood were more efficient than vessels made of steel. None of the tested gear characteristics were important in explaining the lpue variability. The most significant variable reflected the most suitable gear to catch hake, i.e. two panels (single trawl) with a rockhopper.

The importance of the vessel effect could also indicate that the technical variables considered in this study were not reported with sufficient accuracy at the scale of the fleet. This idea is supported by the fact that a notable number of fishing sequences was reported without technical information. An improved level of information on technical variables would contribute to more accurate identification of the importance of the technical variables in explaining variations in catching power, and hence might help to reduce the contribution of the vessel effect.

The biological effects we attempted to quantify in our study are linked to the availability and behaviour of hake. Hake availability is influenced by vertical migrations in the water column at night (Hickling, 1927; Casey and Pereiro, 1995; Bozzano *et al.*, 2005), associated with feeding behaviour of the fish. In our small-scale survey, the trawls were operated at 50-cm off-bottom. Consequently, and as expected, we observed differences in catches between day and night. The size composition of the catches demonstrated that more fish were caught at night and that smaller fish were only caught then.

By day, small-scale video observations in an area (characterized by similar ground and depth) during the same month and close to the current study have revealed that individual hake tend to be randomly distributed in space (Trenkel *et al.*, 2007). The small part of the variance explained by inter-vessel or inter-haul variability and the goodness of fit of the Poisson model seem to confirm the random nature of hake spatial distribution in this area at that time of year.

There were no major differences in catches between the various dates during the survey, a reflection of the absence of short temporal-scale variations at the scale of the survey area. This result was expected considering that the survey took place on four consecutive days, with consistent weather and ocean conditions. On the other hand, there was noticeable variation

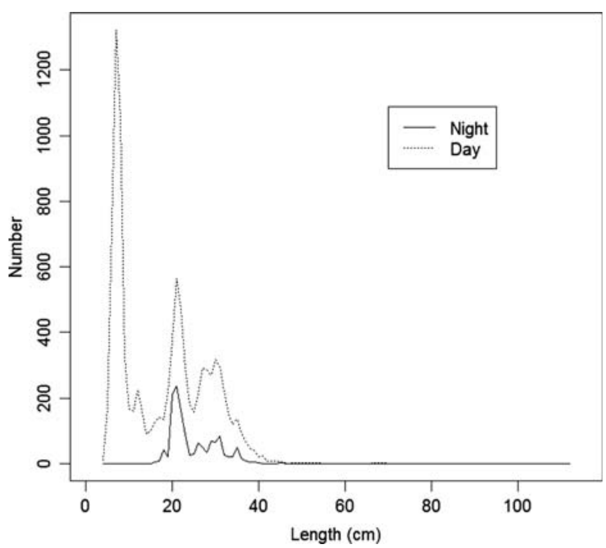

Figure 7. Average length frequency distribution of scientific hake catches by day and night.

Table 8. Estimates of standard errors for random effects and residual variability for linear mixed-effects models, as defined in Table 5.

	Standard error of LMM 1		Standard error of LMM 2		Standard error of LMM 3	
Parameter	Inter-vessel ψ_v	Residual σ_v	Inter-haul Ψ_h	Residual σ_h	Inter-date Ψ_d	Residual σ_d
Lower confidence interval	203.8	4 717	173.9	4 518.1	0	4 790
Estimate	1 176.6	5 512.9	1 341.6	5 443.3	184.6	5 596.3
Upper confidence interval	6 793.8	6 443	10 350.7	6 557.9	1.45E+18	6.54E+03
$\psi_v/(\psi_v^2+\sigma_v^2)^{1/2}$	20.8%		23.9%		3.2%	

The approximate 95% confidence intervals for the estimates were obtained using a normal approximation to the distribution of the (restricted) maximum likelihood estimates.

between vessels and hauls, demonstrating a spatial variation in hake availability at a fine spatial scale. Trawling, even with short tows (30 min in this study), provides an observation of the cumulative accessible proportion of the population over the trawled area. Using acoustic data collected on board one of the vessels during the survey, preliminary results point towards the absence of fine spatial structure and confirm the presence of spatial autocorrelation at the scale of ∼10 km (Doray *et al*., 2010).

The fishery studied operates in an area characterized by a depth of 50–200 m (Figure 1). The survey explored an intermediate depth within the fishery area. The survey's coverage (in both time and space) was limited, and the results need to be confirmed for larger scales. However, the first objective of our study was achieved and our conclusion is that the contribution of hake behaviour and spatial distribution to catchability can be explored by carrying out this type of survey. To extrapolate the conclusions to the scale of a fishery, we would need to conduct a similar sampling survey over a larger part of the region.

The management of some European fisheries relies currently on the control of landings and fishing effort. There are, however, concerns that measuring effort might not be appropriate because it does not comprehensively reflect changes in fleet capacity. When only fishing effort is measured over extended periods, it might not reflect changes brought about by the introduction of new techniques or technologies (technical creep; Kirkley *et al*., 2004; Mahévas *et al*., 2004). To study the various components of catchability, we attempted to quantify the role of these technical aspects. One of our main findings was that fishing power was less affected by technical factors than by anthropogenic factors, and this probably reflects the lack of significant technical developments over the study period. In the absence of technical improvements, variations in catchability were largely linked to a vessel effect, i.e. skippers' differing skill at finding and catching fish. Another useful finding was that hake accessibility/vulnerability varied between areas. This signal was detected at various spatial scales. Catch rates varied between ICES rectangles at an annual scale, but also at a much finer scale between the various hauls during the survey. To conclude, though, there is considerable scope for improvement in measuring effective fishing effort that would require examining the effects described above, especially differences between vessels and between areas. Improving measures of fishing effort would require one to evaluate the situation for much smaller units within the fishing fleet.

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