

Global analysis of depletion and recovery of seabed biota following bottom trawling disturbance

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- 35 model, otter trawl, penetration depth, scallop dredge, systematic review

36 Abstract

37 Bottom trawling is the most widespread human activity affecting seabed habitats. Here, we collate 38 all available data for experimental and comparative studies of trawling impacts on whole 39 communities of seabed macro-invertebrates on sedimentary habitats and develop novel and widely 40 applicable methods to estimate depletion and recovery rates of biota following trawling. Depletion of biota and trawl penetration into the seabed are highly correlated. Otter trawls caused the least 41 42 depletion, removing 6% of biota per pass and penetrating the seabed on average down to 2.4cm, while hydraulic dredges caused the most depletion, removing 41% of biota and penetrating the 43 44 seabed on average 16.1cm. Median recovery times post-trawling (from 50% to 95% of unimpacted 45 biomass) ranged between 1.9 and 6.4y. By accounting for the effects of penetration depth, environmental variation and uncertainty, the models explained much of the variability of depletion 46 47 and recovery estimates from single studies. Coupled with large-scale, high-resolution maps of 48 trawling frequency and habitat, our estimates of depletion and recovery rates enable the assessment of trawling impacts on unprecedented spatial scales. 49

51

52 Significance statement

53 Bottom trawling is the most widespread source of physical disturbance to the world's seabed. 54 Predictions of trawling impacts are needed to underpin risk assessment, and are relevant for the 55 fishing industry, conservation, management and certification bodies. We estimate depletion and 56 recovery of seabed biota after trawling, by fitting novel models to data from a new global data 57 compilation. Trawl gears removed 6% to 41% of faunal biomass per pass and recovery times post-58 trawling were 1.9 to 6.4 y depending on fisheries and environmental context. These results allow the estimation of trawling impacts on unprecedented spatial scales and for data poor fisheries, and 59 60 enables an objective analysis of trade-offs between harvesting fish and the wider ecosystem effects 61 of such activities.

63

64 INTRODUCTION

65 Fisheries using bottom trawls are the most widespread source of anthropogenic physical disturbance 66 to global seabed habitats (1, 2). Almost one quarter of global seafood landings from 2011–2013 67 were caught by bottom trawls (3). Development of fisheries, conservation and ecosystem-based 68 management strategies requires assessments of the distribution and impact of bottom trawling and 69 the relative status of benthic biota and habitats. There are many drivers for such assessments including (i) policy commitments to an ecosystem approach to fisheries, (ii) requirements to take 70 71 account of trawling impacts in fisheries and environmental management plans, (iii) demands from 72 certification bodies to assess fisheries' environmental impacts and (iv) the need to evaluate the 73 effects of alternate management measures to meet conservation and management objectives (4, 5, 74 6). These assessments are used to assess the sustainability of bottom trawl fisheries and formulate 75 priorities for habitat protection and ultimately to achieve a balance between fisheries production 76 and environmental protection. The distribution of bottom trawling is increasingly well characterised 77 by vessel tracking and other monitoring systems (7), but impacts depend on the magnitude of 78 trawling-induced mortality and recovery rates of biota, for which the current evidence base is 79 incomplete, dispersed and often contested (4, 8).

80

Bottom trawls, (here defined as any towed bottom fishing gear, including otter trawls, beam trawls,
scallop dredges and hydraulic dredges) are used to catch fish, crustaceans and bivalves living in, on,
or above the seabed (9). Bottom trawling resuspends sediments (10, 11), reduces topographic
complexity and biogenic structures (12, 13, 14), reduces faunal biomass, numbers and diversity (15,
16), selects for communities dominated by fauna with faster life histories (17) and produces energy

subsidies in the form of carrion (18). These effects lead to changes in community production, trophic
structure and function (19, 20). Given the patchy and dynamic distribution of bottom fishing (21),
fished seabeds comprise a mosaic of undisturbed, recently impacted and recovering benthic
communities and habitats (22). The state of each patch within this mosaic depends on the history
and frequency of past trawling impacts and the recovery rates of the biota present (23).

91

92 Recovery rates following trawling depend on recruitment of new individuals, growth of surviving 93 biota and active immigration from adjacent habitat. Most existing estimates of recovery rates come 94 from experimental studies, with changes in abundance recorded before and after experimental 95 trawling (15, 16). While these experiments provide reliable estimates of immediate mortality, their 96 small scale is likely to underestimate recovery time, in particular for mobile fauna. This is because 97 immigration makes a greater contribution to recovery when biota are relatively more abundant 98 around the impacted site, and because most experiments have been conducted in infrequently and 99 untrawled areas (16). On fishing grounds, impacts occur on larger scales such that untrawled and 100 infrequently trawled areas become scarce when there is more trawling activity. Furthermore, 101 experiments typically focus on recovery following single trawling events, rather than recovery from 102 successive events typical of fishing grounds.

103

The development of satellite-based vessel monitoring systems has enabled scientists to map commercial fishing activity at high resolution (7). Such maps have been used to design studies of the comparative impacts of towed bottom-fishing gears across gradients of commercial fishing frequency (herein = comparative studies). In contrast to experimental studies, these studies account for the spatial extent, frequency and temporal variability in fishing activity, and are expected to provide more representative estimates of recovery rates. When these estimates are coupled with efstimates of the mortality of biota from experimental studies, they can be used to assess status of

impacted biota on fishing grounds. Presently there are too few studies to adopt the alternative approach of analysing large-scale studies directly recording recovery from trawling (24).

113

114 We used the logistic growth equation (25) to describe recovery of benthic fauna because it provides 115 an effective abstraction of the complex recovery dynamics of populations and communities and can 116 be fitted to available data (e.g. 26, 23, 22). This model is identical to the Schaefer models commonly 117 used in fisheries management when the data to implement full age or size-structured models are not 118 available (27). If we assume the recovery of biomass or numbers (hereafter abundance) of biota B following trawling is described by the logistic growth equation, then the equilibrium solution can be 119 120 used to estimate B as a fraction of carrying capacity K in an environment subject to chronic fishing 121 disturbance (28):

122

$$B/K = 1 - F d/r$$
 (eq. 1)

123 where F is trawling frequency, d is the depletion of biota caused by each trawl pass (expressed as a 124 proportion) and r is rate of increase, interpreted here as the recovery rate. Equation (1) only 125 requires estimates of F, d and r to estimate relative abundance B/K (28). Eq. 1 suggests that r is 126 constant, but in communities composed of species with a range of r values, trawling selects for 127 species with faster life histories that are more resilient and therefore r can be expected to increase 128 with F. We found that the relationship between community B/K and F for communities is well 129 approximated by a log–linear relationship (SI appendix, Text S3). We therefore estimated r at F = 0130 and assuming a log-linear relationship between B/K and F (eq. 2). More sophisticated models of 131 recovery can account for differential responses of groups with contrasting life histories and other 132 aspects of community dynamics, and thus provide a better description of underlying processes (19, 133 29), but higher parameter demands limit their application to systems with a substantial amount of 134 available data. Conversely, if d and r can be estimated and associated uncertainties quantified, the 135 logistic model would facilitate assessment of trawling impacts in most marine systems. Different gears and substrata will have different levels of seabed contact or penetration and these factors will influence *d*. Penetration depth is however largely independent of the towing speed (6). If a strong relationship exists between the penetration depth and *d*, this can be used to obtain estimates of depletion for trawl gears for which no empirical depletion estimates are available. Trawling frequency *F* is defined as the swept area ratio, which is the area trawled annually divided by the studied area (km² km⁻² y⁻¹, simplified to y⁻¹), which should ideally be calculated for small cells (ca. 1km²) because trawling tends to be spatially clustered at larger scales.

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Here, we conduct a meta-analysis of experimental studies of trawling impacts to estimate depletion of biota following trawling. We report the effect on the abundance of whole benthic macroinvertebrates communities, including infauna and epifauna. We combine this with the first metaanalysis of results from large-scale comparative studies of trawling effects on fishing grounds, to estimate recovery rates of seabed biota, and describe how they vary with gear characteristics and environment. All data were collated from studies that were quality assured following systematic review methodology, thereby avoiding selection bias (30).

151

152 **RESULTS**

Twenty-four comparative and 46 experimental studies met the criteria for inclusion in our analyses (SI Appendix, Table S1-S3). Studies were mostly temperate and concentrated in NW Europe and NE USA (Figure 1). None of the studies that met the criteria examined the effect of trawling on biogenic habitats, but there were sufficient studies in other habitats. Many gear-habitat combinations were not represented in the studies reviewed because many fishing gears are only suitable for fishing on particular seabed types or species associated with those habitats (SI Appendix, Table S1) and because some habitats are less widespread than others (7).

161 Depletion rates estimated from the experimental studies for biomass and numbers were not 162 significantly different. Thus the pooled estimates of d (SI Appendix, Table S4) apply to both biomass and numbers. Estimates of depletion d and penetration depth P by gear-type were very closely 163 correlated (Figure 2, Pearson's r = 0.980, p = 0.020). Otter trawls (OT) had the smallest impact, 164 165 removing on average 6% of organisms per trawl pass and penetrating on average 2.4cm into the 166 sediment. Median penetration depths were 2.7cm and 5.5cm for beam trawls (BT) and toothed 167 dredges (TD) respectively and the corresponding median depletions per trawl pass were 14% and 168 20%. Hydraulic dredges (HD) had the largest impact, removing on average 41% of organisms per pass 169 and penetrating 16.1cm.

170

171 The effect of trawling frequency on relative biomass estimated from the comparative studies 172 showed a log-linear relationship and with each unit increase in swept-area ratio linked to a mean fall 173 in biomass of 15.5% (Figure 3a). None of the other environmental variables significantly affected this 174 response (Table 1). The effect of sediment composition on community biomass depletion was not 175 significant (Table 1A, SI Appendix, Table S5) but the model estimates for gravel are nevertheless 176 shown in the Table 1a to allow comparison with the significant effects of gravel found for community 177 numbers (Table 1B, SI Appendix, Table S5). Mean community r (estimated using equation S4.1 and 178 S4.2 from d and b) increased with trawling frequency, from 0.82 y⁻¹ when there was no trawling (5-179 95% uncertainty intervals 0.42 - 1.53) to $1.73 (0.89 - 3.23) y^{-1}$ when the trawling frequency was 10 180 y^{-1} (using the mean estimated d across gears OT, BT and TD, d = 0.13, SI Appendix, Figure S1, Table 181 S6). The increase in r, which results from changes in community composition to favour biota with 182 faster life histories, is therefore relatively slight across ranges of trawling frequencies that dominate those on real fishing grounds, e.g. 0 to 1 y^{-1} (e.g. 31, 7, 32). The *r* estimate of 0.82 y^{-1} enables 183 184 estimates of median time to recovery (T) to 0.95K for a range of levels of depletion (Figure 3b). For

example, if the fraction depleted D = 0.5K then recovery time is 3.6 years (5-95% uncertainty intervals: 1.9 - 6.4 years).

187 The effect of trawling on community numbers, estimated from the comparative studies, increased 188 significantly with the gravel content of the sediment (Figure 3c, Table 1B, SI Appendix, Table S5) and 189 this effect persisted when examined among gears. The reduction in benthic community numbers for 190 each unit increase in trawling frequency was 3.1% at 0% gravel content (typical for BT studies), 5.5% 191 at 1% gravel content (typical for OT studies), and 72% at 45% gravel content (typical for TD studies). The estimates of r for community abundance range from 0.18 y⁻¹ for TD on 45% gravel to 4.47 y⁻¹ for 192 193 BT on 0% gravel, with high uncertainty. These r estimates result in a median recovery time T from 194 0.5K to 0.95K of 0.7 to 16.6 y (Figure 3d). Beside gravel content, the inclusion of the ratio of d over 195 primary production also resulted in reduced AIC compared to the model with no additional 196 explanatory variables, with the effect of trawling on numbers increasing with d and decreasing at 197 higher levels of primary production (Table 1B, SI Appendix, Table S5).

198

199 DISCUSSION

200 This is the first attempt to quantify the impacts of bottom trawling and recovery of seabed biota by 201 synthesizing data from trawling studies following a systematic review of the available evidence-base. 202 We developed a novel method to derive the recovery rates of benthic macrofaunal invertebrate 203 communities from trawling by combining results from experimental and comparative studies, and 204 provide new estimates of depletion and recovery including a quantification of uncertainty based on 205 all available data. The method for estimating the recovery rate from comparative studies is novel. 206 Given that realistic and robust r estimates have been largely unavailable previously, this work is 207 critically important. Recovery rates were estimated from changes in the biomass and numbers of 208 biota across fishing grounds, so estimates are likely applicable to trawled shelf-seas in general (at least in temperate waters where most of the studies were carried out). Our new estimates of 209

210 depletion and recovery enable the parameterisation of models to predict the state of the benthic 211 biota as a function of trawling frequency and levels of primary production and % gravel (28). Coupled 212 with the emergence of large-scale estimates of trawling frequency (7) these models will support 213 assessment of trawling impacts on unprecedented spatial scales, because our approach provides a 214 quantitative estimate of status with minimal data requirements (28). The method is widely 215 applicable because it requires relatively few data inputs and could be applied world-wide, including 216 fisheries where trawl impacts remain unassessed. The r and d values that we estimate here with a 217 broad geographic basis are based on the full body of available evidence and are therefore the most 218 robust estimates available. The generality of our approach means that the outputs of assessments 219 are accurate when averaging over larger scales, but that biases may exist when used for local 220 assessments. These results have global policy relevance for conservation and food security policy 221 development as it enables an objective analysis of the efficacy of different methods of harvesting 222 food from the ocean to be considered in the light of the wider ecosystem effects of such activities on 223 the marine environment. The results enable managers to understand the variable resilience of 224 benthic systems to trawl fisheries and to set limits of fishing accordingly.

225

226 Most continental shelves consist of relatively small intensively trawled areas where the trawling 227 frequency is in the range of 1 to 10 y⁻¹ and extensive infrequently trawled areas where the trawling 228 frequency is <1 y^{-1} and predominantly <0.25 y^{-1} (7). Our results show that trawling frequencies of 1 y^{-1} cause average declines of 15.5% in the biomass of benthic biota. Communities on gravel may be 229 230 more sensitive to trawling because they on average have a larger proportion of larger, long-lived and 231 sessile epifauna (33) that are particularly sensitive to trawling (34). Effects were greater for gears 232 that kill a larger fraction of the biota (larger d) because they penetrate the sediment more deeply, 233 and weaker in areas of higher primary production where higher food supply to the benthos may 234 result in a higher recovery rate.

The ranking of different fishing gears with respect to their magnitude of impact reported here is 236 237 similar to the ranking in previous meta-analyses of small-scale experimental studies (15, 16), 238 although our estimates of d are smaller, probably because we adjusted for the number of trawl 239 passes while previous analyses did not. The use of depletion to primary production ratio as a proxy 240 for community resilience to trawling has the advantage of being easily understandable and easy to 241 estimate for new areas and fisheries. The ratio of depletion over primary production might support 242 rapid preliminary large-scale risk assessments of potential trawling impacts on community 243 abundance to guide more region-specific studies. The close relationship between penetration depth 244 and depletion can be used to estimate depletion resulting from the pass of a given trawl gear when 245 no direct depletion estimate is available. Accurate estimates of penetration depth are much easier 246 and cheaper to obtain than estimates of depletion, would support preliminary impact assessments by gear type, and can even be generated using numerical models (11). 247

248

249 Our analyses did not identify any variables other than trawling frequency that affected community 250 biomass. This is surprising given the contrasting results for numbers and that some comparative 251 studies and past meta-analyses of experimental studies have shown interaction effects between 252 gear type and habitat type (e.g. 29, 16). The relatively small number of studies included in the 253 biomass analysis and the high variability associated with benthic sampling, which cannot be fully 254 controlled in a meta-analysis, may have contributed to this discrepancy. Our results for biomass 255 imply that a single estimate of recovery rate r is appropriate when assessing impacts on the different 256 habitat types studied here. They also suggest that differences in time to recovery and expected 257 biomass (B/K) will be driven primarily by gear type (and hence d) and trawling frequency (F).

258

259 Our estimates of biomass recovery times are similar to empirical measurements of recovery taken in 260 three areas where commercial trawling was stopped (4-5 years, 24), but are longer than estimates 261 from small-scale experimental studies, which are in the order of 25–500 days (15, 16). The scale-262 dependency of recovery times has important implications for management because recovery will be 263 faster when trawled areas are closer to less impacted areas from which individuals can recruit or 264 migrate (as also shown by 22). We found that biomass recovery rates were slower and recovery 265 times longer than those for numbers. This result is expected based on the population dynamics of 266 seabed biota. Recovery in numbers is driven more strongly by recruitment than recovery of biomass, 267 which is driven by increases in the size and age structure of the population through growth of 268 individuals. We recommend the use of recovery rates for community biomass when modelling trawl 269 impacts and their consequences. This will give due weight to recovery of body-size and age structure 270 as well as numbers and take account of energy flow through food webs and other ecosystem 271 processes that are linked closely to biomass. Recovery times as estimated from the logistic model 272 nevertheless do not imply that the communities will recover over these times to the species, size 273 and age composition that existed before trawling, but they do imply the recovery of total biomass or 274 numbers and related cross-species ecosystem processes such as aggregate secondary production.

275

276 Uncertainties around mean/median estimates of penetration depth, recovery and depletion were 277 high, despite the careful screening of included data (but which also decreased the sample size and 278 potentially power to detect effects, 30). However, our approach allows us to address directly some 279 aspects of uncertainty, and the broad distribution of resulting depletion and recovery estimates 280 show that large site-specific differences in the response of seabed communities to trawling are 281 expected. The advantage of characterising uncertainty is that it can be propagated in future risk and 282 impact analyses. Given the unexplained variance in r, percentiles from the distribution of plausible 283 values might be selected to reflect the degree of risk aversion in the management system. The

extent of risk aversion is a non-scientific decision (although it would be informed by science) that would likely be made by managers and other stakeholders. Risk aversion would likely depend on the perceived value of a habitat type. A risk-averse approach might adopt a value of *r* from a lower percentile of the distribution (e.g. the 10% or 25%) rather than the median (see SI Appendix, Table S6 for a selection of values).

289

290 Our use of comparative studies provides improved estimates of recovery compared with those from 291 previous small-scale experiments studies because they are based on larger scale measurements 292 from fishing grounds. Comparative studies may however be affected by 'shifting baselines' (35), 293 where historical trawling has removed the most sensitive organisms and only resilient organisms 294 remain. Since trawling selects for species with faster life histories that are more resilient, recovery 295 time will increase with trawling frequency. Our finding that mean community r increases with F 296 conforms with previous observations of shifts towards species with faster life-histories in disturbed 297 communities (e.g. 36). This effect is apparent across a range of plausible trawling frequencies from 298 >0 to 10 y⁻¹ but would be small for the great proportion of most fishing grounds where swept area ratio is less than $1 y^{-1}$ (7). Although this shift means that previously trawled communities may be 299 300 more resilient to further trawling, it does not mean that they will recover any faster to the original, 301 pre-trawling state. For this reason we used the *r* estimate of untrawled communities for estimating 302 recovery times. Selective effects linked to trawling history are likely to be strongest for long-lived 303 sessile epifauna that build biogenic reefs, such as sponges and corals. The estimates of r and T304 presented here are applicable to invertebrate communities living in sedimentary habitats, but not 305 biogenic habitats as no studies of trawling impacts on biogenic habitats met the rigorous selection 306 criteria imposed by the systematic review.

307

308 In summary, we apply novel and widely applicable methods to estimate depletion and recovery rates 309 of benthic invertebrate communities following trawling. By accounting for the effects of gear type 310 and penetration, environmental variation and uncertainty, our analysis explained much of the 311 variability of depletion and recovery estimates from single studies. Coupled with large-scale, high-312 resolution maps of trawling frequency and habitat, our estimates of depletion and recovery rates 313 will enable analysis of trawling impacts on unprecedented spatial scales to inform best-practices to 314 achieve sustainable fishing, and will be of use to policy makers, conservation planners and fisheries 315 managers for risk assessment and the evaluation of management strategies.

316

317 METHODS

318 We present analyses for whole community biomass and numbers of benthic invertebrates. Changes 319 in the abundance of seabed biota following trawling depend on the mortality caused by each pass of 320 a trawl and the rate of recovery of the biota between trawl passes. We estimated the immediate 321 depletion of biota (d) caused by a trawl pass from a meta-analysis of experimental studies of 322 trawling impacts. We estimated the recovery rates (r) of biota from a meta-analysis of comparative 323 studies of trawling impacts. The analyses were structured to assess the effects of gear type, 324 penetration depth and environmental variables (e.g. depth, sediment composition) on depletion and 325 recovery.

326

327 Depletion

328 Depletion was estimated using data collated from experimental studies of trawling impacts 329 identified using systematic review methodology. A comprehensive literature search of journal 330 papers, book chapters and grey literature reports was carried out. Details of literature search terms 331 and databases, study inclusion criteria are provided in the systematic review protocol by Hughes et

al. (30). All included studies quantified the immediate mortality of biota following one or multiple
trawling events. Each identified study had to pass quality assurance criteria before data from the
study were included in the collated dataset.

335

336 We classified gear types as otter trawls, beam trawls, towed dredges or hydraulic dredges (SI 337 Appendix, Text S1). The reduction in abundance of biota resulting from one pass of a trawling gear 338 depends on the characteristics and operation mode of the gear. Different gears are designed to have 339 different levels of seabed contact or penetration, depending on the target species and seabed type, 340 and these factors will influence mortality (37). Consequently, we assessed the relationship between 341 mortality and penetration depth of the gear. Some of these studies were conducted in previously 342 trawled areas with a lowered abundance of biota, but as we are estimating the fraction of organisms 343 removed rather than the absolute amount we expect that this will have had little effect on our 344 estimates of d. Depletion d was estimated using a generalized linear mixed model (GLMM) 345 implemented in the package nlme in R (38, 39), with InRR (the log of the ratio of the biomass or abundance in trawled over untrawled areas) as the response variable, and log₂(time t in days since 346 347 trawling) and gear type as fixed factors, and the study as a random effect assuming a Gaussian error 348 distribution. We weighted *InRR* values by the inverse of their variance as is normal practice in meta-349 analyses. We estimated d as the intercept for the different gears at t = 0.

350

Predicted penetration depth of each gear type into the seabed was estimated from values in the literature by averaging the reported penetration depths of the individual components of the gear (e.g. doors, sweeps, and bridles of an OT) weighted by the width of these components (details in SI Appendix, Text S2).

355

356 Recovery

357 Recovery rates were estimated using data collated from comparative studies of trawling impacts. All 358 included studies sampled the biomass or numbers of whole communities of benthic invertebrates at two or more sites subject to different trawling intensities on commercial fishing grounds. 359 360 Contributing studies were identified following the same procedure as for experimental studies (SI 361 Appendix, Text S1). In the analyses of the comparative studies we assume that both K and observed 362 gradients of trawling effort were unrelated to other environmental drivers, and that the observed 363 state of the biota is in equilibrium with the reported trawling effort. Gradients in trawling effort may 364 be driven by regulation and seabed obstructions, but are also observed in areas of homogenous 365 habitat (e.g. 29). Spatial patterns of trawling effort are also shown to be relatively stable over time in 366 the few fisheries where high-resolution time series have been analyzed (40). K could vary across the 367 trawl grounds because of environmental variations and this will increase the uncertainty around 368 relationships between B and F.

369

In the comparative studies, conversions between units of abundance were not always possible (e.g.
biomass per unit sediment volume could not be converted to biomass per unit sediment area, given
sampling gears with different, but unknown, efficiencies), so absolute *B* or *K* could not be estimated.
We normalized the data by expressing relative biomass or numbers as the *B/K* ratio and used a loglinear approximation for the relationship between community *B/K* and *F* where

375
$$\log_{10}(B/K) \sim b F$$
 (eq. 2)

where *b* is the slope of the relationship (derivation taking account of the log-linear relationship between *B/K* and *F* and the distribution of trawling in SI Appendix, Text S3 and S4). After fitting a linear relationship to $\log_{10} B$ versus *F* for each comparative study, *K* was estimated as the $10^{A^{intercept}}$ of this relationship.

381 The data collated from comparative studies were initially used to estimate relative changes in 382 abundance (B/K) as a function of trawling frequency F. This approach differs from the aforementioned analyses of depletion because the change in abundance with trawling is a response 383 384 to both depletion (per trawl pass) and recovery. Because b = d/r (equation 1), once d is estimated 385 from experimental data, recovery rate r can be estimated from the slope b of equation (2) after 386 taking account of the log-linear nature of this relationship, which implies r increases with F. To 387 propagate uncertainty in the estimates of b and d into the estimate of r we sampled the distributions 388 of b and d estimates to derive the distribution of r (SI Appendix, Text S4). Time to recovery from a 389 given level of depletion D to a defined proportion ϕ of K at which recovery is deemed to have 390 occurred (e.g. 0.95) was derived from the approach of Lambert et al. (22) (SI Appendix, Text S5). 391 When reporting recovery times, we report recovery from 0.5K to 0.95K.

392

393 Variables that determine the effect of trawling in comparative studies

The effect of trawling on seabed biota in comparative studies could be influenced by different variables. Thus we evaluated the explanatory power of several potential factors by including them as covariates in a linear mixed model (39) based on equation (2) and selecting the most parsimonious model using AIC. According to equation (2) the community response to trawling in \log_{10} scale is approximately proportional to *F*, with slope a function of the ratio of *d/r*. The fixed part of the mixed models was therefore:

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401 le

log₁₀ (Response) ~ Trawling frequency + Trawling frequency × other variables

(4)

402

403 where the response variable is community biomass or numbers and where the 'other variables' can 404 be covariates for *d*, *r* or their ratio. The intercept was removed because $\log_{10}(B/K)$ with no impact = 405 0. We modelled 'study' as a random effect, allowing the slope to vary per study. This approach 406 accounted for the non-independence of observations within a study. We checked the assumptions 407 of the linear mixed model by visual inspection of the normalized residuals (38).

408

409 We expected that factors that lead to a higher *d* would strengthen the effect of trawling (e.g. higher 410 penetration depth), while factors that lead to a higher r by affecting growth rates of individuals and 411 populations (higher flow of energy to the seabed because of a higher production or shallower depth, 412 or a higher temperature) would weaken the effect. The closely related penetration depth P 413 (continuous) and gear type (categorical) were examined as covariates for d. The following covariates 414 for r were examined: primary production estimated from the vertically generalized productivity model (mg C m⁻² d⁻¹) (41) and particulate organic carbon flux to depth (POC flux, g C_{org} m⁻² y⁻¹) (42) 415 as proxies for energy availability, mean sea bottom temperature calculated from monthly mean 416 417 bottom temperature for 2009-2011 provided in MyOcean Product; GLOBAL-REANALYSIS-PHYS-001-418 009, depth (from GEBCO if not reported in the original study), habitat type and sediment 419 composition (gravel, sand and mud content). Habitat types were classified as biogenic habitats, 420 gravel, sand, muddy sand/sandy mud, and mud. Sediment gravel, sand and mud content were 421 extracted from the source studies by converting the sediment description to the Folk classification 422 (43) and then converting the Folk classification to percentages based on the means in each category. 423 In addition to analyses using covariates of d or r, we also conducted analyses using covariates of the 424 d/r ratio, here the d/r ratio was approximated as the ratio of d or P to the continuous r covariates. 425 The effect of trawling is expected to increase with water depth owing to the lower levels of natural 426 disturbance in deeper water and the corresponding increase in the relative abundance of individuals

427 with slower life histories (low *r*), so $d \times depth$ was examined as a covariate for d/r, with depth 428 expressed as a negative number.

429

430

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- 539 43. Folk RL (1954) The distinction between grain size and mineral composition in sedimentary-rock
 540 nomenclature. J Geol 62:344-359
- 541

543 Table 1. Linear mixed model (SI Appendix, equation S3.1) fits for the analysis of data from

544 comparative studies of changes in (A) biomass and (B) numbers. For community biomass the model

545 with the lowest AIC included no explanatory variables other than trawling frequency, but for

546 community abundance both 'Gravel content' and 'd/PP' improved the AIC in relation to a model

547 without other explanatory variables. Results for these variables are given under (A) for comparative

548 purposes.

A)	Community	Slope (b)	Std.Error	DF	t-value	p-value	AIC
	biomass						
TF		-0.07522	0.0158	503	-4.732	<0.0001	566.9
TF		-0.07142	0.0172	502	-4.148	<0.0001	568.4
TF: Gravel		-0.00067	0.0010	502	-0.648	0.5168	
TF		-0.08623	0.0325	502	-2.653	0.0082	568.8
TF : (<i>d</i> /PP)		125.6879	373.7966	502	0.336	0.7368	
B)	Community						
	numbers						
TF		-0.21185	0.1342	141	-1.577	0.1169	89.5
TF		-0.01451	0.0942	140	-0.153	0.8778	81.1
TF: Gravel content		-0.01206	0.0035	140	-3.377	0.0009	
TF		0.25300	0.2145	140	1.048	0.2964	86.1
TF: (<i>d</i> /PP)		-6892.96900	2676.5453	140	-2.575	0.0111	

549

550 TF = Trawling frequency d = depletion estimate from experimental studies (fraction per trawl pass, SI 551 Appendix, Table S4), PP = Primary production (mg C m⁻² d⁻¹), Gravel = sediment composition in % by

552 weight

555 Figure captions



Figure 1. Maps of the locations of the studies. The higher resolution maps of the northwest and
northeast Atlantic give more detail for two areas with high concentration of studies. The 200 m
depth contour is shown in blue.



561

562

563 Figure 2. The relationship between the penetration depth *P* and depletion *d* of macrofaunal

564 community biomass and numbers caused by a single trawl pass for different trawl gears. Means ±

565 SD.



567



569 Figure 3. The relationship between trawling frequency and total community biomass (a) and 570 numbers (c). The thicker lines are the fixed effects, grey lines the random effects of the individual 571 studies (not all visible because many studies had small ranges and low trawling frequencies). Recovery time to 0.95K for depleted total community biomass (b) and numerical abundance (d) as a 572 573 function of estimated r and initial depletion D. In (a) and (b) lines are the median estimate based on 574 the mean d across all gears. In (c) and (d), lines are the median estimates for the three different gear types, based on the mean gravel content in the areas where studies using these gear types were 575 carried out. The shaded areas indicate the 5–95% uncertainty intervals for estimates. 576