

Availability of deep-water fish to trawling and visual observation from a remotely operated vehicle (ROV)

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ABSTRACT: Visual observations were collected using video from a remotely operated vehicle (ROV) for a number of deep-water species on the continental slope of the Bay of Biscay, Northeast Atlantic. Relative trawl availability was defined as the ratio of population density estimates from a scientific bottom-trawl survey to those derived from visual strip transects. Several natural and reaction behaviour variables were explored to explain between-species variation in relative trawl availability. The variable with most explanatory power was spatial dispersion, with aggregating species showing lower relative availability than those that were randomly or uniformly distributed. This variable was also strongly correlated with ROV density estimates (aggregated species had the highest densities). Mean distance off the ground and mean body length of a species were positively related to relative trawl availability. In contrast, the way different species reacted to the ROV did not appear to be correlated with relative trawl availability.

KEY WORDS: Remotely operated vehicle · ROV · Catchability · Spatial distribution · Continental slope

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INTRODUCTION

Scientific trawl surveys provide relative abundance indices for fish stock assessments. The constant of proportionality between these indices and the true population density is commonly referred to as the catchability coefficient. Catchability is known to have many components and can vary in response to factors such as species, population density, season, time of day and body size, which all interact with the fishing gear. For a given population, trawl catchability is commonly broken down into horizontal and vertical availability and gear efficiency (Godø 1994). Horizontal availability, which is the probability that an individual is found in the fishing area, is not studied in this paper. Vertical availability is the probability that an individual is at the right distance from the bottom in order to be caught by

the particular fishing gear. Gear efficiency, defined as the probability that an individual that encounters the gear ends up in the catch, is determined by mesh size and reactions to the approaching gear. Most of the information on the different components of catchability comes from field studies of a few continental shelf species, in particular cod, haddock and some flatfish (Parrish et al. 1962, Hemmings 1973, Walsh 1991, Wardle 1993, Engås 1994, Godø 1994, Bublitz 1996). Laboratory studies have contributed to our understanding of fish reaction to gear, with respect to swimming ability (Harden Jones 1963, He 1993), hearing spectra (Chapman 1973, Hawkins 1973) and vision (Muntz 1983).

Little is currently known about the catchability of deep-sea species. The main insights come from comparative trawl studies, which indicate large differences in the relative catchabilities of different deep-sea spe-

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cies, depending on the kind of trawl and rigging used (Gordon & Duncan 1985, Merrett et al. 1991, Gordon & Bergstad 1992). An increase in towing speed and larger net openings seem to favour catches of large, fast swimming species such as *Alepocephalus bairdii* and *Aphanopus carbo* (Gordon & Duncan 1985). Single warp rigging of a semi-balloon trawl leads to increased catches of the small anguilliform species, *Synbranchus kaupii*, compared to the traditional paired warp rigging previously used (Gordon & Bergstad 1992). These authors claim that this difference can be explained by the higher physical disturbance created by the single warp. Thus, the catchability coefficient strongly depends on the trawl design and mode of deployment.

Spatial distributions of deep-water species, such as the aggregating orange roughy *Hoplostethus atlanticus*, have been found to vary between years, likely having major impacts on trawl catchability (Clark 1996, Kirchner & McAllister 2002). Clark (1996) found that the variance of orange roughy biomass in New Zealand waters increased when high-density aggregations seemed to have formed after a closure of the fishery. Francis et al. (2003) showed clear evidence of annual variability in catchability when analysing trawl survey data for many New Zealand species. Moreover, high clustering, i.e. strongly skewed spatial distributions, leads to large variances of estimated abundances (Fréon et al. 1993).

If a method existed that provided true population density estimates, then a simple comparison with the relative trawl abundance indices would allow estimation of catchability coefficients (Somerton et al. 1999). Krieger & Sigler (1995) estimated rockfish catchability to be between 0.97 and 1.27, assuming submersible counts provided true population density estimates. However, the hypothesis that visual observations collected from remotely operated vehicles (ROVs) or submersibles might provide such unbiased estimates for all species has not been confirmed, at least for deep-water species (Trenkel et al. 2004). In particular, the restricted vertical observation field and far distance avoidance reactions are suspected to bias certain population density estimates. Thus, visual observations are also subject to 'catchability' and species-specific differences in availability are to be expected. Nevertheless, visual observations are useful as a relative measure to study catchability of bottom trawls at a given site and point in time. As ROVs do not actually catch fish, we will adopt the terminology of relative availability for the remainder of this paper. Thus, we define relative trawl availability as the ratio obtained when dividing population density estimates derived from bottom trawl data by density estimates based on visual strip transects.

In this paper, we investigate the factors that could explain overall between-species differences in relative trawl availability to a commercial deep-sea trawl and to visual observation using an ROV. The data were collected on the continental slope of the Bay of Biscay, Northeast Atlantic (see also Trenkel et al. in press). In order to assess the effect of vertical availability, as well as that of gear efficiency, 4 explanatory factors were considered for each species (or family in certain cases) (1) average individual distance off the ground, (2) average body size, (3) type of spatial distribution and (4) average reaction to the approaching ROV.

MATERIALS AND METHODS

Study sites. Three sites were surveyed during late August 2002 with the IFREMER ROV 'Victor 6000' in the Bay of Biscay. The ROV 'Victor 6000' is a deep-diving ROV (3.1 × 1.8 × 2.1 m, 4 t) equipped with 8 frontal flood lights (total 2700 W). The sites visited were Meriadzek Terrace, St Nazaire Terrace and Belle Ile Canyon (Fig. 1). At each site, the survey depth ranged from 1100 to 1500 m, with the ROV working up the slope and operating in an identical way in all 3 areas. ROV operations at each site were carried out continuously over an approximately 75 h period. In addition, scientific trawling was carried out on the 2 terraces shortly after the ROV passed.

ROV data collection. The ROV travelled at constant speed (0.25 m s⁻¹) and altitude (0.8 m) along pre-defined transect lines; the forward facing video camera recorded ahead and transmitted the images, in real time, to the IFREMER RV 'L'Atalante'. The survey design consisted of perpendicular transect strips (nominal lengths: 300 m along depth gradients and 60 m across) arranged in 6 (7 at Meriadzek Terrace) segments of roughly equal length, with total lengths of 24 (Meriadzek Terrace), 20 (St Nazaire Terrace) and 20 km (Belle Ile Canyon). Further details on sampling design can be found in Trenkel et al. (2004). Strip transect width was calibrated to 5 m, at a distance of 1.5 m ahead of the ROV, by keeping all survey parameters constant (0.8 m above ground, fixed camera settings). All fish observed within the strip transect were counted in real time.

Individuals were later identified from video replays, where possible to species level. A number of species were grouped at the family level, as visual identification to species level was judged unreliable (see Appendix 1). For example, nearly all Moridae were North Atlantic codling *Lepidion eques*, but some common mora *Mora moro* and slender codling *Halargyreus johnsonii* were also encountered, and it was often difficult to confirm which identification was correct. In this

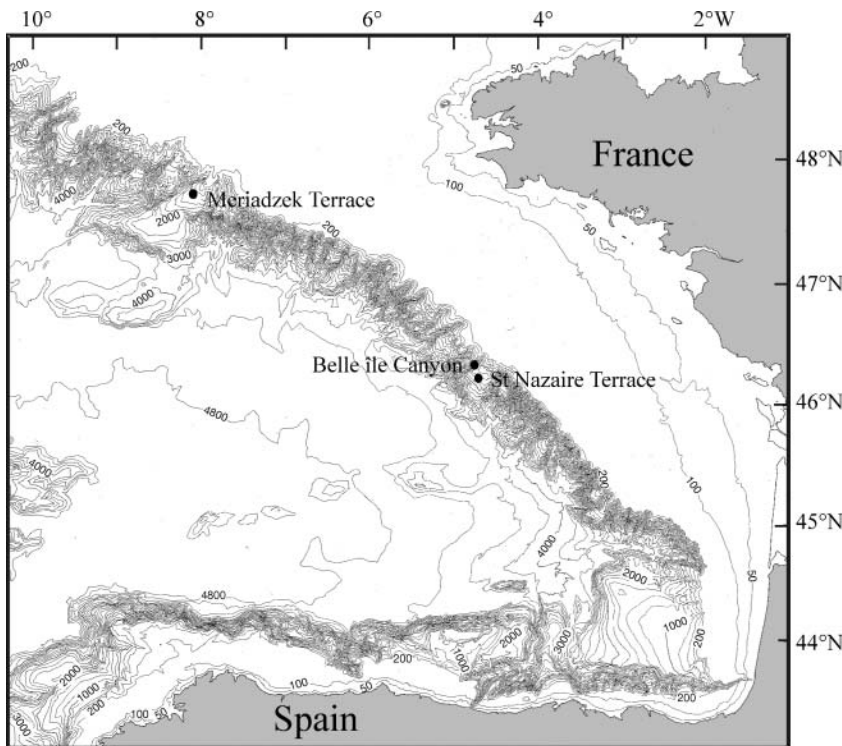


Fig. 1. Study areas: Meriadzek terrace, St Nazaire terrace and Belle Ile canyon. Isobaths are for 50, 100, 200 m and then every 200 m

study, we concentrate on species and families that were observed in sufficient numbers. We used the video replays to categorise individual distance off the ground and reaction to the ROV for the selected species.

Individual distance off the ground was classified relative to body size and the following categories were defined: sitting, touching, less than 1 body length, 1 to 3 body lengths and more than 3 body lengths. Reaction to the ROV was categorised into no reaction, escaping at a distance or reacting but allowing the ROV to catch up with the individual.

Fish size was measured using laser beams while the ROV was cruising in random directions outside the strip transect design. The size measurements should, therefore, provide a random sample from the respective populations. Four parallel red laser pointers (10 mW, 635 nm) were mounted around the main camera housing. The distance between 2 opposite lasers was 232 mm. The measurement method involved projecting the laser beams onto the target fish. The laser spots, visible on the video, gave size information both in real time and in video replay. The measurement principle is simple, but measurement is only correct for objects perpendicular to the laser beam axis. Hence, it proved impossible to measure fast moving, active fish species while coefficients of variations up to 24 % were obtained for the slow swimming Chimaeridae (M. J.

Rochet, J. F. Cadiou, V. M. Trenkel unpubl. data). For roundnose grenadier *Coryphaenoides rupestris*, total length (TL) was converted to pre-anal length (PAL) using the relationship $PAL = 0.2 TL + 1.68$ (P. Lorance unpubl. data).

Trawl data. Ten hauls with a standard commercial bottom trawl were carried out on the 2 terrace areas a few days after the ROV operation. Gear parameters for the net were: codend 60 mm, door spread 82 to 145 m, average headline height 4 to 5 m and wing spread around 20 m. Tow duration was 45 to 60 min and towing speed 3 knots. The tows were carried out at 25 m depth intervals in each of the depth strata 1200 to 1300 m (e.g. 1200, 1225, 1250, 1275 and 1300 m) and 1400 to 1500 m, following depth contours. All species in the catch were identified, counted and measured. For the roundnose grenadier, pre-anal length instead of total body length was measured.

Estimation of relative trawl availability. The visual strip transect method (Seber 1982) provided population density (D) estimates as:

$$D_{ROV} = \sum_i N_i / \sum_i A_i \quad (1)$$

where N_i is the number of a given species encountered along transect leg i and A_i is the corresponding transect leg area. To estimate the uncertainty of density estimates, a non-parametric bootstrap (1000 resamples) of transect legs was carried out.

For the bottom-trawl data, swept area was estimated using horizontal net opening (taken as half the headline length due to lack of measurements) and trawled distance (trawl duration multiplied by trawl speed). Overall population density per study site was then estimated by summing all catches and dividing by the total swept area, ignoring depth stratification.

Relative trawl availability for species r (q_r) was calculated as the ratio of the swept area-based density estimates to the ROV density estimates:

$$\hat{q}_r = \hat{D}_{trawl} / \hat{D}_{ROV} \quad (2)$$

with corresponding variance:

$$\hat{V}(\hat{q}_r) = \hat{V}[\hat{D}_{trawl}] / (\hat{D}_{ROV})^2 + (\hat{D}_{trawl})^2 \hat{V}[\hat{D}_{ROV}] / (\hat{D}_{ROV})^4 \quad (3)$$

following Kendall & Stuart (1977), as the 2 density estimates were independent. Relative availability was calculated for each terrace separately.

Creating explanatory variables. From the observations collected with the ROV, 4 explanatory variables based on observed natural and reaction behaviours were created. Due to the limited number of observations for certain species, data from all 3 study sites were combined. Hence, there was only 1 set of explanatory variables per species/family.

Distance off ground: The distribution of individual distances from the sea floor determines the average probability of a given species being observed by the ROV or caught by the trawl. The mean distance off the ground for each species was derived in the following way. The observation categories for distance off ground were translated into body lengths (bl) using the midpoints of each category, i.e. sitting = touching = 0 bl, 1 to 3 body lengths = 1.5 bl, >3 body lengths = 3 bl. An estimated distance off the ground was then calculated for each fish by multiplying this distance by the average body size of the species. Thereby, an average absolute measure of body position in the water column was obtained.

Body size: Smaller species are expected to have a lower probability of being retained by the trawl, while body size does not affect observability by the ROV. An index of species body size was derived from the average body size measured by the ROV (combining all study sites and depths). For slickheads (coded FMALEPO), rabbit fish (FMCHIMA) and false boarfish (NECYHEL), the average size was obtained from the catch data. As these species have rather large body sizes, average size based on catch data should provide a good estimate of average size in the population.

Reaction: Reactions to an approaching trawl can impact the probability of being retained by fishing gear. Although the reactions in front of the trawl were not directly observed, those observed with the ROV were used as proxies. Individuals showing no reaction were assigned a score of zero, while individuals that reacted but allowed the ROV to catch up with them got a score of +1 and those that escaped ahead of the ROV were marked -1. This classification is based on the hypothesis that individuals that react, but allow the ROV to catch up with them, are most likely to be herded by the trawl sweeps and bridles and thus have an increased chance of being caught by a bottom trawl, hence the positive score. In contrast, individuals escaping from the ROV path would reduce their chances, which justifies the negative score. No reaction is considered neutral (score zero); these species are not herded, but will be caught if in the path of the net mouth. A reaction variable was created by calculating the average score for each species.

Many small species (spiderfish, false boarfish, morid cods and Kaup's arrowtooth eel) were assigned a value of zero for the reaction variable, as real time observa-

tions showed that individuals did not essentially react to the ROV. However, no video replays with detailed characterisation of individual behaviours were carried out for these species.

Spatial distribution: The spatial distribution of a species will determine the distribution of numbers per transect line or numbers per haul and, as a consequence, the variability of abundance estimates. The baseline spatial distribution is a random distribution. Deviations from this can occur in 2 directions. At one end, individuals form clusters, and at the other, they show regular spatial patterns. Spatial distributions of ROV counts were analysed by fitting generalised linear models (McCullagh & Nelder 1989) to total numbers per transect line. To account for systematic effects of environmental variables, such as study site, depth stratum, current speed category, relative survey direction with respect to current direction and day-night differences, a step-wise procedure was used to create the best fitting model for each species. Only second order interactions were included. The models were fitted using a quasi-likelihood method with variance proportional to the mean. If the spatial distribution was random, then the counts would follow a Poisson distribution and the variance would be equal to the mean. The estimated dispersion parameter of the fitted error distribution was used as an indicator for the spatial distribution. Spatial dispersion factor values around 1 indicate a random spatial distribution. Values greater than 1 imply that the species aggregates, while those less than 1 suggest individuals tend to avoid each other, resulting in a more uniform distribution. The spatial dispersion factors were ln-transformed before use as explanatory variables, so that values were of the same scale.

Modelling relative trawl availability. For analysis purposes, the estimated relative trawl availabilities for the 2 terraces were combined by taking the average. The relationship between relative trawl availability and each of the explanatory variables was explored using generalised additive models (GAMs) (Hastie & Tibshirani 1990). Relative trawl availability was ln-transformed to normalise variances. To deal with values of zero, a small value (0.001) was added before taking logarithms. All explanatory variables were modelled by smooth functions (cubic B-splines) with fixed degrees of freedom ($df = 3$). Where the relationship appeared linear, linear models were also fitted. For this, the explanatory variables were centred in order to decorrelate intercept and slope estimates.

Trawl selectivity as a function of length is traditionally modelled by a sigmoid curve. Thus, the probability (p_i) that a species of average length l_i is retained by the gear is given by:

$$p_i = \frac{\exp(v_1 + v_2 l_i)}{1 + \exp(v_1 + v_2 l_i)} \quad (4)$$

If ROV availability is assumed to be independent of body size, then relative trawl availability might be approximated as $q_r \approx p$, ignoring any other factors. Hence, considering the ln-transformed relative trawl availability, the relationship with body size becomes:

$$\ln(q_r) \approx v_1 + v_2 l_i - \ln[1 + \exp(v_1 + v_2 l_i)] \quad (5)$$

This function, referred to as the asymptotic model, was fitted to the data using non-linear least squares estimation.

The goodness-of-fit for each single factor model was evaluated using the Akaike information criterion (AIC) (Akaike 1974), calculated as:

$$\text{AIC} = n \ln(\text{RSS}/n) + 2p \quad (6)$$

where n is the number of observations, RSS the residual sums of squares and p the number of model parameters.

RESULTS

Explanatory variables

A number of species, in particular slickheads (FMALEPO) and dogfish sharks (FMSQUAL), were primarily seen higher up in the water column (Table 1). At the other end of the spectrum, the spiny scorpionfish (TRASCRI) and spiderfish (BATPDUB) were always sitting on the seabed. The small body size of a number of species makes efficient capture by the trawl with a codend mesh of 60 mm unlikely (Table 1). In particular, spiderfish and Kaup's arrowtooth eel (SYNAKAU) are very small bodied and rarely appeared in the catch, but were seen from the ROV. Observations from the visual transect showed that morid cods (FMMORID) were dominated by North Atlantic codlings *Lepidion eques*, a relatively small species, while in the catch, the slender codling *Halargyreus johnsonii*, which is of a similar size, was dominant. For the 2 species (spiderfish and North Atlantic codling) with sufficient size data collected

Table 1. Fish species coding, body distance off sea floor and mean body size (standard deviation) as estimated from the ROV parallel laser beam measurements and from the bottom trawl catches. See Appendix 1 for full list of species names

Species	Mean distance off ground			Mean body length (ROV)		Mean body length (Catch)	
	N	body lengths	cm	N	cm	N	cm
FMALEPO	17	1.8	90				
<i>Alepocephalus bairdii</i>				2	46.7 (5.7)	856	65.6 (13.1)
BATPDUB	794	0	0	103	20.3 (3.6)	25	21.1 (4.8)
FMCHIMA	21	0.6	48				
<i>Chimaera monstrosa</i>				6	97.3 (10.6)	93	80.9 (16.7)
<i>Hydrolagus affinis</i>				1	82.8	1	30
<i>H. mirabilis</i>				3	71.7 (7.8)	1	76
CORYRUP	92	0.5	22.5	23	10.5 (1.8) ^a	1192	11.4 (3.1) ^a
HOPLATL	23	0.6	21	6	33.0 (3.5)	307	44.5 (10.4)
NECYHEL	22	0.7	18.48			5	26.4 (1.5)
FMMORID	82	0.2	6				
<i>Halargyreus johnsonii</i>						340	38.3 (3.6)
<i>Lepidion eques</i>	82	0.2 ^b		170	27.6 (4.8)	245	29.3 (3.6)
<i>Mora moro</i>				3	56.9 (12.4)	1	41
FMSCYLI	18	1.1	36.3				
<i>Galeus melastomus</i>				1	31.8		
FMSQUAL	20	1.1	110				
<i>Centroscymnus coelolepis</i>						35	101.3 (10.6)
<i>Deania calceus</i>						495	88.2 (7.6)
SYNAKAU	233	0.5 ^c	15	7	30.0 (6.4)		
TRASCRI	19	0	0	15	42.8 (7.6)	77	36.8 (4.7)

^aPre-anal length
^bFrom Uiblein et al. (2003)
^cFrom Uiblein et al. (2002)

from the ROV, mean size was calculated as being about 1 cm smaller in the *in situ* measurement than in the catch (Table 1).

In terms of reactions to the approaching ROV, 30% of roundnose grenadier (CORYRUP) and 9% of orange roughy (HOPLATL) started swimming ahead of the ROV but were finally caught up by it, while 9% and 4% respectively avoided the ROV, resulting in an average reaction variable of 0.22 and 0.05, respectively (Table 2). This included a few orange roughy individuals observed descending rapidly from above the ROV and seeking refuge near the bottom. The lowest average reaction scores were obtained for dogfish sharks (FMSQUAL: -0.39) and slickheads (FMALEPO: -0.12).

The spatial distributions of a number of species showed systematic distribution patterns (spatial dispersion factor <1 ; Table 2). Only morid cods were more or less randomly distributed with a spatial dispersion factor close to 1. Two small species, spiderfish and Kaup's arrowtooth eel, exhibited clustering (spatial dispersion factor >1).

The exploration of relationships between explanatory variables revealed some strong patterns (Fig. 2).

There seemed to be a tendency for larger species to be found further away from the sea-bottom (Fig. 2a). The spatial dispersion factor was negatively related to both body size and distance off ground (Fig. 2b,c). For exploratory purposes, the ln-transformed spatial dis-

Table 2. Reaction in front of the ROV and dispersion factor from a generalised linear model (GLM) (Poisson error with log-link) for the best fitting model for total numbers (N) per transect leg

Species	N	Reaction	Spatial dispersion factor
FMALEPO	17	-0.12	0.04
BATPDUB	597	0	2.45
CORYRUP	90	0.22	0.56
FMCHIMA	55	0.14	0.43
HOPLATL	23	0.05	0.06
FMMORID	710	0	1.39
NECYHEL	44	0	0.13
FMSCYLI	74	0.15	0.35
FMSQUAL	41	-0.39	0.14
SYNAKAU	3434	0	6.58
TRASCRI	19	0	0.1

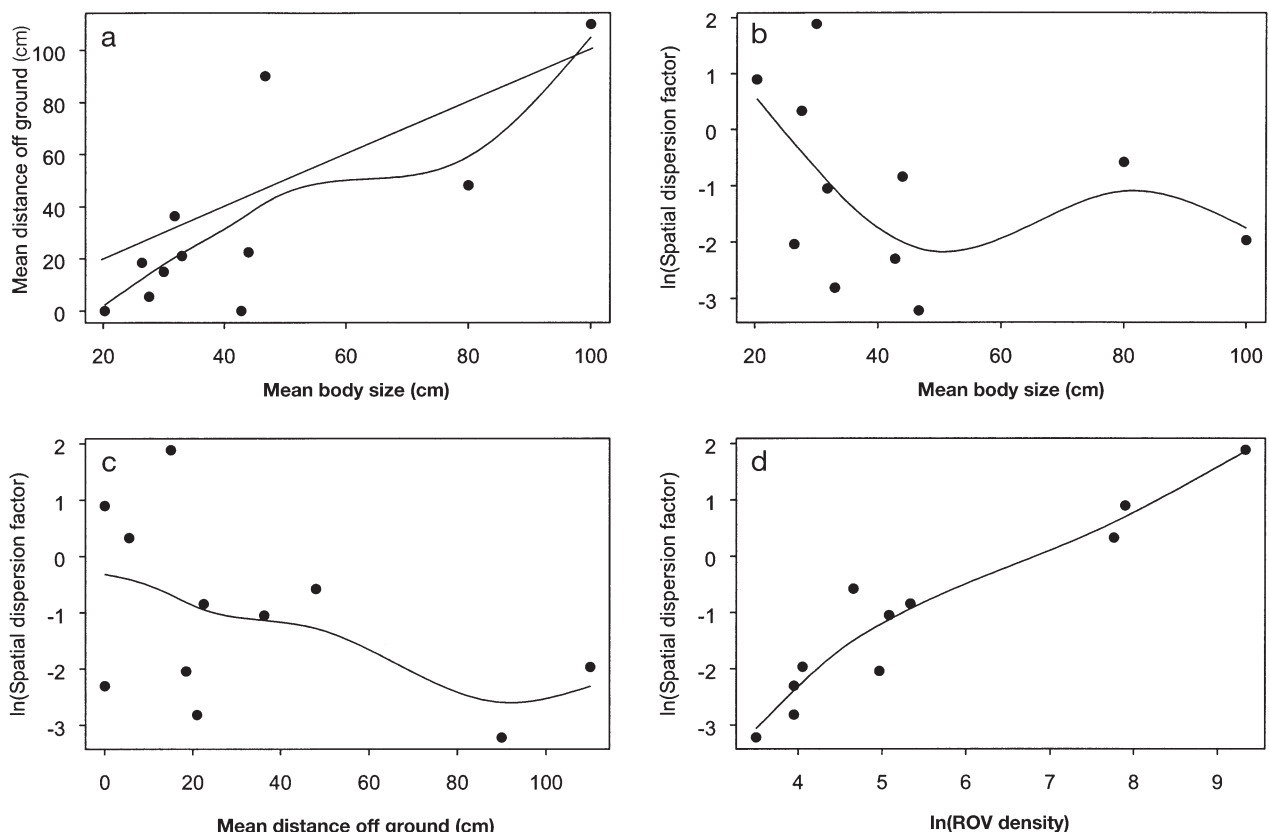


Fig. 2. Relationship between explanatory variables, (a) mean distance off ground versus mean body size; (b) spatial dispersion factor versus mean body size; (c) spatial dispersion factor versus mean distance off ground; (d) spatial dispersion factor versus ROV density. Non-parametric models were fitted using generalised additive models (GAMs)

persion factor was also regressed against the ln-transformed average ROV density estimates (Fig. 2d). The observed correlation between the 2 factors was strong (correlation coefficient = 0.95).

Explanatory factors for relative trawl availability

Relative trawl availabilities estimated for the 2 terrace sites were similar, and the largest values had the highest estimation uncertainty (Table 3). Kaup's arrowtooth eel (SYNAKAU) was never caught in the trawl, and hence, had a relative availability of zero and no estimate of standard deviation. Similarly, no false boarfish (NECYHEL) were caught on St Nazaire terrace, although a few individuals were caught on Meriadzek terrace.

The single factor model with the best fit overall was the linear model with ln(spatial dispersion factor) as explanatory variable (Table 4). This showed that aggregating species were relatively less available to the trawl. The asymptotic model of body size came second, while the linear model with distance off ground as covariable and the smooth model of reaction performed similarly to each other and somewhat worse than the first 2 models.

Table 3. Relative trawl availability (q_r) for selected species with standard deviation (SD)

Species	Meriadzek terrace		St Nazaire terrace	
	q_r	SD	q_r	SD
FMALPO	113.15	85.08	21.67	12.81
BATPDUB	0.005	0.002	0.004	0.001
FMCHIMA	0.46	0.15	0.52	0.24
CORYRUP	5.50	2.44	5.79	2.62
HOPLATL	23.21	24.18	3.44	2.58
FMMORID	0.17	0.03	0.15	0.03
NECYHEL	0.04	0.03	0	
FMSCYLI	0.02	0.01	0.03	0.02
FMSQUAL	5.34	2.52	8.76	5.97
SYNAKAU	0		0	
TRASCRI	1.16	0.68	0.839	0.51

Table 4. Goodness-of-fit for single factor models of relative trawl availability. RSS = residual sums of squares; df = degrees of freedom; AIC = Akaike information criterion

Model factor	Model	df	RSS	AIC
ln(spatial dispersion factor)	Linear	9	48.10	19.08
Body size	Asymptotic	9	67.95	22.19
Reaction	Smooth	8	75.52	23.96
Distance off ground	Linear	9	85.74	24.29

The mean distance off ground δ (δ^* when centred) was linearly related to ln-transformed relative trawl availability (Fig. 3a). The fitted relationship was $\ln(q_r) = -2.9 - 0.06\delta^*$ (SD intercept = 1.29; SD slope = 0.03; $r^2 = 0.32$). Mean species body size was also linearly related to relative trawl availability, up to body sizes of around 30 cm (Fig. 3b). The fitted selectivity curve provided a good description of the data for species with smaller body lengths but not for species of intermediate size. The estimated parameters of the selectivity function were $v_1 = 2.69$ (4.78 SD) and $v_2 = 0.39$ (0.28 SD). No simple relationship was detected between the reaction variable and relative trawl availability (Fig. 3c). The spatial dispersion factor γ (ln-transformed) showed a clear negative linear relationship (Fig. 3d). The fitted linear model for this was $\ln(q_r) = -1.06 - 1.74 \ln(\gamma)^*$ (SD intercept = 0.70; SD slope = 0.46; $r^2 = 0.62$).

DISCUSSION

Relative trawl availability

In this study, we estimated 4 factors that might affect trawl availability for a number of deep-water species using visual observations obtained with an ROV: mean distance off ground, mean body size, spatial dispersion factor and reaction to the ROV. The first 3 factors showed strong relationships with relative trawl availability. These relationships can either be due to availability to ROV observation, availability to trawl catches or to both. The fact that relative trawl availability increased as a species was found further from the sea floor is most likely due to the difference in vertical coverage between the ROV (~2.5 m) and the commercial trawl (4 to 5 m). In contrast, the effect of body length will be due to trawl selectivity. The fitted model derived from the sigmoidal selectivity model provided a good description for smaller species but not for larger species, as, in addition to body size, other factors will impact relative trawl availability.

The different explanatory variables were independent of each other, with the exception of mean body size and mean distance off ground. Mean distance off ground was obtained by converting relative distance measured in body lengths into absolute distance by multiplying with mean body size. If all species had the same average distance off the ground in body lengths, the relationship would be exactly linear. However the results (Fig. 2a) show that the relationship is somewhat nonlinear. Hence, we believe that the variable distance off ground carries some independent information.

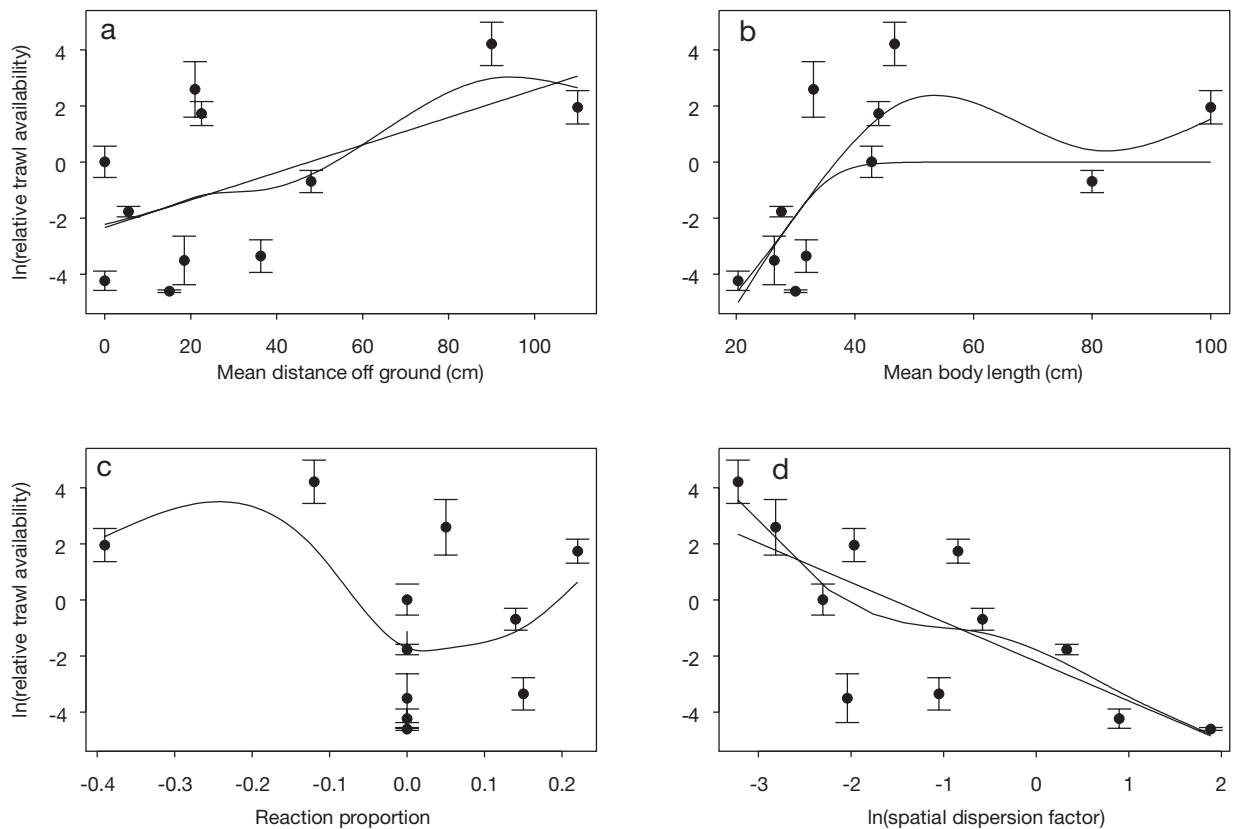


Fig. 3. Relationship between relative trawl availability (ln-scale) and explanatory variables: (a) mean distance off ground; (b) mean body length; (c) reaction; (d) spatial dispersion factor. Error bars indicate 1 SD. Non-parametric models fitted using GAMs

The best fitting single factor model was obtained when using the spatial dispersion factor as explanatory variable (ln-transformed). Conceptually, the spatial dispersion factor represents the relationship between the mean population density and its variance. As this factor was estimated using a Poisson model for which the variance is equal to the mean, the fact that the dispersion factor is a power function of the mean density [$\ln(\text{dispersion factor}) = a + b\ln(\text{density})$] indicates that the variance of the population density is a power function of its mean. This might, thus, lead to the interpretation that the relative trawl availability depends on the underlying population density, which in turn determines the spatial distribution. However, the underlying causal mechanism could also involve other non-explored factors related to species biology. In this study, smaller species had lower relative trawl catchability. They also had higher ROV densities, which implies a higher spatial dispersion factor. These 2 relationships may have contributed to the strong negative correlation between relative trawl catchability and spatial dispersion factor. On the other hand, Tuck et al. (1997) also found a log-linear relationship when comparing the ratios of trawl population density estimates of Norway lobster *Nephrops norvegicus* to video

survey-based estimates in areas with different burrow densities. In their case, the relationship cannot be due to species differences as only one species was involved.

Bottom trawl velocity was about 16 times that of the ROV surveying velocity. There is some evidence that the probability of reacting to the approaching ROV depends on surveying speed (P. Lorance & V. M. Trenkel unpubl. data). Gordon & Duncan (1985) noted that fast swimming species such as squalid sharks and Alepocephalidae have been caught in larger numbers by fast trawls with large vertical openings than by smaller, slower trawls. Hence, it cannot be excluded that, to some degree, the slow survey speed of the ROV led to an unrepresentatively low number of encounters for larger species. As a consequence, it seems important to investigate an explanatory variable which expresses swimming ability in future studies. Visual observations from a staffed submersible have been used to determine swimming speed relative to body size (Uiblein et al. 2002). Acoustic tags hidden in baits have also been employed to measure fish swimming speed (Armstrong et al. 1992). Further experiments combining these methods might allow assessment of both cruising and maximum velocity of different deep-water fish species.

The findings of this paper apply to a set of deep-water species caught by the standard commercial trawl used in the area. Hence, it seems reasonable to assume that, although some variations in trawl rigging might occur within the deep-water fishery of the European Atlantic waters, these should have small effects on trawl availability and should not change the form of its relationship with different factors, as determined in this study.

Suitability of ROV observations

The number of available observations was rather limited for most species. Due to this, and also because of problems with identification, some species were analysed at the family level. Even after grouping into families, numbers of observations were low and so results have to be interpreted with caution. A drawback of analysing some species at family level is that, while related species share certain life history traits, they might differ in terms of spatial distributions, natural behaviour or reactions. This was clear for dogfish sharks (FMSQUAL), where birdbeak dogfish *Deania calceus* individuals were observed swimming fast and well off the bottom, far ahead of the ROV, while 1 kitefin shark *Dalatias licha* swam slowly close to the bottom and did not seem to avoid the ROV.

Data for the explanatory variables were also pooled over the 3 sites. There are some topographic, hydrological and fishing intensity differences between these sites (see Trenkel et al. 2004), but we do not believe that this had any effect on our analysis. The relative catchabilities were similar on both terraces and no clear difference was seen between sites in terms of the selected explanatory variables, apart from some differences in population densities.

In this study, reactions to the ROV were used as proxies for fish reactions occurring in front of the approaching trawl. The fact that no strong relationship was found between the reaction variable and relative trawl availability might be due to other factors being more important (e.g. local habitat conditions, time of day or depth) or indicate that reactions observed in front of the ROV were not representative. Although the ROV and the trawl are rather different observation platforms, they both will have provided auditory and, to some degree, visual stimuli for the fish. The noise emitted by the different engine parts of ROV 'Victor 6000' has been measured to be particularly strong at low frequencies (20 to 800 Hz, P. Arzelies pers. comm.). This corresponds to the range of sharpest hearing of many fish species (Hawkins 1973), although no measurements are currently available for deep-water fish. Unfortunately, no measurements are available for the

noise emitted by the commercial trawl, so it is impossible to comment on the potential auditory stimulus. In addition to the noise, the floodlights of the ROV might have triggered reactions. It also seems likely that the moving trawl enhanced bioluminescence locally and, consequently, both the ROV and the trawl provided visual stimuli. However, the difference in the light spectrum of visual stimulus could be of some importance, as the vision of deep-water fish species has been found to be well adapted to the prevailing light frequencies in deeper waters (Muntz 1983). Two contrasting hypotheses can be formulated. Firstly, introducing artificial light might have blinded some species so that they did not show the same reaction towards the ROV as towards the trawl. Secondly, the lights could have triggered a reaction which was independent of light intensity or frequency and, hence, similar for the ROV and the trawl. In this study, roundnose grenadier and orange roughy were observed swimming ahead of the ROV. This behaviour can be explained by the optomotor reflex which leads to fish keep a fixed distance to a moving object, for example trawl wings or moving stripes in an experimental tank (Harden Jones 1963, Wardle 1993). The same behaviour should lead to herding by a trawl. Indeed, McClatchie et al. (2000) have reported herding of orange roughy by trawls.

CONCLUSION

Although the study was carried out for a selection of Bay of Biscay deep-water species at a particular time of the year using a particular trawl, the results should be of relevance for other situations. Firstly, the trawl used corresponded to the standard commercial deep-water trawl in operation in the Bay of Biscay. Secondly, the shape of the observed relationships between factors should apply in other cases. However, the results obtained in this study are based on observations of scattered deep-water fish, not on large aggregates as are known to appear in many areas for a certain number of deep-water species. Thus, the relationship between relative trawl availability and spatial dispersion factor or ROV population density might be expected to be different in these cases. Thirdly, the methodological approach used in this paper can be applied to any species, whether it is a deep-water or a shelf species. Thus, instead of primarily focusing on the comparison of visual density estimates obtained by ROVs, staffed submersibles or divers to catch-based density estimates in order to estimate catchability (Uzmann et al. 1977, Kulbicki & Wantiez 1990, Krieger 1992, Krieger & Sigler 1995), visual observations should also be used to provide insights into the importance of different behavioural and ecological factors.

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Appendix 1. Names of deep-water species studied and identities of species being regrouped in the analysis

Code	Species	Family	English name
FMALEPO	<i>Alepocephalus bairdii</i> <i>A. rostratus</i>	Alepocephalidae	Slickheads
BATPDUB	<i>Bathypterois dubius</i>	Ipnopidae	Spiderfish
FMCHIMA	<i>Chimaera monstrosa</i> <i>Hydrolagus affinis</i> <i>H. mirabilis</i>	Chimaeridae	Rabbit fish
CORYRUP	<i>Coryphaenoides rupestris</i>	Macrouridae	Roundnose grenadier
HOPLATL	<i>Hoplostethus atlanticus</i>	Trachichthyidae	Orange roughy
NECYHEL	<i>Neocyttus helgae</i>	Oreosomatidae	False boarfish
FMMORID	<i>Lepidion eques</i> <i>Halargyreus johnsonii</i> <i>Mora moro</i>	Moridae	Morid cods
FMSCYLI	<i>Apristurus</i> sp. <i>Galeus melastomus</i>	Scyliorhinidae	Cat sharks
FMSQUAL	<i>Centroscymnus coelolepis</i> <i>C. crepidater</i> <i>C. squamosus</i> <i>Deania calceus</i> <i>Dalatias licha</i> <i>Etmopterus princeps</i> <i>E. spinax</i> <i>Scymnodon ringens</i>	Squalidae	Dogfish sharks
SYNAKAU	<i>Synaphobranchus kaupii</i>	Synaphobranchidae	Kaup's arrowtooth eel
TRASCRI	<i>Trachyscorpia cristulata echinata</i>	Scorpaenidae	Spiny scorpionfish

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