ICES Journal of Marine Science: Journal du Conseil
May 2010, Volume 67(4): Pages 668-676
http://dx.doi.org/10.1093/icesjms/fsp277
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Estimating gear efficiency in a combined acoustic and trawl survey, with reference to the spatial distribution of demersal fish

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Abstract:

Few analyses have been performed to estimate the efficiency of trawls targeting demersal fish using the ratio of catches and acoustic densities. In summer 2006, acoustic and fishing data were collected simultaneously over 3 d by three fishing vessels equipped with identical pelagic trawls in the Bay of Biscay. Variography identified moderate spatial autocorrelation in the acoustic backscatter at a mean scale of 3 km, a scale slightly smaller than the mean haul length (3.5 km), indicating that fish horizontal availability did not influence trawl efficiency. Acoustic backscattering densities expressed as nautical area scattering coefficients (NASCs) recorded in the trawled layer were compared with equivalent NASC (ENASC) values calculated from the species composition in the trawl, fish-length structure, and available relationships between target strength and fish length. Estimates of trawl efficiency for hake-dominated trawls were computed as the slopes of the relationships ENASC = 0.008 NASC and ENASC = 0.18 $NASC^{0.31}$ for trawls made by day and night, respectively. For the whole demersal community, the relationships were ENASC = 0.022 NASC and ENASC = 0.17 $NASC^{0.33}$ for trawls made by day and night, respectively.

Keywords: availability, Bay of Biscay, catchability, generalized linear model, geostatistics, hake, vulnerability

1. Introduction

Estimating ‘trawl efficiency’ (Q), i.e. the constant of proportionality relating trawl catch per unit effort to the true fish population density, is necessary to derive absolute abundance estimates from trawl survey data (Fraser *et al.*, 2007), as well as to refine the estimation of catchability in stock assessment models (Somerton *et al.*, 1999). The choice of trawling location (depth and track) determines the actual amount of fish found within the swept area, which depends on fish ‘availability’ i.e. the abundance and spatial distribution of fish populations. The actual proportion Q of available fish hauled up on the deck is essentially determined by gear technology (net selectivity, gear rigging, fishermen skills) and fish reactions to the approaching gear (herding, escapement) (Godø, 1994).

Trawl efficiency can be estimated directly using gear comparison experiments where gear efficiency is estimated as the quotient of fish density (catch per area swept) from the fishing gear to density estimates from an other investigative tool believed to be completely efficient, such as visual or acoustic transects (Somerton *et al.*, 1999). Few analyses have been performed to estimate trawl efficiency using the ratio of trawl catches and acoustic densities (O'Driscoll *et al.*, 2002). This might be because the relationship between acoustic and bottom trawl data can be rather vague, as demonstrated for example for the North Sea demersal fish community (Mackinson *et al.*, 2005). However, a clear relationship was found between the two data types for rockfish (Krieger *et al.*, 2001) with a bottom trawl and for capelin using a midwater trawl (O'Driscoll *et al.*, 2002). For cod, the relationship varied between size classes, on a daily and seasonal basis and with the assumed fishing height of the bottom trawl (Hjellvik *et al.*, 2003; Gauthier and Rose, 2005).

Here, we analyse the data obtained during a semi-controlled combined acoustic-trawl survey to compute direct estimates of trawl efficiency for an assemblage of demersal fishes exploited by semi-pelagic trawlers. Acoustic and fishing data were collected simultaneously during a short time period (three days) by three comparable fishing vessels equipped with identical pelagic trawls, in a relatively homogeneous fishing ground of the Bay of Biscay. To account for eventual changes in fish availability during the survey, the spatio-temporal structure in the fish assemblage was first assessed by: i) monitoring the evolution of the catch composition, and ii) estimating the spatial autocorrelation in the continuous fish acoustic densities at the survey scale (tens of km). At the fishing operation scale, trawl efficiency is also known to vary according to the level of spatial structuring of fish. Schooling species often aggregate locally in high numbers, hence greatly increasing the potential for catching a large number of fish in a short time (Fréon and Misund, 1999; Gauthier and Rose, 2005). Fish spatial autocorrelation was then assessed at the trawl haul scale (km), to evaluate its potential effects on trawl efficiency estimates. Direct diel trawl efficiency estimates were computed for a mixture of demersal species dominated by hake (*Merlucius merluccius*), blue whiting (*Micromesistius poutassou*) and horse mackerel *(Trachurus trachurus)*.

2. Material and Methods

2.1. Data collection

In July 2006, acoustic and catch data were collected in the Bay of Biscay during three days by three twenty meters long chartered fishing vessels (F/V “Davidson”, F/V “Hebeilan” and F/V “Océanie”) equipped with identical semi-pelagic trawls (4 doors, headline: 54 m, foot rope: 50 m). The survey was conducted in a 30 x 12 nautical miles (n.mi.; 1 n.mi. = 1852 m) flat muddy area of constant bathymetry (100 m depth), known to be a major hake fishing ground. The three vessels, sailing side by side at about 200m from one another, simultaneously sampled twenty-eight stations positioned along five pseudo-linear transects (one transect per diel period, Figure 1a), yielding a total of 84 hauls.. A subset of 72 hauls for which acoustic recordings were available were selected for further analysis. These hauls were performed at 24 trawl stations (12 daytime and 12 night-time stations). Every hour between 0:00 and 20:00, all three vessels towed a trawl, with a net opening of 40 (horizontal) by 20 m (vertical), approximately 0.5 m above the seabed. Trawls were 30 minutes long and covered 3.5 km with a mean vessel speed of 4 knots. Catches were sorted and all or a subsample was measured and weighted. In the case of a very large catch, total weight was estimated visually. One vessel (F/V Davidson) was equipped with a portable Simrad ER60 echosounder connected to a 11° beam angle, spherical split-beam transducer, operating vertically at the 70 kHz frequency. The transducer was operated at a 0.512 ms pulse length in a paravane towed between 3 and 5 knots about 2 m below the sea surface on the port side of the vessel during and between fishing stations. *In situ* on-axis calibration of the echosounder was performed before the cruise using standard methodology (Foote, 1982). Acoustic data were replayed with the Movies+ software (Weill *et al.*, 1993) and archived in the international hydro-acoustic data format (HAC) (Simard *et al.*, 1997) at a -80 dB threshold. The paravane had to be retrieved when the trawl was hauled onboard, introducing gaps in the linear transects (Figure 1a).

2.2. Acoustic data treatment

Volume backscattering coefficients (s_V) (MacLennan *et al.*, 2002) larger than –60 dB were allocated to fish and integrated with Movies+ software over 80 standard bottom depth channels of thickness 0.5 m from 0.5 to and 40.5 m above the bottom, and over 36 depth channels of tickness 2 m from the altitude of 40.5 m to the sea surface. Fish Nautical Area Scattering Coefficient (NASC) (MacLennan *et al.*, 2002) per depth channels were averaged over 20 pings , creating 0.02 n.m. (40 m) long elementary sampling units (ESUs) at a mean speed of 4 knots. Fish NASC per depth channels were then summed over the depth range sampled by the pelagic trawl, considered to extent from 0.5 to 40.5 m off the bottom. This depth stratum will be referred to as ‘trawled layer’, even when no trawl haul was performed, i.e. between trawling stations. Although the vertical trawl opening was 20 m, the effective fishing height of the trawl was in fact expected to be higher, as fish have been recorded to dive down in response to vessel noise (Hjellvik *et al.*, 2003). As the majority of bottom fish backscatters were detected between 0 to 20 m above the seafloor (Figure 1b) the actual limit was not important. Total nautical area scattering coefficient values, $NASC_{tot}(t)$ recorded onboard F/V Davidson during trawl station *t* were then calculated as the average NASC values in the trawled layer in ESUs located along the haul tracks.

2.3. Catch data treatment

To transform catch data to equivalent acoustic data, Estimated Nautical Area Scattering Coefficients (Simmonds and MacLennan, 2005), $ENASC_s(t,v)$, were computed for each of the main species *s,* caught at station *t* by vessel *v* as for Mackinson *et al.* (2005):

$$ENASC_s(t,v)=\frac{4\pi \hat{N}_s(t,v)\sigma_{bs-s}}{A}, \qquad (1)$$

where: *A* is the area swept during a trawl haul (in squared nautical miles), $\hat{N}_s$ is the (estimated) catch in numbers of species *s* at station *t* by vessel *v*, and σ_{bs-s} is the theoretical backscattering cross-section (MacLennan *et al.*, 2002) of species *s*. *A* was estimated based on trawl geometry data recorded on vessels Hebeilan and Océanie, using Scanmar systems. σ_{bs-s} values were computed as $\sigma_{bs-s}=10^{TS/10}$, where *TS* are theoretical target strength values from the literature presented in Table 1. As species specific TS-length relationships were not available in the literature at the 70 kHz frequency, we used equations of closely related species at available frequencies (38kHz) (‘reference’ species in Table 1).

$ENASC_s(t,v)$ of all species were summed per haul to compute total ENASC values, $ENASC_{tot}(t,v)$, for trawl station *t* and vessel *v*.

2.4. Diel variations

Diel differences in the fish vertical distribution were assessed by computing mean vertical profiles of fish acoustic densities for each linear transect.

The following procedure was then applied to remove the influence of vertical diel migrations from fish log-transformed acoustic densities recorded in the trawled layer. Let us denote *NASC(i)* the mean NASC value recorded in the trawled layer in ESU *i*. *NASC(i)* values were ln(x+1) transformed to approach a normal distribution.

The diel trend, *m(t),* in the fish log-transformed *NASC(i)* values was modelled as a cosine function of time *t* (Rivoirard and Wieland, 2001):

$$\ln\left(NASC(i)+1\right)=m(t)+\varepsilon(i)=a\cos\left(2\pi\frac{t-12}{24}\right)+b+R(i) \qquad (2)$$

where *a* and *b* are the model coefficients. Residual fish log-transformed acoustic densities without diel trends, *R*, were used in further spatial analyses. These analyses were performed on data collected during and between trawl hauls for all transects, except those conducted during day 1 and night 1, for which data were too scarce. The spatial structure of diel-detrended fish acoustic densities was studied over survey portions showing the highest spatial continuity, i.e. along each linear transect.

2.5. Fish horizontal distribution

Ideally, trawl efficiency estimates should be computed based on trawl samples of fish communities, comprised of more or less randomly distributed fish density, to avoid mixing spatial variance (i.e. variance originating from fish availability) with the intrinsic variability of the catching process (originating from fish reaction to the gear). Based on the continuous acoustic data, we assessed the dominant spatial scales at which species densities were varying and compared them to the sampling scales. At the survey scale, we first checked that the mean length of the sampling units (trawl hauls of 3.5 km) was larger than the mean width of the unit objects (fish patches), to verify whether fish patches were on average, effectively sampled (Dungan *et al.*, 2002). Secondly, we checked that fish distributions along haul tracks were random, to ensure that trawl efficiency estimates were computed based on homogeneous fish communities.

Survey scale. Diel-detrended, log-transformed, fish acoustic densities, *R,* integrated in ESUs of length 20 pings were first averaged within larger units of 0.1 nautical miles (185.2 m) to adapt the spatial resolution (or 'support') of acoustic data to the extent of the survey area (30 x 12 nautical miles). Experimental variograms of geolocalised *R* values (Equation 2)*,* were first computed for each linear transect. The basic multiple of lag distance is the new support size (0.1 nautical miles). Models composed of spherical functions with nugget term were fitted by eye to the experimental variograms of each transect. The sills were determined to ensure that the sample variance and the model dispersion variance were close to each other (Rivoirard *et al.*, 2000). Variogram models were fitted over distance lags with significant number of pairs (generally up to half the maximum sample extent). Mean dimensions of aggregative patterns were estimated by the variogram model range, i.e. the distance beyond which the correlation between point values vanishes (Petitgas, 2001). The amount of spatial variance in the data was estimated by computing the ratio: spherical component sill / (nugget sill + spherical component sill) for each transect.

Trawl haul scale. To study the fish spatial structure at the haul scale (40 m- 4 km), empirical variograms of ln(x+1) transformed, diel-detrended, NASC values recorded in 40 m long ESUs were computed and scaled to the data variance (normalisation) for each trawl station.

Normalised variograms values were averaged within each variogram distance class for all day and night-time stations, as well as for day/night stations dominated by hake. Resulting mean daytime and night-time normalised variograms were analysed to assess the spatial structure of the global demersal fish community, as well as the fish assemblage dominated by hake.

2.6. Trawl efficiency estimates

The relationship between catch, C (number of fish), and true fish density, N (nb. of fish per m^3), can be expressed as:

$$C = qEN^b \,, \tag{3}$$

where q is catchability, E is (nominal) fishing effort represented in our case by the trawled volume (in m^3) and b is a parameter. If b is 1, the relationship between catches and density is linear and for b<1 non linear.

We assume that the $NASC_{tot}(t)$ value recorded onboard F/V Davidson during station t is a reasonable estimate of the true density of demersal fish encountered along the haul track by all three vessels. So, replacing N in Equation 3 by $NASCtot(t)$, we obtain the relationship:

$$ENASCtot(t,v) = q(v)E(t,v)\left[NASCtot(t)\right]^b = Q(v)\left[NASCtot(t)\right]^b \tag{4}$$

where $Q(v)$ is the trawl efficiency, defined as the proportion of animals within the swept volume which are captured by the trawl of vessel v (Somerton *et al.*, 1999).

$Q(v)$ and b were estimated by fitting generalised linear models of the form:

$$\mathrm{g}\left(\mathrm{E}\left[\mathrm{ENASC_{tot}(t,v)}\right]\right) = \mathrm{b}\log\left(\mathrm{NASC_{tot}(t)}\right) + \log\left(\mathrm{Q(v)}\right) \tag{5}$$

where $g()$ is the link function.

The choice of the distribution and link function ($g()$) was made to ensure no violation of GLM assumptions (homoscedasticity, normality of residuals). Daytime and night-time hauls were analysed separately. To test for differences in gear efficiency between species, diel trawl efficiency coefficients were estimated for subsets of trawl stations where the proportion in weight of one species was higher than 50% in at least one of the three parallel trawl hauls. Trawl efficiency coefficients were also computed for all stations combined (day and night), as an estimate of the mean trawl efficiency of the demersal fish community in the area. Systematic vessel effect was also tested.

Statistical analyses were implemented using the R statistical environment (R Development Core Team, 2009), supplemented with the package ‘geoR’ (Ribeiro and Diggle, 2001) for geostatistical computations.

3. Results

3.1. Species composition of trawl hauls

Overall trawl catches were dominated in weight by hake (38%), horse mackerel (33%) and blue whiting (23%). Hake catches were fairly constant throughout the survey (Figure 2). However, dramatic diel variations were observed in the size distribution of this species. Hake mean size was about 30 cm during daytime and a second length mode appeared at night, with catches of smaller fish of mean length 20 cm (Mahévas *et al.*, 2008). High horse mackerel catches were recorded during day 2 (Figure 2), at the same time dense schools were detected by acoustics (results not shown).

The hake proportion in weight in the catches was higher than 50% in the catch of at least one vessel for 5 trawl stations (14 hauls, one vessel skipped one station) during daytime and 6 stations (18 hauls) during night-time. The mean species compositions in weight of hake dominated hauls were: hake: 47% day, 72% night; horse mackerel: 27% day, 6% night; blue whiting: 18% day, 16% night. The horse mackerel proportion in weight in catches was higher than 50% in at least one trawl haul for 8 trawl stations (24 hauls) during daytime. The mean species composition of horse mackerel dominated hauls was: hake: 18%, horse mackerel: 69% and blue whiting: 9%.

3.2. Diel variations

Diel vertical variations were observed in the acoustic data throughout the survey. During the day, fishes were concentrated close to the seafloor and their total abundance fluctuated from one day to another. (broken lines in Figure 1b). At night, fishes were distributed closer to the surface in scattered layers (continuous lines in Figure 1b) and displayed less inter-day abundance variations. At the survey scale, a significant diel trend ($R^2 = 0.3$, F-test p-value: $< 2.2e-16$) was found in the data (Figure 3) and removed before further spatial analyses.

3.3. Fish horizontal distribution

Survey scale. Variograms of diel-detrended log-transformed fish acoustic densities revealed the presence of spatial autocorrelation in the fish distribution for all transects (Figure 4). No significant difference was found in the spatial correlation range or magnitude between day and night, according to the spreading of confidence intervals around diel means, under normality assumption (Table 2). The spatial structure in the data was moderate, the spatial variance accounting for 48% of the total variance on average (SD 11%) (Table 2). The mean range of spatial patches was 2.7 km (SD 1.9 km) (Table 2).

The variogram sum of sills were systematically higher during the day than at night, meaning that the total variability in fish density along any transect line was higher during the day (Figure 4).

The mean range of fish patches was 2.7 km, slightly smaller than the mean length of a trawl haul (3.5 km). In other words, the sampled object unit was smaller than the sampling unit, so we could assume that our observation scale was appropriate to reasonably capture the fish spatial structure.

Trawl haul scale. Day and night-time mean empirical variograms were generally flat and for hake dominated hauls showed no sign of spatial structure in the fish acoustic densities (Figure 5). The fact that no spatial correlation was found at the haul scale confirms that trawl efficiency estimates should not be biased by fish availability.

3.4. Trawl efficiency estimates

After controlling for fish availability effects, we computed trawl efficiency estimates by modelling ENASC as a function of NASC values.

In the case of daytime or night-time hake-dominated hauls and overall night-time hauls, the best-fitting model was a generalised linear model assuming a gamma distribution and a log link function. No suitable model was found for horse-mackerel dominated hauls. In the case of overall daytime hauls, the best-fit model was a log-linear model assuming a Gaussian distribution for residuals.

The average trawl efficiency coefficient of daytime hake-dominated hauls was 0.008 (50% deviance explained; Figure 6a, Table 3). The estimated exponent *b* was 0.91 and not significantly different from 1 (Table 3). At night-time, the average trawl efficiency of hake-dominated hauls was higher than during daytime: 0.18 (23% deviance explained; Figure 6b,

Table 3). The exponent estimate was 0.31 (Table 3), thus *b* was significantly different from 1. Trawl efficiency coefficients did not vary systematically between fishing vessels in the case of hake-dominated hauls (results not shown).

All daytime and night-time trawl hauls, whatever the species composition, were considered in the last analysis. A total of 8 daytime hauls out of 38 were comprised of very large amounts of horse mackerel, whose total weight was imprecisely estimated visually. Hence, we considered that *ENASCtot* values computed for those hauls were dubious and excluded them from the analysis. The average daytime trawl efficiency estimate of the demersal community for pelagic trawls was 0.022 (14% variance explained; Figure 6c, Table 3) with an exponent of 0.68 (Table 3) which was not significantly different from 1. At night, estimations differed markedly from those during the day, with higher trawl efficiency: 0.17 (25% deviance explained; Table 3) and an exponent of 0.33 (Table 3) which is significantly different from 1. Again, trawl efficiency did not vary systematically between fishing vessels in the case of the whole demersal community.

4. Discussion

This study demonstrates that catch efficiency estimates of pelagic trawls targeting demersal species can be computed at a coarse scale (tens of km), by combining fishing and acoustic data, provided that fish density is: i) distributed randomly along haul tracks, and ii) positioned slightly above the bottom. Night-time exponents and trawl efficiency estimate markedly differed from those estimated for daytime. Observed discrepancies in trawl efficiency were probably due to the presence of more, mainly smaller (20 cm length class) hake within the trawl zone, not observed in catches during daytime (Mahévas *et al.*, 2008). Besides differences in avoidance reactions due to different light levels or fish diel activity (accounted for by the trawl efficiency coefficient), estimates of $b<1$ in fact represent a net reduction of the amount of hake biomass available to the trawl, which could be explained by a higher trawl selectivity for the smaller hake present at night-time.

Spatial information in acoustic data has been used in the past to increase the precision and accuracy of trawl-based abundance estimates (Bez *et al.*, 2007). The originality of our approach resides in the quantitative study of fish spatial distribution prior to trawl efficiency computations, to control for fish availably effects. Hake was caught in relatively constant proportions during all hauls and appeared to be widely and randomly distributed in the area. This is corroborated by small-scale video observations conducted in an area close to the current study (Trenkel *et al.*, 2007). We therefore assume that the spatial distribution and trawl efficiency coefficient of this species was reasonably well assessed with our survey design. The comparison with other trawl efficiency coefficients from the literature is not straightforward, as fishing efficiency is expected to drastically vary according to, namely, species, size, geographic area, season and fishing gears. Our trawl efficiency estimate of hake dominated daytime trawls is one order of magnitude smaller than those calculated based on survey trawl catches for hake in the Celtic Sea (Trenkel and Skaug, 2005) and in the North Sea (Fraser *et al.*, 2007). This difference might in part be explained by differences in fishing gear and protocol, as previous studies used Grande Ouverture Verticale bottom trawls. The GOV provides access to fish positioned very close to the bottom (difference in fish availability) and also prevents fish escaping below the footrope (difference in trawl efficiency), compared to our pelagic trawl which was set at about 0.5 m above the bottom. Moreover, the trawl haul composition was relatively variable and diverse in our data. This could have been due to mobile schools of species such as horse mackerel or blue whiting moving throughout the area. As the accurate allocation of fish acoustic energy to each of the species found in the catches was not possible, our trawl efficiency estimates represent the vulnerability of a mixture of demersal species towards a pelagic trawl. Conducting a large number of hauls is hence required to maximize the odds of getting a sufficient number of haul catches dominated by a particular species, to allow for the computation of species specific trawl efficiency estimates. This multispecies environment and the absence of species and frequency specific TS-length equations to compute ENASC values (Table 1) were limiting factors in our work, compared to studies focusing on single well known species, such as cod (Hjellvik *et al.*, 2003), rockfish (Gauthier and Rose, 2005) or capelin (O'Driscoll *et al.*, 2002). Within the range of acoustic frequencies commonly used in fisheries acoustics (12 – 200 kHz), fish species which possess air-filled swim bladders have very similar multifrequency acoustic signatures due to the dominance in backscattering of the swim bladder (SIMFAMI, 2005). We therefore assume that the use of TS-length equations established at the 38 kHz frequency (or at the 29 kHz frequency in the case of blue whiting, Table 1) did not introduce a major bias in the computations of ENASC estimates derived from acoustic backscatters recorded at the 70 kHz frequency. Dealing with the lack of species-specific TS-length relationships, Foote's (1987) equation is considered a fair description of the target strength of clupeoid-like fish such as sardine (Simmonds and MacLennan, 2005). On the other hand, no species-specific TS-length equations were available for physoclistous fish such as hake and horse mackerel. The equations we used were established for species of the same families in other locations (Table 1). Their b_{20} parameter being close to those proposed by Foote (1987) for physoclistous fish, we assume that their use did not introduce a large bias in the ENASC computations, compared to the results that would have been obtained with the generic equation. However, establishing specific TS-length equations for these species is a priority to improve the precision of fishing efficiency estimates in the study area. Another question that arises when comparing acoustic densities and trawl catches of demersal fishes is whether the trawls and the echosounder actually measure the same thing. In our case, the footrope of the semi-pelagic net worked 0.5 m above the bottom, i.e. above the acoustic dead zone extending 0.5 m above seabed at a 0.512 ms pulse length. A 0.5 m bottom offset was used for the echo-integration of fish backscatters to exclude echoes from the dead zone and ensure that fish acoustic densities and catches were measured in the same depth range. However, besides classical avoidance reactions accounted for by the estimated trawl efficiency coefficients (i.e. swimming down the footrope or up the headrope), some demersal fish located under the footrope might have reacted to the disturbance caused by the trawl by swimming up into the net. The vertical distribution of *M. merluccius* being poorly documented, one cannot rule out the possibility that *ENASC* values might have been biased upward, due to such vertical avoidance reactions. However a combined acoustic/trawl study conducted in Namibia showed that *Merluccius paradoxus* of size similar to those of *M. merluccius* caught during daytime in our study, were generally more abundant 5-50 m off the bottom, whereas larger *Merluccius capensis* dominated just over the seabed (Huse *et al.*, 1998). If such a diurnal size at-depth distribution also prevails for *M. merluccius*, the abundance of 30 cm hake located within the 0.5 m unsampled layer would have been low during daytime. In this case, one could assume that the bias introduced in *ENASC* values by the vertical avoidance of this fraction of unsampled hake into the trawl was small.

Besides very localised horse mackerel schools, significant spatial correlation was found in the demersal fish spatial distribution at the scale of 3 km. This aggregation scale corresponds to school clusters, previously evidenced in the case of Pacific hake (*Merluccius productus*) (Swartzman, 1997).

Estimated trawl efficiency estimates varied between species and diel periods and one can assume that they would potentially change from one fishing ground or season to another. Such gear efficiency coefficients could be routinely computed based on trawl survey data or catches and acoustic data recorded onboard commercial vessels equipped with calibrated echosounders and automatic data loggers. This would provide useful insights into the larger scale variability of the catching process, as well as catchability estimates to be used in stock assessment in the absence of long time series of fisheries statistics (Somerton *et al.*, 1999).

Acknowledgement

This study received financial support from the European funding scheme IFOP. The authors thank the crews of F.V. Davidson, Hebeilan and Océanie for their assistance during the CHAPAUV survey. We thank our colleagues C. d'Ardeville, B. Mesnil, P. Lorance, L. Pennors, and A. Péronnet for assisting with the onboard data collection during the CHAPAUV survey. The referees and the editor are thanked for thoughtful comments, which greatly improved the manuscript.

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Tables

Table 1. Values used to compute theoretical TS of sampled species, as a function of fish length L. TS = 20log(L)+b_{20}.

Sampled species	Reference species	b_{20}	Frequency (kHz)	Reference
Hake (*Merluccius merluccius)*	*Merluccius gayi*	-68.5	38	Lillo *et al.*, 1996
Blue whiting (*Micromesistius poutassou)*	*Micromesistius poutassou*	-71.9	29	Robinson, 1982
Sardine (*Sardina pilchardus)*	*physostome*	-71.9	38	Foote, 1987
Horse mackerel (*Trachurus trachurus)*	*Trachurus trachurus capensis*	-66.8	38	Barange *et al.*, 1996
Mackerel (*Scomber scombrus)*	*Scomber scombrus*	-84.9	38	Edwards *et al.*, 1984

Table 2. Variogram models of diel-detrended log-transformed fish acoustic densities for each transect (D2 = day 2; N2 = night 2; D3 = day 3; N3 = night 3; D4 = day 4). . The percentage of spatial variance is the ratio Sill / (Sill+Nugget).

Transect	**Variogram model**	**Nugget**	**Sill**	**Range (km)**	**Perc. spatial variance**
D2	spherical	0.69	0.39	5.6	36%
N2	spherical	0.19	0.34	2.2	64%
D3	spherical	0.5	0.61	3.3	55%
N3	spherical	0.26	0.2	1.1	43%
D4	spherical	0.46	0.35	1.1	43%
Day average (SD)		0.55 (0.12)	0.45 (0.14)	3.3 (2.2)	45% (10%)
Night average (SD)		0.23 (0.05)	0.27 (0.10)	1.7 (0.8)	54% (14%)
Overall average (SD)		0.42 (0.20)	0.38 (0.15)	2.7 (1.9)	48% (11%)

Table 3. Estimates of trawl efficiency coefficients (Q) and exponents (b) from the models relating Equivalent NASC derived from trawl catches to observed NASC, along with the percentage of deviance explained by the model, standard deviations in brackets

Species	4.1.1. Error distribution	4.1.2. Diel period	**Q estimate**	**b estimate**	**% deviance explained**
Hake	Gamma	Day	0.008 (0.026)	0.91 (0.28)	50%
Hake	Gamma	Night	0.180 (0.045)	0.31 (0.14)	23%
All species	Normal	Day	0.022 (0.051)	0.68 (0.28)	14%
All species	Gamma	Night	0.170 (0.065)	0.33 (0.1)	25%

Figures

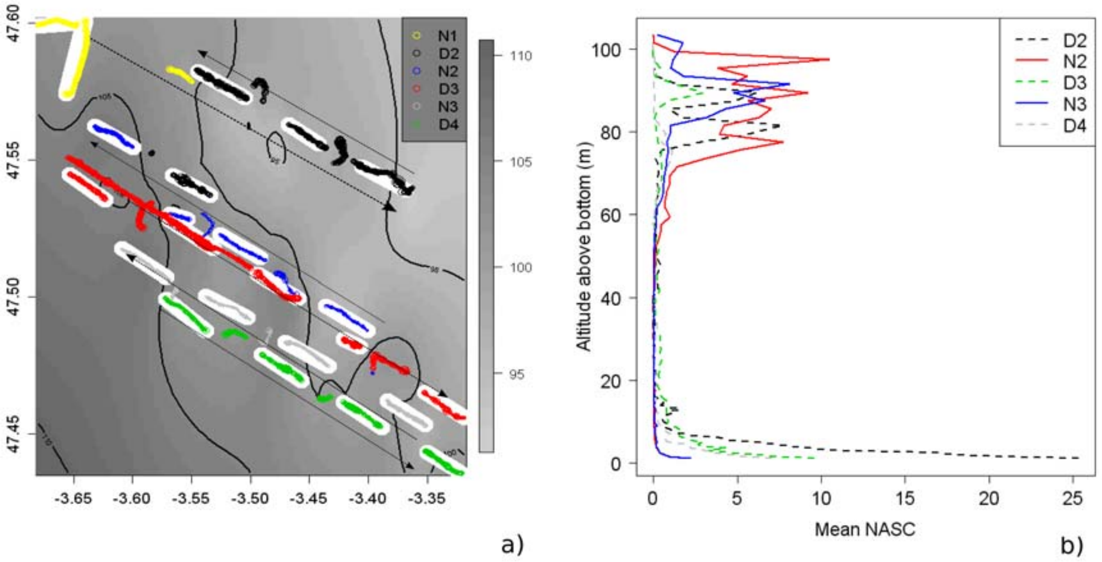

Figure 1. a) Kriged bottom depths (shades of grey) and trawled areas (in white) in the study area with log-transformed fish Nautical Area Scattering Coefficients per successive diel periods (transects). Successive transects (D2 = day 2; N2 = night 2; D3 = day 3; N3 = night 3; D4 = day 4) and vessels' headings are represented with different colours and grey arrows, respectively. The three vessels sailed side by side at about 200m from one another along the transects. b) Mean vertical profiles of fish acoustic densities (NASC in m².NM^{-2}) recorded along successive transects represented with different colours. Broken lines: daytime, straight lines: night-time.

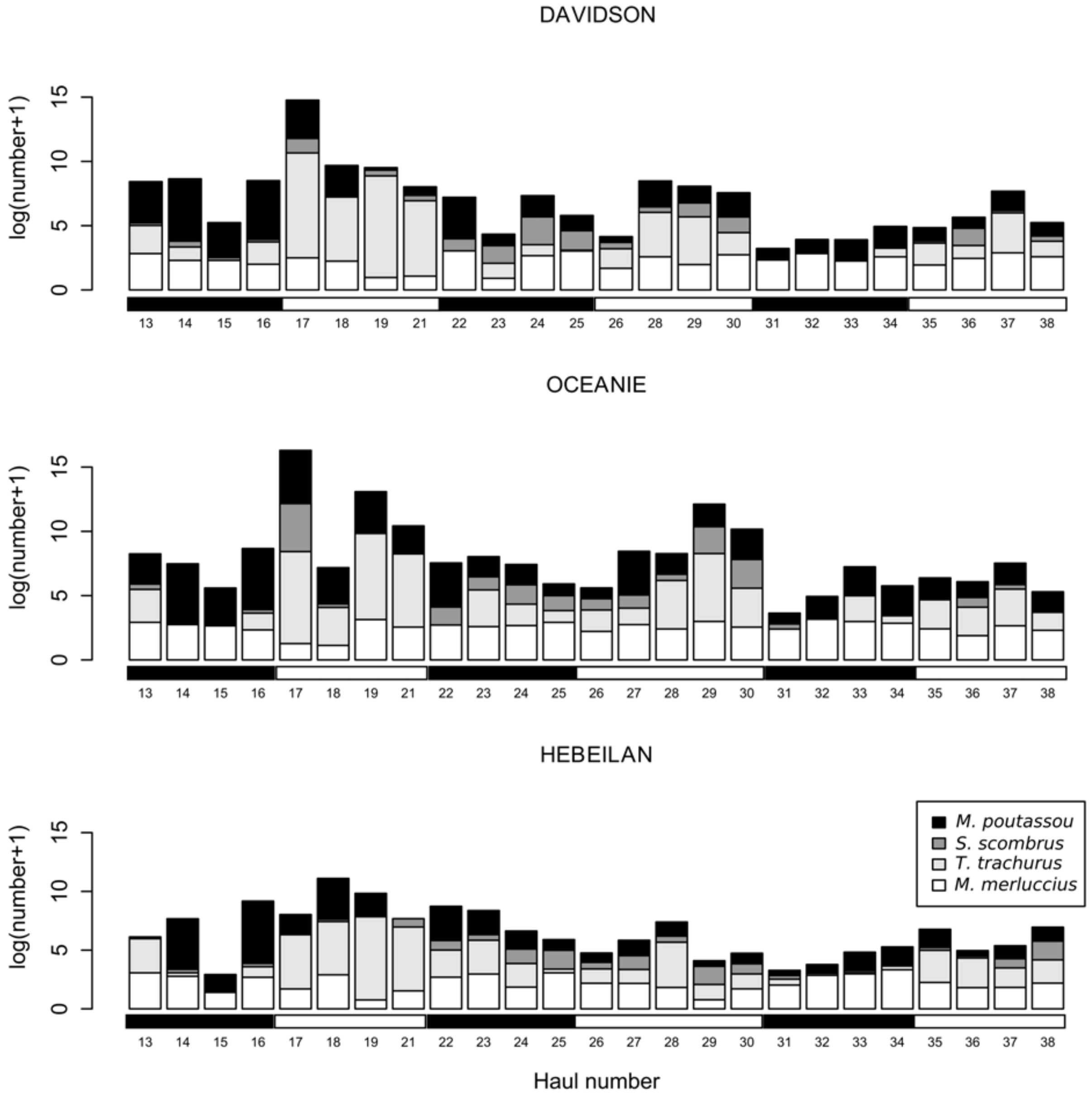

Figure 2. Species composition per trawl station for the different fishing vessels. For species names refer to Table 1. Diel periods are represented by a coloured bar above station numbers: black: night-time, white: daytime.

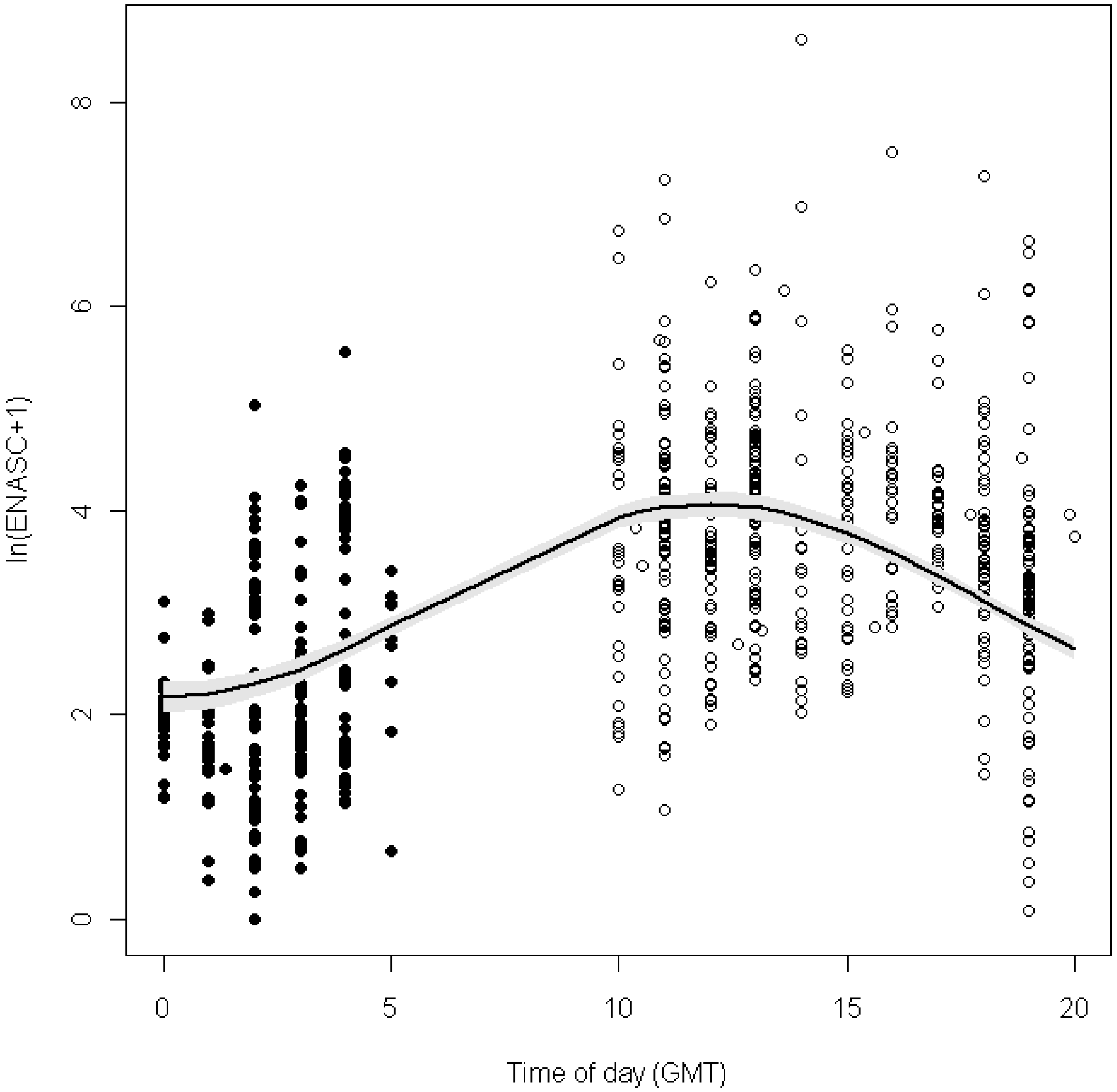

Figure 3. Fit of the diel trend model (black line), with confidence intervals (grey area), overlaid on log-transformed daytime(open dot) and night-time (solid dot) fish acoustic densities.

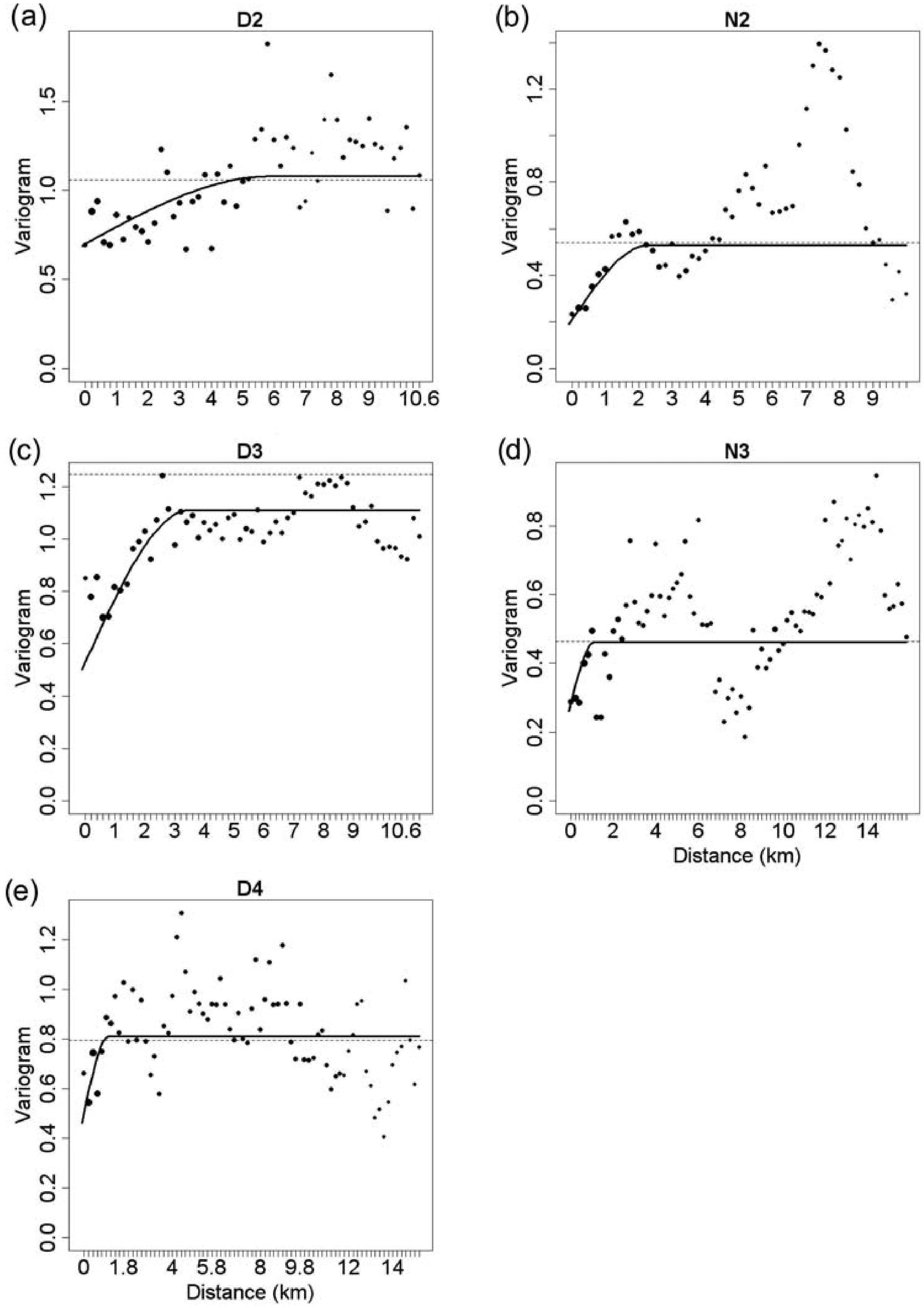

Figure 4. Data variance (horizontal broken line), experimental variogram (solid dots, diameter

proportional to the number of pairs in distance lags) and variogram model (continuous lines) of log-transformed, diel-detrended fish acoustic densities, for transects: a) D2 = day 2, b) N2 = night 2, c) D3 = day 3, d) N3 = night 3, and e) D4 = day 4. Distance lags are 0.1 nautical miles (0.1825 km).

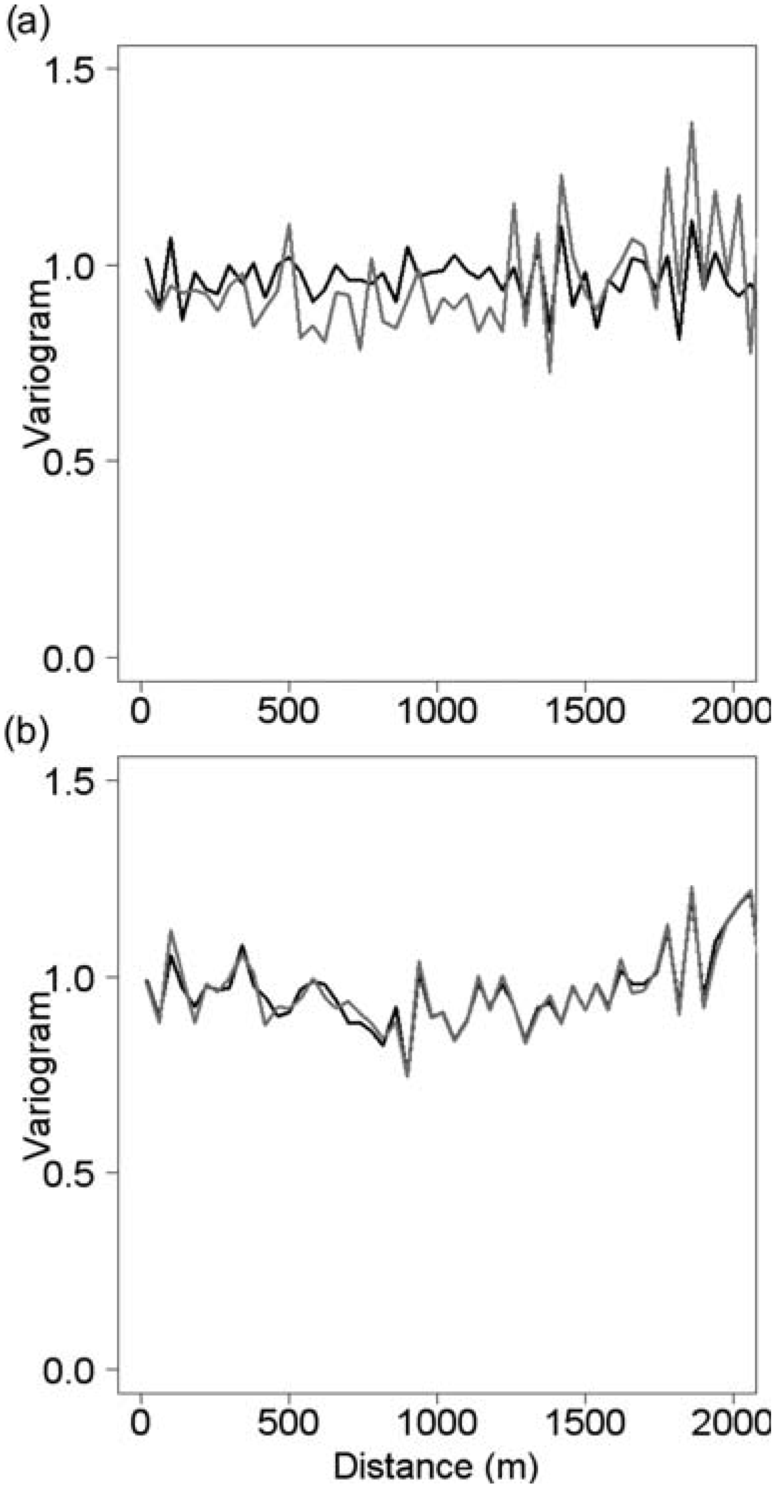

Figure 5. Mean normalised variograms of log-transformed, diel-detrended fish acoustic densities computed for: a)all daytime trawl hauls (black line) and hake-dominated day hauls (grey line), and b) all night-time trawl hauls (black line) and hake-dominated night hauls (grey line). Distance lags are the acoustic elementary sampling units (40 m).

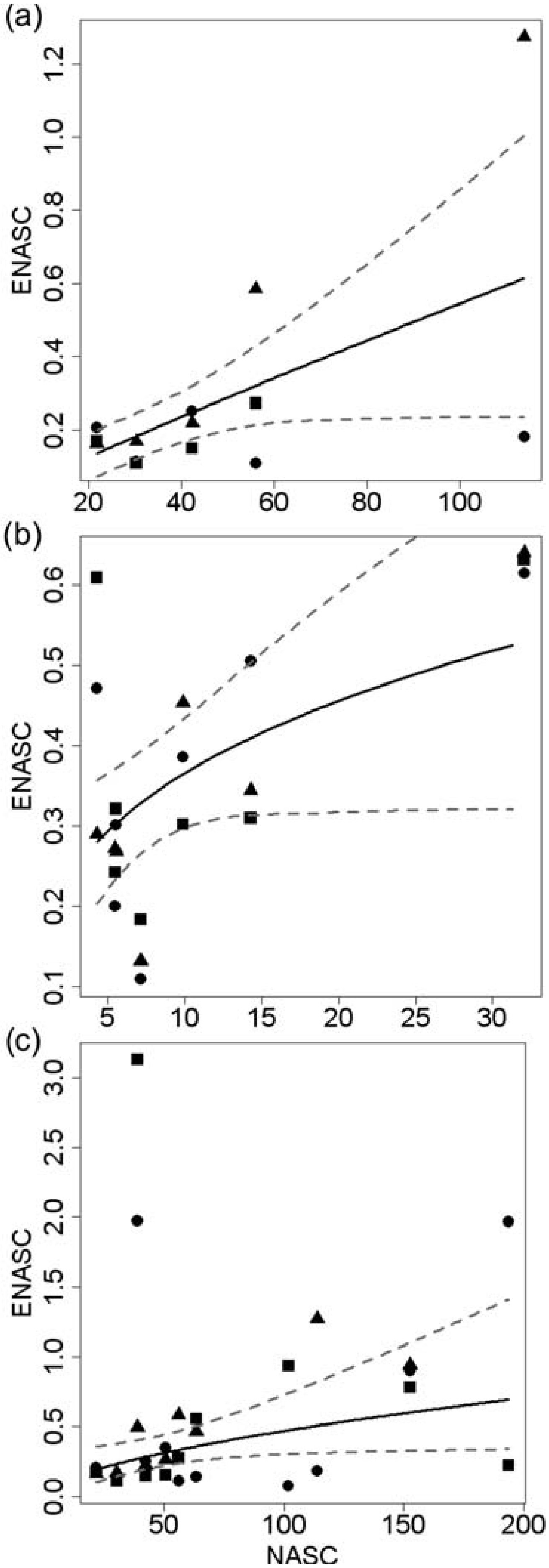
(a)
ENASC
0.2
0.4
0.6
0.8
1.0
1.2
20
40
60
80
100
(b)
ENASC
0.1
0.2
0.3
0.4
0.5
0.6
5
10
15
20
25
30
(c)
ENASC
0.0
0.5
1.0
1.5
2.0
2.5
3.0
50
100
150
200
NASC

Figure 6. Relationship between total ENASCs per haul and vessel (circles: Davidson, triangles: Océanie, crosses: Hebeilan) and total NASCs per haul recorded on F/V Davidson (straight line) with confidence intervals (broken lines), computed in the case of: a) hake dominated daytime hauls, b) hake dominated night-time hauls, and c) all daytime hauls.