International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

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Catchability of pelagic trawls for sampling deep-living nekton in the mid North Atlantic

Mikko Heino (mikko.heino@imr.no)
Filipe M. Porteiro (filipe@uac.pt)
Tracey T. Sutton (tsutton@vims.edu)
Tone Falkenhaug (tone.falkenhaug@imr.no)
Olav Rune Godø (olav.rune.godoe@imr.no)
Uwe Piatkowski (upiatkowski@ifm-geomar.de)

Approved by

Ulf Dieckmann
Program Leader, EEP

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M. Heino, F. M. Porteiro, T. T. Sutton, T. Falkenhaug, O. R. Godø, and U. Piatkowski

We use the material collected in summer 2004 from the Mid-Atlantic Ridge between Iceland the Azores with three pelagic trawls to estimate relative catchabilities for the common fish, cephalopod, decapod and jellyfish species. Catchability is defined as the ratio of numbers or weight caught between two trawls, standardised for towed distance. We estimate taxon-specific catchability coefficients for two large pelagic trawls with graded meshes, using a smaller pelagic trawl with uniform mesh size as the reference trawl. Two of the trawls were equipped with multiple opening-closing codends that allowed for sampling in different depth layers. Generalized linear and mixed models suggest that most of the taxa have catchabilities much less than expected from the area of opening alone, indicating that only a few species are herded by the large meshes in the mouth of larger trawls. Catchability coefficients across taxa show a very large spread, indicating that the sampled volume for the larger trawls with graded meshes were highly taxon-specific. Part of this variability can be explained with body size and taxonomic group, the latter probably reflecting differences in body form and behaviour. The catchability estimates presented here form the basis for combining data for quantitative analyses of community structure.

Keywords: catchability, gear comparison, Mid-Atlantic Ridge, nekton, pelagic ecosystems, sampling.

Mikko Heino: Department of Biology, University of Bergen, Box 7803, N-5020 Bergen, Norway, and Institute of Marine Research, Bergen, Norway, and International Institute for Applied Systems Analysis, Laxenburg, Austria. F. Porteiro: Department of Oceanography and Fisheries, University of the Azores, PT-9901-862 Horta, Portugal. T. Sutton: Virginia Institute of Marine Science (VIMS), P.O. Box 1346, Gloucester Point, VA 23062, USA. T. Falkenhaug: Institute of Marine Research, Flødevigen Marine Research Station, N-4817, His, Norway. O. Godø: Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway. U. Piatkowski: Leibniz Institute of Marine Sciences, IFM-GEOMAR, Düsternbrooker Weg 20, D-24105 Kiel, Germany.

Correspondence to M. Heino: tel: +47 55584544; fax: +47 55584450; e-mail: mikko.heino@imr.no.

Introduction

Trawls are an effective and widely used method for sampling nekton as they sample large volumes of often sparsely distributed organisms and allow direct species identification and further individual-level observations (e.g., length measurements, aging, and stomach contents analysis) to be made from specimens taken on board. However, one type of trawl cannot perform well for all types of nekton that range in size from few millimetres to metres: overall trawl size — which largely determines its ability to capture fast-swimming organisms — has to be traded off against mesh size, which determines the retention of small organisms. Furthermore, fine-meshed trawls cannot be towed with speeds high enough to capture species that show avoidance behaviour. A natural solution is to use more than one type of trawl with complementary characteristics. However, combining data from different gears is not trivial (e.g., Kashkin and Parin, 1983; Wassenberg *et al.* 1997; Pelletier, 1998; von Szalay and Brown, 2001; Fock *et al.*, 2002; West, 2002; Helser *et al.*, 2004; Lewy *et al.*, 2004; Porteiro, 2005).

Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic (MAR-ECO) is a Census of Marine Life project that is set up to describe and understand the patterns of distribution, abundance and trophic relationships of the organisms inhabiting the mid-oceanic North Atlantic, and to identify and model ecological processes that cause variability in these patterns (Bergstad and Godø, 2002; Bergstad *et al.*, 2008; see also www.mar-eco.no). A major contribution to this project was a two-month cruise of the RV "G.O. Sars" in summer 2004 surveying the ecosystems along the Mid-Atlantic Ridge from Iceland to the Azores (Wenneck *et al.*, 2008). In order to get quantitative and representative samples from various types and size classes of pelagic nekton, three different trawls were used (Table 1): a macrozooplankton trawl and two fish trawls, the medium-sized Åkra trawl and the larger Egersund trawl. These trawls differ substantially in their overall size as well as in mesh sizes. Both the Åkra and macrozooplankton trawls were used systematically, following a predetermined sampling scheme (respectively 15 and 17 successful hauls), whereas the Egersund trawl was used opportunistically to sample acoustically “interesting” registrations (four successful hauls). For analyzing these data, for example to characterize the species assemblages (Sutton *et al.*, 2008), it would be desirable to combine data from all three gears. However, simply merging of the data across gears would be questionable as the trawls differ considerably in their essential characteristics that determine how efficient they are catching pelagic organisms.

In this paper we aim to estimate relative catchabilities for the three different midwater trawls used on the RV “G.O. Sars” in summer 2004 (Wenneck *et al.*, 2008). Catchability is here defined as the expected ratio of catch in numbers for two trawls fishing in the same area with the same effort (here, the distance trawled). Catchability can be defined at different levels of biological organization; here we focus on species and higher taxonomic levels. A first indication of catchability is provided by the ratio of opening areas (Table 1). However, nominal opening area is but one major factor affecting catchability. In general, catchability is determined both by properties of trawl and by characteristics of the organisms encountered, and the interactions between them. There are four major factors that are expected to cause systematic differences in the catchability of the trawls used in this study:

- *Area of opening*. Filtered volume is proportional to the mouth area of trawl, but strict proportionality between filtered volume and catches is expected only when there is no avoidance and all individuals in the filtered volume are retained (Barkley, 1972). Expected effect on catchabilities: Egersund>Åkra>macrozooplankton.
- *Ease of avoidance*. This is closely related to the size of trawl (Barkley, 1964, 1972; Bethke *et al.*, 1999) and towing speed (Barkley, 1964, 1972; Winger *et al.*, 2000; Gabriel *et al.*, 2005): for organisms showing avoidance behaviour, increasing diameter of a trawl

should increase catchability, and increasing towing speed should have a similar effect, to the extent that the so-called bucket effect does not come into the play. Also rigging may affect the noise and bioluminescence caused by the approaching trawl (Jamieson *et al.*, 2006) and thus the likelihood of early detection and avoidance, but we have no data on these parameters. Expected effect on catchabilities: Egersund>Åkra>macrozooplankton.

- *Retention through mesh selection*. Mesh selection depends on the mesh size relative to the size of individuals as well as their body shape and form (Barkley, 1972; Gartner *et al.*, 1989; Millar, 1992; Wileman *et al.*, 1996; Bethke *et al.*, 1999). Expected effect on catchabilities: Egersund<Åkra< macrozooplankton.
- *Herding effect*. In pelagic trawls with decreasing meshes toward the codend, capture is based not only on filtering but also on behavioural response known as herding (Lee *et al.*, 1996; Valdemarsen, 2001): fish inside the trawl try to avoid the meshes and do not swim through the meshes even if they could do so, but are instead herded in the middle of the trawl, eventually encountering meshes that are small enough for retention. In bottom trawls, trawl doors and bridles cause the herding (Wardle, 1993; Ramm and Xiao, 1996; Sangster and Breen, 1998; Winger *et al.*, 2004), but the extent that this happens in pelagic trawls is unknown. Visual detection of trawls in deep water is made possible by bioluminescence caused by the trawl itself (Jamieson *et al.*, 2006). Expected effect on catchabilities: potentially important in Egersund and Åkra trawls, probably unimportant in macrozooplankton trawl.

The estimated catchability coefficient will reflect all of the abovementioned factors, plus measurement noise arising from, e.g., spatial heterogeneity and variability in gear performance (Byrne *et al.*, 1981; Pelletier, 1998).

The value of catchability estimates comes from three sources. First, catchability coefficients form the quantitative basis on which data collected with different gears can be compared. Furthermore, catchability coefficients allow for description of the performance of trawls, for example, effective mouth area. Taken together, catchability estimation contributes to improved monitoring strategies for the deep ocean. And finally, catchability estimates also provide indirect information on behaviour of deep-living biota.

Materials and methods

Wenneck *et al.* (2008) give a detailed account on methods employed in collecting the material. We include fishes, cephalopods, decapods and large medusae (disc diameter >1 cm) in our analyses. The analyses were run at five taxonomic levels, at the level of species, genus, family, order and class, following taxonomy by Nelson (2006) for fishes, Sweeney and Roper (1998) for cephalopods, and Crosnier and Forest (1973) and Vereshchaka (2000) for decapods. *Atolla*, *Mastigoteuthis* and *Hymenodora* were not identified to species level, but for simplicity we refer to them also as ‘species’.

Sampling was based on pre-determined ‘superstations’ where both the macrozooplankton and Åkra trawl trawls were used, whereas the Egersund trawl was used opportunistically (Wenneck *et al.*, 2008). The macrozooplankton and Åkra trawls were equipped with a “MultiSampler” (Engås *et al.*, 1997), a multiple opening-closing device that enabled respectively five and three samples to be obtained from pre-programmed depths during a single haul. Because estimation of the sampling volume was straightforward only for the macrozooplankton trawl, this trawl was used as the reference trawl against which the Åkra and Egersund trawls were compared. In statistical sense the sampling unit was a specific depth layer and superstation where both gears being compared were successfully used. In analyses specific to a taxon, data from sampling units where the taxon was not observed in either trawl were omitted. The data thus contain informative zeros from sampling units where only one gear captured the taxon, and are balanced with respect to trawl.

Even though the macrozooplankton and Åkra trawls were equipped with a multiple opening-closing device, surface contamination can occur. When single specimens of abundant epi- or mesopelagic species were captured well below their continuous depth distribution in the current data, and below their reported depth range, they were considered contaminants and removed from the data. This led to deletion of few observations of *Entelurus aequoreus*, *Maurolicus muelleri* and seven species of myctophids.

In comparisons with the Åkra trawl, macrozooplankton trawl catches were aggregated into three layers that showed the closest match with the depth layers sampled by the other trawl at the same stations; sometimes a macrozooplankton trawl sample had to be discarded as there was no corresponding Åkra trawl sample (e.g., the horizontal macrozooplankton trawl hauls). This lead to a balanced setup where samples could be compared as pairs representing the same station and depth interval but different trawl (Appendix). Because the Egersund trawl was used opportunistically outside the pre-determined standard stations, the samples were paired afterwards by matching stations based on geographic distance and species composition (Appendix).

In the final analyses involving the Åkra trawl we only included taxa that had three or more positive records with both trawls being compared; species that were not frequent enough for species-level analyses still contributed to analyses at higher taxonomic levels. For species-level analyses involving the Åkra trawl, our material includes 52 fish species, 19 species of crustaceans, five species of cephalopods and two species of medusae (total 78 species). Because the Egersund trawl was successfully used only four times, we relaxed the data selection criterion and included taxa that had two or more positive records with both the Egersund and macrozooplankton trawls. The material includes eight fish species, five decapods, one cephalopod and two medusae.

Samples were classified as daytime, dusk, night or dawn samples using sunrise and sunset times calculated for each sampling location and date. Sunrise and sunset times were calculated using the CBM model of Forsythe *et al.* (1995) to estimate day length and the equation of time and longitude to estimate solar noon. A dusk sample was defined as a sample that was at least partially taken during the period from one hour before sunset to one hour after. Similarly, dawn samples were those that overlapped with the period from one hour before sunrise to one hour after sunrise. Our sampling was imbalanced with respect to gear and diel phase: the macrozooplankton trawl was used more often during night (11 samples, or 26% of the total) than the Åkra trawl (1 sample, 2.4%); the proportions of dusk and dawn samples were similar (respectively six and seven samples).

Statistical methods

We assume that selectivity of trawl *y* relative to the reference trawl *x* can be expressed with the linear relationship $C_y \sim \rho C_x$, where *C* refers to a catch standardised for towed distance and ρ is relative catchability; $\rho = 1$ corresponds to equal catchability whereas smaller ($0 \leq \rho < 1$) or larger values indicate that trawl *y* is respectively less or more effective than the reference trawl *x*. The most intuitive way to estimate ρ is to apply a logarithmic transformation on both sides of this equation (e.g., Wassenberg *et al.*, 1997), yielding $\log(C_y) \sim a_0 + \log(C_x)$, where $a_0 = \log(\rho)$. However, this model has a major disadvantage, namely that information in zero catches cannot be used. Therefore, we chose to use a more general approach, expressing catch using the generalized linear model

$$\log(c_i) \sim a_X + a_Y \mathrm{trawlY} + \log(d_i),$$

where c_i is catch numbers of trawl *i*, a_X is an estimated parameter that corresponds to the mean logarithmic catch of the reference trawl *x*, a_Y gives the mean logarithmic difference in catch between the two trawls, trawl Y is an indicator variable that is 1 for trawl Y and 0 otherwise, and d_i is trawled distance treated as an offset variable. This model allows great flexibility. In particular, we can treat catches in numbers as counts, assumed to represent a random variable with a discrete distribution that includes zero. Poisson and negative binomial distributions are obvious choices, in which case the logarithm on the left hand side of equation (1) is naturally treated as the link function. Because our data are mostly more variable than the Poisson distribution would suggest (seen as overdispersion in Poisson models), we chose to use the negative binomial distribution; inspection of the fitted models suggested that the model describes the data well. Nevertheless, it was encouraging that the choice of the error distribution had generally minute influence on the catchability estimates.

Including additional explanatory variables could improve catchability estimates in terms of precision and accuracy. We considered depth and diel variation in comparisons between the macrozooplankton and Åkra trawl; for the Egersund trawl there were too few observations. Alas, diel effects could not be routinely considered because for many species data were too imbalanced, with not all combinations of day and night versus gear type being present at those superstations where a species occurred. Therefore diel effects were considered only for species with sufficiently balanced data as an additional check of robustness of the results.

Depth, calculated as the average of a haul's starting and finishing depth (see Appendix), could be used routinely. However, because our measure of depth is not precise, we did not use depth for species that had a relatively narrow vertical range of <500 metres (*E. aequoreus* and five myctophids: *Lampanyctus pusillus*, *Vinciguerria poweriae*, *Diaphus rafinesquii*, *Symbolophorus veranyi* and *Electrona risso*). For all other species, we centered the depth data so that species-specific mean depth was zero and estimated models with linear and/or quadratic depth terms (the quadratic term allows for catch rates to peak at intermediate depths). The model that had the lowest Akaike Information Criterion (with correction for small sample sizes, AIC_c) was chosen as the final model. A depth term was included for 51 out of 78 species in our data (65%). Nevertheless, in the majority of cases estimates of catchability were little influenced by consideration of depth effects. In a few cases where larger changes occurred, these were supported by non-negligible improvements in AIC_c and were considered biologically sensible. For example, catchability for *Lampanyctus crocodilus* was $\rho = 0.43$ without depth effect, and $\rho = 1.2$ with linear depth effect ($\Delta AIC_c = -4.7$); neither estimate is significantly different from 1 but the latter one is more reasonable for a relatively large-sized species. Furthermore, when the best model involved a depth term, the standard error for the catchability was usually somewhat smaller than without the depth term.

All analyses were carried out in R 2.9.0 (R Development Core Team, 2009). We used function ‘glm.nb’ by Venables and Ripley (2002) for fitting the negative binomial models. When taxon was included as an explanatory variable and treated as a random effect, package ‘lme4’ by Bates and Maechler (2009) was used for fitting generalized mixed models. When exact p-values for hypothesis testing are not given, $p = 0.05$ is used as the limit of statistical significance.

Results

Macrozooplankton versus Åkra trawl

Catchability of the Åkra trawl relative to the macrozooplankton trawl for all fishes was 2.3 (95% confidence interval for catchability 1.6...3.4, $a_Y = 0.838$, s.e. 0.197) for catch in numbers. For all cephalopods, the catchability of the Åkra trawl was estimated to be 0.38 (95% confidence interval 0.14...1.03, $a_Y = -0.966$, s.e. 0.510). For large medusae, the catchability of the Åkra trawl was estimated to be 3.05 (95% confidence interval 0.50...19,

$a_Y = 1.12$, s.e. 0.926). For decapods, the catchability of the Åkra trawl was estimated to be 0.57 (95% confidence interval 0.35...0.93, $a_Y = -0.566$, s.e. 0.251). Thus, the Åkra trawl was more efficient in catching fishes than the macrozooplankton trawl, whereas the opposite was true for decapods. For medusae and cephalopods the results were inconclusive, although the results were suggestive of a tendency of the macrozooplankton trawl to catch more cephalopods than the Åkra trawl.

We were able to estimate catchability for 52 fish species (Figure 1). The estimates range from 0.0066 (snake pipefish, *Entelurus aequoreus*) to 45 (platytroctid, *Normichthys operosus*). For 31 of the species (60%) the Åkra trawl was significantly more efficient than the macrozooplankton trawl ($\rho > 1$), but only for 12 species (23%) the theoretical catchability derived from the ratio of mouth areas ($\rho = 18$) was within the confidence limits of the estimate. However, there were three species for which macrozooplankton trawl was significantly more efficient, all of them small (two species of bristlemouths, *Cyclothone*) or very thin-bodied (*E. aequoreus*).

We estimated catchability for 26 invertebrate species (Figure 2). For the majority of these (65%), the Åkra and macrozooplankton trawls were not significantly different, and only for the decapod shrimp *Sergestes corniculum* did the confidence limits overlap with the theoretical catchability derived from the ratio of mouth areas ($\rho = 18$). Decapods in general showed a very large spread of catchabilities, ranging from 0.033 in *Hymenodora* to 8.4 in *S. corniculum*, with five species having catchability significantly less than one, whereas two species (both from genus *Sergestes*) had catchability that was significantly larger than one. Also one medusa (*Atolla*) and one cephalopod (*Pyroteuthis margaritifera*) had catchabilities significantly larger than one.

We estimated catchability also at higher taxonomic levels (Figure 3). In some cases there were considerable differences within a genus or family. Of families represented by more than one species, the Platytroctidae had the highest catchability while the Gonostomatidae had the lowest. The estimate for the Gonostomatidae was strongly influenced by small but abundant *Cyclothone* species, while other genera in the family had higher catchabilities.

Some variability in the catchability estimates can be explained by body size: catchability was positively related to mean body weight (linear model with log-transformation of both variables: $F_{1,76} = 12.0$, $p = 0.001$), and on average, doubling the body weight increased catchability by a factor of 1.46 (95% confidence interval 1.18...1.80). However, the relationship was noisy (Figure 4) and only a small proportion of variability in the data could be explained ($R^2 = 14\%$). Taxon-specific differences remained: including 'order' as an explanatory variable significantly improved the fit ($F_{12,64} = 3.28$, $p = 0.001$, $R^2 = 47\%$); the effect was weaker but still significant ($F_{9,64} = 2.16$, $p = 0.037$, $R^2 = 36\%$) if three orders represented by only one species (Gadiformes, Saccopharyngiformes, Syngnathiformes) were excluded. Without mono-specific orders and using the abundantly-sampled lanternfishes (Myctophiformes) as the reference order, we saw that eels (order Anguilliformes), decapods and cephalopods (Oegopsida) had a lower catchability than their weight would suggest; medusae and other fish orders were not significantly different from lanternfishes. Similarly, the fit could be improved using family (instead of order) as an explanatory variable, either with ($F_{27,49} = 2.86$, $p = 0.001$, $R^2 = 66\%$) or without mono-specific families ($F_{12,49} = 3.41$, $p = 0.001$, $R^2 = 58\%$). Without mono-specific families and using the abundantly-sampled lanternfishes (Myctophidae) as the reference family, we saw that when accounting for weight differences, two fish families (Gonostomatidae and Serrivomeridae) and one decapod (Oplophoridae) and one cephalopod family (Cranchiidae) had a lower catchability than their weight would suggest. Treating order or family as a random effect, instead of a fixed effect as above, gave a similar estimate for the average effect of doubling the body size (order as a random effect: 1.49, 95% confidence interval 1.17...1.90; family as a random effect: 1.58, 95% confidence interval 1.25...1.99) as obtained above for the model without taxonomic information (1.46). We also considered taxon-specific weight effects on catchability but our data were too few to allow detecting significant effects.

Diel effects could also influence catchability. However, our data were imbalanced, such that diel and gear effects could become confounded. To reduce this problem, we analysed diel effects only at higher taxonomic levels. For fishes, including diel phase (day, dusk, night and dawn; see the methods) did not significantly improve the model where gear was used as the explanatory variable ($\chi_3^2 =$ 4.25, p = 0.236), but it did so when also ‘order’ was included ($\chi_3^2 =$ 8.47, p = 0.037). The latter model suggested that day-time catches tended to be higher compared night-time catches; dawn and dusk catches were not significantly different from night catches. This effect could arise from the Åkra trawl having more daytime samples than the macrozooplankton trawl.

In order to make the data more balanced, we therefore regrouped dawn and dusk catches with night-time catches. Analysing the data by order suggested that night-time catches were significantly higher for orders Osmeriformes and Syngnathiformes. A significant gear × day/night interaction was detected for Anguilliformes, Osmeriformes, and Stomiiformes, suggesting that the Åkra trawl was relatively more efficient during darkness for the two first orders, but the opposite held true for the last one. For cephalopods, a significant diel effect was apparent ($\chi_3^2 =$ 8.19, p = 0.042), but this disappeared if a single large dusk catch of *Gonatus steenstrupi* was omitted. Also for medusae, the data suggested a diel effect ($\chi_3^2 =$ 8.00, p = 0.046): dawn catches appeared on average higher than night-time catches. In contrast to the aforementioned groups, diel effects appeared relatively strong in decapods:

inclusion of the diel phase greatly improved the model fit ($\chi_3^2 = 27.0$, $p < 0.001$), with dusk catches being much higher than night-time catches. Furthermore, there was a significant interaction between trawl and diel phase ($\chi_3^2 = 30.7$, $p < 0.001$): the Åkra trawl appeared less efficient in catching decapods during the day and dusk compared to the macrozooplankton trawl.

In addition to the Åkra and macrozooplankton trawls often catching different numbers of individuals of a species for the same effort, they also had tendency to catch differently sized individuals: for 56 of 78 species, mean individual weight was higher in the Åkra compared to the macrozooplankton trawl (Figure 5). This tendency was evident across the main taxonomic groups, but was more pronounced in small species; linear regression fitted on log-log scale yielded a significantly positive intercept but a slope that was significantly less than one.

Macrozooplankton versus Egersund trawl

Because the Egersund trawl was only used four times, catchability of the Egersund trawl relative to the macrozooplankton trawl could only be estimated for a few species. Notice also that the material only included relatively large species as smaller ones were not caught by the large-meshed Egersund trawl often enough.

Catchability of the Egersund trawl relative to the macrozooplankton trawl for fishes in general was 57 (95% confidence interval 19…168, $a_Y = 4.04$, s.e. 0.55). For all decapods, the catchability of the Egersund trawl was estimated to be 0.35 (95% confidence interval 0.01, …, 18, $a_Y = –827$, s.e. 1.91). For medusae, the catchability of the Egersund trawl was estimated to be 7.8 (95% confidence interval 0.06…1070, $a_Y = 2.06$, s.e. 2.51). Only one cephalopod, *G. steenstrupi*, was common enough for estimation, and even the estimate for this species was highly uncertain (2.8, confidence interval 0.37...21). The Egersund trawl was thus more efficient than the macrozooplankton trawl for fishes, but for the other groups there was no detectable difference.

Figure 6 shows catchability estimates obtained for all species fulfilling our data selection criteria. For one species (decapod, *Acanthephyra pelagica*) the macrozooplankton trawl was significantly more efficient than the Egersund trawl, whereas the Egersund trawl was significantly better catching six fish and one medusa species. The ratio of opening areas (137) was within the confidence limits of catchability estimates for three fish species; for two of these species the point estimate was similar to the ratio of opening areas, but the estimate was very imprecise.

Regressing log catchability against log body weight showed a significant positive effect of body weight on catchability; the regression could explain 26% of the variance (Figure 7). However, the relationship was heavily influence by decapods that are relatively small and had low catchabilities; treating order as an explanatory variable resulted in a weaker positive weight effect that no longer was significant ($p = 0.51$). Egersund trawl had a marked tendency to catch larger individuals of a certain species than the macrozooplankton trawl (Figure 8).

Discussion

The catchability estimates presented in this paper showed large variability among different species of fish, cephalopods and large medusae. Towing the relatively small macrozooplankton trawl at the same depth and area for the same distance as the medium-sized Åkra trawl would be expected to yield, on average, 150 times as many pipefish, *Entelurus aequoreus,* but only about 1/45 of the catch of the platytroctid *Normichthys operosus*. Many of the smallest species caught with the macrozooplankton trawl were entirely missed by the large Egersund trawl. These findings call for care when data from different gears are synthesized.

Our analysis was based on pairs of trawl hauls taken with two gears being compared, which is the standard approach in gear comparisons (Wileman *et al.*, 1996). However, because comparing catchability of different trawls was not the primary goal of the sampling, the pairs are inherently more different than what could be achieved in a targeted study (Pelletier 1998; von Szalay and Brown, 2001; Lewy *et al.*, 2004). In particular, depth ranges were not always closely matching. This is likely to add noise to our data but not introduce a systematic bias. Furthermore, because total tow durations were long and only a single vessel was used, samples were often taken under different light regimes. This is potentially more problematic because the macrozooplankton trawl was used more often during darkness than the Åkra trawl. However, diel migrations do not change overall abundance of organisms at the station level, so the potential for bias arises only if the night-time samples with the macrozooplankton trawl were distributed unevenly between the depth layers. At the level of the whole data, the distribution was only mildly uneven (5, 3 and 3 samples from depth layers 1–3), but for individual species, imbalance might be more serious. In conclusion, we do not expect diel migrations to bias our catchability estimates in general, but for individual species this can happen.

Some species often get entangled in large meshes in the forenet and never enter the codend (e.g., Kashkin and Parin, 1983). This applies in particular to cephalopods, large specimens of jellyfish, and species like eels and the dragonfish *Stomias boa ferox*. The cause of entanglement could be fully passive (jellyfish), or an active behavioural response, i.e., an animal attacking the trawl (possibly triggered by bioluminescence) as suggested by *Stomias* that were often found hanging with their teeth in the net.

Catchabilities showing the macrozooplankton trawl to be more efficient per towed distance than the larger trawls ($\rho < 1$) probably reflect mesh selection in the codend (e.g., Gartner *et al.*, 1989; Wileman *et al.*, 1996). These are mostly small species (Figure 4, 7). Our results also show that the small-meshed macrozooplankton trawl catches, on average, smaller specimens than the large-meshed trawls (Figure 5, 8). Mesh selection is probably contributing this difference, but also the ability of larger trawls to catch large specimens able to avoid the smaller trawls might be important. Disentangling these mechanisms requires individual size data that we did not systematically collect; the size data we have suggest that both mechanisms are operating but not always simultaneously (unpublished results).

For a perfectly herded species where mesh selection in the forenet is unimportant, we would expect catchability similar to the ratio of the opening areas. For a number of fish species, the estimated catchability was in the vicinity this theoretical catchability (with the theoretical catchability within the confidence limits; Figure 1). The species with the highest catchability estimates included two platytroctids, a deepsea smelt, and a number of lanternfishes. Because the body size of these species was small to moderate (the largest individuals had a total length of about 20 cm), much of the opening area of the larger trawls had so large meshes that retention could not possibly account for the high catchability. Two complementary explanations then remain. First, herding and avoidance of large forenet meshes were important. Second, these species were relatively successful in avoiding the smaller trawl. With our data it is not possible to disentangle these mechanisms, and probably both played some role.

Both mechanisms mentioned above imply that the fish species with a high catchability must be able to maintain relatively high swimming speeds for some time. ROV observations provide some support for this statement (Trenkel *et al.*, 2004; Jon Moore, pers. comm.). This contradicts the stereotypic view of deep-sea fishes, at least the non-migrant ones, being typically phlegmatic energy savers. This stereotypic view might have been too much coloured by sit-and-wait predators, such as dragonfishes. The high catchability estimates for some species in our material, together with their relatively sleek body shapes, suggest that perhaps they are more active predators than previously thought

Only very few invertebrates had a catchability larger than one. For one decapod, *Sergestes corniculum*, the best estimate was rather high, and the confidence limit overlaps with the theoretical catchability (Figure 2). This is a relatively small species (average body weight <1 g) that must be capable of quite high swimming speed relative to its body size to be able to display behaviour implied by its catchability estimate; indeed, *S. corniculum* is known for extensive vertical migration (Roe, 1984). Alternatively, it could be that the ‘true’ catchability is much less than the best current estimate. Catchability could be estimated for two other, albeit slightly smaller, *Sergestes* species, one of which had catchability just barely larger than one, whereas the other, and the most common of the three, *S. arcticus*, had catchability much less than one. Also one medusa, *Atolla*, had a relatively high catchability. As *Atolla* are poor swimmers but often quite large, mesh selection outside the codend is probable explanation for the catchability of this animal.

A trawl does not necessarily scare off all animals. A trawl moving in water stimulates bioluminescence (Jamieson *et al.*, 2006), and light can attract fishes and is often used in fish capture (Pascoe, 1990; Gabriel *et al.*, 2005). To what extent this process influences catchability of deep-pelagic nekton is unknown, although attaching electric lights to trawls is known to increase their catchability at least for certain species (Clarke and Pascoe, 1985, 1998; Clarke *et al.*, 1986; Swinney *et al.*, 1986), but also to decrease catchability of certain other species (Clarke *et al.*, 1986). Whether attraction caused by bioluminescence is differently influencing the trawls considered here is unknown. Another source of attraction are the animals in the trawl itself: codend feeding by active predators such as cephalopods is known to occur (Herring, 2002). Such predators are unlikely to be caught by the trawl, but their feeding in the codend would reduce catches of prey species. Also species not attracted by the catch but opportunistically feeding in codend would have a similar effect. While codend feeding is difficult to show, there was nothing suggesting that this was important in our samples.

Our analyses suggest some diel effects on catchability. Because we sampled more or less the whole water column, diel migrations alone are not sufficient to cause systematic diel catchability effects. However, imbalanced day and night-time sampling with respect to the trawl could give rise to artefactual diel effects. This could explain the higher day-time catches when gear × day/night interaction was not allowed. With the interaction term present, the analyses tended to suggest higher catches during darkness. This is compatible with visual avoidance of trawls in the upper parts of the water column with some daylight.

Traditionally, trawl comparisons have focused primarily on differences in size selectivity (e.g., Millar, 1992; Erickson *et al.*, 1996; Wileman *et al.*, 1996; Millar and Holst, 1997; Millar and Fryer, 1999; Bethke *et al.*, 1999; Kvamme and Isaksen, 2004). There has been less focus on differences in catch rates at species level (Wassenberg *et al.*, 1997; Sangster and Breen, 1998, Fock *et al.*, 2002; West, 2002; Lewy *et al.*, 2004; Porteiro, 2005). Studies of fishing power of survey vessels may involve different trawls but these are confounded with vessel effects (von Szalay and Brown, 2001; Helser *et al.*, 2004). Common to most of these studies is the methodological similarity to this study in that they analyzed effort-standardized catch rates using linear statistical models. Porteiro (2005) adopted a different approach, using multivariate statistics to account for gear differences. The studies by Wassenberg *et al.* (1997), West (2002), Lewy *et al.* (2004) and Porteiro (2005) point to big differences between different trawls in catchability as well as species that are caught. On the other hand, von Szalay and Brown (2001) and Helser *et al.* (2004), comparing research and commercial fishing vessels using bottom trawls, showed moderate differences in catchability of key species and that combining data from different platforms is possible and possibly worthwhile.

Helser *et al.* (2004) treated gear (or more precisely, vessel) as random effect. This is sensible when many gears are being compared and one is interesting in overall gear effects, not specific gear types. In this paper, gear was treated as a fixed effect because there were only three trawl types (of which only two could be compared at time) and we were interested in those very trawls, so that the data from different trawls could ultimately be merged. Our approach necessitates choosing one trawl as the reference trawl, here the macrozooplankton trawl. Dividing catches obtained with one of the large trawls by the corresponding catchability estimate gives an estimate of catch that would have been caught with the macrozooplankton trawl, given the same effort in terms of towed distance. As the effective mouth area of the macrozooplankton trawl is known, catches per towed distance with the other trawls can be converted to density estimates in volume that would have been caught with the macrozooplankton trawl. Notice, however, that this does not imply that the estimate is 'correct', even if the catchability estimate is correct. If a species is rather successful in avoiding the macrozooplankton and less so with a larger trawl (this would be seen as a catchability estimate exceeding the ratio of the opening areas), converting the observations from the large trawl to the macrozooplankton trawl scale underestimates the abundance. Using the macrozooplankton trawl as the reference trawl must therefore be seen as a pragmatic choice.

Main application of our catchability estimates is community characterization of pelagic fauna along the Mid-Atlantic Ridge. If data from different gears are analyzed together, ordination methods tend to cluster them separately, as observed in other studies (e.g., West, 2002). However, correction with catchability estimates nests the Åkra trawl samples within the macrozooplankton trawl samples in multivariate analysis (Sutton *et al.*, 2008). Thus, the systematic differences between the gears appear to be successfully removed. Of course, the catchability estimates obtained here only apply for the material studied in this paper. The estimates provide some guidance for other areas and times, but care should be taken, especially during different seasons and where populations with different size composition are encountered.

The focus of this paper on catchability tends to highlight challenges rather than the benefits arising from complementary characteristics of different gears. The first impression is that relatively little is gained or lost with using larger trawls. For the Åkra trawl, catchabilities estimated for major taxonomic groups showed that the macrozooplankton trawl was significantly more efficient than the Åkra trawl for decapods, whereas the opposite was true for fishes; for other groups the difference was insignificant and none of the differences were large in magnitude. The results are similar for the Egersund trawl, except that the efficiency gain for fishes was substantial. However, this ignores the fact that the Egersund trawl missed many smaller species, the specimens in the catch were more damaged, and that the trawl is more time-consuming to operate. On the other hand, even within a species, the small and large trawls did not necessarily catch similar specimens: larger trawls with large meshes tended to miss smaller specimens, but also to catch larger specimens than the small trawl. Indeed, some of the specimens appeared unusually large for the species. A study targeting the whole life cycle of a species might therefore need to use both small and large trawls.

Furthermore, different trawls may catch entirely different species. Because of the data selection applied here, our results only apply to species caught with both trawl types under comparison. However, several species were caught only with one trawl type (corresponding to a catchability approaching either zero or infinity). The macrozooplankton trawl caught 31 fish species not caught with the Åkra trawl, whereas the corresponding number for the Åkra trawl is 96; 108 species were caught with both trawls. For rare species this is likely by chance alone, and the total sampling effort in terms of distance trawled was greater for the Åkra trawl, so care is needed before drawing conclusions from these numbers. Preliminary analyses using a randomization approach (e.g., Manly, 1997), pooling macrozooplankton trawl samples so that the distance trawled was similar to the Åkra trawl samples, suggested that both Åkra and macrozooplankton caught slightly more species than expected by chance, but that the differences are not significant. Results for cephalopods were similar.

Using different gears to sample an ecosystem is both an opportunity and a challenge. The results presented here and in Sutton *et al.* (2008) suggest that the challenges are potentially manageable. It must be acknowledged that two trawls will sample a broader range of species as well as a broader size spectrum within a species than a single trawl, and that something is lost if only one trawl type can be employed. Whether the extra effort and costs needed to operate more than one trawl type are warranted will depend on the specific goals. For routine monitoring the answer might well be negative, whereas more comprehensive ecosystem studies or faunal inventories should seriously consider using more than one trawl. Indeed, the need to use more than one sampling method is often acknowledged in faunal surveys of terrestrial and freshwater systems (e.g., Southwood and Henderson, 2000; Gunzburger, 2007; Ribeiro-Júnior *et al.*, 2008), but less so in deep oceanic surveys. If one then chooses a multi-trawl approach, care is needed so that the sampling design is sufficiently balanced to allow quantitatively merging data from different sources.

Supplementary material

The following supplementary material is available at ICESJMS online:

Details of the macrozooplankton and Åkra trawl hauls included in the analysis (Table S1).

Details of the Egersund trawl hauls included in the analysis (Table S2).

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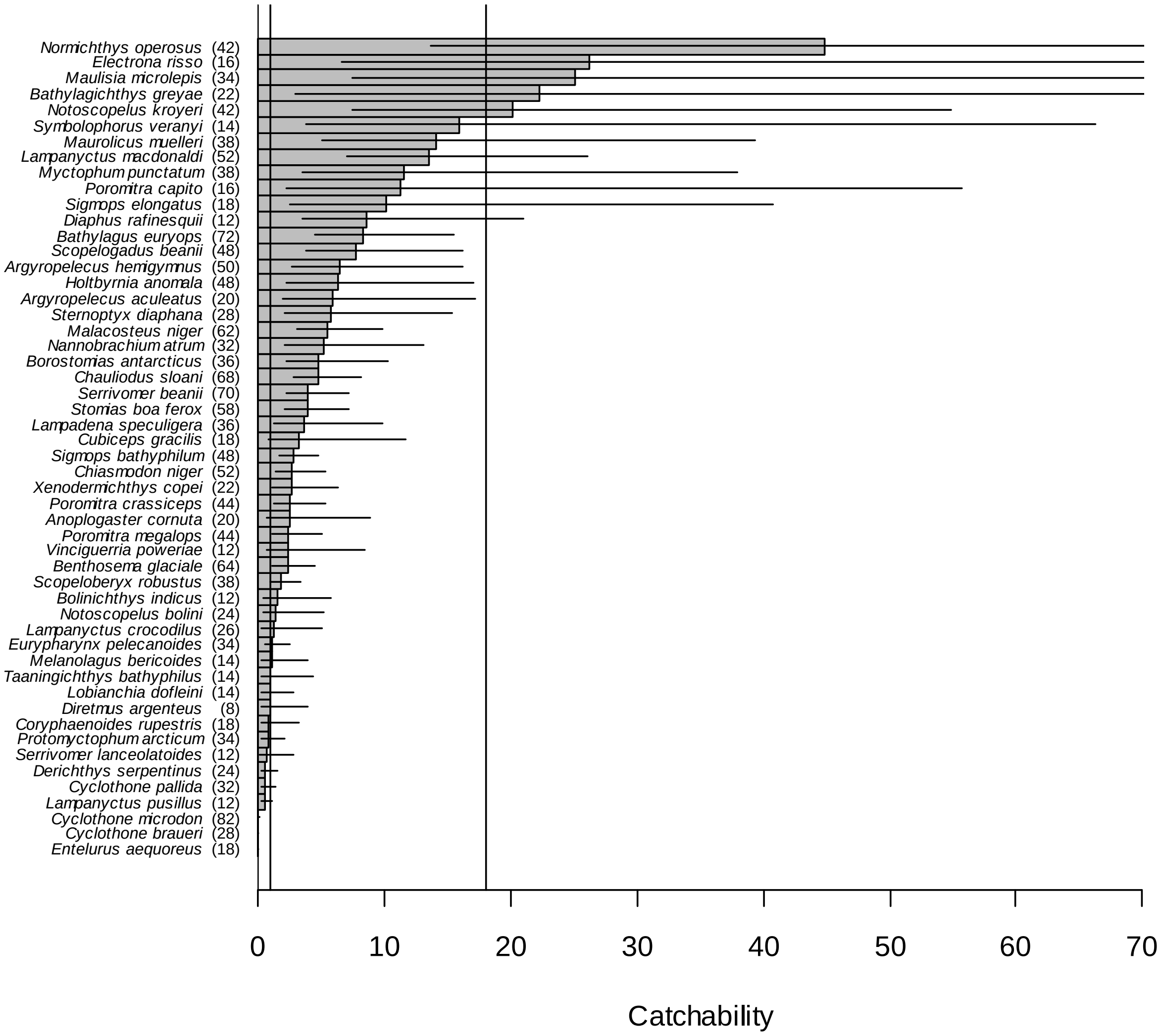

Figure 1. Estimates of catchability of 52 fish species with the Åkra trawl, a medium-sized pelagic trawl with graded meshes, relative to the macrozooplankton trawl. Horizontal bars give 95% confidence limits (for *N. operosus*, *E. risso*, *M. microlepis* and *B. greyae* these extend outside the plot area to respectively 148, 104, 85 and 170). Vertical lines give reference values that correspond to equal catchability (1) and to the ratio of opening areas (18). Sample size is indicated in parenthesis after the species name.

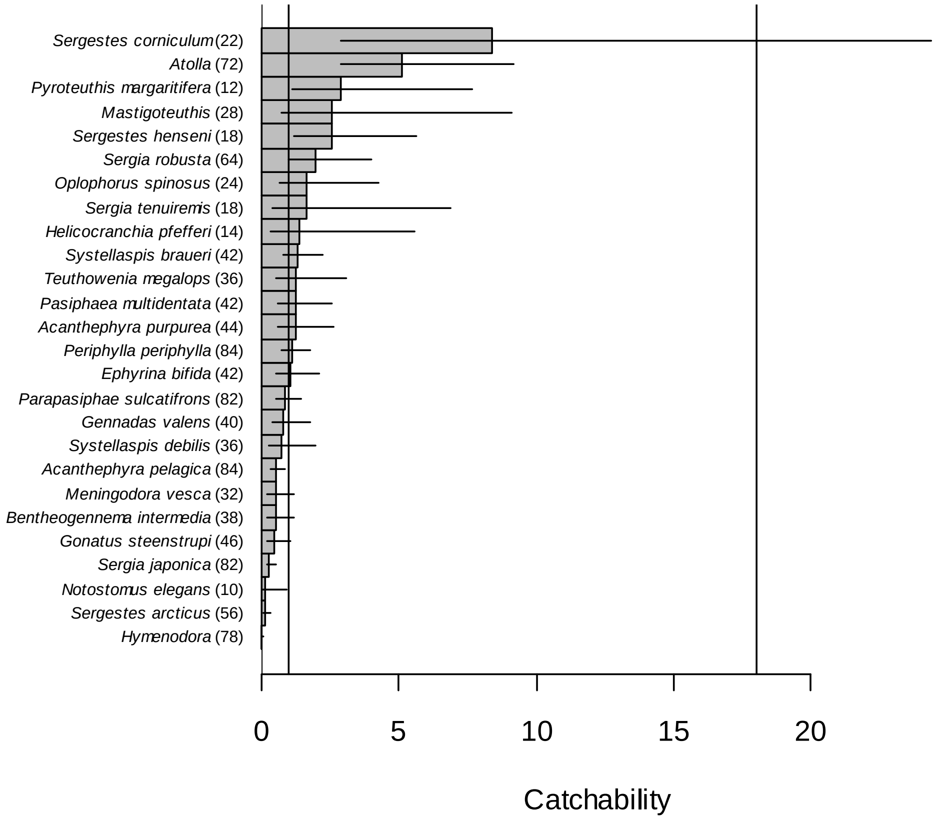

Figure 2. Estimates of catchability of two medusa, five cephalopod and 19 decapod species (or genera) with the Åkra trawl relative to the macrozooplankton trawl. Horizontal bars give 95% confidence. Vertical lines give reference values that correspond to equal catchability (1) and to the ratio of opening areas (18). Sample size is indicated in parenthesis after the species name.

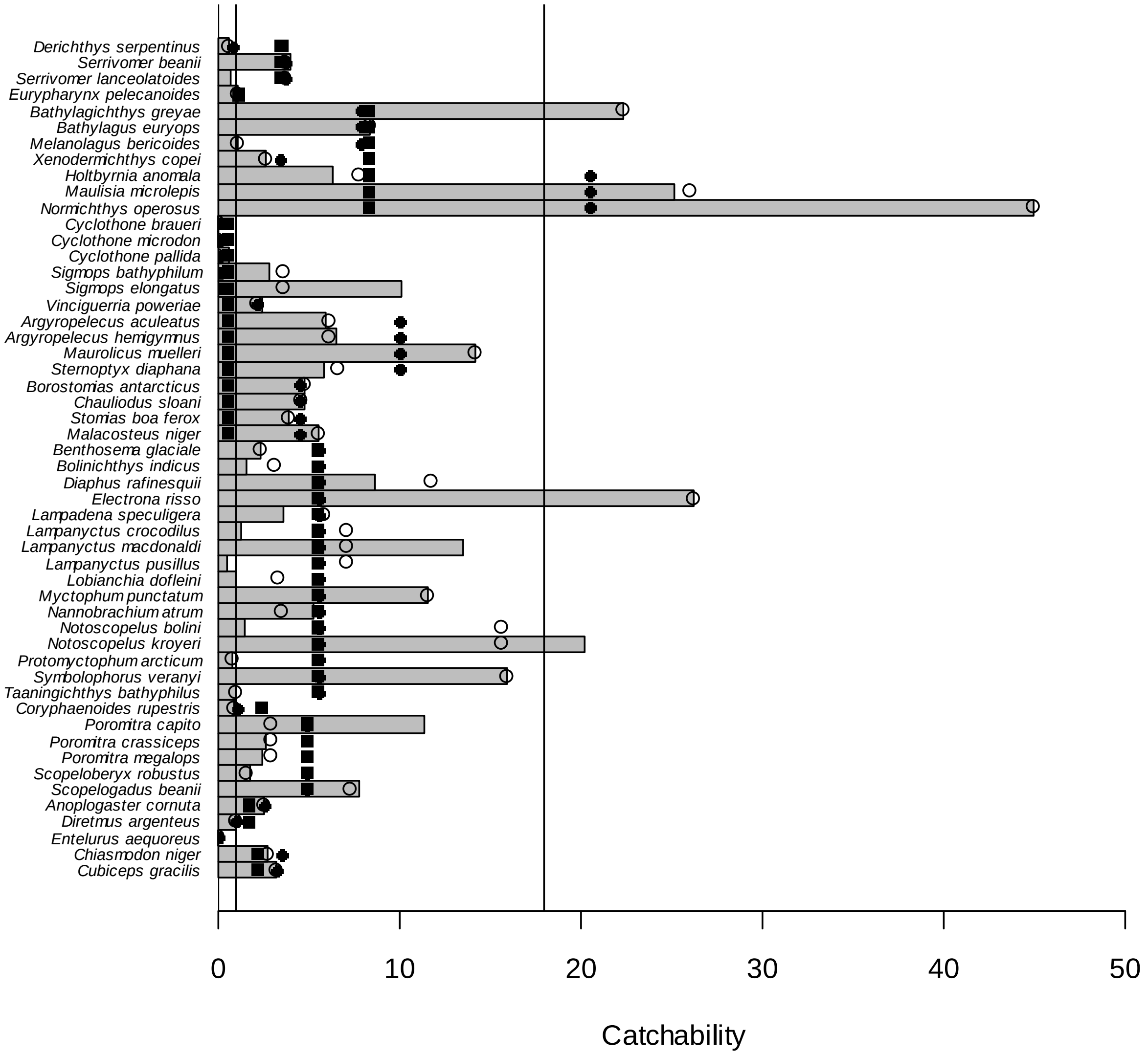

Figure 3. Estimates of catchability (in numbers) of fish taxa for the Åkra trawl relative to the macrozooplankton trawl. For each fish for which catchability was estimated at species level (grey bars), we also give the estimates at the generic (open circles), familial (black circles) and ordinal levels (black squares). For some orders there was only one species and all estimates are identical. The taxa are sorted following Nelson (2006).

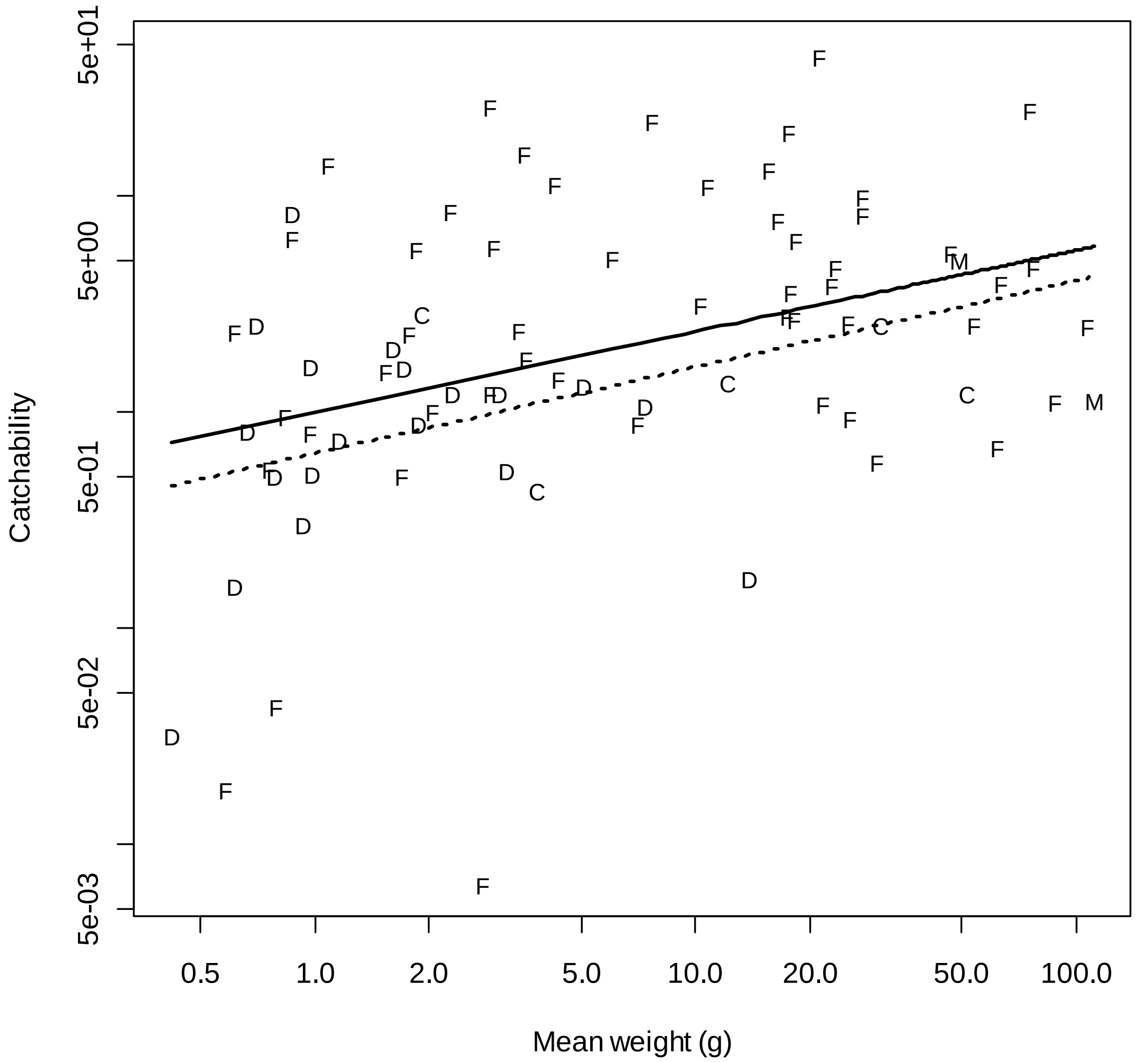

Figure 4. Relationship between the mean species-specific weight and the estimated catchability for the Åkra trawl relative to the macrozooplankton trawl. Letters are used to indicate a taxon: F = fish, D = decapod, C = cephalopod, M = medusae. Mean weight is calculated as the mean individual weight (catch weight/catch numbers) over all trawl hauls in the comparison. Thick regression line is for an ordinary regression, and the dotted regression line is for a mixed model treating order as a random effect. Notice the logarithmic scale on both axes.

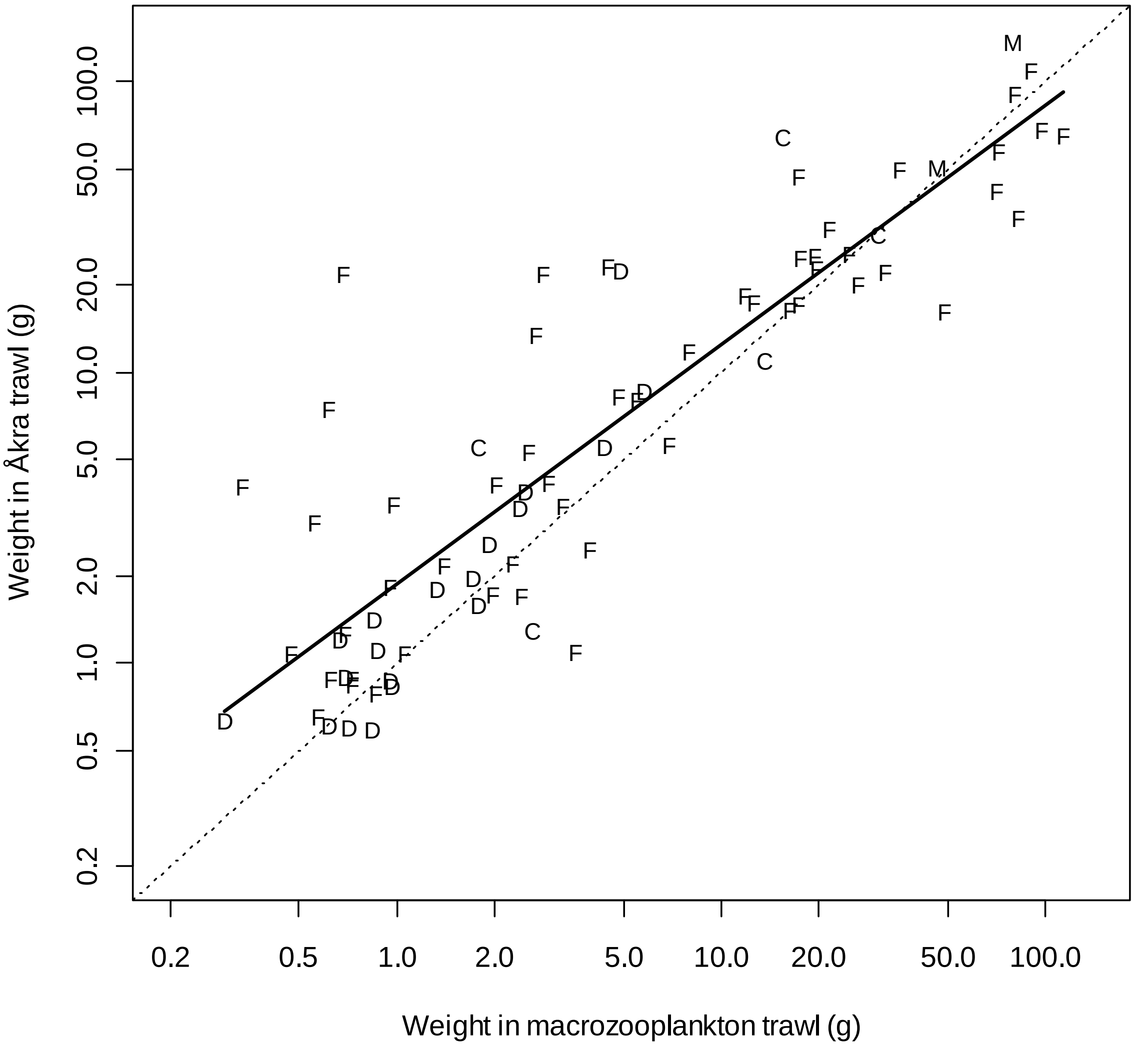

Figure 5. Relationship between the mean species-specific weight between the macrozooplankton and Åkra trawl catches. The corresponding regression model is illustrated by a thick line (R^2 = 78%). Letters are used to indicate a taxon: F = fish, D = decapod, C = cephalopod, M = medusa. Mean weight is calculated as the mean individual weight (catch weight/catch numbers) for each combination of species and trawl type. Diagonal is shown as dotted line. Notice the logarithmic scale on both axes.

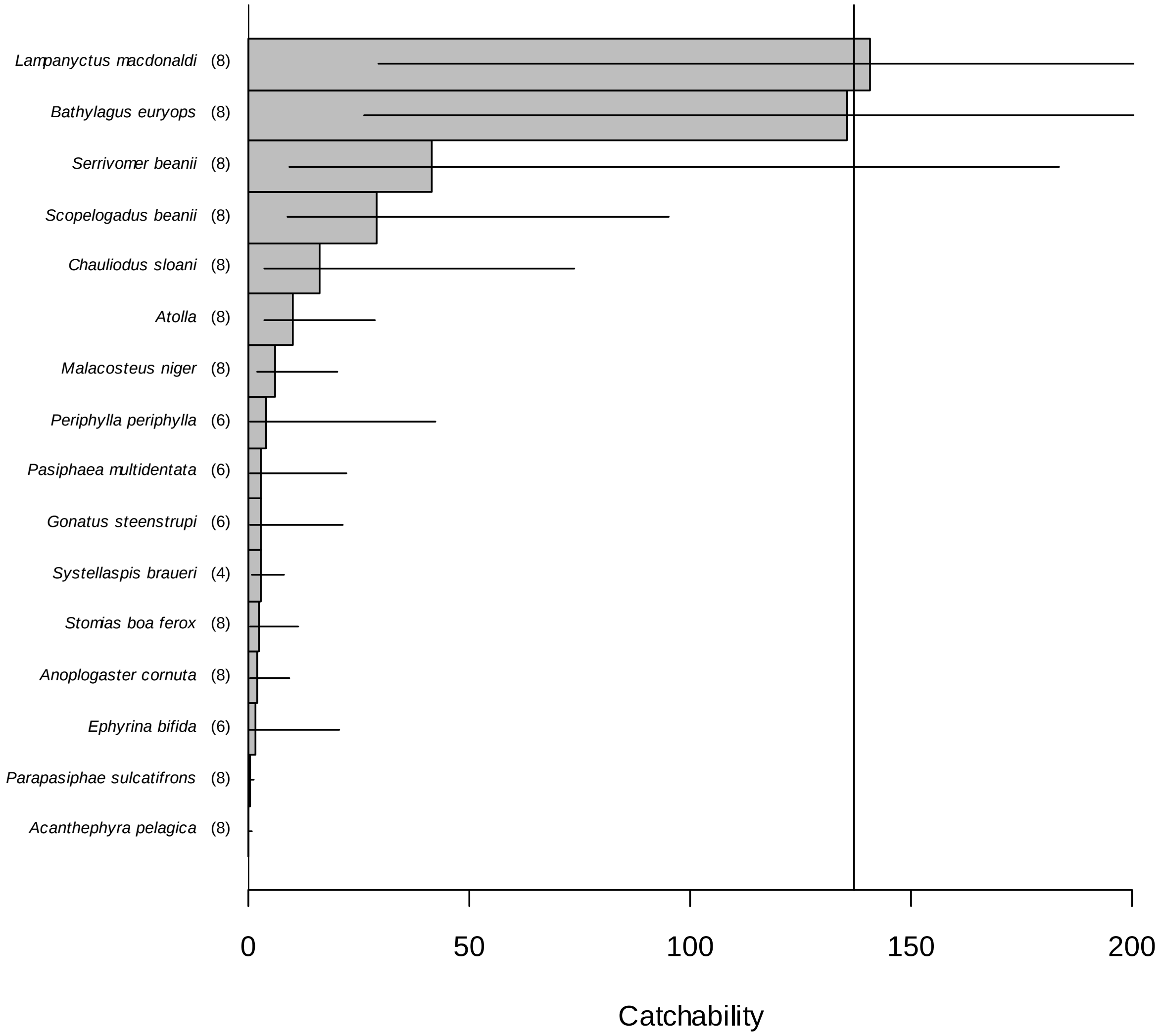

Figure 6. Estimates of catchability of eight fish and eight invertebrate species with the Egersund trawl, a large pelagic trawl with graded meshes, relative to the macrozooplankton trawl. Horizontal bars give 95% confidence limits (for *Lampanyctus macdonaldi* this extends outside the plot to 674 and for *Bathylagus euryops* to 697). The vertical line gives a reference value that corresponds to the ratio of opening areas (137). Sample size is indicated in parenthesis after the species name.

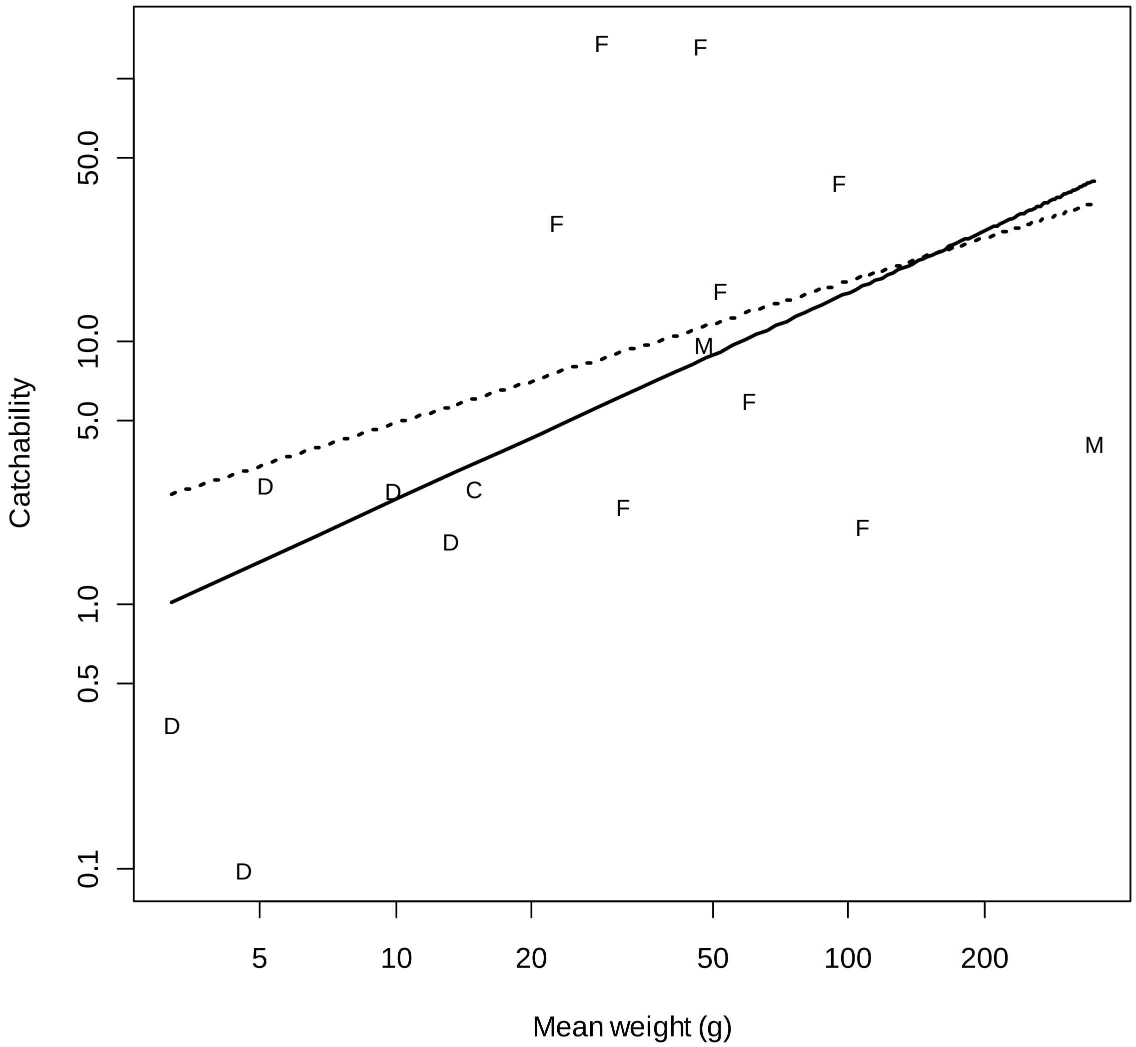

Figure 7. Relationship between the mean species-specific weight and the estimated catchability for the Egersund trawl relative to the macrozooplankton trawl. See Figure 4 for further explanations.

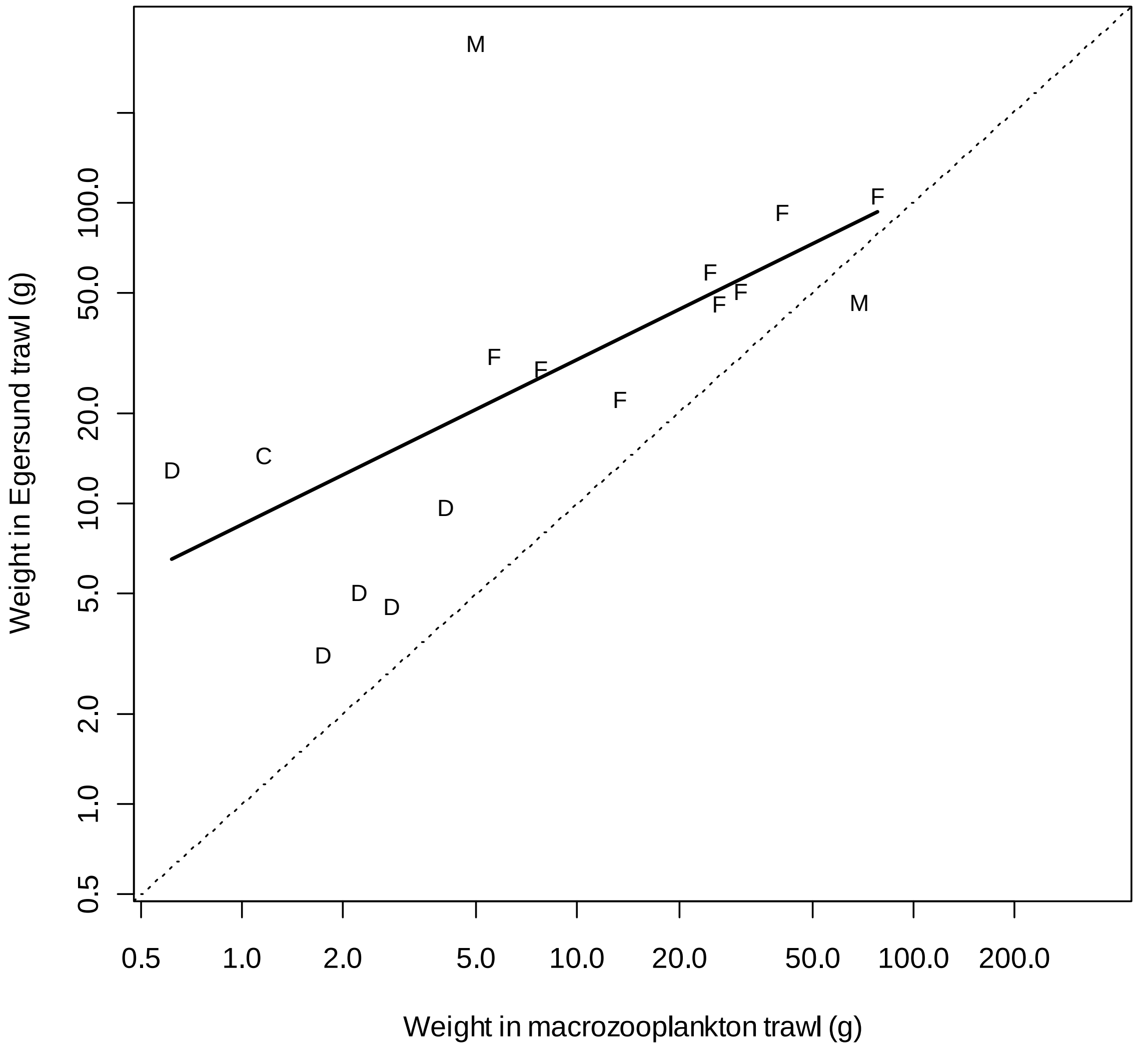

Figure 8. Relationship between the mean species-specific weight between the macrozooplankton and Egersund trawl catches. The corresponding regression model is illustrated by a thick line ($R^2 = 42\%$). See Figure 5 for further explanations.

Tables

Table 1. Trawls used on the RV "G.O. Sars" during the MAR-ECO cruise in summer 2004 (see Wenneck *et al.*, 2008, for further details). Macrozooplankton and Åkra trawls were equipped with a "MultiSampler" that enabled opening and closing several codends at pre-programmed depths (Engås *et al.*, 1997).

Trawl	Description	Mesh size (stretched) in the codend (mm)	Approximate opening area (m^2)	Ratio of opening areas (macrozooplankton trawl = 1)	Typical towing speed (nm h^{-1})
Macrozooplankton	5 codends, uniform meshes	6	36	1	2
'Åkra' (medium-sized fish trawl)	3 codends, graded meshes	22	660	18	3
'Egersund' (large fish trawl)	1 codend, graded meshes	50	5 000	137	3