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

3

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6

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

22

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

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## 38 Introduction

39 Trawls are an effective and widely used method for sampling nekton as they sample large  
40 volumes of often sparsely distributed organisms and allow direct species identification and  
41 further individual-level observations (e.g., length measurements, aging, and stomach contents  
42 analysis) to be made from specimens taken on board. However, one type of trawl cannot  
43 perform well for all types of nekton that range in size from few millimetres to metres: overall  
44 trawl size — which largely determines its ability to capture fast-swimming organisms — has  
45 to be traded off against mesh size, which determines the retention of small organisms.  
46 Furthermore, fine-meshed trawls cannot be towed with speeds high enough to capture species  
47 that show avoidance behaviour. A natural solution is to use more than one type of trawl with  
48 complementary characteristics. However, combining data from different gears is not trivial  
49 (e.g., Kashkin and Parin, 1983; Wassenberg *et al.* 1997; Pelletier, 1998; von Szalay and  
50 Brown, 2001; Fock *et al.*, 2002; West, 2002; Helser *et al.*, 2004; Lewy *et al.*, 2004; Porteiro,  
51 2005).

52 *Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic* (MAR-ECO) is a  
53 Census of Marine Life project that is set up to describe and understand the patterns of  
54 distribution, abundance and trophic relationships of the organisms inhabiting the mid-oceanic  
55 North Atlantic, and to identify and model ecological processes that cause variability in these  
56 patterns (Bergstad and Godø, 2002; Bergstad *et al.*, 2008; see also [www.mar-eco.no](http://www.mar-eco.no)). A major  
57 contribution to this project was a two-month cruise of the RV “G.O. Sars” in summer 2004  
58 surveying the ecosystems along the Mid-Atlantic Ridge from Iceland to the Azores (Wenneck  
59 *et al.*, 2008). In order to get quantitative and representative samples from various types and  
60 size classes of pelagic nekton, three different trawls were used (Table 1): a macrozooplankton  
61 trawl and two fish trawls, the medium-sized Åkra trawl and the larger Egersund trawl. These

62 trawls differ substantially in their overall size as well as in mesh sizes. Both the Åkra and  
63 macrozooplankton trawls were used systematically, following a predetermined sampling  
64 scheme (respectively 15 and 17 successful hauls), whereas the Egersund trawl was used  
65 opportunistically to sample acoustically “interesting” registrations (four successful hauls). For  
66 analyzing these data, for example to characterize the species assemblages (Sutton *et al.*,  
67 2008), it would be desirable to combine data from all three gears. However, simply merging  
68 of the data across gears would be questionable as the trawls differ considerably in their  
69 essential characteristics that determine how efficient they are catching pelagic organisms.

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

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

87 should increase catchability, and increasing towing speed should have a similar effect, to  
88 the extent that the so-called bucket effect does not come into the play. Also rigging may  
89 affect the noise and bioluminescence caused by the approaching trawl (Jamieson *et al.*,  
90 2006) and thus the likelihood of early detection and avoidance, but we have no data on  
91 these parameters. Expected effect on catchabilities: Egersund>Åkra>macrozooplankton.

92 • *Retention through mesh selection.* Mesh selection depends on the mesh size relative to the  
93 size of individuals as well as their body shape and form (Barkley, 1972; Gartner *et al.*,  
94 1989; Millar, 1992; Wileman *et al.*, 1996; Bethke *et al.*, 1999). Expected effect on  
95 catchabilities: Egersund<Åkra< macrozooplankton.

96 • *Herding effect.* In pelagic trawls with decreasing meshes toward the codend, capture is  
97 based not only on filtering but also on behavioural response known as herding (Lee *et al.*,  
98 1996; Valdemarsen, 2001): fish inside the trawl try to avoid the meshes and do not swim  
99 through the meshes even if they could do so, but are instead herded in the middle of the  
100 trawl, eventually encountering meshes that are small enough for retention. In bottom  
101 trawls, trawl doors and bridles cause the herding (Wardle, 1993; Ramm and Xiao, 1996;  
102 Sangster and Breen, 1998; Winger *et al.*, 2004), but the extent that this happens in pelagic  
103 trawls is unknown. Visual detection of trawls in deep water is made possible by  
104 bioluminescence caused by the trawl itself (Jamieson *et al.*, 2006). Expected effect on  
105 catchabilities: potentially important in Egersund and Åkra trawls, probably unimportant in  
106 macrozooplankton trawl.

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

110 The value of catchability estimates comes from three sources. First, catchability  
111 coefficients form the quantitative basis on which data collected with different gears can be

112 compared. Furthermore, catchability coefficients allow for description of the performance of  
113 trawls, for example, effective mouth area. Taken together, catchability estimation contributes  
114 to improved monitoring strategies for the deep ocean. And finally, catchability estimates also  
115 provide indirect information on behaviour of deep-living biota.

## 116 Materials and methods

117 Wenneck *et al.* (2008) give a detailed account on methods employed in collecting the  
118 material. We include fishes, cephalopods, decapods and large medusae (disc diameter >1 cm)  
119 in our analyses. The analyses were run at five taxonomic levels, at the level of species, genus,  
120 family, order and class, following taxonomy by Nelson (2006) for fishes, Sweeney and Roper  
121 (1998) for cephalopods, and Crosnier and Forest (1973) and Vereshchaka (2000) for  
122 decapods. *Atolla*, *Mastigoteuthis* and *Hymenodora* were not identified to species level, but for  
123 simplicity we refer to them also as ‘species’.

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

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

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

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



160 Samples were classified as daytime, dusk, night or dawn samples using sunrise and sunset  
161 times calculated for each sampling location and date. Sunrise and sunset times were  
162 calculated using the CBM model of Forsythe *et al.* (1995) to estimate day length and the  
163 equation of time and longitude to estimate solar noon. A dusk sample was defined as a sample  
164 that was at least partially taken during the period from one hour before sunset to one hour  
165 after. Similarly, dawn samples were those that overlapped with the period from one hour  
166 before sunrise to one hour after sunrise. Our sampling was imbalanced with respect to gear  
167 and diel phase: the macrozooplankton trawl was used more often during night (11 samples, or  
168 26% of the total) than the Åkra trawl (1 sample, 2.4%); the proportions of dusk and dawn  
169 samples were similar (respectively six and seven samples).

## 170 Statistical methods

171 We assume that selectivity of trawl  $y$  relative to the reference trawl  $x$  can be expressed with  
172 the linear relationship  $C_y \sim \rho C_x$ , where  $C$  refers to a catch standardised for towed distance  
173 and  $\rho$  is relative catchability;  $\rho = 1$  corresponds to equal catchability whereas smaller ( $0 \leq \rho <$   
174  $1$ ) or larger values indicate that trawl  $y$  is respectively less or more effective than the reference  
175 trawl  $x$ . The most intuitive way to estimate  $\rho$  is to apply a logarithmic transformation on both  
176 sides of this equation (e.g., Wassenberg *et al.*, 1997), yielding  $\log(C_y) \sim a_0 + \log(C_x)$ , where  
177  $a_0 = \log(\rho)$ . However, this model has a major disadvantage, namely that information in zero  
178 catches cannot be used. Therefore, we chose to use a more general approach, expressing catch  
179 using the generalized linear model

$$180 \quad \log(c_i) \sim a_x + a_y \text{trawl}_i + \log(d_i),$$

181 where  $c_i$  is catch numbers of trawl  $i$ ,  $a_x$  is an estimated parameter that corresponds to the  
182 mean logarithmic catch of the reference trawl  $x$ ,  $a_y$  gives the mean logarithmic difference in

183 catch between the two trawls, trawl Y is an indicator variable that is 1 for trawl Y and 0  
184 otherwise, and  $d_i$  is trawled distance treated as an offset variable. This model allows great  
185 flexibility. In particular, we can treat catches in numbers as counts, assumed to represent a  
186 random variable with a discrete distribution that includes zero. Poisson and negative binomial  
187 distributions are obvious choices, in which case the logarithm on the left hand side of  
188 equation (1) is naturally treated as the link function. Because our data are mostly more  
189 variable than the Poisson distribution would suggest (seen as overdispersion in Poisson  
190 models), we chose to use the negative binomial distribution; inspection of the fitted models  
191 suggested that the model describes the data well. Nevertheless, it was encouraging that the  
192 choice of the error distribution had generally minute influence on the catchability estimates.

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

201 Depth, calculated as the average of a haul's starting and finishing depth (see Appendix),  
202 could be used routinely. However, because our measure of depth is not precise, we did not use  
203 depth for species that had a relatively narrow vertical range of <500 metres (*E. aequoreus* and  
204 five myctophids: *Lampanyctus pusillus*, *Vinciguerria poweriae*, *Diaphus rafinesquii*,  
205 *Symbolophorus veranyi* and *Electrona risso*). For all other species, we centered the depth data  
206 so that species-specific mean depth was zero and estimated models with linear and/or  
207 quadratic depth terms (the quadratic term allows for catch rates to peak at intermediate

208 depths). The model that had the lowest Akaike Information Criterion (with correction for  
209 small sample sizes,  $AIC_c$ ) was chosen as the final model. A depth term was included for 51  
210 out of 78 species in our data (65%). Nevertheless, in the majority of cases estimates of  
211 catchability were little influenced by consideration of depth effects. In a few cases where  
212 larger changes occurred, these were supported by non-negligible improvements in  $AIC_c$  and  
213 were considered biologically sensible. For example, catchability for *Lampanyctus crocodilus*  
214 was  $\rho = 0.43$  without depth effect, and  $\rho = 1.2$  with linear depth effect ( $\Delta AIC_c = -4.7$ ); neither  
215 estimate is significantly different from 1 but the latter one is more reasonable for a relatively  
216 large-sized species. Furthermore, when the best model involved a depth term, the standard  
217 error for the catchability was usually somewhat smaller than without the depth term.

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

## 224 Results

### 225 Macrozooplankton versus Åkra trawl

226 Catchability of the Åkra trawl relative to the macrozooplankton trawl for all fishes was 2.3  
227 (95% confidence interval for catchability 1.6...3.4,  $a_Y = 0.838$ , s.e. 0.197) for catch in  
228 numbers. For all cephalopods, the catchability of the Åkra trawl was estimated to be 0.38  
229 (95% confidence interval 0.14...1.03,  $a_Y = -0.966$ , s.e. 0.510). For large medusae, the  
230 catchability of the Åkra trawl was estimated to be 3.05 (95% confidence interval 0.50...19,

231  $a_Y = 1.12$ , s.e. 0.926). For decapods, the catchability of the Åkra trawl was estimated to be  
232 0.57 (95% confidence interval 0.35...0.93,  $a_Y = -0.566$ , s.e. 0.251). Thus, the Åkra trawl was  
233 more efficient in catching fishes than the macrozooplankton trawl, whereas the opposite was  
234 true for decapods. For medusae and cephalopods the results were inconclusive, although the  
235 results were suggestive of a tendency of the macrozooplankton trawl to catch more  
236 cephalopods than the Åkra trawl.

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

245 We estimated catchability for 26 invertebrate species (Figure 2). For the majority of these  
246 (65%), the Åkra and macrozooplankton trawls were not significantly different, and only for  
247 the decapod shrimp *Sergestes corniculum* did the confidence limits overlap with the  
248 theoretical catchability derived from the ratio of mouth areas ( $\rho = 18$ ). Decapods in general  
249 showed a very large spread of catchabilities, ranging from 0.033 in *Hymenodora* to 8.4 in *S.*  
250 *corniculum*, with five species having catchability significantly less than one, whereas two  
251 species (both from genus *Sergestes*) had catchability that was significantly larger than one.  
252 Also one medusa (*Atolla*) and one cephalopod (*Pyroteuthis margaritifera*) had catchabilities  
253 significantly larger than one.

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

259 Some variability in the catchability estimates can be explained by body size: catchability  
260 was positively related to mean body weight (linear model with log-transformation of both  
261 variables:  $F_{1,76} = 12.0$ ,  $p = 0.001$ ), and on average, doubling the body weight increased  
262 catchability by a factor of 1.46 (95% confidence interval 1.18...1.80). However, the  
263 relationship was noisy (Figure 4) and only a small proportion of variability in the data could  
264 be explained ( $R^2 = 14\%$ ). Taxon-specific differences remained: including ‘order’ as an  
265 explanatory variable significantly improved the fit ( $F_{12,64} = 3.28$ ,  $p = 0.001$ ,  $R^2 = 47\%$ ); the  
266 effect was weaker but still significant ( $F_{9,64} = 2.16$ ,  $p = 0.037$ ,  $R^2 = 36\%$ ) if three orders  
267 represented by only one species (Gadiformes, Saccopharyngiformes, Syngnathiformes) were  
268 excluded. Without mono-specific orders and using the abundantly-sampled lanternfishes  
269 (Myctophiformes) as the reference order, we saw that eels (order Anguilliformes), decapods  
270 and cephalopods (Oegopsida) had a lower catchability than their weight would suggest;  
271 medusae and other fish orders were not significantly different from lanternfishes. Similarly,  
272 the fit could be improved using family (instead of order) as an explanatory variable, either  
273 with ( $F_{27,49} = 2.86$ ,  $p = 0.001$ ,  $R^2 = 66\%$ ) or without mono-specific families ( $F_{12,49} = 3.41$ ,  $p =$   
274  $0.001$ ,  $R^2 = 58\%$ ). Without mono-specific families and using the abundantly-sampled  
275 lanternfishes (Myctophidae) as the reference family, we saw that when accounting for weight  
276 differences, two fish families (Gonostomatidae and Serrivomeridae) and one decapod  
277 (Oplophoridae) and one cephalopod family (Cranchiidae) had a lower catchability than their  
278 weight would suggest. Treating order or family as a random effect, instead of a fixed effect as

279 above, gave a similar estimate for the average effect of doubling the body size (order as a  
280 random effect: 1.49, 95% confidence interval 1.17...1.90; family as a random effect: 1.58,  
281 95% confidence interval 1.25...1.99) as obtained above for the model without taxonomic  
282 information (1.46). We also considered taxon-specific weight effects on catchability but our  
283 data were too few to allow detecting significant effects.

284 Diel effects could also influence catchability. However, our data were imbalanced, such  
285 that diel and gear effects could become confounded. To reduce this problem, we analysed diel  
286 effects only at higher taxonomic levels. For fishes, including diel phase (day, dusk, night and  
287 dawn; see the methods) did not significantly improve the model where gear was used as the  
288 explanatory variable ( $\chi^2_3 = 4.25$ ,  $p = 0.236$ ), but it did so when also 'order' was included  
289 ( $\chi^2_3 = 8.47$ ,  $p = 0.037$ ). The latter model suggested that day-time catches tended to be higher  
290 compared night-time catches; dawn and dusk catches were not significantly different from  
291 night catches. This effect could arise from the Åkra trawl having more daytime samples than  
292 the macrozooplankton trawl.

293 In order to make the data more balanced, we therefore regrouped dawn and dusk catches  
294 with night-time catches. Analysing the data by order suggested that night-time catches were  
295 significantly higher for orders Osmeriformes and Syngnathiformes. A significant gear  $\times$   
296 day/night interaction was detected for Anguilliformes, Osmeriformes, and Stomiiformes,  
297 suggesting that the Åkra trawl was relatively more efficient during darkness for the two first  
298 orders, but the opposite held true for the last one. For cephalopods, a significant diel effect  
299 was apparent ( $\chi^2_3 = 8.19$ ,  $p = 0.042$ ), but this disappeared if a single large dusk catch of  
300 *Gonatus steenstrupi* was omitted. Also for medusae, the data suggested a diel effect ( $\chi^2_3 =$   
301 8.00,  $p = 0.046$ ): dawn catches appeared on average higher than night-time catches. In  
302 contrast to the aforementioned groups, diel effects appeared relatively strong in decapods:

303 inclusion of the diel phase greatly improved the model fit ( $\chi^2_3 = 27.0$ ,  $p < 0.001$ ), with dusk  
304 catches being much higher than night-time catches. Furthermore, there was a significant  
305 interaction between trawl and diel phase ( $\chi^2_3 = 30.7$ ,  $p < 0.001$ ): the Åkra trawl appeared less  
306 efficient in catching decapods during the day and dusk compared to the macrozooplankton  
307 trawl.

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

#### 314 Macrozooplankton versus Egersund trawl

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

319 Catchability of the Egersund trawl relative to the macrozooplankton trawl for fishes in  
320 general was 57 (95% confidence interval 19...168,  $a_y = 4.04$ , s.e. 0.55). For all decapods, the  
321 catchability of the Egersund trawl was estimated to be 0.35 (95% confidence interval 0.01, ...,  
322 18,  $a_y = -827$ , s.e. 1.91). For medusae, the catchability of the Egersund trawl was estimated  
323 to be 7.8 (95% confidence interval 0.06...1070,  $a_y = 2.06$ , s.e. 2.51). Only one cephalopod,  
324 *G. steenstrupi*, was common enough for estimation, and even the estimate for this species was  
325 highly uncertain (2.8, confidence interval 0.37...21). The Egersund trawl was thus more

326 efficient than the macrozooplankton trawl for fishes, but for the other groups there was no  
327 detectable difference.

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

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

341

## 342 Discussion

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



349 large Egersund trawl. These findings call for care when data from different gears are  
350 synthesized.

351 Our analysis was based on pairs of trawl hauls taken with two gears being compared,  
352 which is the standard approach in gear comparisons (Wileman *et al.*, 1996). However,  
353 because comparing catchability of different trawls was not the primary goal of the sampling,  
354 the pairs are inherently more different than what could be achieved in a targeted study  
355 (Pelletier 1998; von Szalay and Brown, 2001; Lewy *et al.*, 2004). In particular, depth ranges  
356 were not always closely matching. This is likely to add noise to our data but not introduce a  
357 systematic bias. Furthermore, because total tow durations were long and only a single vessel  
358 was used, samples were often taken under different light regimes. This is potentially more  
359 problematic because the macrozooplankton trawl was used more often during darkness than  
360 the Åkra trawl. However, diel migrations do not change overall abundance of organisms at the  
361 station level, so the potential for bias arises only if the night-time samples with the  
362 macrozooplankton trawl were distributed unevenly between the depth layers. At the level of  
363 the whole data, the distribution was only mildly uneven (5, 3 and 3 samples from depth layers  
364 1–3), but for individual species, imbalance might be more serious. In conclusion, we do not  
365 expect diel migrations to bias our catchability estimates in general, but for individual species  
366 this can happen.

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

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

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

394 Both mechanisms mentioned above imply that the fish species with a high catchability  
395 must be able to maintain relatively high swimming speeds for some time. ROV observations  
396 provide some support for this statement (Trenkel *et al.*, 2004; Jon Moore, pers. comm.). This  
397 contradicts the stereotypic view of deep-sea fishes, at least the non-migrant ones, being

398 typically phlegmatic energy savers. This stereotypic view might have been too much coloured  
399 by sit-and-wait predators, such as dragonfishes. The high catchability estimates for some  
400 species in our material, together with their relatively sleek body shapes, suggest that perhaps  
401 they are more active predators than previously thought

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

414       A trawl does not necessarily scare off all animals. A trawl moving in water stimulates  
415 bioluminescence (Jamieson *et al.*, 2006), and light can attract fishes and is often used in fish  
416 capture (Pascoe, 1990; Gabriel *et al.*, 2005). To what extent this process influences  
417 catchability of deep-pelagic nekton is unknown, although attaching electric lights to trawls is  
418 known to increase their catchability at least for certain species (Clarke and Pascoe, 1985,  
419 1998; Clarke *et al.*, 1986; Swinney *et al.*, 1986), but also to decrease catchability of certain  
420 other species (Clarke *et al.*, 1986). Whether attraction caused by bioluminescence is  
421 differently influencing the trawls considered here is unknown. Another source of attraction  
422 are the animals in the trawl itself: codend feeding by active predators such as cephalopods is

423 known to occur (Herring, 2002). Such predators are unlikely to be caught by the trawl, but  
424 their feeding in the codend would reduce catches of prey species. Also species not attracted  
425 by the catch but opportunistically feeding in codend would have a similar effect. While  
426 codend feeding is difficult to show, there was nothing suggesting that this was important in  
427 our samples.

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

435 Traditionally, trawl comparisons have focused primarily on differences in size selectivity  
436 (e.g., Millar, 1992; Erickson *et al.*, 1996; Wileman *et al.*, 1996; Millar and Holst, 1997; Millar  
437 and Fryer, 1999; Bethke *et al.*, 1999; Kvamme and Isaksen, 2004). There has been less focus  
438 on differences in catch rates at species level (Wassenberg *et al.*, 1997; Sangster and Breen,  
439 1998, Fock *et al.*, 2002; West, 2002; Lewy *et al.*, 2004; Porteiro, 2005). Studies of fishing  
440 power of survey vessels may involve different trawls but these are confounded with vessel  
441 effects (von Szalay and Brown, 2001; Helser *et al.*, 2004). Common to most of these studies  
442 is the methodological similarity to this study in that they analyzed effort-standardized catch  
443 rates using linear statistical models. Porteiro (2005) adopted a different approach, using  
444 multivariate statistics to account for gear differences. The studies by Wassenberg *et al.*  
445 (1997), West (2002), Lewy *et al.* (2004) and Porteiro (2005) point to big differences between  
446 different trawls in catchability as well as species that are caught. On the other hand, von  
447 Szalay and Brown (2001) and Helser *et al.* (2004), comparing research and commercial

448 fishing vessels using bottom trawls, showed moderate differences in catchability of key  
449 species and that combining data from different platforms is possible and possibly worthwhile.

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

468 Main application of our catchability estimates is community characterization of pelagic  
469 fauna along the Mid-Atlantic Ridge. If data from different gears are analyzed together,  
470 ordination methods tend to cluster them separately, as observed in other studies (e.g., West,  
471 2002). However, correction with catchability estimates nests the Åkra trawl samples within  
472 the macrozooplankton trawl samples in multivariate analysis (Sutton *et al.*, 2008). Thus, the

473 systematic differences between the gears appear to be successfully removed. Of course, the  
474 catchability estimates obtained here only apply for the material studied in this paper. The  
475 estimates provide some guidance for other areas and times, but care should be taken,  
476 especially during different seasons and where populations with different size composition are  
477 encountered.

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

492 Furthermore, different trawls may catch entirely different species. Because of the data  
493 selection applied here, our results only apply to species caught with both trawl types under  
494 comparison. However, several species were caught only with one trawl type (corresponding to  
495 a catchability approaching either zero or infinity). The macrozooplankton trawl caught 31 fish  
496 species not caught with the Åkra trawl, whereas the corresponding number for the Åkra trawl  
497 is 96; 108 species were caught with both trawls. For rare species this is likely by chance

498 alone, and the total sampling effort in terms of distance trawled was greater for the Åkra  
499 trawl, so care is needed before drawing conclusions from these numbers. Preliminary analyses  
500 using a randomization approach (e.g., Manly, 1997), pooling macrozooplankton trawl samples  
501 so that the distance trawled was similar to the Åkra trawl samples, suggested that both Åkra  
502 and macrozooplankton caught slightly more species than expected by chance, but that the  
503 differences are not significant. Results for cephalopods were similar.

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

## 517 Supplementary material

518 The following supplementary material is available at ICESJMS online:

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

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

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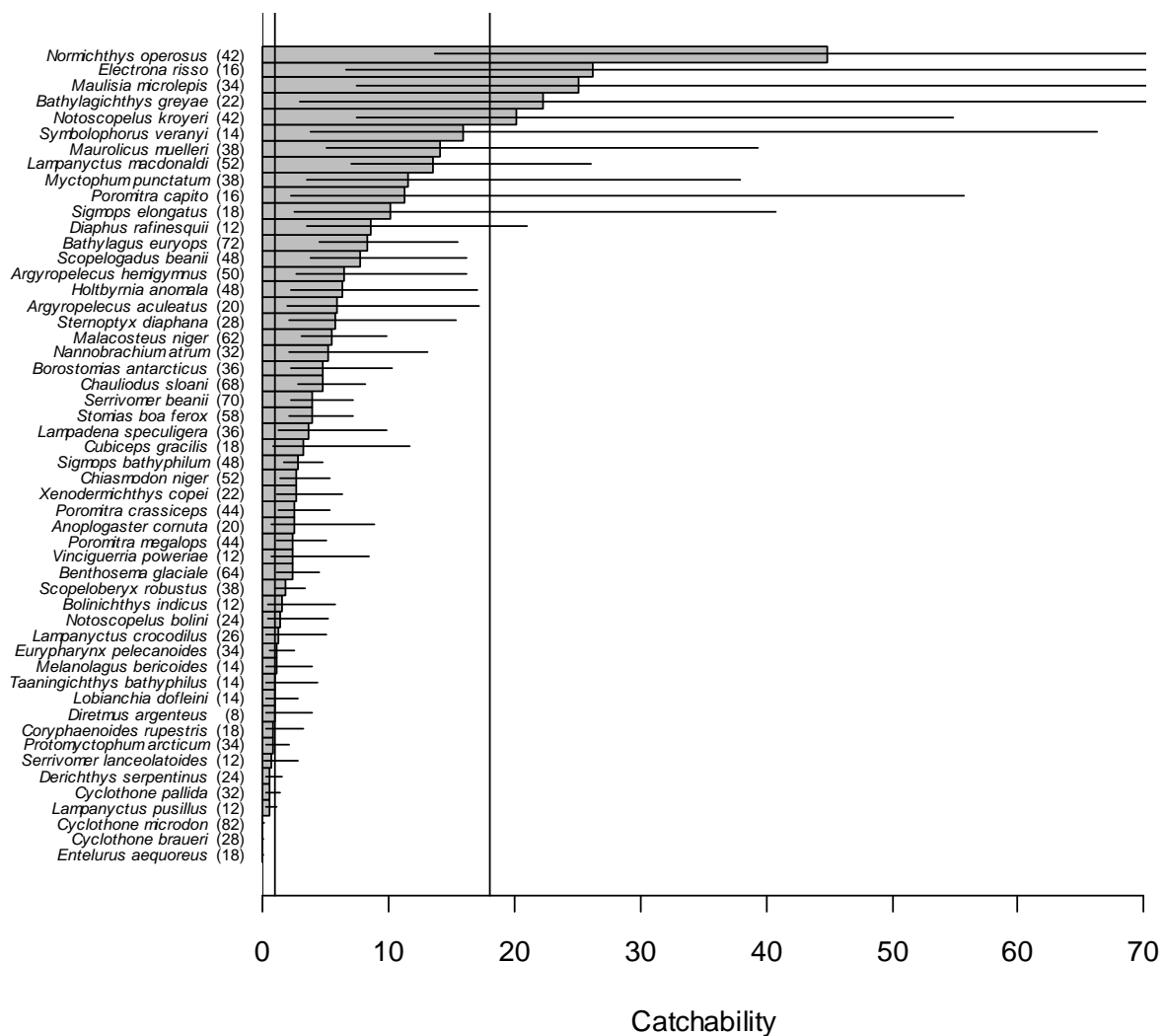
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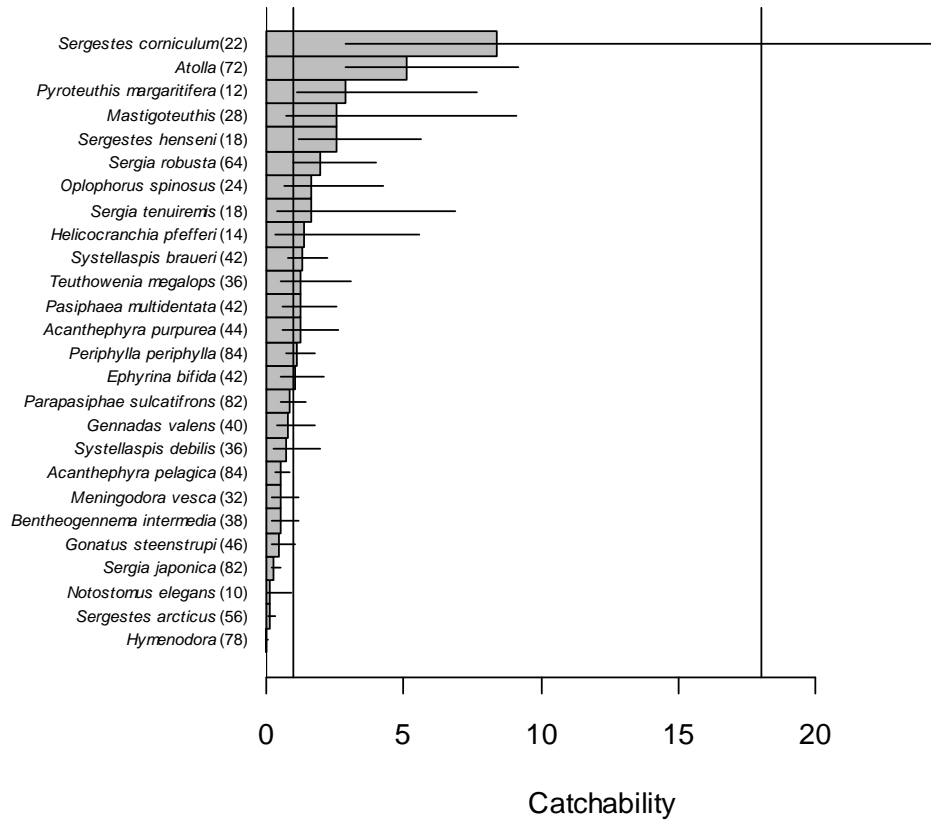
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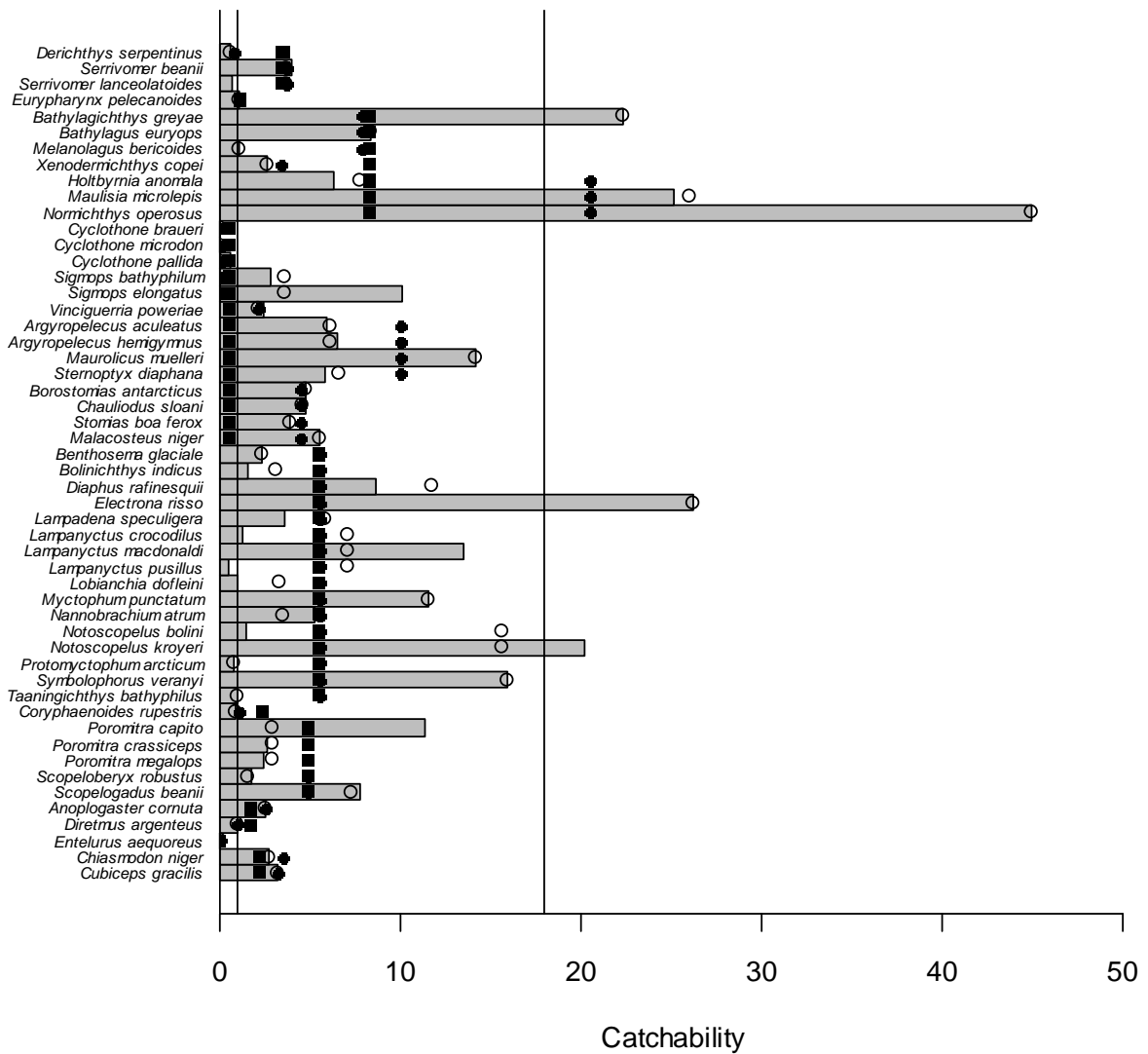
663  
 664 Figure 1. Estimates of catchability of 52 fish species with the Åkra trawl, a medium-sized  
 665 pelagic trawl with graded meshes, relative to the macrozooplankton trawl. Horizontal bars  
 666 give 95% confidence limits (for *N. operosus*, *E. risso*, *M. microlepis* and *B. greyae* these  
 667 extend outside the plot area to respectively 148, 104, 85 and 170). Vertical lines give  
 668 reference values that correspond to equal catchability (1) and to the ratio of opening areas  
 669 (18). Sample size is indicated in parenthesis after the species name.



670

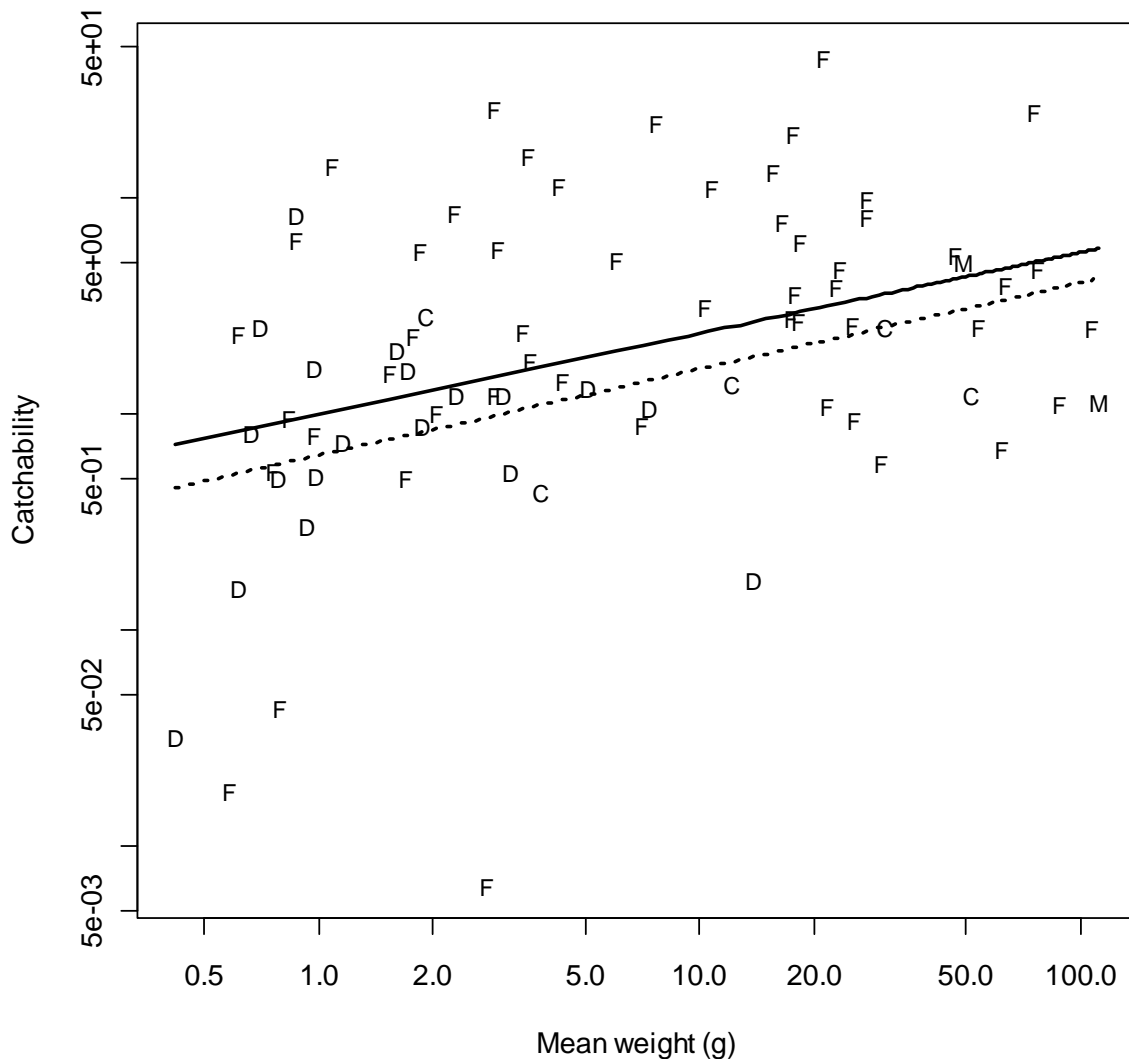
671 Figure 2. Estimates of catchability of two medusa, five cephalopod and 19 decapod species  
 672 (or genera) with the Åkra trawl relative to the macrozooplankton trawl. Horizontal bars give  
 673 95% confidence. Vertical lines give reference values that correspond to equal catchability (1)  
 674 and to the ratio of opening areas (18). Sample size is indicated in parenthesis after the species  
 675 name.





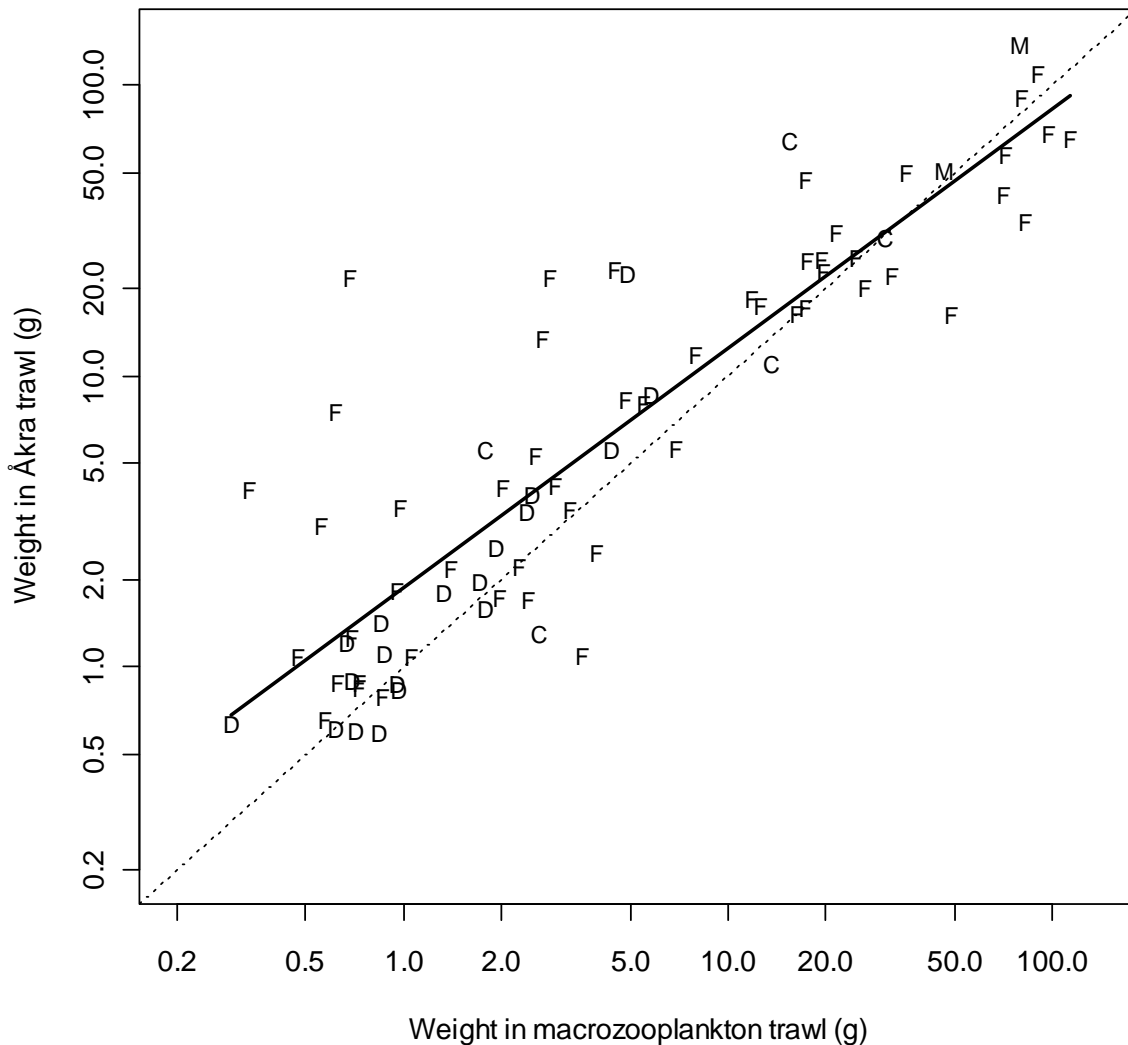
676

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



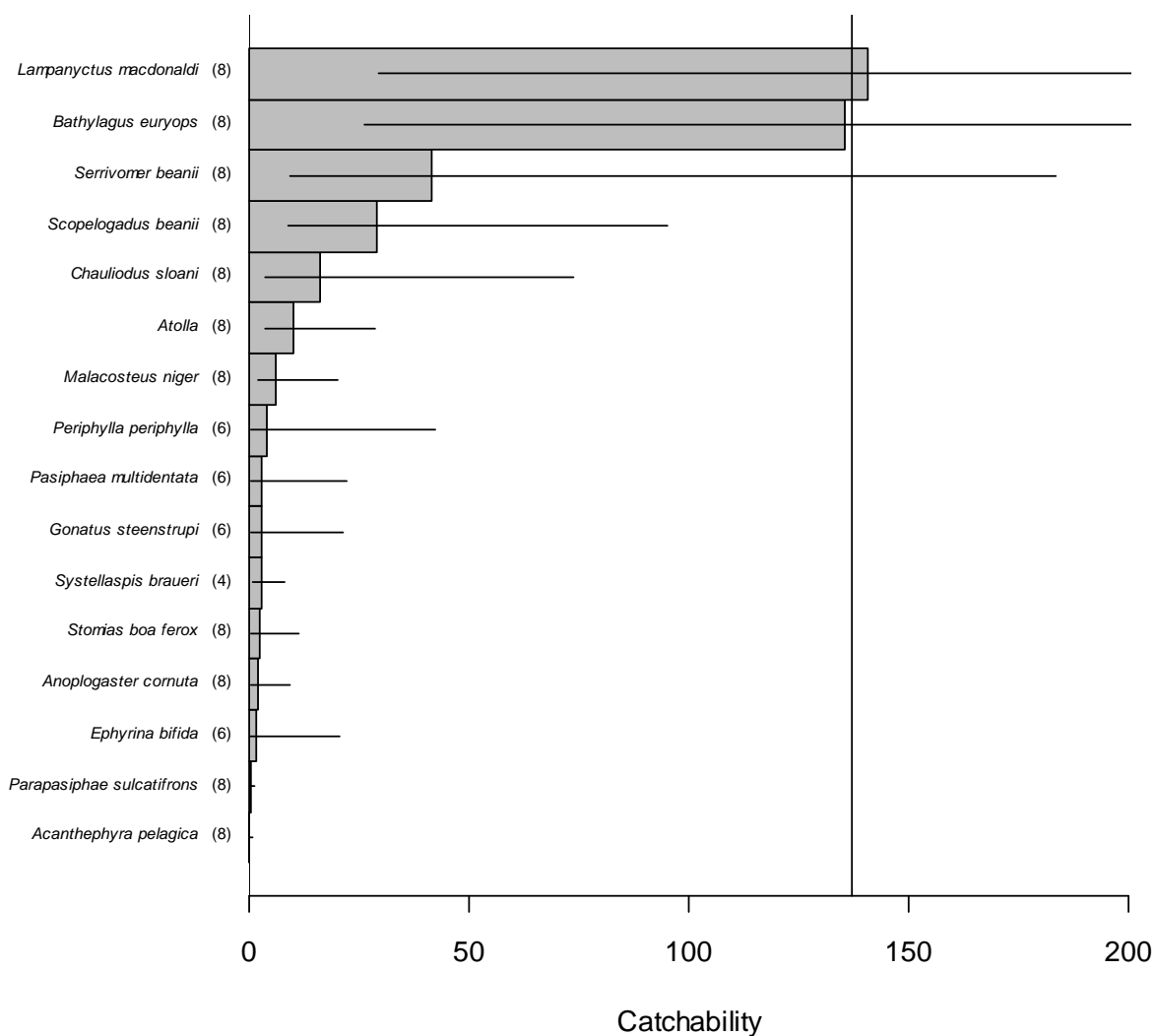
682

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

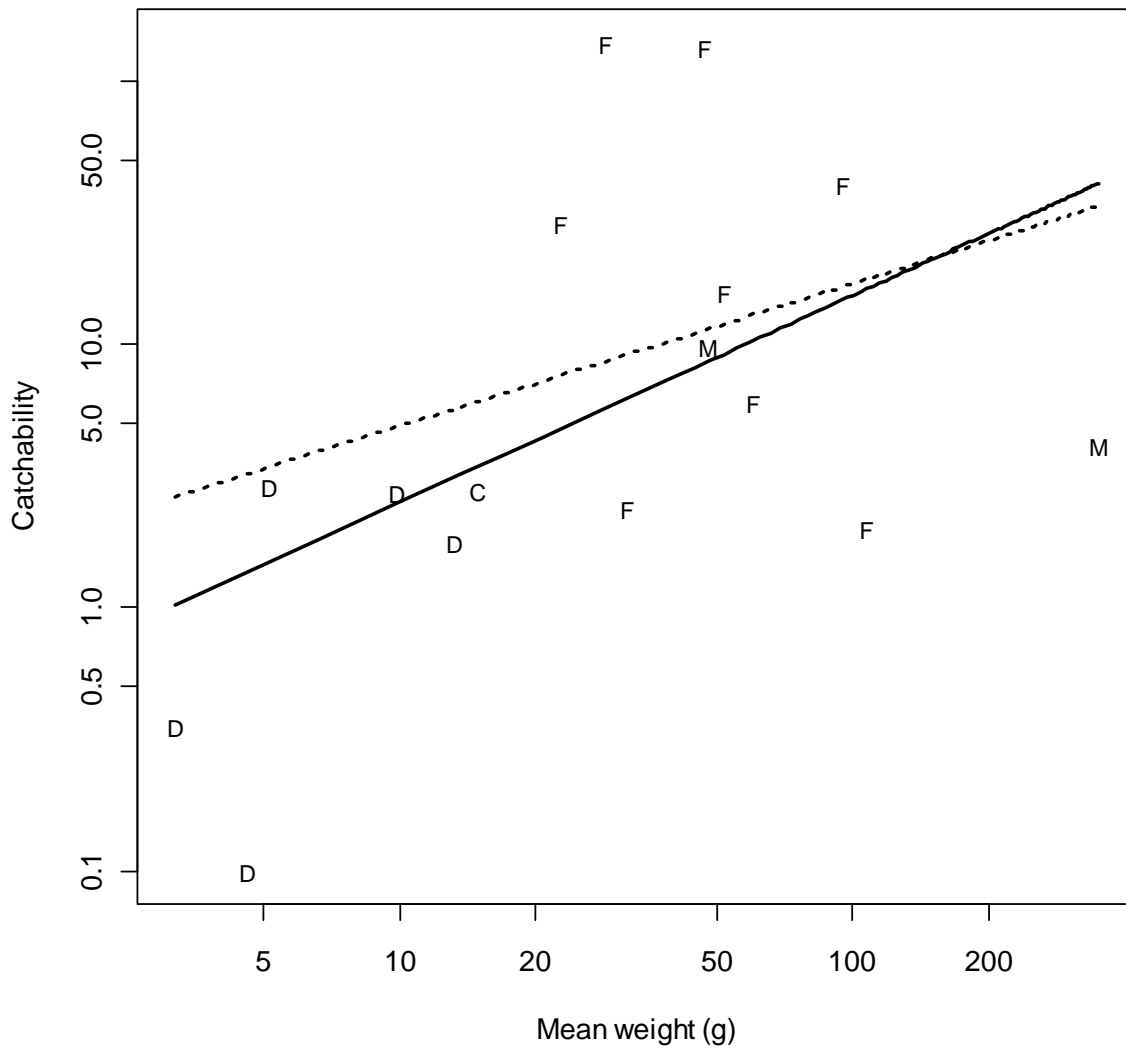


690

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

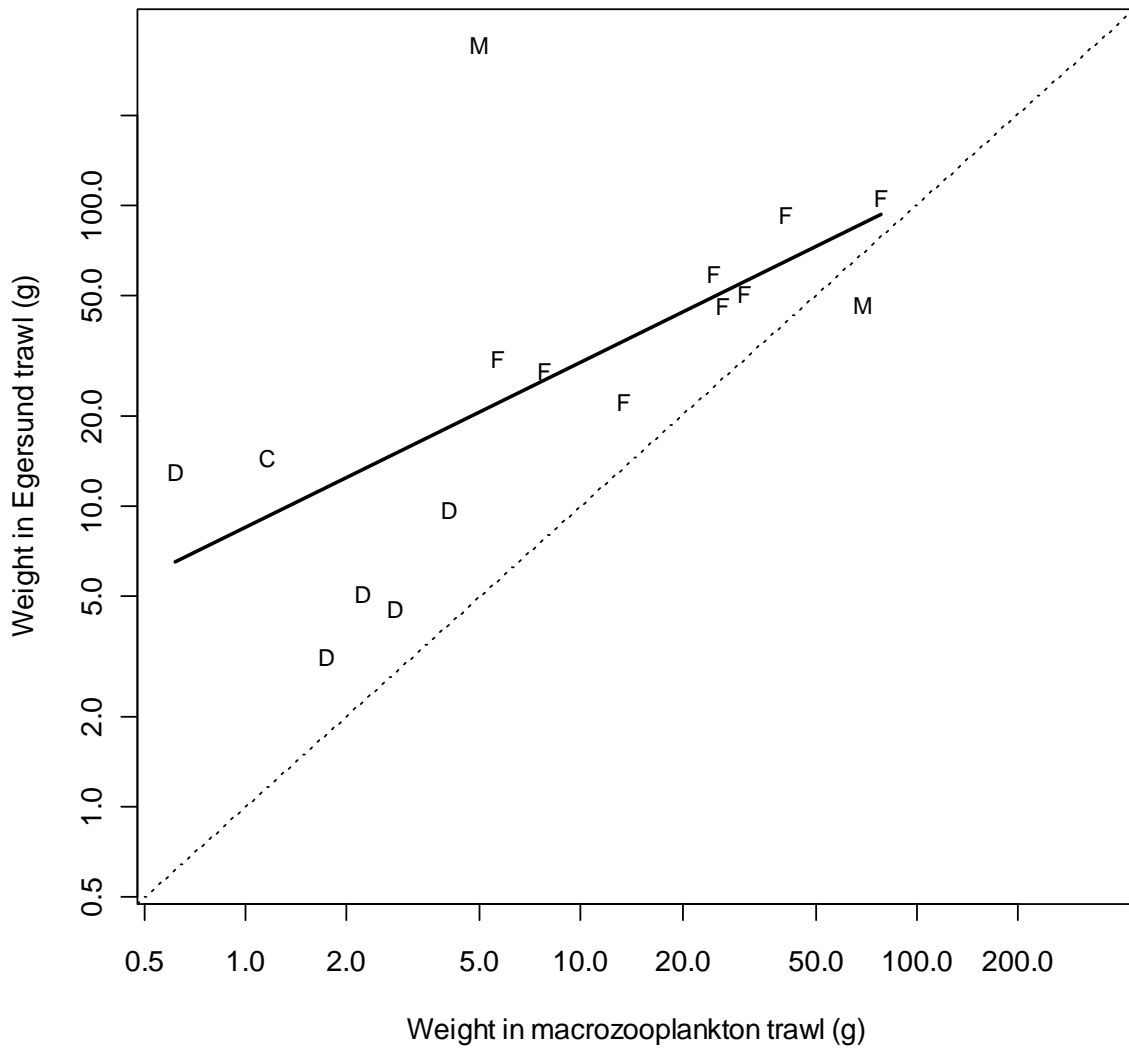


697  
 698 Figure 6. Estimates of catchability of eight fish and eight invertebrate species with the  
 699 Egersund trawl, a large pelagic trawl with graded meshes, relative to the macrozooplankton  
 700 trawl. Horizontal bars give 95% confidence limits (for *Lampanyctus macdonaldi* this extends  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



704

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



708

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

712

713 Tables

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

718

Trawl	Description	Mesh size (stretched) in the codend (mm)	Appro- ximate opening area (m <sup>2</sup> )	Ratio of opening areas (macro- zooplankton trawl = 1)	Typical towing speed (nm h <sup>-1</sup> )
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

719