

Diel variation in trawl catchability: is it as clear as day and night?

Jill M. Casey and Ransom A. Myers

Abstract: Diel variation in the catchability of over 50 species was examined using research vessel surveys conducted off the coast of Newfoundland and Labrador from 1972 to 1995. Catchability during the day and night was estimated for several seasons and geographic areas in the Northwest Atlantic using two generalized linear models. In general, species exhibiting diel vertical migrations, such as redfish (*Sebastes* sp.), northern sand lance (*Ammodytes dubius*), and haddock (*Melanogrammus aeglefinus*), were caught in higher proportions during the day. Nonmigrating species, such as flatfish, skate, and scuplin, which rely on visibility of the trawl as a means of escapement, were caught in higher proportions during the night. Analysis of the effect of depth indicated that catchability during the day, relative to the night, increased significantly with depth for 21 species. We demonstrate that the accepted methods of estimating standard errors for generalized linear models are not valid for survey trawl data and suggest alternative methods.

Résumé : De 1972 à 1995, nous avons mené des campagnes de recherche au large de la côte de Terre-Neuve et du Labrador afin d'étudier les variations nyctémérales de la capturabilité de plus de 50 espèces. Pour estimer la capturabilité de jour et de nuit de ces espèces, nous avons utilisé deux modèles linéaires généralisés que nous avons appliqués à des données recueillies sur une période de plusieurs saisons et dans diverses régions du nord-ouest de l'Atlantique. En général, les espèces effectuant des migrations verticales nyctémérales comme le sébaste (*Sebastes* sp.), le lançon du nord (*Ammodytes dubius*) et l'aiglefin (*Melanogrammus aeglefinus*) ont été capturées en plus grande proportion le jour. Quant aux espèces non migratrices comme les poissons plats, la raie et le chabot, qui peuvent échapper au chalut lorsqu'il est visible, elles étaient capturées en plus grand nombre la nuit. Nous avons analysé l'effet de profondeur et constaté que, par comparaison à la capturabilité de nuit, la capturabilité de jour de 21 espèces augmente dans une mesure significative en fonction de la profondeur. Pour finir, nous démontrons que les méthodes acceptées pour l'estimation de l'écart-type des modèles linéaires généralisés ne sont pas valables lorsqu'on traite des données de chalutage, et nous en proposons d'autres.

[Traduit par la Rédaction]

Introduction

Many countries conduct bottom trawl surveys for the purpose of estimating abundance of commercial species. Determining the efficiency of survey gear, however, is a key component of estimating abundance and interpreting these survey results. The survey vessel, time of year, and time of day affect the survey trawl efficiency. Fish behaviour in response to physical factors, such as light intensity, has been shown to affect the efficiency of the survey gear over a 24-h period (Walsh 1991). Abundance of species exhibiting diel vertical migration would be overestimated from surveys conducted during the day as compared with surveys conducted at night, when these species would be out of the vertical range of the trawl (Michalsen et al. 1996). Increased visibility of the trawl during the day (Glass and Wardle 1989) could result in lower catches of nonmigrating species and thus abundance would be underestimated. Consequently, estimated abundance of species with variable patterns of diel

catchability may be inaccurate. Analysis must be carried out to determine if diel variability in catchability exists, and if so, to correct for this difference.

Several studies of diel catchability have made use of designed experiments in which a predetermined number of tows was carried out under controlled conditions (Walsh 1991; Walsh and Hickey 1993; Engs and Soldal 1992). While important information on fish behaviour in the vicinity of survey gear has been obtained, the number of tows completed have often been too few to give precise estimates. Furthermore, the results may not take into account regional or seasonal changes in catchability.

The purpose of this paper is to present a simple method that allows the relative efficiency of fishing gear during the day and night to be rigorously estimated using data routinely collected during research surveys. Our approach combines data from many years and several geographic areas.

A further motivation for this work is to provide correction factors for older research surveys of the Canadian Department of Fisheries and Oceans, many of which were conducted almost exclusively during daylight hours. As data collected from commercial vessels are thought to be unreliable, more emphasis is being placed on research vessel surveys. Correction factors for diel variation in trawl catchability are essential in determining absolute abundances from these surveys.

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Methods

Data

Research surveys have been conducted by the Canadian Department of Fisheries and Oceans off the coast of Newfoundland since 1946 (Templeman 1966). Prior to 1972, however, surveys were primarily conducted during daylight hours. We examined stratified random surveys conducted around the Island of Newfoundland and the coast of Labrador (Pitt et al. 1981) from 1972 (when both day and night surveys were conducted in roughly equal proportion) to 1995 during which time approximately 20 000 research tows were successfully made. Only tows with a duration of 30 min were selected for this analysis. Data from seven Northwest Atlantic Fisheries Organization (NAFO) subdivisions (Fig. 1), each with different bottom topographies, were included in this study. Seasons of the surveys are given in Table 1.

Species were selected for analysis if they occurred in more than 100 tows, and only strata in which individual species were caught in more than five tows were included. Sunrise and sunset were determined using the day of year and latitude of the tows (Brock 1981). Tows that occurred within 1 h of sunrise and sunset were excluded so that successive tows would not be compared (e.g., the last tow of the night and the first tow of the day).

Model

Model 1

Consider a survey in year y , in which C_{ysl} fish are caught in stratum s during the time of day (i.e., day or night) l . The catchability associated with time of day l is S_l , where the catchability will be scaled so that the catchability during the night will be 1. We construct a simple model in which an equal proportion of fish will be in each stratum in all years. The expected value of the catch, $E[C_{ysl}]$, is

$$E[C_{ysl}] = N_y P_s S_l$$

where N_y is the number of fish in the population in year y , P_s is the proportion of fish stratum s , and S_l is the combined availability and vulnerability of each species to the survey gear (or catchability) associated with time of day, l . The simplest model for the probability of catching C_{ysl} fish is a Poisson distribution. This is not a realistic model, however, because fish usually aggregate (i.e., in schools) and, as such, are not captured independently. Also, habitat within a stratum is not equally suitable. An overdispersed, i.e., extra-Poisson model, is preferred in which overdispersion is modeled using a scale factor for the variances (McCullagh and Nelder 1989). The scale factor only affects the variance but not the parameter estimates. The data can be analyzed in terms of a generalized linear model (GLIM) with a log link.

The main assumption of this model is that an equal proportion of fish will be in each stratum in all years. This may not be a valid assumption, however, as it is unlikely that the distribution of fish will remain constant from year to year.

Model 2

To remove the assumption of a constant stratum and year effect, the data considered will be restricted to strata within years in which at least one day and night tow has occurred.

Let C_{ysd} be the total catch in numbers during the day in a particular year and stratum, and C_{ysn} be the total catch for the day and the night in the same year and stratum. T_{ysd} and T_{ysn} will be the corresponding number of day and night tows, respectively. Let the probability that a fish caught in a year, y , and stratum, s , is caught during the day be p_{ys} and $1 - p_{ys}$ for night catches. If there is no difference between day and night catchability, then we would expect

$$\frac{p_{ys}}{1 - p_{ys}} = \frac{T_{ysd}}{T_{ysn}}$$

We are interested, however, in whether or not a different proportion of fish are caught during the day and night, and so the catchability term, S_d , is multiplied to the right-hand side of the above equation. After a log transformation we have

$$\log\left(\frac{p_{ys}}{1 - p_{ys}}\right) = \log(S_d) + \log\left(\frac{T_{ysd}}{T_{ysn}}\right)$$

The left side of the equation represents the logit transformation of p_{ys} . The term on the far right is the offset (McCullagh and Nelder 1989), a known quantitative variate, which will account for the number of day and night tows. The log of the catchability during the day, S_d , is the intercept and will be estimated.

If fish of a given species are captured independently, and if the probability of catching a fish during the day is constant for individuals of that species, then the probability of catching a fish during the day in a particular year and stratum (C_{ysd}), given the total number of fish caught in that year and stratum (C_{ys}), is binomial. Overdispersion must also be taken into account with model 2. An extra-binomial model is preferred in which overdispersion is modeled using a scale factor for the variances (McCullagh and Nelder 1989). A GLIM with a logit link and an offset is used to analyze the data. The method of programming is given in the Appendix.

This model also makes a potentially unrealistic assumption that the same proportion of fish will remain in a stratum during the survey period for a given year. Many species make seasonal migrations that take them into and out of the arbitrarily assigned strata and, as such, would not be expected to restrict their distribution during the year.

It is not clear that either of the above models is superior as both make assumptions that may not be valid for research survey data. For simplicity, model 2 was chosen for this analysis, although reference will be made to the results of model 1 as a method of comparison.

Regional and seasonal differences in diel catchability

Differences in bottom topographies associated with each NAFO area could possibly affect diel catchability. Banks within the study area range from 150–300 m in depth surrounded by troughs of 450–500 m in the north, to depths of 100 m with 150–200 m deep troughs in the south (Litvin and Rvachev 1963).

Seasonal changes in diel catchability have been suggested for various groundfish species (Beamish 1965). Since the degree of vertical migration within the water column may vary seasonally, research surveys conducted in different seasons were examined separately.

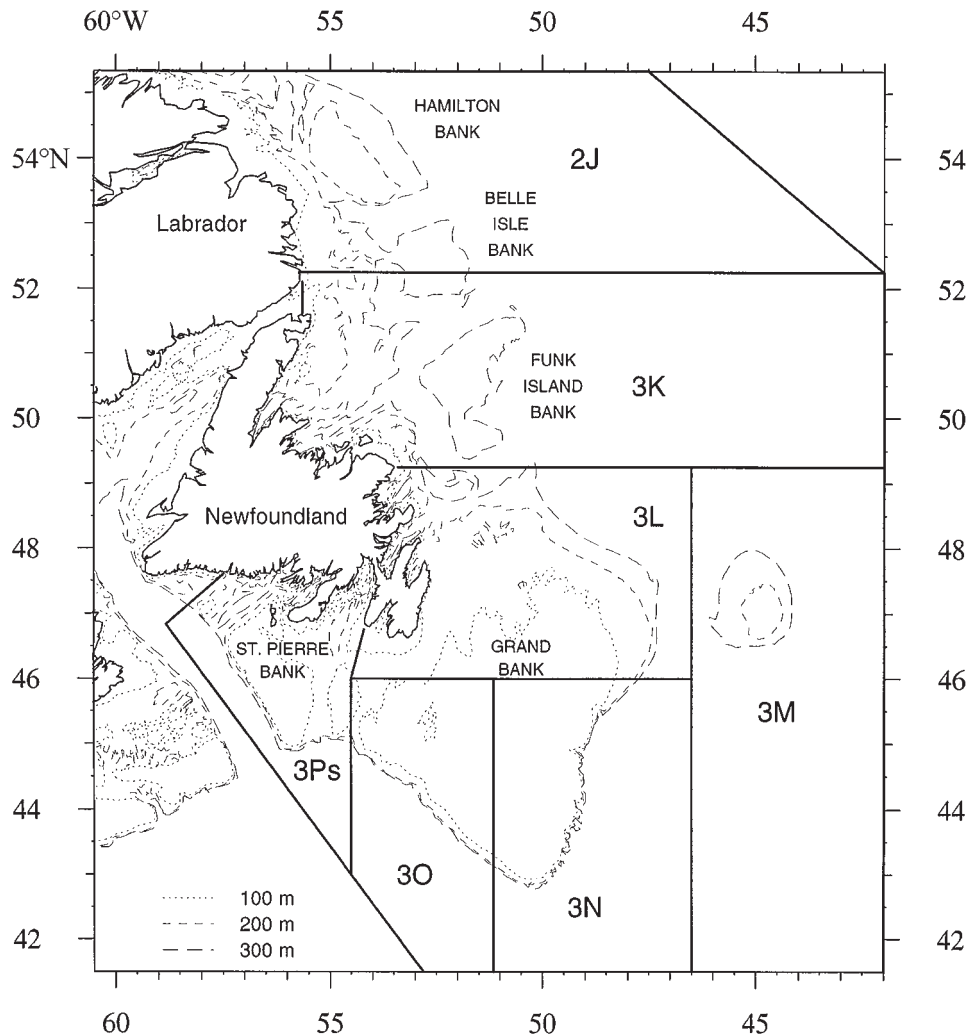
This analysis examines nine region and season combinations over which estimates of diel catchability will be compared.

Randomization tests

The reliability of confidence limits and significance tests for the day–night effect was assessed using a randomization test (Manly 1991). For each area–season combination studied (Table 1), the catchability of day tows was estimated using model 2 and the original data, with half of the data randomly assigned to the day and half to the night. Significance was determined by calculating the 95% confidence interval based on the standard errors of the GLIM estimates. The proportion of significant tests from 100 randomizations was then determined.

The randomization tests showed that the standard significance levels and standard errors of the parameter estimates were not reliable. Figure 2 shows the proportion of significant tests from the 100 randomizations for each species and region–season combina-

Fig. 1. Map of NAFO areas. The 100- (dotted line), 200- (short-dashed line), and 300-m (long-dashed line) isobaths are given for reference.



tion. With a significance level of 5%, the proportion of nominally significant tests should have been 0.05. For only 33% of the species and region–season combinations, however, was the proportion of significant tests less than or equal to 0.05.

Fish species that are known to school, such as capelin (*Mallotus villosus*), redfish (*Sebastes* sp.), Atlantic cod (*Gadus morhua*), and arctic cod (*Boreogadus saida*), tended to have a higher proportion of significant tests, while with solitary species, such as wolffish, the proportion of significant tests was closer to 0.05. In subdivision 3M, where the number of species and number of observations were the lowest for all subdivisions, the proportion of significant tests tended to be lower. In subdivisions with many observations, such as 3L and 3NO, the opposite was true.

Alternative estimates of reliability were constructed as the standard deviation of the mean of the parameter estimates from the 100 randomizations. These estimates of reliability in Table 1 represent the standard errors under the null hypothesis (i.e., no difference between day and night catchability) and are used in hypothesis testing (Manly 1991).

Depth effects

Depth, which has been thought to contribute to the variability in diel catchability (Pitt 1967), was examined using model 2. Tows were categorized into approximately 100-m depth classes that corresponded with the average depth of the strata included in this

study (Bishop 1994). The model was run initially as a regression analysis with depth as a covariate. Since the standard significance tests are considered to be liberal, any species for which depth was not significant was eliminated. For the remaining species, estimates of reliability for the depth effect were then determined with the depth categories randomly assigned in the same proportion as would normally be observed for each species. For example, it would be unlikely that a species normally found at shallow depths would be caught in equal proportions at the greatest depths. The standard deviation of the estimates from 100 randomizations were used in hypothesis testing. Estimates of diel catchability in each depth class were then determined using model 2.

Results

Estimates of diel catchability were obtained for all region–season combinations (Table 1, Fig. 3). Negative estimates indicated higher catchabilities at night. The summary refers to estimates determined over all regions and seasons. Of the 32 species with significant differences over all regions and seasons, 12 were caught significantly more during the day and 20 were caught significantly more at night.

Estimates for the family Gadidae differed among species. Arctic cod was caught significantly more during the day in

Table 1. Comparison of species catchability during day and night trawls.

Species	2J Fall	3K Fall	3L Fall	3L Spring	3L Summer	3M Spring	3NO Fall	3NO Spring	3Ps Spring	Summary
Clupeiformes										
Clupeidae										
<i>Clupea harengus</i> (herring)								2.02 (0.53)	0.81 (0.22)	0.91 (0.22)
Gadiformes										
Gadidae										
<i>Boreogadus saida</i> (Arctic cod)	0.24 (0.23)	-0.25 (0.16)	0.5 (0.14)	0.38 (0.17)	-0.04 (0.53)		0.95 (1.22)		-1.12 (0.24)	0.27 (0.08)
<i>Gadus morhua</i> (Atlantic cod)	-0.23 (0.08)	-0.15 (0.14)	-0.15 (0.1)	-0.05 (0.09)	0.09 (0.14)	1.16 (0.43)	0.26 (0.11)	0.23 (0.09)	-0.26 (0.15)	0.05 (0.05)
<i>Gadus ogac</i> (Greenland cod)	-0.28 (0.38)									-0.28 (0.42)
<i>Melanogrammus aeglefinus</i> (haddock)			-1.29 (1.08)		1 (0.97)		-1.32 (0.83)	0.87 (0.25)	0.34 (0.17)	0.51 (0.2)
<i>Merluccius bilinearis</i> (silver hake)							-0.99 (0.66)	0.02 (0.24)	0.37 (0.2)	0.26 (0.18)
<i>Pollachius virens</i> (pollock)								0.99 (0.75)	0.11 (0.36)	0.2 (0.32)
<i>Urophycis chesteri</i> (longfin hake)						-0.95 (0.16)	-1.55 (0.73)	-1.01 (0.26)	-0.42 (0.11)	-0.58 (0.09)
<i>Urophycis tenuis</i> (white hake)							-0.18 (0.46)	0.24 (0.15)	0.01 (0.09)	0.04 (0.07)
Macrouridae										
<i>Coryphaenoides rupestris</i> (roundnose grenadier)	-0.9 (0.65)	-1.38 (0.59)								-1.3 (0.49)
<i>Macrourus berlax</i> (roughhead grenadier)	0.08 (0.06)	0.09 (0.05)	0.41 (0.13)	-0.12 (0.09)	0.35 (0.14)	0.1 (0.11)	0.87 (0.48)	0.15 (0.16)		0.19 (0.04)
<i>Nezumia bairdi</i> (marlin-spike)	0.21 (0.24)	-0.14 (0.1)	0.11 (0.16)	0.39 (0.26)	-0.1 (0.24)	-0.27 (0.1)	-0.5 (0.31)	-0.39 (0.18)	0.04 (0.05)	-0.02 (0.04)
Moridae										
<i>Antimora rostrata</i> (blue hake)	-0.72 (0.42)	-0.43 (0.32)				-0.14 (0.18)				-0.27 (0.14)
Lophiiformes										
Lophiidae										
<i>Lophius americanus</i> (monkfish)								1.12 (1.33)	0.19 (0.12)	0.14 (0.12)
Myctophiformes										
Myctophidae										
Other (lanternfishes)	0.12 (0.22)	0.78 (0.49)	-0.25 (0.27)	3.56 (0.69)	1.84 (3.94)	-0.4 (0.43)		-1.22 (1.07)	-0.6 (0.43)	-0.18 (0.18)
Paralepididae										
Other (Barracudina)	-0.35 (0.54)	0.09 (0.3)	1.07 (0.43)	0.4 (0.25)	0.05 (0.26)				0.43 (0.3)	0.48 (0.16)

Table 1 (continued).

Species	2J Fall	3K Fall	3L Fall	3L Spring	3L Summer	3M Spring	3NO Fall	3NO Spring	3Ps Spring	Summary
Synphobranchidae										
<i>Synphobranchus kaupi</i> (longnose eel)	-0.16 (0.44)	-0.28 (0.5)								-0.24 (0.37)
Myxiniformes										
Myxinidae										
<i>Myxine glutinosa</i> (Atlantic hagfish)									-0.65 (0.18)	-0.65 (0.2)
Notocanthiformes										
Notocanthidae										
Other (spiny eels)		-0.74 (0.38)	0.75 (0.79)	0.11 (1.17)	1.47 (0.98)	-0.58 (0.29)				-0.19 (0.24)
Perciformes										
Agonidae										
<i>Agonus decagonus</i> (northern alligatorfish)	-0.34 (0.14)	-0.15 (0.11)	-0.44 (0.15)	-1 (0.2)	-0.2 (0.6)					-0.56 (0.11)
<i>Aspidoporoidea olriki</i> (common alligatorfish)	-2.69 (0.93)		-1.06 (0.27)	-0.81 (0.48)			-2.38 (0.98)			-1.01 (0.21)
Ammodytidae										
<i>Ammodytes dubius</i> (northern sand lance)			1.09 (0.3)	1.78 (0.42)	1.91 (2.34)		2.43 (0.38)	2.7 (0.4)	3.58 (2)	1.59 (0.19)
Anarhichadidae										
<i>Anarhichas denticulatus</i> (broadhead wolffish)	-0.2 (0.05)	-0.02 (0.08)	0.16 (0.12)	-0.11 (0.23)	0.01 (0.18)	-0.14 (0.19)				-0.11 (0.04)
<i>Anarhichas lupus</i> (striped wolffish)	-0.09 (0.08)	-0 (0.05)	0.29 (0.11)	-0.03 (0.1)	-0.12 (0.16)	-0.87 (0.09)	-0.82 (0.32)	-0.71 (0.12)	-1.19 (0.19)	-0.29 (0.04)
<i>Anarhichas minor</i> (spotted wolffish)	-0.12 (0.09)	0.32 (0.15)	-0.17 (0.14)	0.07 (0.13)	0.09 (0.25)	-0.63 (0.12)		2 (0.77)		-0.09 (0.06)
Cottidae										
<i>Artediellus</i> sp. (hooker sculpin)	-1.73 (0.59)	-0.89 (0.13)	-2.13 (0.24)	-1.87 (0.55)						-2.02 (0.2)
<i>Cottunculus microps</i> (Arctic deepsea sculpin)	-0.63 (0.23)	0.23 (0.16)	-0.14 (0.78)	0.56 (0.44)						0.01 (0.11)
<i>Hemitripterus americanus</i> (sea raven)				0.25 (0.3)			-1.08 (0.26)	-0.52 (0.08)	-0.51 (0.08)	-0.56 (0.06)
<i>Myoxocephalus octodecemspinosus</i> (longhorn sculpin)			-3.55 (1.06)	-0.56 (0.55)			-1.33 (0.24)	-1.2 (0.31)	-1.84 (0.44)	-1.44 (0.19)

Table 1 (continued).

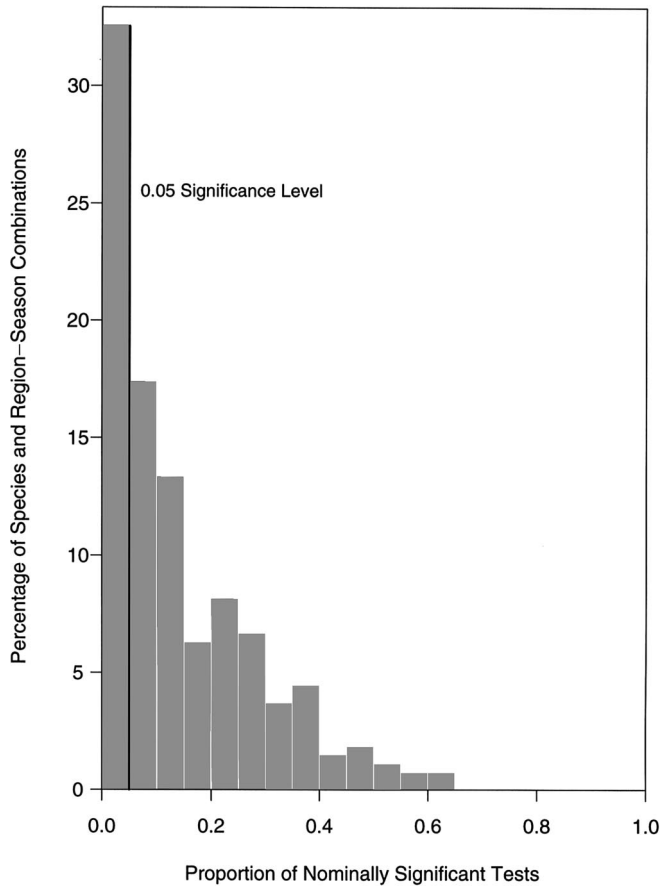
Species	2J Fall	3K Fall	3L Fall	3L Spring	3L Summer	3M Spring	3NO Fall	3NO Spring	3Ps Spring	Summary
<i>Myoxocephalus scorpius</i> (shorthorn sculpin)			-0.78 (0.34)	0.55 (0.26)			0.43 (0.6)	-0.05 (0.25)	0.2 (0.15)	0.19 (0.1)
<i>Triglops</i> sp. (mailed sculpin)	-1.96 (0.38)	-1.39 (0.63)	-0.83 (0.17)	-0.78 (0.25)	-1.82 (0.29)		-0.52 (0.27)	-1.12 (0.29)	-1.13 (0.33)	-0.78 (0.14)
Cyclopteridae										
<i>Cyclopterus lumpus</i> (common lumpfish)	1.29 (0.42)	0.95 (0.49)	1.84 (0.67)	0.45 (0.27)				1.21 (0.24)	0.56 (0.2)	0.57 (0.14)
<i>Eumicrotremus spinosus</i> (spiny lumpfish)	-1.52 (0.23)		-1.21 (0.12)	-2 (0.2)	-2.13 (0.64)		-1.95 (0.54)	-1.83 (0.33)	-2.68 (0.28)	-1.54 (0.08)
Liparidae										
Other (seasnails)	-1.17 (0.87)	-1.96 (0.65)	-1.28 (0.16)	-0.95 (0.25)			-3.75 (1.59)			-1.31 (0.14)
Scorpaenidae										
<i>Sebastes</i> sp. (redfish)	0.65 (0.26)	0.28 (0.38)	0.59 (0.23)	0.2 (0.16)	1.01 (0.37)	0.94 (0.15)	0.99 (0.3)	1.24 (0.23)	0.63 (0.08)	0.8 (0.07)
Stichaeidae										
<i>Eumesogrammus praecisus</i> (fourline snakeblenny)			-1.37 (0.7)							-1.37 (0.62)
<i>Lumpenus lumpretaeformis</i> (snake blenny)			0.51 (0.28)				0.36 (0.44)			0.43 (0.27)
<i>Lumpenus maculatus</i> (shanny)			0.28 (0.32)	-1.05 (1.05)						0.12 (0.25)
Zoarcidae										
<i>Lycodes reticulatus</i> (Arctic eelpout)	-0.26 (0.09)	-0.46 (0.12)	-0.7 (0.11)	-0.38 (0.08)	-0.44 (0.09)		-0.12 (0.39)	-0.53 (0.15)	-0.27 (0.18)	-0.54 (0.06)
<i>Lycodes</i> sp. (eelpout)	0.28 (0.21)	0.19 (0.29)	-0.86 (0.68)	0.13 (0.07)				-0.35 (0.56)		0.1 (0.07)
<i>Lycodes vahlii</i> (Vahl's eelpout)	-0.18 (0.13)	-0.24 (0.06)	-0.19 (0.1)	-0.1 (0.11)	-0.58 (0.16)	-0.06 (0.16)	-1.79 (1.48)	0.42 (0.27)		-0.21 (0.04)
Pleuronectiformes										
Pleuronectidae										
<i>Glyptocephalus cynoglossus</i> (witch flounder)	0 (0.1)	0.25 (0.1)	0.19 (0.16)	0 (0.11)	-0.32 (0.1)	0.28 (0.16)	-0.59 (0.14)	-0.62 (0.13)	-0.09 (0.08)	-0.1 (0.05)
<i>Hippoglossoides platessoides</i> (American plaice)	0.3 (0.09)	0.16 (0.05)	0.38 (0.08)	0.39 (0.05)	0.23 (0.08)	0.21 (0.13)	0.03 (0.07)	-0.38 (0.07)	-0.29 (0.11)	0.2 (0.03)
<i>Hippoglossus hippoglossus</i> (Atlantic halibut)								0.26 (0.13)	0.41 (0.16)	0.34 (0.12)
<i>Limanda ferruginae</i> (yellowtail flounder)			-0.76 (0.19)	-0.68 (0.23)	-0.62 (0.28)		-1.02 (0.17)	-1.06 (0.11)	-0.32 (0.22)	-1 (0.1)

Table 1 (concluded).

Species	2J Fall	3K Fall	3L Fall	3L Spring	3L Summer	3M Spring	3NO Fall	3NO Spring	3Ps Spring	Summary
<i>Reinhardtius hippoglossoides</i> (Greenland halibut)	-0.01 (0.06)	-0.07 (0.05)	0.28 (0.07)	0.32 (0.08)	-0.08 (0.1)	-0.05 (0.09)	0.78 (0.15)	0.1 (0.11)	0.02 (0.08)	0.02 (0.03)
Rajiformes										
Rajidae										
<i>Raja radiata</i> (thorny skate)	-1.07 (0.12)	-0.64 (0.06)	-0.8 (0.08)	-0.75 (0.09)	-0.77 (0.12)	-1.19 (0.13)	-0.74 (0.08)	-0.98 (0.12)	-1.15 (0.13)	-0.87 (0.04)
<i>Raja senta</i> (smooth skate)	-0.64 (0.24)	-0.61 (0.1)	-0.8 (0.36)	-0.13 (0.29)		-1.49 (0.43)	-1.54 (0.64)	-1.03 (0.36)	-0.43 (0.1)	-0.62 (0.07)
Salmoniformes										
Argentinidae										
<i>Argentina silus</i> (Atlantic argentine)								2.03 (0.64)	0.83 (0.2)	0.93 (0.19)
Osmeridae										
<i>Mallotus villosus</i> (capelin)	0.59 (1.21)	0.32 (0.19)	0.23 (0.13)	1.82 (0.2)	1.33 (0.62)		1.16 (0.78)	0.34 (0.36)	1.4 (0.74)	0.95 (0.12)
Squaliformes										
Squalidae										
<i>Centroscyllium fabricii</i> (black dogfish)	-0.03 (0.25)	-0.66 (0.85)				-0.47 (0.47)			0.11 (0.06)	0.1 (0.06)
<i>Squalus acanthias</i> (spiny dogfish)								1.39 (3.65)	-0.34 (0.51)	-0.33 (0.49)

Note: Values in parentheses are SEs computed using a randomization procedure (see text). Estimates for all regions and seasons are combined in Summary.

Fig. 2. Frequency of the proportion of nominally significant tests obtained from the randomizations for all species and region–season combinations (as in Table 1). The frequency is given as the percentage of species and region–season combinations ($n = 266$).



subdivision 3L in both the fall and spring surveys, while the estimate for subdivision 3Ps indicated a higher night catchability. The estimates for Atlantic cod were also variable with higher day catchabilities in subdivisions 3M and 3NO and a higher night catchability in subdivision 2J. Haddock (*Melanogrammus aeglefinus*) was caught significantly more during the day, while the opposite was true for longfin hake (*Urophycis chesteri*). Only arctic cod, haddock, and longfin hake had significant results across all regions and seasons.

All of the flatfish species included in this analysis had significant differences in diel catchability, although no consistent pattern among the species could be found. Witch flounder (*Glyptocephalus cynoglossus*) was caught significantly more during the night in 3L (summer only) and 3NO. Higher daytime catchability for witch flounder was found in subdivision 2J only. Atlantic halibut (*Hippoglossus hippoglossus*) and Greenland halibut (*Reinhardtius hippoglossoides*) were caught significantly more during the day, while yellowtail flounder (*Limanda ferruginae*) was caught significantly more at night. Estimates for American plaice (*Hippoglossoides platessoides*) differed regionally with catchability in 3NO and 3Ps spring surveys higher at night. In the north, catches were higher during the day.

Higher catchabilities during the day were found for sev-

eral deepwater species, such as Atlantic argentine (*Argentina silus*) and roughhead grenadier (*Macrourus berax*), and pelagic species, such as capelin and herring (*Clupea harengus*). Redfish and northern sand lance (*Ammodytes dubius*), which have higher daytime catchabilities, have a demersal existence during the day but become pelagic feeders at night (Scott and Scott 1988).

Estimates for each species of lumpfish were consistent for all regions and seasons. Common lumpfish (*Cyclopterus lumpus*) catches, however, were significantly higher during the day, while spiny lumpfish (*Eumicrotremus spinosus*) had a significantly higher catchability at night across all regions and seasons.

For species of wolffish, sculpin, skate, and eelpout, catches were higher at night. Both striped (*Anarhichas lupus*) and spotted wolffish (*Anarhichas minor*), however, also exhibited higher day catchabilities in subdivision 3L (fall only) and 3K surveys, respectively.

Parameter estimates for catchability during the day were generally not different for models 1 and 2 (Fig. 4). The only exceptions were roundnose grenadier (*Coryphaenoides rupestris*) and northern sand lance. The fact that two models, using two variations on the same data set (model 2 used a much smaller proportion of the model 1 data set), would have such similar results, suggests that the results of this analysis are believable.

Significant estimates for the effect of depth on diel catchability were obtained for 24 species (Table 2). For the majority of these species, depth was positively associated with higher catchabilities during the day relative to the night. At shallow depths, these species were more likely to be caught in greater proportions during night tows, but at greater depths, catchability was likely to be higher during the day. Only three species had a negative association with depth.

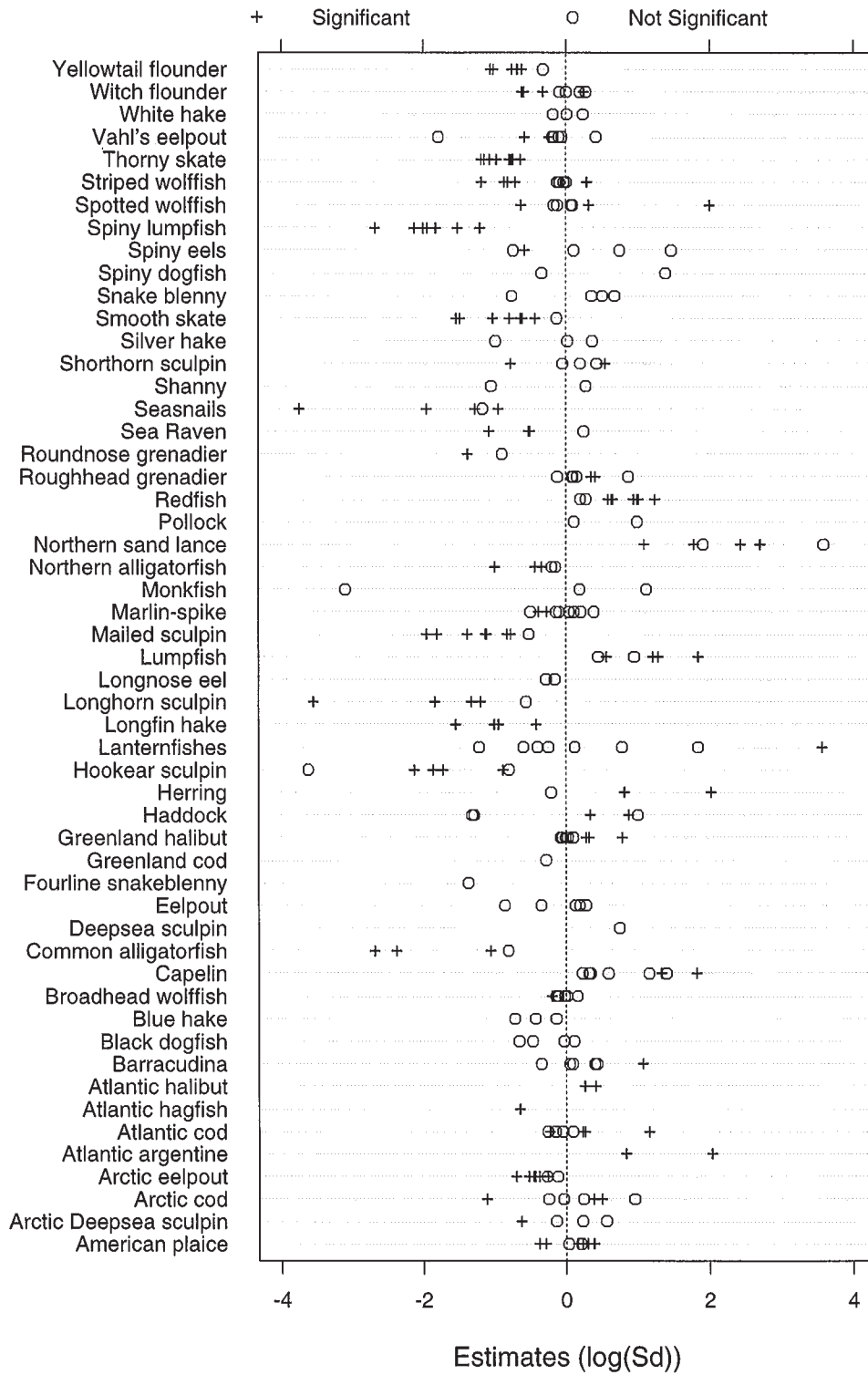
Catchability was not affected by the type of vessel used over the time period. Estimates of diel catchability obtained for each region, season, and vessel combination did not differ significantly from those obtained using only region and season combinations.

Discussion

The observed diel variation in catchability may be attributed to patterns of vertical migration, and escapement associated with visibility of the trawl. Redfish and northern sand lance are known to migrate vertically at night in search of food high in the water column (Scott and Scott 1988). The high catchability during the day for both species is consistent with this type of diel vertical migration. Atkinson (1989) and Beamish (1965) found similar results for redfish in the Northwest Atlantic.

Previous studies of Atlantic cod and haddock have shown that catches were higher during the day (Engs and Soldal 1992; Walsh and Hickey 1993; Michalsen et al. 1996). Using acoustic techniques, Beamish (1965) found that both species were found in higher concentrations on the bottom during the day. Our results for haddock are consistent with these studies. For Atlantic cod, however, diel catchabilities were variable among regions. The previous studies considered surveys conducted over a small geographic area and a

Fig. 3. Estimates of the day–night effect for all region and season combinations (as in Table 1). Negative results indicate higher catchability at night. Significant (+) and nonsignificant (o) results are differentiated, and a reference line at zero is provided for comparison.

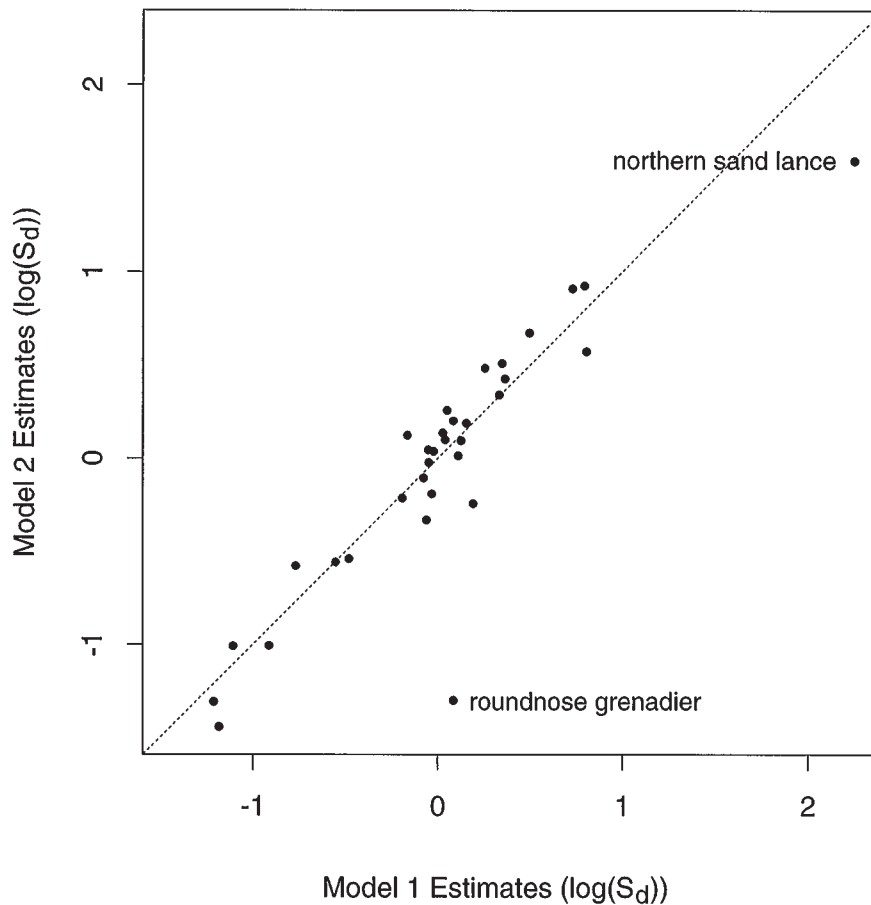


short period of time and thus may not represent the variability of these species over their entire range.

Visibility is important to the ability to escape the trawl during daylight hours for some species (Glass and Wardle 1989), e.g., underwater video cameras have shown that some flatfish are able to avoid the trawl during the day (Walsh

1988; Walsh and Hickey 1993). In this study, however, not all flatfish showed higher catchabilities during night tows. Atlantic halibut, a deepwater species, was caught significantly more during the day indicating that this species may be migrating up into the water column at night, a previously undocumented phenomenon. The same may be true for Am-

Fig. 4. Comparison of the parameter estimates combined over all regions and seasons for models 1 and 2. Each point represents an individual species. A one-to-one reference line is also given.



erican plaice found in deep water. Walsh (1991) carried out experiments on the Grand Banks and found higher catchabilities of American plaice at night, while Beamish (1965), who examined data from the Scotian Shelf and the Gulf of St. Lawrence, found the opposite. These regional differences, however, may be confounded by the effects of depth on diel catchability. In our analysis, estimates of diel catchability for American plaice were higher during the day in the northern regions which also have the deepest strata. In the south, where strata are shallower, catchabilities were higher at night.

Analysis of the influence of depth indicated that catchability during the day, relative to the night, increased significantly with depth for 21 species. When diel catchability was examined for each depth zone, the greatest differences were between the shallowest depth (<91 m) and the rest of the zones. If light does not penetrate farther than the shallowest depth, then the diel catchability should not necessarily differ beyond this depth. This increase in catchability during the day with depth may be the result of diel vertical migrations.

This study has shown that there are clear differences between day and night catchabilities for many species in the Northwest Atlantic and that depth and geography are also important factors. Size and abundance of species, although not considered in this analysis, may also be important in determining the diel variation in trawl catchability (Korsbrekke

and Nakken 1997). These differences should be taken into account in the assessment of fish stocks to improve estimates of abundance.

Stratified random surveys are conducted annually for the purpose of estimating abundance of commercial species. Our analysis has shown that this data can be used to augment other studies that require the use of specified controlled experiments. Research surveys provide many replicates of data necessary for rigorous hypothesis testing and should not be overlooked as a source of valuable information. Our results will allow the time series of groundfish research surveys to be extended back 45 years, which was previously not possible because the earlier surveys occurred mostly during the day. Such an analysis is crucial for resolving major ecological issues (Greenstreet and Hall 1996).

An important general statistical issue has been raised as a result of this analysis. The standard methods for dealing with extra-Poisson and extra-binomial variation in GLIMs do not appear to provide an adequate basis for inference and hypothesis testing when dealing with stratified random research survey data. Our randomization testing clearly demonstrated that the variation in both models could not be explained by the scale factor, which inflates the binomial and Poisson variances in GLIMs. We suggest that, for research survey data and perhaps for other highly variable fisheries data, randomization testing be undertaken to dem-

Table 2. Influence of depth on diel catchability.

Species	Estimate of the depth effect	Depth zone (m)				
		<91	92–183	184–274	275–366	367–549
American plaice	0.39 (0.03)	-0.28 (0.06)	0.42 (0.06)	0.51 (0.1)	0.24 (0.11)	0.28 (0.28)
Arctic cod	0.29 (0.12)	-0.47 (0.32)	0.35 (0.15)	0.22 (0.18)	0.93 (0.43)	
Arctic eelpout	0.38 (0.09)	-1.09 (0.13)	-0.58 (0.11)	-0.14 (0.15)	-0.38 (0.15)	
Atlantic haggfish	0.99 (0.35)		-3.33 (19.1)	-1.05 (0.48)	-0.13 (0.4)	0.21 (21.91)
Barracudina	0.56 (0.25)			-0.16 (0.43)	0.46 (0.31)	0.96 (0.26)
Capelin	-0.44 (0.13)	1.41 (0.44)	1.12 (0.2)	0.2 (0.21)	0.72 (0.43)	0.49 (9.24)
Common alligatorfish	1.06 (0.29)	-3.41 (0.69)	-1.25 (0.3)	-0.05 (0.39)	-0.11 (0.53)	
Common lumpfish	-0.52 (0.21)	1.28 (0.36)	0.34 (0.31)	0.87 (0.67)	-0.1 (0.51)	0.66 (0.34)
Hookear sculpin	0.84 (0.22)	-2.38 (0.75)	-2.18 (0.27)	-0.55 (0.3)	-0.34 (0.54)	
Longfin hake	0.46 (0.14)			-0.96 (0.32)	-0.82 (0.16)	-0.12 (0.12)
Longhorn sculpin	0.89 (0.37)	-1.48 (0.22)	-0.39 (0.47)	-1.42 (5.33)		
Longnose eel	-1.87 (0.52)				1.11 (17.02)	-0.76 (0.7)
Marlin-spike	0.15 (0.07)		-0.09 (14.34)	0.02 (0.14)	-0.27 (0.14)	0.07 (0.07)
Northern alligatorfish	0.67 (0.22)	-1.52 (3.84)	-1.17 (0.21)	-0.39 (0.31)	0.15 (0.28)	
Sea raven	0.39 (0.11)	-0.72 (0.08)	-0.35 (0.14)	0.13 (0.47)		
Seasnails	0.79 (0.23)	-4.05 (0.35)	-1.22 (0.21)	-0.84 (0.2)	-0.28 (0.27)	
Shorthorn sculpin	0.94 (0.29)	-0.22 (0.17)	0.72 (0.22)			
Smooth skate	0.32 (0.09)	-1.33 (9.36)	-0.99 (0.12)	-0.59 (0.13)	-0.3 (0.18)	-0.06 (0.23)
Spiny eels	1.79 (0.35)				-1.46 (0.71)	0.33 (0.29)
Spiny lumpfish	0.99 (0.18)	-2.51 (0.18)	-1.43 (0.12)	-0.55 (0.41)		
Striped wolffish	0.22 (0.05)	-0.77 (0.12)	-0.37 (0.08)	-0.16 (0.07)	0.01 (0.09)	-0.78 (0.56)
Thorny skate	0.14 (0.04)	-0.93 (0.1)	-0.99 (0.07)	-0.82 (0.08)	-0.44 (0.11)	-0.13 (0.17)
Vahl's eelpout	0.16 (0.06)	0.09 (6.55)	-0.49 (0.17)	-0.21 (0.08)	-0.06 (0.1)	-0.06 (0.14)
Witch flounder	0.22 (0.06)	-0.96 (0.17)	-0.24 (0.17)	-0.11 (0.1)	0.1 (0.13)	0.17 (0.11)

Note: The second column is the estimate of the slope from the regression analysis, where positive estimates indicate higher catches during the day relative to the night as depth increases. Values in parentheses are SEs under the null hypothesis (as in Table 1). Only those species with significant estimates are shown. Estimates of diel catchability in each depth zone, which correspond to average depths of the strata, are given for comparison.

onstrate the reliability of inferences. We have demonstrated, however, that by examining data from many geographical areas, the reliability of inferences can often be determined.

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References

- Atkinson, D.B. 1989. Diel movements of beaked redfish and the implications of these for stratified random bottom trawl estimates of biomass and abundance. *N. Am. J. Fish. Manage.* **9**: 163–170.
- Beamish, F.W.H. 1965. Vertical migration by demersal fish in the Northwest Atlantic. *J. Fish. Res. Board Can.* **23**: 109–139.
- Bishop, C.A. 1994. Revisions and additions to stratification schemes used during research vessel surveys in NAFO Subareas 2 and 3. NAFO SRC Doc. No. 94/43.
- Brock, T.D. 1981. Calculating solar radiation for ecological studies. *Ecol. Modell.* **14**: 1–19.
- Engs, A., and Soldal, A.V. 1996. Diurnal variations in bottom trawl catch rates of cod and haddock and their influence on abundance indices. *ICES J. Mar. Sci.* **49**: 89–95.
- Glass, C.W., and Wardle, C.S. 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. *Fish. Res. (Amsterdam)*, **7**: 249–266.
- Greenstreet, S.P.R., and Hall, S.J. 1996. Fishing and the groundfish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *J. Anim. Ecol.* **65**: 557–598.
- Korsbrenke, K., and Nakken, O. 1997. Length and species dependent diurnal variation in catch rates in the Norwegian Barents Sea bottom trawl surveys. *ICES C.M. W:20*.
- Litvin, V.M., and Rvachev, V.D. 1963. The bottom topography and sediments of the Labrador and Newfoundland fishing areas. *In Soviet fisheries investigations in the Northwest Atlantic. Edited by Y.Y. Marti. Israel Program for Scientific Translations, Jerusalem.* pp. 100–112.
- Manly, B.F. 1991. Randomization and Monte Carlo methods in biology. Chapman & Hall, New York.
- McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. *Monogr. Stat. Appl. Prob.* Chapman & Hall, London.
- Michalsen, K., God, O.R., and Ferno, A. 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. *ICES J. Mar. Sci.* **53**: 389–395.
- Pitt, T.K. 1967. Diurnal variation in the catches of American plaice, *Hippoglossoides platessoides* Fabr., from the Grand Bank. *ICNAF Res. Bull.* **4**: 53–58.
- Pitt, T.K., Wells, R., and Mckone, W.D. 1981. A critique of research vessel otter trawls by the St. John's Research and Resource Services. *In Bottom trawl surveys. Edited by W.G. Doubleday and D. Rivard. Fisheries and Oceans Canada, Ottawa, Ont.* pp. 42–61.

Scott, W.B., and Scott, M.G. 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. No. 219.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. No. 154.

Walsh, S.J. 1988. Diel variability in the trawl catches of juvenile and adult yellowtail flounder on the Grand Banks and the effect on resource assessment. N. Am. J. Fish. Manage. **8**: 1261–1272.

Walsh, S.J. 1991. Diel variation in availability and vulnerability of fish to a survey trawl. J. Appl. Ichthyol. **7**: 147–159.

Walsh, S.J., and Hickey, W.M. 1993. Behavioural reactions of demersal fish to bottom trawls at various light conditions. ICES Mar. Sci. Symp. **196**: 68–76.

Appendix. Estimation in SAS

This appendix demonstrates how to fit the proposed model 2 to catch data from stratified random surveys.

Create a data set with seven variables per observation: species, region, season (season), number caught during the day (C_{ysd}) in a particular year and stratum, total number caught (C_{ys}) in a particular year and stratum, number of tows during the day (T_{ysd}), number of tows during the night (T_{ysn}), and time of day (daytime). A sample of what the data set should look like is given in Table A1.

The following is a brief description of the method of program Christiane Hudon in SAS:

```
data d1;
  infile survey; input species season Cysd Cys Tysd Tysn
  daytime;
  offset = Tysd/Tysn;
proc sort; by species season;
proc genmod; by species season;
class daytime;
model Cysd/Cys = daytime/link = logit dist =
  binomial offset = offset dscale noint;
```

Table A1. Sample data set to be used with model 2 (Appendix).

y	s	C_{ysd}	C_{ys}	T_{ysd}	T_{ysn}	Offset
72	383	62	65	1	1	0
72	359	73	78	1	2	-0.69
72	382	154	358	2	2	0
72	381	83	228	2	2	0
73	374	8	10	3	1	1.1
73	376	1	1	1	2	-0.69
73	354	15	22	1	2	-0.69
73	359	13	59	1	2	-0.69
74	378	129	484	1	2	-0.69
74	381	5	23	1	3	-1.1
74	379	32	296	1	2	-0.69
74	380	8	16	1	1	0
75	376	17	23	1	1	0
75	377	81	110	1	1	0
75	333	169	169	1	1	0
76	354	32	60	2	1	0.69
76	333	15	15	1	1	0
76	334	0	2	1	1	0

Note: The data represent Atlantic cod in subdivision 3NO from the spring research surveys.