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- 1 Estimating the abundance of benthic invertebrates from trap-catch data 2 3 Jan Geert Hiddink¹ Matt Coleman¹ 4 5 Stephen Brouwer² 6 Isobel Bloor¹ 7 Stuart Jenkins¹ 8 9 1. School of Ocean Sciences, Bangor University, United Kingdom, j.hiddink@bangor.ac.uk 2. Saggitus Environmental Science Limited, New Zealand 10 11 12 Short running title: Analysis of trap-distance experiments 13
- 14 IJMS

15 Abstract

16 Trap fisheries targeting invertebrates are economically important but many of the target species lack 17 stock assessments. One reason for this is the difficulty of estimating density. One important means by which density can be estimated uses the catch rates of baited traps that are spaced at different 18 19 distances. With declining spacing, the sphere of attraction will increasingly overlap, leading to 20 reductions in catches, allowing for the estimation of the density that is catchable by traps on the 21 seabed. Here we review the analytical methods adopted across a range of studies and find that no 22 consensus on robust methods exists. We propose an analytical method that assumes the trapping 23 area is circular and that the chance of catching an individual declines linearly with distance from the 24 trap. We apply this method to estimate the density and the trapping radius of crabs and gastropods 25 from real and simulated datasets. The method estimated a trapping radius of between 4 and 86 26 metres, and densities that are up to 2.5 times less and 13 times greater than estimates provided in 27 the original sources, illustrating the sensitivity to methodology. In conclusion, we provide and test a standardized method to estimate the density of benthic invertebrates. 28 29 30 Keywords: stock assessment, Cancer pagurus, Buccinum undatum, pot, creel, static fishing gear 31

33 Introduction

34 Trap, pot and creel fisheries targeting crustaceans and gastropods are economically important 35 worldwide, with growth of wild capture crustacean fisheries outpacing all other major species groups 36 since 1990. Global landings have nearly doubled from 4.4% of total landed biomass to 7.8% and they 37 account for 21.3% of global marine fisheries value (Boenish et al. 2022). The socio-economic 38 importance of wild capture crustacean and gastropod fisheries is further evident at local scales. For 39 example, in the UK whelk Buccinum undatum, brown crab Cancer pagurus and European lobster 40 Hommarus gammarus landings are worth ~£77Million annually at the first point of sale (Marine 41 Management Organisation 2022). However, many of the target species of these fisheries, including 42 those in the UK, are still classed as data deficient. Globally, in 2016 only 12% of crustacean stocks were managed using biomass reference points (Boenish et al. 2022), limiting the ability to maximize food 43 production while minimizing environmental impacts (Emmerson et al. 2022; Hilborn et al. 2020; Lart 44 45 2019). In the European union, managers are predominantly reliant on fisheries dependent data to 46 assess stock status in trap fisheries (ICES 2021; Marine Institue and Bord Iascaigh Mhara 2022; 47 Mesquita et al. 2023) despite recognition of the potential limitations of such approaches in provision 48 of management advice (Emmerson et al. 2022; Maunder and Piner 2014). Fisheries independent 49 approaches to determining stock abundance for crustaceans and gastropods are relatively limited. In 50 using traps to generate estimates of stock abundance one of the key pieces of information that is 51 currently missing is understanding of the area of the sea floor fished.

52

53 Traps are usually baited and deployed on a line with multiple traps spaced at regular intervals, and 54 left on the seabed for one or more days (called the soak time). During this time, crustaceans and 55 gastropods (and sometimes fish) will detect the plume of bait and start moving towards the trap, and some of those that reach the trap will enter. The area of seafloor that is effectively sampled by a trap 56 57 is, however, poorly understood. Bait plume detection will depend on the bait type, habitat complexity 58 (Tremblay and Smith 2001), currents (Lees et al. 2018; Moore et al. 1991) and target species 59 sensitivity, while distance moved in relation to soak time depends on behaviour and movement speed 60 of the target species (Himmelman 1988; Lees et al. 2018; Van Tamelen 2001). The probability of 61 capture has been shown to be influenced by numerous environmental and biotic factors such as intra-62 and inter-species interaction (Skerritt et al. 2020), seasonality and temperature (Emmerson et al. 63 2022), reproductive state (Skinner and Hill 1987) and fishers' targeting behaviour and associated local 64 ecological knowledge (Pantin et al. 2015). This means that the size of the trapping area is likely to 65 depend on the species, location and fishing operations.

66

67 Estimates of the area from which commercial crustaceans are caught have primarily been undertaken 68 using telemetry, with these estimates derived through the recording of behavioural responses before 69 and after baited trap deployment (Homarus americanus - Watson III et al. (2009); Homarus gammarus 70 - Lees et al. (2018); Cancer pagurus - Skajaa et al. (1998)). The use of such technology, though useful, 71 requires: a) a significant number of individuals to be tracked; b) a suitable sized sampling area to 72 encompass home ranges; and c) significant financial cost. Furthermore, studies are heavily reliant on 73 subjective assessment of behavioural responses to bait. There is an overall lack of standardisation in 74 describing bait detection behaviours. For example, some studies used change in angle of movement 75 (Lees et al. 2018; Watson III et al. 2009), while others used changes in walking speed (Skajaa et al. 76 1998), to infer bait detection.

78 Given that traps are generally deployed at regular intervals along lines, there is clear potential for the 79 area over which traps attract target species to overlap, resulting in adjacent traps 'competing' (Arena 80 et al. 1994). This is confirmed through observations that catch rates are often highest at the ends of 81 lines (Bell et al. 2001); given trap spacing close enough to allow overlap of trapping areas, end of line 82 traps are competing with only one other trap, while mid-line traps are competing with two other traps. 83 The overlap in the trapping area between closely-spaced traps is potentially large, and therefore it can 84 be assumed that with increasing spacing, catch rates increase up to the point where trapping areas no 85 longer overlap and catch rates stabilize (Aedo and Arancibia 2003; Arena et al. 1994; Skud 1978). This 86 means that trap-by-trap catch data from traps that are spaced at different distances, or end vs. mid-87 line traps, contains information on both the size of the attraction area and the density of the target 88 species. The analysis of catch rates at different trap spacing can therefore potentially be used to 89 estimate density. However, such methods are rarely used in the assessment of the abundance of 90 benthic invertebrates and when they are used, they have not been used consistently.

91

Here we review the analytical methods used in a range of trap-spacing experiments to estimate the density of invertebrates that can be caught by traps. Based on this, we propose a standardized terminology and operationalise a method that has only a few assumptions, and test this method on new and existing data.

96

97 Review of methods and terminology

98 The basis for the use of trap-spacing experiments originates in the work initially undertaken by Eggers 99 et al. (1982) in which teleost fish abundance was estimated using traps/hooks at different spacing, 100 with the theoretical methodology associated with using overlapping trapping areas developed and 101 refined by Arena et al (1994). This methodology forms the basis on which current research and its 102 application to commercial trap fisheries are based. Our comprehensive search identified 7 published 103 studies that develop theory (Arena et al. 1994; Bell et al. 2001) and/or apply it (Aedo and Arancibia 104 2003; Brouwer and Wichman 2020; Cores et al. 2019; Gros and Santarelli 1986). Table 1 gives an 105 overview of the terminology used and the assumptions for each of these studies. The main differences 106 among studies are found in the terminology used, the assumed shape of the trapping area, the 107 probability of capture as a function of the distance from the trap, and if/how the interaction of the 2D 108 nature of the trapping area with the probability of capture is captured mathematically.

109

110 A variety of terms and definitions have been used to define the area from which animals were trapped 111 (Table 1). Bell et al. (2001) defined the trapping area as the area within which the probability of 112 capture of an individual during the deployment time of the trap is greater than zero. Other definitions 113 were more ambiguous, such as the 'Attraction area', 'Effective capture field', and 'Effective fishing 114 area'. The effective fishing area is a purely notional area containing as many animals as were trapped, 115 and is the product of the trapping area and the average capture probability within this area. The 116 attraction area is more complex to understand because it defines the area of chemical influence of 117 the bait rather than the area from which animals are caught.

118

The horizontal shape of the area from which animals were assumed to be caught was either circularor elliptical (Table 1). The mathematics and statistics are more straightforward for circular areas

(which require the estimation of only the radius, which is two fewer parameters than ellipses for which the elongation and direction also need to be estimated). In reality, none of the studies estimated these last two parameters and instead fixed them based on assumption about the direction and strength of the tidal currents (e.g. Gros and Santarelli 1986). None of these papers evaluated if the added complexity was worthwhile, and it seems unlikely that any statistical models would be able to estimate these extra parameters unless experiments using multiple lines of traps in many different directions

- 127 are carried out. To date, such experiments have not been undertaken.
- 128

129 The studies treated the probability of capture as a function of the distance from the trap quite 130 differently. Some studies assumed a constant probability of capture up to a knife-edge distance, where 131 the probability dropped to zero (Arena et al. 1994; Brouwer and Wichman 2020; Gros and Santarelli 132 1986). Other studies used exponential (Aedo and Arancibia 2003; Bell et al. 2001; Cores et al. 2019) or 133 linear (Bell et al. 2001) declines in capture probability. Although the mathematics for a constant 134 probability are most straightforward, it is unlikely that this assumption holds true in reality 135 (Himmelman 1988), although a simulation by Bell et al. (2001) suggests that such a pattern can result 136 from highly directional movements of mobile animals when the plume detection itself shows a knife-137 edge response, or through long soak times. Exponential and linear declines with distance seem more 138 plausible for most target species (although the long tail of an exponential decline is unlikely to be 139 accurate), and can be mathematically described using only two parameters (one defining the density 140 of the target species and one defining the rate of decline (exponential) or the radius of the trapping 141 area (linear).

142

143 Combining the shape of the trapping area with the probability of capture results in a 3-dimensional 144 shape, i.e. a cone in the case of a circular trapping area and a linear decline, Figure 1). The volume of 145 this 3D shape is equivalent to the total catch in a trap (this shape is unrelated to whether a species 146 uses their habitat in 3D (e.g. pelagic fish) or 2D (e.g. a gastropod), but relates only to how the 147 probability of capture declines with distance). This assumption underpins the work by Bell et al. (2001) 148 and Gros and Santarelli (1986). However, two of the studies did not take account of the 3D nature of 149 this shape (Aedo and Arancibia 2003; Cores et al. 2019), and instead solved the mathematics based 150 on a 1D probability-distance relationship alone, and will therefore have obtained incorrect estimates. 151 Some of the studies fitted statistical models where the parameters have no theoretical meaning, i.e. 152 the model provides a fit to the data but does not estimate the parameters we are interested in (the 153 trapping area or the density (e.g. Arena et al. 1994; Brouwer and Wichman 2020)). These parameters 154 are then estimated indirectly from these fits in another step. Such an indirect estimation of 155 parameters is less elegant but not necessarily invalid.

156

This brief review shows that the terminology used is inconsistent among existing studies and that no consensus on robust methods exists. Some of the published methods based on empirical data may be hard to replicate, have logical flaws, or require estimation of many parameters from noisy data. In addition, some assumptions are difficult to justify, or models used are too complex to fit on noisy data. In our opinion the theoretical study by Bell et al. (2001) is the most robust yet simple approach for application to real datasets, and we operationalise a proposed method based on the principles presented in their work.

165 Description of chosen method, justification of assumptions

The review above suggests that using an assumption of a circular trapping area and a linearly declining capture probability may be a reasonable trade-off between capturing the complexity of the catch~spacing relationships vs. having enough data to estimate all parameters in the chosen relationships. We evaluate the validity of these assumptions in the rest of this paper. These assumptions have the advantage that this results in a mathematical framework that can be analytically solved, and meaningful parameters can be estimated statistically. This framework requires the following parameters:

- Trapping radius: *r*. The radius from the trap within which the probability of capture of an individual during the deployment time of the trap is greater than zero.
- 175 Trapping area: $A = \pi r^2$
- Density of the target species: *H*.
- Capture probability for animals <u>at the trap</u>: *P*. This value is likely to be <1 in all fisheries including trap fisheries as not all animals that are next to the trap will enter it.
- Probability of capture <u>at distance x from the trap</u>: p_x . This is assumed to decline linearly with 180 distance from the trap, from $p_{x=0} = P$ directly at the trap, to $p_{x\geq r} = 0$.
- The density catchable by traps: h = HP. This is the density of catchable animals on the ground, which is the density corrected for the fact that not all animals present in an area have the inclination to enter the trap even when right next to it (P<1). It is the measure of abundance we are interested in estimating here. This density of animals could theoretically be caught within the trapping area if p_x did not decrease with distance from the trap. The catchable density directly correlates to the catches if traps are not competing with each other, and is equivalent to the integration of p_xH over A.
 - Half the distance between traps in the experiment: *d*

189 When thinking about this in 1D for non-competing traps, the catch coming from a particular distance 190 x equals $H p_x$.

191

188

192 The key assumptions of this framework are that:

193 1) Catch rates decrease linearly with distance from the trap.

We found three studies that were suitable to evaluate the validity of this assumption. Himmelman 194 195 (1988) released a large number of tagged whelks Buccinum undatum at 6 distances from a baited trap 196 (refreshed every 24 hours) and recorded their recovery in the trap over a period of 15 days. Using the 197 full period leads to an exponential decline in catch rates with distance, but using a period of 48 hours, 198 which is a much more realistic period of soak time in most coastal fisheries, leads to a linear decline 199 in capture probability (Figure 2). Observations of marked snow crabs Chionoecetes opilio (Brethes et 200 al. 1985) and brown crab Cancer pagurus (Ungfors 2008) show similar patterns that do not clearly 201 deviate from a linear decline. It is worth noting that each of these studies does show large variations 202 that could justify other shapes (concave and convex curves), but such shapes would not allow a mathematical solution of the equations. 203

- 203 204
- 2) The area from which animals are attracted is circular.

3) The importance of current on the shape and area of attraction of baited traps or hooks has
been identified by numerous studies (Lees et al. 2018; Olsen and Laevastu 1983; Taylor et al.
207 2013; Wilson and Smith 1984). The area of attraction is indicative of the direction and
strength of the prevailing currents during a full tidal cycle, resulting in a shape that is not

209 predictable or uniform (Himmelman 1988; Lapointe and Sainte-Marie 1992). The area of 210 attraction has been estimated by a number of different shapes, described by either a circle 211 (Bell et al. 2001), rectangle (Melville-Smith 1986) or an ellipse (Gros and Santarelli 1986). In 212 locations of less intense tidal current flow, the area of attraction might average out as circular 213 over the course of the tidal cycle, even if it is not circular at any given point in time. Given the 214 complexity of bait plume dispersal and lack of current data we therefore assume that circular 215 is a good assumption for convenience and mathematical solvability. Catch from overlapping 216 trapping areas are divided equally between traps.

- 217 We assume that animals in an area where trapping areas overlap will move towards the closest trap.
- 218 219

4) The likelihood of traps capturing the target species is not affected by the presence of

previously caught animals in a trap.

220 Trap saturation caused predominantly by inter- and intraspecific interactions is known to affect 221 catches in trap fisheries (Fogarty and Addison 1997). For example Emmerson et al (2022) showed that 222 interaction with European lobster Homarus gammarus led to a reduction in catch rates of targeted 223 brown crab Cancer pagurus while Rayner and McGaw (2019) documented that trap saturation by non-224 target invasive green crab Carcinus maenas had a negative impact on American lobster Homarus 225 americanus catches. Trap saturation seems to be particularly common in lobster fisheries (e.g. Clark 226 et al. 2018; Watson and Jury 2013) which can result in a lack of a correlation between lobster catches 227 and lobster abundance (Courchene and Stokesbury 2011; Watson and Jury 2013).

228

229 Despite these observations, intra- and interspecific interactions are highly variable across species, and 230 hence for simplicity we have chosen to assume that over the soak time chosen, traps continue to 231 accumulate the target species.

232

Following from these assumptions, the catch in a single trap is equal to the volume of a cone, which is defined by a circular base defined by the trapping area *A*, and a height defined by the density that is catchable by traps *h*. The density *h* is the absolute density of animals on the seabed *H* multiplied by the probability $P(p_{x=0})$ that an animal at the trap will enter it. The use of a cone shape is driven by the assumption of a linear decline in the probability of capture with distance from the trap (Figure 2). The total volume of this cone equals:

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241

240 *Cone volume* = $(1/3) \times \pi \times r^2 \times h$

(equation 1)

where *r* is the radius of the cone and *h* is the density catchable by traps that we are interested in estimating, and the height of the cone.

244

The interference between two adjacent traps (i.e. reduction in catch) can be quantified as the volume of the two cones that overlap. If *d* is half the distance between the two traps (i.e. the distance from the centre of the cone to the centre of the area of overlap), then the overlapping volume equals (Rajpoot 2016):

250 Overlapping volume =
$$\frac{h}{3r} \left[r^3 \cos^{-1}\left(\frac{d}{r}\right) - 2rd\sqrt{r^2 - d^2} + d^3 \log\left(\frac{r + \sqrt{r^2 - d^2}}{d}\right) \right]$$
(equation 2)
251

If d > r, there is no overlap between the two cones and the *Overlapping volume* = 0. The catch of a 252 253 trap that is competing with n traps with overlapping trapping areas (n = 1 at the end of a line, and n = 12 in the middle of a line) is therefore: 254

- 255
- 256

258

(equation 3)

- *Catch* = *Cone volume n Overlapping volume* 257
- 259 When fishing at close trap spacings, or where attraction areas are large, interactions may extend 260 beyond just adjacent traps (i.e. the overlaps may themselves be overlapping), but given that we 261 assume that all animals move to the closest trap, this does not affect our estimates of h and r.
- 262

263 The relationship between the catch and d can therefore be statistically fitted on data by equation 3 using a non-linear ordinary least-squares regression, which assumes a Gaussian error distribution, 264 265 which provides estimates of the parameters of interest, catchable density h and trapping radius r. 266 Even though a Poisson error distribution may have been more appropriate for the count data that 267 underly the catch rates, a non-linear ordinary least-squares regression does not allow other error 268 structures than Gaussian. Given that the distribution of the residuals did not deviate from a normal 269 distribution on visual inspection, using non-linear ordinary least-squares regression seems 270 appropriate here. R code using both non-linear regression and Bayesian statistics and an example 271 dataset are provided in the Supplementary Material of this paper. The non-linear regression is more 272 straightforward to use and is recommended for users that are not familiar with Rstan (Stan 273 Development Team 2020).

274

Estimation of catchable density h and trapping radius r for 8 studies 275

276 We collated 6 studies that carried out trap-spacing experiments (Aedo and Arancibia 2003; Brouwer 277 and Wichman 2020; Cores et al. 2019; Gros and Santarelli 1986; Sinoda and Kobayasi 1969; Williams 278 and Hill 1982), one study that simulated a trap-spacing experiment (Bell et al 2001), and we carried 279 out one new experiment on Cancer pagurus in the Isle of Man (Table S1). The methods for this new 280 experiment are described in the Supplementary Material. Seven of these datasets were for 281 crustaceans (of which one was simulated) and one for a gastropod. For the simulation study in Bell et 282 al. (2001), we used the simulation for 'crabs', and the scenario where other traps are ignored if the 283 crab is not caught in the first trap they encounter, because this simulation most closely matched our 284 assumption of a lack of trap saturation.

285

286 The non-linear regression was successfully fitted, and provided estimates of the catchable density of 287 crabs and gastropods, for all-but-one of the datasets (Table 2, Figure 3). Where applicable Figure 3 fits 288 two separate curves, one in grey for traps at the end of the line and one in black for traps in the middle 289 of a line. The end of line curves have a catch rate that is half the maximum catch rate when d = 0 (i.e. 290 the theoretical situation when traps are in the same location) because half the trapping area overlaps 291 with the next trap (each trap catches half as much as it would as without the competing trap). The 292 mid-line curves have a catch rate of 0 at d = 0, because their trapping area fully overlaps with the 293 trapping area of the adjacent traps and the catch is therefore theoretically shared between an infinite 294 number of traps that are in the same location. The plots only show data points for end of line traps 295 and for mid-line traps where the distance to both adjacent traps was equal (as it is hard to visualize 296 mixed distances on the x axis), but all data points were used for fitting the curves. All estimates of h297 and r were significantly different from zero, except for the studies that had only 3 and 5 data points 298 respectively (Cores et al. 2019; Williams and Hill 1982). One dataset showed a decrease in catch with 299 trap spacing and failed to fit the model (Sinoda and Kobayasi 1969). Some of the datasets show 300 relatively tight fits, while for others there is a lot of remaining variation around the fitted curves. 301 Visually, the model fit for the study on whelks by Gros and Santarelli (1986) does not look convincing 302 because there are very few traps that were spaced at a distance where *d* < *r* and it is therefore difficult 303 to judge if initial part of the curve matches the observations.

304

305 The method estimates a trapping radius (the radius of the area within which the probability of capture of an individual is greater than zero) of between 4 and 86 metres for the real crustaceans and whelks. 306 307 The method estimated a catchable density (the product of the density and the probability of capture 308 for animals right next to the trap) between 15.3 individuals per 100 m⁻² for Portumnus latipes, 0.052 individuals per 100 m⁻² for *Cancer pagurus* to 0.043 individuals per 100 m⁻² for *Scylla serata*. These 309 estimates of h are between 0.4 to 13 times relative to the estimates provided in the original sources, 310 311 which illustrates that these estimates are highly sensitive to the method used (Table 2). Although the 312 studies on Cancer porter (Aedo and Arancibia 2003) and Portumnus latipes (Cores et al. 2019) reported 313 that they used the same analytical technique, our estimate of h using their data was 0.41 times that of Aedo and Arancibia (2003), but 5.88 times that of Cores et al. (2019). This differing divergence from 314 315 original estimates suggests that they did not in fact use the same analysis and points to the lack of 316 clarity across studies in general.

317

In the simulated dataset from Bell et al. (2001) the density H of crabs on the seabed and probability 318 319 of capture P were defined, and this dataset therefore allowed an evaluation of how precisely our 320 method estimates the catchable density $h = H \times P$. The density H of crabs in the simulation was 321 0.078/100 m², while P = 0.5, which means that the real catchable density $h = 0.039 / 100 \text{ m}^2$. Our model estimated $h = 0.061 / 100 \text{ m}^2$ (95% confidence interval 0.048 to 0.075 / 100 m²) and therefore 322 323 overestimated h by a factor 1.57. The overestimate is related to the violation of the assumption of a 324 linear decline in the probability of capture p_x with distance in the simulation. The way the model was 325 set up by Bell et al (2001) dictates that virtually all crabs that were within 100m of a trap were caught 326 during the soak time regardless of their initial distance from the trap, and hardly any from further 327 away. Therefore, p did not start to decline until d > 100m (a pattern that is not supported by empirical 328 observations of marked animal capture (Brethes et al. 1985; Himmelman 1988; Ungfors 2008)). It is 329 therefore not surprising we overestimated h. The overestimate is relatively modest though for such a 330 major violation of our assumption.

331

The estimates of *h* and *r* generated using the *nls* function in the *stats* packages in R (R Core Team 2021)
(Table 2) were fairly similar to the estimates generated using *rstan* (Stan Development Team 2020)
(Table S2).

335

336 The effect of the shape of the attraction area

In our analysis we assume a circular attraction area and a linearly declining capture probability with distance. Although the empirical evidence to support these assumptions is not strong, this model could be solved mathematically, and as a result could directly estimate the parameters *h* and *r* for 340 most datasets and fitted them well. Although other shapes are plausible (e.g. an exponential decline 341 in p_x with distance, elliptical trapping areas), they would make it much more difficult to mathematically 342 solve the equations and estimate the parameters. This would introduce several further parameters to 343 estimate, which would be difficult on the datasets that only have a few data points.

344

345 To test the effect of more elliptical attraction areas on the estimate of the density h, we simulated the catches of pairs of traps spaced at different distances (1 to 150 m), where 'crabs' were seeded 346 347 randomly in space at a density of 0.03125 m⁻², and where the probability of capture p_x declines linearly with distance from $p_{x=0} = 1$ to $p_{x=50} = 0$ for crabs that are inside the ellipse. We estimated h for attraction 348 349 areas that ranged from perfectly circular to extremely elliptical, expressed by the eccentricity ranging 350 from 0 to 0.99. Figure 4 shows that the estimate of density *h* is not biased by the shape of the trapping 351 area until the shape parameter is > 0.85 (which represents ellipses that are about 3 times as long as 352 wide), above which point the density is increasingly underestimated. We therefore consider our 353 choice of a circular attraction area a reasonable trade-off between capturing the complexity of the 354 relationship versus the ability to usefully estimate the desired parameters.

- 355
- 356

357 Discussion

358

359 The methods and analyses presented in this paper show that trap-spacing experiments can be used 360 to estimate both the trapping area and the density of benthic fauna that is catchable in traps. Our 361 comparison of the outputs from our analysis with the outputs in the original papers show that the 362 estimates of the catchable density h and the trapping area are highly sensitive to assumptions and 363 analytical method used. It is therefore important to use analytical methods that are both ecologically 364 and mathematically plausible. The large variety in terminology that has been used to describe the area 365 from which animals are caught or attracted has also been confusing this field of study. We therefore 366 propose a standardized set of terms, assumptions and parameters that have clear ecological meaning, 367 and link them to a mathematical framework that formalises these.

368

The method that we used failed to estimate *h* and *r* for one of the datasets where catch rates did not increase with distance, and the estimates *h* and/or *r* were not significant for two of the other studies where only a few datapoints could be extracted. This is unsurprising and illustrates the limitations of this (and any other) approaches in fitting curves on too few data points (i.e. fitting a 2 parameter curve through 3-5 points is always going to be challenging).

374

Based on our analysis, we make these recommendations for carrying out trap-spacing experiments:

- The traps that are spaced closest to each other need to be close enough to each other to interfere with each other's catches. If they are not, it will be difficult to estimate the trapping area *r*, and because *r* and catchable density *h* are interdependent in the analysis, estimation of *h* will also be problematic.
- 380 2) For the traps that are furthest apart, *d* needs to be much larger than *r* to allow a robust
 381 estimate of the trapping area and maximum catch rates.

- 382 3) Mixed distances between traps should be avoided because this makes fitting the curves
 harder for the statistical algorithms. Having traps at the end of lines that only have one
 neighbour is useful (and unavoidable).
- 385 4) Shorter soak times are better, because they avoid trap saturation and are more likely to lead 386 to a linear decline in p_x with distance. This is particularly important in lobster fisheries, where 387 trap saturation seems to be prevalent than in other fisheries (Clark et al. 2018; Watson and 388 Jury 2013)
- 3895) A critical issue to consider is that the efficiency of traps (just like all forms of fishing gear390whether used commercially or in scientific sampling) will always be lower than 100%, i.e. P<1.</td>391In order to estimate actual densities of target species on the seabed, that is estimate the392absolute density *H* from the catchable density *h*, an estimate of *P* is required. Mark-recapture393experiments are probably the most effective means of achieving this (e.g. Ungfors et al. 2007).
- 394

In our model we implicitly assume that the area from which animals could be arriving increases quadratically with the distance from the trap (based on the trapping area being circular), while the probability of capture declines linearly. This means that most of the animals caught will arrive from an intermediate distance from the trap (Figure 5). As the time at which animals arrive in a trap is likely to correlate to the distance they travelled to reach the trap, monitoring the arrival time at traps using cameras or frequent trap lifts may be useful as a way of testing the assumption about how the probability of capture relates to distance.

402

The failure of the model fitting for *Chionocetes japonicus* because catches declined with trap spacing (Figure 3H) may be interesting in its own right. The observed pattern could imply non-independent trap entry probabilities through an aggregation response, which doesn't satisfy the assumptions of our model. Similarly, antagonistic interactions between individual crustaceans (e.g. *Homarus gammarus, (Bennett 1974)*) could result in lower trap entry probabilities than expected at higher lobster densities, and underestimate *r* and *h*.

- 409
- 410 Uncertainty remains regarding the importance of the shape of the attraction area and the 411 relationship between the distance from the trap and probability of capture on the accuracy of the 412 density estimate. Future studies could use further simulations to evaluate how different attraction 413 area ellipse shapes and ellipse directions, and the variation in the directions of such ellipses over the 414 tidal cycle, affect the relationship between the catches and density estimates in trap-spacing 415 experiments. Further simulations should also evaluate the effect of different relationships between 416 the probability of capture and the distance from the trap, besides the linear relationship assumed 417 here. If such simulations show that such variations cause strong biases in the estimated densities, 418 further fieldwork will be needed to more precisely determine the actual shape of these relationship, 419 and further development of the mathematical framework may be needed.
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- 421

1 Implications for trap spacing and soak time in commercial fishing operations.

422

The continued use of fleets using closely spaced traps such as those used in the British Isles for targeting *C. pagurus* may be inefficient. Currently, the spacing between traps in the commercial brown crab fishery in the Isle of Man is 18 - 27m. Our estimates (reported in detail in Supplementary material) show this spacing achieves catch rates at only 20 to 30% of the maximum possible per trap, which 427 would be obtained at a trap spacing of 171.6m (2 x r, 95% CI: 88.5 - 252.2m). Obtaining these higher 428 catch rates using such a large trap spacing would require the use of much longer mainlines. The open 429 access nature of the fishery means there high competition between vessesl, with limited ground and 430 therefore vessles may need to deploy all their pots over a smaller area due to a lack of available 431 suitable ground. Increasing trap spacing could potentially increase catch rates. However, there would 432 be operational implications because while the catch per trap could go up substantially, the catch per 433 unit of line would decline by almost 50%. Lower catch per trap may therefore be outweighed by higher 434 overall catch per unit of 'fishing effort', as lower trap catch rates may be offset by the ability to lift 435 more traps, leading to an overall higher catch per fishing day. However, if ground availability and the 436 length of the mainline that can be deployed are not a limiting factor, this presents the opportunity to 437 reduce trap numbers whilst maintaining the desired overall catch. Wider trap spacing could reduce 438 ecosystem impacts related to seabed abrasion (Gall et al. 2020) and reduce bait use, and could reduce 439 costs and CO_2 emissions (but could increase the entanglement of marine mammals). In regions where 440 trap limits are imposed this presents the opportunity to maintain the viability of the fishery by 441 developing single trap deployment zones, e.g. coinciding with priority marine features or limited 442 gear/limited access areas.

443

444 Changes in trap spacing to maximise efficiency could add to technology creep in trap fisheries with 445 important implications for pressure on stocks and the use of long term fisheries dependent data in 446 management. Technology creep is poorly understood in trap fisheries, but is recognised to significantly 447 influence catch rates and efficiency. Kleiven et al. (2022) demonstrated how slight changes in gear 448 design in static gear can affect the catch composition available to the fishery. This was demonstrated 449 by comparing the catch efficiency and catch composition of traditional wooden traps from 1928 to 450 modern semi-synthetic traps in the Norwegian H. gammarus fishery. That study established that since 451 1928, traps have been fitted with incrementally larger entrance eyes, multi-chamber designs and 452 longer lasting manufactured material. These small changes alter the efficiency of traps and have been 453 highlighted as potential contributors to the stock collapse in Norway by potentially masking stock 454 decline by keeping catch rates high (Erisman et al. 2011). Such an instance of unaccounted technical 455 creep was recorded in Pacific halibut fisheries, with shifts to wider longline hook spacing resulting in 456 misleading CPUE trends (Skud 1978). This is of concern owing to the declines recorded in both the Isle 457 of Man Cancer pagurus fisheries (Bangor University, 2021) and those around the UK (Mesquita et al. 458 2021).

459

460 **Conclusions**

461 We provide and test a standardized method that is widely applicable to estimate the catchable density 462 of benthic invertebrates. We provide code and example data that will allow more extensive use of this 463 underused method for estimating the catchable density of benthic invertebrates. This work highlights 464 the importance of recording trap spacing in fishery dependent surveys given that it affects the CPUE, 465 and may allow retrospective CPUE standardisation. Further work is needed, however, to better 466 understand the effect of trap spacing on catch efficiency relative to seasonal fluctuations in catch rates 467 and different soak times (Monnahan and Stewart 2018). Although we applied this method to trap 468 fisheries, it has been shown to be applicable to hook spacing in longline fisheries, where catch of 469 Pacific halibut increase with increasing hook spacing (Skud 1978). However, the estimate of density 470 may be harder to interpret in such fisheries on highly mobile target species, and much larger spacing 471 is likely to be necessary to achieve a good estimate of the distance at which hooks stop interfering.

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- 478

479 Data and Code Availability Statement

480 The code created and an example dataset are available in the supplementary material, using both 481 frequentist and Bayesian methods. Most datasets were extracted from the literature and are

- 482 therefore freely available, and the only new dataset is available in the supplementary material.
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Tables

Study	Terminology used	Shape of	Probability of capture as	Weaknesses
		attraction	a function of the	
		area	distance from the trap	
(Arena et al.	Area of influence – not defined explicitly.	Circular	Constant, i.e. assuming	Simplifies the mathematics to fit a
1994)			no decline with distance.	curve with parameters that have no
			A decline with distance is	theoretical meaning. Does not take
			mentioned in the paper	account of the decreasing catches
			but not implemented	with distance.
			mathematically.	
Gros and	Effective capture field - the area within which every whelk	Ellipse	Constant, i.e. assuming	Assumption of ellipsoid adds in two
Santarelli	present can detect the bait for a sufficient period of time		no decline with distance,	more parameters to estimate. In
(1986)	to enable it to travel to the place where the bait is located,		assuming homogeneous	reality, these can only be estimated
	which is included within the area of chemical influence.		capture probabilities	if multiple experiments with lines in
			within the Effective	different directions are carried out.
			capture field	
Aedo and	Attraction area - the area of chemical influence of the bait	Circular	Negative exponential	Does not correct for the 2D nature
Arancibia	Effective fishing area - notional area containing as many		decline, which is	of a circle when modelling the
(2003) &	animals as were trapped.		converted to knife-edge	probability of capture. Fits a curve
Cores et al.			distance, estimated as	with parameters that have no
(2019)			the distance from which	theoretical meaning. Arbitrary
			half of the catch comes.	definition of the attraction area.
Brouwer and	Effective Fishing Area - The area around the trap that is	Circular	Constant, i.e. assuming	No statistical model fitted. Effective
Wichman	close enough for individuals to find and detect the bait		no decline with distance,	Fishing Area assumed to be the area
(2020)	plume and to reach the trap during the soak time.		assuming homogeneous	within the bait plume.
			capture probabilities	
			within the whole	
			Effective Fishing Area.	

Table 1. Terminology and assumptions of previous studies and models used for estimating 'catchable density' using trap spacing experiments.

(2001)	of capture of an individual during the deployment time of					•
	of capture of an individual during the deployment time of	Circular	or	exponential o	r other	fully developed and too complex to
	the trap is greater than zero.	ellipse				apply to <i>in situ</i> data.
	The effective area fished, which is a purely notional area					
	containing as many animals as were trapped. Effective area					
	fished is a compound of two quantities: the trapping area					
	and the overall average capture probability within this					
	area.					
	Capture probability – in reality the product of density and					
	capture probability					

Table 2. Comparison of the estimated catchable density from the original sources and the non-linear model fitted here, plus the trapping radius estimated here. p-values indicate whether a value was significantly different from zero.

Study	Original Units This study study						
		Catchable density <i>h</i> (100 m ⁻²)	Catchable density <i>h</i> (100 m ⁻²)	p-value h	Trapping radius <i>r</i> (m)	p-value r	Estimated maximum catch rate per trap
A) Cancer pagurus, Isle of Man	Numbers	NA	0.052	0.041	85.8	<0.001	3.85
B) <i>Cancer porter</i> (Aedo and Arancibia 2003)	Numbers	13.0	5.40	0.002	36.1	<0.001	73.87
C) Portumnus latipes (Cores et al. 2019)	Numbers	2.6	15.29	0.101	4.1	0.024	2.69
D) Jasus caveorum (Brouwer and Wichman 2020)	Weight (kg)	Not given	0.13	0.018	54.3	<0.001	4.09
E) <i>Buccinum undatum</i> (Gros and Santarelli 1986)	Weight (kg)	0.72 ¹	9.30	0.043	4.7	<0.001	2.15
F) Simulated crabs (Bell et al. 2001)	Numbers	0.039 ²	0.061	<0.001	150.1	<0.001	14.47
G) Scylla serata, (Williams and Hill 1982)	Numbers	Not given	0.043	0.133	54.9	0.073	1.36
H) <i>Chionoecetes japonicus,</i> (Sinoda and Kobayasi 1969)	Relative numbers	Not given	Failed to fit b	ecause catch	es decline wi	th spacing	

¹ Converted assuming 55 whelks per kg from (Gros and Santarelli 1986).

² Catchable density in the simulation.

Figures



Figure 1. Trap interaction geometry. a) A 3-dimensional view of a cone with the overlapping volume estimated by equation 2. The height of the cone equals h, the radius of the cone equals r, while the slope of the cone is defined by how the capture probability p_x declines with distance b) Trap interaction geometry: circles represent overlapping trapping areas, of radius r, for four baited traps that are spaced at a distance of 2d; (c) overlaps of functions relating capture probability, to distance from trap with capture probability modelled as a linear function of distance. Catchable density right next to the trap equals h, the density of the target species. The overlapping probability surfaces can be viewed as volumes of intersection between cones in a). Figure b and c are modified from Bell et al. (2001).



Figure 2. The cumulative catch of marked *Buccinum undatum* released at different distances from a trap, calculated from data collected by Himmelman (1988). None were caught from further than 18m in within 48h. The black line indicates a linear regression (R^2 =0.78, $F_{1,2}$ =12.166, p=0.073). The red point, where catches is zero, is not included in the regression.



Figure 3. The relationship between the catch per trap and the distance between traps, and the fitted relationship for mid-line (adjacent traps in both directions, black points and line) and end of line traps (adjacent trap in one direction only, grey points and line). Some datasets had traps where the distance to the two adjacent traps were not equal (Brouwer and Wichman 2020; Gros and Santarelli 1986), these are not plotted here but they are used in fitting the lines.



Figure 4. The simulated effect of the eccentricity of the attraction area (0 is circular, with values towards 1 approaching elongated ellipses) on the estimated density *h*, from a simulation. The error bars are 95% confidence intervals of the estimates. The horizontal grey line is the true density of animals in the simulated area.



Figure 5. Example of the distance from which catch originates for the *Cancer pagurus* study presented here. The probability of capture (blue) declines linearly with distance from the trap, but the area (red) increases quadratically with distance from the traps. The catch (black) is the product of these two, and on average caught crabs move 50m to the trap. All y-axis values here are scaled so the maximum equals 1.

Supplementary material

Table S1. Summary of the trap-spacing experiments included in our analysis

Study	Type of trap used	Experimental Design	Trap spacing	Soak time
A) Cancer pagurus, Isle of Man	Traditional single chamber, double soft eyed crab trap. Approx. 30" x 19 x 18". 10" soft eyes.	Eight different trap spacing treatments were established comprising of a single line with 5 traps, and fished over 3 separate 24 hour periods (ie using a 24 hour soak time between each haul event). When hauled the number of individuals per trap was recorded. Individuals were sexed and measured	Distance between traps per treatment were; 15, 22.5, 35,75,105,135.165 and 224 m	24 hours
B) <i>Cancer porter</i> (Aedo and Arancibia 2003)	The Fathom Plus trap was used as the experimental fishing gear and measured 87 cm \times 69 cm \times 29 cm (length, width and depth, respectively), and had a high- density polyethylene structure and framework, mesh openings of 4.5 cm \times 1.8 cm (length and width) and upward-tilted tunnels on both sides of the trap which lead into it through a semicircular opening of 16.7 cm \times 8.6 cm (length and width).	16 fishing events were Conducted. Each longline had 10 traps. There were four replicates per distance.	Distances between traps were 15.0, 22.5, 30.0 and 37.5 m.	An average time of 26 h per event
C) Portumnus latipes (Cores et al. 2019)	Metal Baited stakes baited with sardines on the beach	Stakes were used to attract the crabs that were caught by hand.	1, 2, 4, 8 and 16 m	10 minutes

		After 10 min, each stake was visited and crabs found feeding on the bait, on the surface or buried beneath the bait, were caught by hand. This procedure was repeated five times during each of the three days of sampling, with a 10 min waiting period between each sampling, resulting in a total of 300 samples.		
D) <i>Jasus caveorum</i> (Brouwer and Wichman 2020)	Top loading cone shaped traps set on longlines. Traps used were 150cm diameter at the base, 75cm high and 50cm diameter at the top. The entrance to the trap was 35cm in diameter and the trap was covered with netting of 5cm mesh.	Each experimental fishing line was set with 30 traps, and the traps were divided into six groups, each group set at varying distances apart. Traps were set on a longline by the vessel with the instructions to set three lines a day, parallel to one another and at least 300m apart.	Six groups on a single line. Group 1 - inter-trap distance 20m, followed by a 40m space. Group 2 - inter-trap distance 40m, followed by a 60m space. Group 3 - inter-trap distance 60m, followed by a 90m space. Group 4 - inter-trap distance 90m, followed by a 140m space. Group 5 - inter-trap distance 140m, followed by a 190m space. Group 6 - inter-trap distance 200m	24 hours
E) <i>Buccinum undatum</i> (Gros and Santarelli 1986)	Whelk traps containing two types of bait (crab and fish)	Whelk traps spaced at different distances, with mostly mixed distances in the two directions. The ground line was set three times.	6, 11.9, 23.8 and 35.7 m	24 hours
F) Simulated crabs (Bell et al. 2001)	For crabs, entry probability does not change with increasing catch.	Two traps spaced at different distances.	1-500 m at intervals increasing from 15 to 120m.	Number of time steps = 200. A crab can

	Probability of capture = 0.5 when closer than 1m from the trap.	Animals that approached but did not enter a trap ignored all traps in the arena for the rest of the simulation.		move 1m per time step. If we assume crabs move at around 200 m a day (Ungfors et al. 2007), this would represent about a 24h soak time.
G) <i>Scylla serata</i> , (Williams and Hill 1982)	Two types of traps were used in approximately equal numbers, firstly a collapsible trap 240 mm high made of a rectangular steel frame (900 x 600 mm), covered with 38ram mesh nylon net. The second trap was a commercial design, it had a circular base of approximately 1 m diameter, was 300 mm high and made of a steel frame covered with wire mesh having 40 mm diameter openings. Both types of traps had two entrance funnels (minimum opening 200 x 80 mm) at opposite ends.	Traps organised in rectangular grids.	50 m spacing - 49 traps in a 7 x 7 grid (2 replications); 100 m spacing - 63 traps in a 7x9 grid (8 replications); 200m spacing -20 traps in a 5 x 4 grid (8 replications).	24 hours
H) Chionoecetes japonicus, (Sinoda and Kobayasi 1969)	The pudding-shaped trap used is about 80cm in diameter on the upper surface and about 120cm on the lower, and 75cm high, it has an opening 40cm in diameter on the top. Iron rods about 9-12mm in diameter are used for framing and the entrance tunnel is a cylinder of	Lines of traps. The traps which were adjacent to next span and were set on the end of ground rope were omitted in this analysis. In our analysis 46mm mesh excluded to balance the dataset.	 13 traps were set at 33m intervals, 27 traps at 50m, 10 traps at 67m. 	Generally 24h.

polyethylene. Four different mesh sizes used (46, 90, 120, 150).

Table S2. Comparison of the estimated catchable density from the original sources and the Bayesian model fitted here, plus the trapping radius estimated here.

		Catchable			Trapping			Estimated
		density h			radius r			maximum catch
Study	Units	(100 m ⁻²)	h lower Cl	h upper Cl	(m)	r lower Cl	r upper Cl	rate per trap
A) Cancer pagurus, Isle of Man	Numbers	0.0939	0.0419	0.2817	58.5	32.0	93.3	3.37
B) Cancer porter (Aedo and	Numbers					10 F		
Arancibia 2003)		6.2179	2.8754	15.4498	32.8	19.5	51./	69.96
C) <i>Portumnus latipes</i> (Cores et al. 2019)	Numbers	14.6996	5.1804	27.2348	4.2	2.8	9.0	2.68
D) Jasus caveorum (Brouwer and Wichman 2020)	Weight (kg)	0.8925	0.0749	4.7116	18.7	7.7	75.1	3.27
E) <i>Buccinum undatum</i> (Gros and Santarelli 1986)	Weight (kg)	8.6559	6.2931	9.9332	4.8	4.4	5.7	2.08
F) Simulated crabs (Bell et al. 2001)	Numbers	0.0596	0.0498	0.0710	152.2	138.7	168.1	2.08
G) <i>Scylla serata,</i> (Williams and Hill 1982)	Numbers	7.2104	0.0402	27.8649	4.2	2.0	60.6	1.31

Supplementary Code 1. Code for estimating h and r using a non-linear regression in base R. The script can be run using Supplementary data 1. ***** # function needs a dataframe with column names Catch, Distance.1, Distance.2 # convergence errors can usually be solved by choosing more realistic starting values for h and r estimate.h.r<- function(dataset=df,h=0.10,r=50) { dataset\$Neighbour.1=1 dataset\$Neighbour.2=1 dataset\$Neighbour.1[is.na(dataset\$Distance.1)]=0 dataset\$Neighbour.2[is.na(dataset\$Distance.2)]=0 dataset\$Distance.1[is.na(dataset\$Distance.1)]=min(c(dataset\$Distance.1,dataset\$Distance.2),na. rm=T) #needed to avoid errors, has no effect because value ignored in nls dataset\$Distance.2[is.na(dataset\$Distance.2)]=min(c(dataset\$Distance.1,dataset\$Distance.2),na. rm=T) #needed to avoid errors, has no effect because value ignored in nls dataset\$x.1=dataset\$Distance.1/2 dataset\$x.2=dataset\$Distance.2/2 fit.1=nls(Catch~ ifelse ((x.1 < r & x.2 <r), #this is not fully correct because it allows mixed with and within the r data points, but we cannot select here because we don't know r vet ({1/3 * pi * r^2 * h} -Neighbour.1* {(h/(3*r))*{r^3 * acos(x.1/r) 2*r*x.1*sqrt(r^2-x.1^2) + x.1^3*log({r+sqrt(r^2-x.1^2)}f/x.1) }} # to next pot -Neighbour.2* { $(h/(3*r))*(r^3 * acos(x.2/r))$ $2*r*x.2*sqrt(r^2-x.2^2) + x.2^3*log({r+sqrt(r^2-x.2^2)}/x.2) }), # to previous pot {1/3 * pi * r^2 * h}),$ data=dataset, start=list(h=h, r = r),algorithm = "port", control=nls.control(maxiter = 500, warnOnly = F, printEval = F, tol = 1e-05), trace = TRUE) # fit again but now excluding data points that mix with and within the preliminary r-estimate data points, where \boldsymbol{r} is based on fit.1, and starting values based on fit.1 r=coefficients (fit.1)[2] #speed up things by using starting values for nls from previous fit. h=coefficients(fit.1)[1] #speed up things by using starting values for nls from previous fit. dataset=subset(dataset, ((x.1 < r) & (x.2 < r)) | ((x.1 > r) & (x.2 > r))) subset(dataset, (x.1 < r & x.2 < r)) subset(dataset, (x.1 > r & x.2 > r)) fit=nls(Catch~ ifelse ((x.1 < r & x.2 <r), ({1/3 * pi * r^2 * h} -Neighbour.1* { $(h/(3*r))*(r^3 * acos(x.1/r))$ 2*r*x.1*sqrt(r^2-x.1^2) + x.1^3*log({r+sqrt(r^2-x.1^2)}/x.1) }} # to next pot -Neighbour.2* {(h/(3*r))*{r^3 * acos(x.2/r) 2*r*x.2*sqrt(r^2-x.2^2) + x.2^3*log({r+sqrt(r^2-x.2^2)}/x.2) }}), # to previous pot {1/3 * pi * r^2 * h}), data=dataset, start=list(h=h, r = r). algorithm = "port", control=nls.control(maxiter = 5000, warnOnly = F, printEval = F,tol = 1e-10),trace = TRUE) fit } plot.hr<- function(dataset,fit,label="A",ylab){</pre> h=coefficients(fit)[1] r=coefficients(fit)[2] dataset\$x=rowMeans(cbind(dataset\$Distance.1,dataset\$Distance.2),na.rm=T)/2 dataset\$x.1= dataset\$Distance.1/2 dataset\$x.2= dataset\$Distance.2/2

```
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```

```
plot(data=dataset,Catch~x,xlim=c(0,0.55*max(dataset$Distance.1,na.rm=T)),ylim=c(0,max(dataset$
Catch)*1.2), xaxs="i", yaxs="i", ylab=ylab, xlab="", col="white", pch=19)
# plot(data=dataset, Catch~x, ylab="Catch", xlab="Half the distance
                                                                                between pots d
(m)", col="black", pch=19)
    points(data=dataset,Catch~x.1,subset=is.na(dataset$Distance.2),col="grey",pch=19)
    points(data=dataset,Catch~x.2,subset=is.na(dataset$Distance.1),col="grey",pch=19)
    if (nrow(subset(dataset,x.1==x.2))>1)
    points(data=dataset,subset=x.1==x.2,Catch~x,col="black",pch=19) }
    dataset$Neighbour.1=1
    dataset$Neighbour.2=1
    dataset$Neighbour.1[is.na(dataset$Distance.1)]=0
    dataset$Neighbour.2[is.na(dataset$Distance.2)]=0
    mid.string=2
    if ( max(rowSums(cbind(dataset$Neighbour.1,dataset$Neighbour.2)),na.rm=T)==2){
curve(expr={1/3 * pi * r^2 * h} - mid.string*{(h/(3*r))*{r^3 * acos(x/r)}
2*r*x*sqrt(r^2-x^2) + x^3*log({r+sqrt(r^2-x^2)}/x) }},add=T,lwd=2,from = -1,
                                                                                          to
max(dataset$x,na.rm=T),col="black")
       lines(x=c(r,250),y=c(1/3 * pi * r^2 * h,1/3 * pi * r^2 * h),col="black",lwd=2)
    end.string=1
    if ( {sum(dataset$Neighbour.1==0) + sum(dataset$Neighbour.2==0) }>0) {
    curve(expr={1/3 * pi * r^2 * h} - end.string*{(h/(3*r))*{r^3 * acos(x/r)}

                           x^3*log({r+sqrt(r^2-x^2)}/x) }},add=T,lwd=2,from =-1, to
2*r*x*sgrt(r^2-x^2) +
max(dataset$x,na.rm=T),col="grey")
    lines(x=c(r,250),y=c(1/3 * pi * r^2 * h,1/3 * pi * r^2 * h),col="grey",lwd=2)
    }
     legend(legend=substitute(paste(italic(label))),"topleft",bty="n")
}
stat.table<-function(fit) {</pre>
   h=coefficients(fit)[1]
    r=coefficients(fit)[2]
    Asymptotic.distance=2*r
    Catchable.Densitv=h
    max.catch.rate={1/3 * pi * r^2 * h}
    p.h=summary(fit)$parameters[1,4]
    p.r=summary(fit)$parameters[2,4]
c(h,p.h, r,p.r, max.catch.rate)
***********
# analysis starts here
****
#setwd("C:/Users/ossc06/OneDrive - Bangor University/Documents/Projects/17. IoM")
setwd("C:/Users/Jan Geert Hiddink/Documents/Projects/17. IoM")
IoM=read.csv("Crab Survey.csv")
IoM=aggregate(data=IoM,Catch~string.position+Distance+Treatment,FUN=mean) #it may be necessary
to take the means of data points
IoM=aggregate(data=IoM,Catch~string.position+Distance,FUN=mean)
                                                                            #it may be necessary
to take the means of data points
IoM$Distance.1=IoM$Distance
IoM$Distance.2=IoM$Distance
IoM$Distance.2[IoM$string.position==1]=NA
fit.IoM=estimate.h.r(dataset=IoM, h=4.998e-04, r=8.576e+01)
windows (width=18, height=14)
par(mfrow=c(1,1),xaxs="i",yaxs="i",mar=c(4,4,1,1),oma=c(2,0,0,0),tck=0.01,mgp=c(2.25,1,0))
plot.hr(dataset=IoM,fit=fit.IoM,label="A) Cancer pagurus, IoM",ylab="Mean catch per pot
(numbers)")
legend(legend=c("mid
                                                                                    string", "end
string"), col=c("black", "grey"), pch=19, "bottomright", cex=1.25, bty="n")
```

mtext(side=1,expression(paste("Half the distance between pots",italic(' d '),"(m)")),outer=T)

stats=stat.table(fit.IoM)



names(stats)=c("Density (h)","p-value h","Cone radius (r)","p-value r","Maximum catch rate")
stats

158159 # The expected output using Supplementary data 1 using nls.

160 Supplementary Code 2. Code for estimating h and r using a Bayesian statistics in rstan. The script 161 can be run using Supplementary data 1.

```
163
       require(rstan)
164
165
       require(rethinking)
166
167
        168
        *****
169
170
        # The first function fits the Bayesian model using rstan
171
        # function needs a dataframe with column names Catch, Distance.1, Distance.2
172
173
       # convergence errors can usually be solved by choosing more realistic starting values for h and
       r
174
175
       Bayesian.estimate.h.r<- function(dataset=df,prior.h=c(10^-6,0.20),prior.r=c(1,200)) {</pre>
176
177
       dataset$Neighbour.1=1
       dataset$Neighbour.2=1
178
179
180
       dataset$Neighbour.1[is.na(dataset$Distance.1)]=0
       dataset$Neighbour.2[is.na(dataset$Distance.2)]=0
181
       dataset$Distance.1[is.na(dataset$Distance.1)]=min(c(dataset$Distance.1,dataset$Distance.2),na.
182
183
184
185
186
187
188
       rm=T) \#needed to avoid errors, has no effect because value ignored in nls
       dataset$Distance.2[is.na(dataset$Distance.2)]=min(c(dataset$Distance.1,dataset$Distance.2),na.
       rm=T) #needed to avoid errors, has no effect because value ignored in nls
       dataset$x.1=dataset$Distance.1/2
       dataset$x.2=dataset$Distance.2/2
189
       dataset$x1= dataset$x.1
190
191
192
       #dataset=subset(dataset,x1<150)</pre>
193
       Catch=dataset$Catch
194
195
196
197
       x1 = dataset$x.1
       Neighbour1 = dataset$Neighbour.1
       Neighbour2 = dataset$Neighbour.2
198
       data list <- list(
199
         Catch = Catch,
200
201
         x1 = x1,
         N = length(Catch),
202
         Neighbour1=Neighbour1,
203
         Neighbour2=Neighbour2,
204
         priorh = prior.h
priorr = prior.r
205
206
207
       )
208
209
210
       model conditional<- '</pre>
211
       data{
212
               int<lower=1> N:
213
214
215
               vector[N] Catch;
               vector[N] x1;
              vector[N] Neighbour1;
216
               vector[N] Neighbour2;
217
218
219
220
               vector[2] priorh;
               vector[2] priorr;
               }
221
222
222
223
224
225
       parameters{
               real<lower=1e-06,upper=0.2> h;
               real<lower=.1,upper=300> r;
               real<lower=0> sigma;}
226
227
228
       model{
               vector[N] mu;
              sigma ~ exponential( 1 );
229
230
231
232
              r ~ uniform(priorr[1], priorr[2] );
              h ~ uniform( priorh[1], priorh[2] );
               for ( i in 1:N ) {
233
                   if (x1[i] < r) {
234
               mu[i] = (pi() * r^2 * h)/3
```

```
- (Neighbour1[i] * ((h/(3 * r)) * (r^3 * acos(x1[i]/r) - 2 * r * x1[i] * sqrt(r^2 -
x1[i]^2) + x1[i]^3 * log((r + sqrt(r<sup>2</sup> - x1[i]<sup>2</sup>))/x1[i]))) -
(Neighbour2[i] * ((h/(3 * r)) * (r<sup>3</sup> * acos(x1[i]/r) - 2 * r * x1[i] * sqrt(r<sup>2</sup> -
x1[i]^2) + x1[i]^3 * log((r + sqrt(r^2 - x1[i]^2))/x1[i]))))
       } else {mu[i] = ((pi() * r^2 * h)/3) ;}
       mu[i] = log(mu[i]);}
       Catch ~ lognormal( mu , sigma );}
generated guantities{
       vector[N] log_lik;
       vector[N] mu;
       for ( i in 1:N ) {
          if (x1[i] < r) {
       mu[i] = (pi() * r^2 * h)/3 - ((h/(3 * r)) * (r^3 * acos(x1[i]/r) - 2 * r * x1[i] *
sqrt(r^2 - x1[i]^2) + x1[i]^3 * log((r +
                                                                 sqrt(r^2 - x1[i]^2))/x1[i])));
       } else {mu[i] = ((pi() * r^2 * h)/3);}
       mu[i] = log(mu[i]);
    }
for ( i in 1:N ) log_lik[i] = lognormal lpdf( Catch[i] | mu[i] , sigma );
}
.
fit <- stan(model_code = model_conditional,</pre>
                     data = data list)
fit
}
### this second function plots that data and the fitted relationship
**********
plot.hr<- function(dataset, fit, label="A", ylab) {</pre>
post <- extract.samples(fit)</pre>
h=median(post$h)
r=median(post$r)
    dataset$x=rowMeans(cbind(dataset$Distance.1,dataset$Distance.2),na.rm=T)/2
    dataset$x.1= dataset$Distance.1/2
    dataset$x.2= dataset$Distance.2/2
plot(data=dataset,Catch~x,xlim=c(0,0.55*max(dataset$Distance.1,na.rm=T)),ylim=c(0,max(dataset$
Catch)*1.2),xaxs="i",yaxs="i",ylab=ylab,xlab="",col="white",pch=19)
#
         plot(data=dataset,Catch~x,ylab="Catch",xlab="Half the distance
                                                                               between pots d
(m)", col="black", pch=19)
    points(data=dataset,Catch~x.1,subset=is.na(dataset$Distance.2),col="grey",pch=19)
    points(data=dataset,Catch~x.2,subset=is.na(dataset$Distance.1),col="grey",pch=19)
    if (nrow(subset(dataset,x.1==x.2))>1)
    points(data=dataset, subset=x.1==x.2, Catch~x, col="black", pch=19) }
    dataset$Neighbour.1=1
    dataset$Neighbour.2=1
    dataset$Neighbour.1[is.na(dataset$Distance.1)]=0
    dataset$Neighbour.2[is.na(dataset$Distance.2)]=0
    mid.string=2
    if (max(rowSums(cbind(dataset$Neighbour.1,dataset$Neighbour.2)),na.rm=T)==2){
curve(expr={1/3 * pi * r^2 * h} - mid.string*{(h/(3*r))*{r^3 * acos(x/r)}
2*r*x*sqrt(r^2-x^2) + x^3*log({r+sqrt(r^2-x^2)}/x) }},add=T,lwd=2,from = -1,
                                                                                         to
max(dataset$x,na.rm=T),col="black")
       lines(x=c(r,250),y=c(1/3 * pi * r^2 * h,1/3 * pi * r^2 * h),col="black",lwd=2)
    }
    end.string=1
    if ( {sum(dataset$Neighbour.1==0) + sum(dataset$Neighbour.2==0)}>0) {
```

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```
310
             curve(expr={1/3 * pi * r^2 * h} - end.string*{(h/(3*r))*{r^3 * acos(x/r)}
311
                         + x^3*log({r+sqrt(r^2-x^2)}/x) }},add=T,lwd=2,from =-1,
      2*r*x*sqrt(r^2-x^2)
                                                                                        tο
      max(dataset$x,na.rm=T),col="grey")
313
          lines(x=c(r,250),y=c(1/3 * pi * r^2 * h,1/3 * pi * r^2 * h),col="grey",lwd=2)
314
315
          }
316
317
           legend(legend=substitute(paste(italic(label))),"topleft",bty="n")
320
321
322
323
      }
      # this function makes a table of the estimated parameter values
      ***********
326
327
328
      stat.table<-function(fit) {</pre>
      post <- extract.samples(fit)</pre>
330
      h=median(post$h)
      r=median(post$r)
      h.ci=quantile(post$h,c(0.025,0.975))
334
      r.ci=quantile(post$r,c(0.025,0.975))
335
336
          Asymptotic.distance=2*r
          Catchable.Density=h
338
          max.catch.rate={1/3 * pi * r^2 * h}
339
340
341
      c(h, h.ci,r, r.ci,max.catch.rate)
      }
343
344
      *****
      # analysis starts here
      *****
349
350
351
352
      #### IoM Cancer pagurus ####
      #setwd("C:/Users/ossc06/OneDrive - Bangor University/Documents/Projects/17. IoM")
      setwd("C:/Users/Jan Geert Hiddink/Documents/Projects/17. IoM")
      IoM=read.csv("Crab Survey.csv")
353
      IoM=aggregate(data=IoM,Catch~string.position+Distance+Treatment,FUN=mean) #it may be necessary
      to take the means of data points
      IoM=aggregate(data=IoM,Catch~string.position+Distance,FUN=mean)
                                                                           #it may be necessary
356
357
      to take the means of data points
      IoM$Distance.1=IoM$Distance
      IoM$Distance.2=IoM$Distance
      IoM$Distance.2[IoM$string.position==1]=NA
360
      fit.IoM=Bayesian.estimate.h.r(dataset=IoM,prior.h=c(0.00001,0.05),prior.r=c(10,200)) #priors
      need to be chosen to fit the dataset
      ##diagnostics
364
      pairs(fit.IoM,pars=c("sigma","h","r"))
365
      traceplot(fit.IoM, pars=c("sigma", "h", "r"))
      windows (width=18, height=14)
      par(mfrow=c(1,1),xaxs="i",yaxs="i",mar=c(4,4,1,1),oma=c(2,0,0,0),tck=0.01,mgp=c(2.25,1,0))
369
370
      plot.hr(dataset=IoM,fit=fit.IoM,label="A) Cancer pagurus, IoM",ylab="Mean catch per pot
      (numbers)")
      mtext(side=1,expression(paste("Half the distance between traps",italic(' d '),"(m)")),outer=T)
373
374
      legend(legend=c("mid
                                                                                   string", "end
      string"),col=c("black","grey"),pch=19,"bottomright",cex=1.25,bty="n")
      # run this is you want to plot a sample of the possible lines you can expect
      #post=extract(fit.IoM)
      #alpha=0.005
      #mid.string.col=adjustcolor( "black",alpha.f = alpha)
      #end.string.col=adjustcolor( "blue", alpha.f = alpha)
      #for (x in 1:length(post$r)) {
      # h=post$h[x]
383
      # r=post$r[x]
         curve(expr={1/3 * pi * r^2 * h} - 1*{(h/(3*r))*{r^3 * acos(x/r)}
                                                                       -2*r*x*sqrt(r^2-x^2) +
      x^3 \log (\{r+sqrt(r^2-x^2)\}/x)\}, add=T, lwd=2, from =-1, to = r, col=end.string.col)
```

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384

```
386  # curve(expr={1/3 * pi * r^2 * h} - 2*{(h/(3*r))*{r^3 * acos(x/r) -2*r*x*sqrt(r^2-x^2) +
387 x^3*log({r+sqrt(r^2-x^2)}x) },add=T,lwd=2,from =-1, to = r,col=mid.string.col)
388  # lines(x=c(r,250),y=c(1/3 * pi * r^2 * h,1/3 * pi * r^2 * h),col=mid.string.col,lwd=2)
389  # lines(x=c(r,250),y=c(1/3 * pi * r^2 * h,1/3 * pi * r^2 * h),col=end.string.col,lwd=2)
390  #}
391  #
392
393
394  stat.table(fit.IoM)
anemes(stats)=c("Density (h)","h lower CI","h upper CI","Cone radius (r)","r lower CI","r upper
CI","Maximum catch rate")
397  stats
398
399
400
401
```



404 # The expected output using Supplementary data 1 using rstan.

405	Supp	plementary dat	a 1. The da	ataset for Is	le of Man t	trap-distance	experim	ent for Cancer pagurus
406		Treatment	String	Pot_No.	Date	Distance	Catch	string.position
407	1	T1 1	Т1	1	05-Aug	15.0	1	1
408	2	т2_1	Т2	1	05-Aug	22.5	0	1
409	3	т3_1	Т3	1	05-Aug	35.0	1	1
410	4	т4_1	Т4	1	05-Aug	75.0	2	1
411	5	 т5_1	т.5	1	05-Aug	105.0	2	1
412	6	т6_1	 т6	- 1	05 - Aug	135 0	5	- 1
412 //12	7	то <u></u> 1	τ0 	1	$05 - \Delta u \sigma$	165 0	2	1
413 /1/	2 Q	ту_1 то_1	т и т Q	1	05 Aug	225 0	2 0	1
414 //15	0	10_1 m1_1	10 m1	1	05 Aug	15 0	2	⊥ 1
415	10		тт ш0	1	00-Aug	1J.U	2	1
410	1 U		12	1	06-Aug	22.0	2	1
417		T3_1	T3	1	06-Aug	35.0	3	1
418	12	1'4_1	'1'4	1	06-Aug	/5.0	6	1
419	13	15_1	Τ5	1	06-Aug	105.0	9	1
420	14	T6_1	Т6	1	06-Aug	135.0	7	1
421	15	T7_1	т7	1	06-Aug	165.0	6	1
422	16	T8_1	Т8	1	06-Aug	225.0	5	1
423	17	T1_1	Т1	1	07-Aug	15.0	3	1
424	18	T2_1	Т2	1	07-Aug	22.5	4	1
425	19	Т3_1	Т3	1	07-Aug	35.0	1	1
426	20	Т4 1	Τ4	1	07-Aug	75.0	3	1
427	21	т5_1	т5	1	07-Aug	105.0	1	1
428	22	т6_1	Тб	1	07-Aug	135.0	4	1
429	23	т7_1	т7	1	07-Aug	165.0	4	1
430	24	т8_1	Т8	1	07-Aug	225.0	9	1
431	25	т1_2	Т1	2	05-Aug	15.0	0	2
432	26	т2_2	т2	2	05-Aug	22.5	1	2
433	27	т.3_2	т.3	2	05-Aug	35.0	1	- 2
434	28	т4_2	т4	2	05 - Aug	75.0	0	2
435	29	т <u>-</u> т5-2	т- т-5	2	05 - Aug	105 0	4	2
436	30	те_2	т6 Т	2	05 - Aug	135 0	0	2
437	31	то <u>2</u> то <u>2</u>	±0 Ͳ7	2	05 - Aug	165 0	1	2
437	32	тя 2	т Я	2	$05 - \Delta u \sigma$	225 0	2	2
130	22	то_2 т1_2	т0 т1	2	05 Aug	15 0	2 /	2
439	21		11 m0	2	06-Aug	10.0	4	2
440	24	12_2 m2_2	۲۲ سر	2	06 Aug	22.J	⊥ 2	2
441	30	T3_Z	T3	2	06-Aug	35.0	3	2
442	30	14_Z	1'4 mc	2	06-Aug	105.0	I C	2
443	37	T5_2	T5	2	06-Aug	105.0	6	2
444	38	T6_2	Т6	2	06-Aug	135.0	5	2
445	39	T/_2	'T' /	2	06-Aug	165.0	6	2
446	40	T8_2	Т8	2	06-Aug	225.0	1	2
447	41	T1_2	T1	2	07-Aug	15.0	1	2
448	42	T2_2	Т2	2	07-Aug	22.5	3	2
449	43	Т3_2	Т3	2	07-Aug	35.0	3	2
450	44	Т4_2	Т4	2	07-Aug	75.0	4	2
451	45	т5_2	Т5	2	07-Aug	105.0	2	2
452	46	т6_2	Тб	2	07-Aug	135.0	2	2
453	47	т7_2	т7	2	07-Aug	165.0	6	2
454	48	Т8_2	Т8	2	07-Aug	225.0	2	2
455	49	т1_3	T1	3	05-Aug	15.0	0	2
456	50	Т2 З	Т2	3	05-Aug	22.5	0	2
457	51	т3_3	Т3	3	05-Aug	35.0	1	2
458	52	т4_3	Т4	3	05-Aug	75.0	1	2
459	53	т5_3	Т5	3	05-Aug	105.0	2	2

460	54	т6_3	Т6	3	05-Aug	135.0	1	2
461	55	т7 З	т7	3	05-Aug	165.0	5	2
462	56	т8_3	Т8	3	05-Aug	225.0	2	2
463	57	т1_3	Τ1	3	06-Aug	15.0	0	2
464	58	Т2_3	Т2	3	06-Aug	22.5	3	2
465	59	Т3_3	ТЗ	3	06-Aug	35.0	2	2
466	60	Т4_3	Т4	3	06-Aug	75.0	4	2
467	61	т5_3	Т5	3	06-Aug	105.0	3	2
468	62	т6_3	Т6	3	06-Aug	135.0	4	2
469	63	т7_3	т7	3	06-Aug	165.0	11	2
470	64	T8_3	Т8	3	06-Aug	225.0	8	2
471	65	T1_3	T1	3	07-Aug	15.0	2	2
472	66	T2_3	T2	3	07-Aug	22.5	Ţ	2
4/3	67	T3_3	T3	3	07-Aug	35.0	0	2
474	68	'1'4_3 m	'1'4 m5	3	07-Aug	/5.0	4	2
475	69 70	T5_3	1'5 mC	3	07-Aug	105.0	2	2
470	70	10_3	10	3 2	07-Aug	135.0	2	2
477 170	71	1/_3 mo_3	1 / mo	ン っ	07-Aug	105.0	9	2
470 170	72	10_3 m1_4	10 m1	7	07-Aug	15 0	2	2
475	73	тт <u></u> т2_4	тт Т	- Д	05 Aug	22 5	0	2
480	75	т2 <u>-</u> т т3_4	т2 т3	4	05-Aug	35 0	0	2
482	76	т <u>3</u> 1 т4 4	т4	4	05 - Aug	75.0	4	2
483	77	т.5 4	т.5	4	05-Aug	105.0	.3	2
484	78	т6_4	<u>т</u> 6	4	05-Aug	135.0	1	2
485	79	т7_4	т7	4	05-Aug	165.0	1	2
486	80	т84	Т8	4	05-Aug	225.0	0	2
487	81	т1 4	Т1	4	06-Aug	15.0	2	2
488	82	т2_4	Т2	4	06-Aug	22.5	0	2
489	83	т3_4	ТЗ	4	06-Aug	35.0	2	2
490	84	T4_4	Т4	4	06-Aug	75.0	4	2
491	85	Т5_4	Т5	4	06-Aug	105.0	2	2
492	86	Т6_4	Т6	4	06-Aug	135.0	4	2
493	87	т7_4	т7	4	06-Aug	165.0	7	2
494	88	T8_4	T8	4	06-Aug	225.0	3	2
495	89	T1_4	T1	4	07-Aug	15.0	1	2
496	90	T2_4	T2	4	07-Aug	22.5	0	2
497	91	13_4	T3	4	07-Aug	35.0	Ţ	2
498	92	1'4_4 m_	'1'4 mc	4	07-Aug	/5.0	4	2
499 500	93	T5_4 T6_4	1'5 	4	07-Aug	125.0	ю 5	2
500	94	10_4 m7_4	10 m7	4	07-Aug	165 0	1	2
502	96	1/_4 T8_/	т Я	7	07 Aug	225 0	2	2
502	97	то <u></u> т ттт 5	то т1	- 5	05-Aug	15 0	0	2
503	98	T2 5	т2	5	05 - Aug	22.5	0	1
505	99	тз <u>5</u>	т3	5	05 - Aug	35.0	4	1
506	100	T4 5	т4	5	05-Aug	75.0	2	1
507	101	T5 5	т5	5	05-Aug	105.0	3	1
508	102	т6 5	Т6	5	05-Aug	135.0	1	1
509	103	т7_5	т7	5	05-Aug	165.0	2	1
510	104	т8_5	Т8	5	05-Aug	225.0	5	1
511	105	т1_5	Т1	5	06-Aug	15.0	1	1
512	106	т2_5	Т2	5	06-Aug	22.5	0	1
513	107	т3_5	ТЗ	5	06-Aug	35.0	1	1
514	108	т4_5	Т4	5	06-Aug	75.0	1	1
515	109	т5_5	Т5	5	06-Aug	105.0	6	1

516	110	т6 5	Т6	5	06-Aug	135.0	4	1
517	111	т7_5	т7	5	06-Aug	165.0	6	1
518	112	т8_5	Т8	5	06-Aug	225.0	5	1
519	113	T1_5	Т1	5	07-Aug	15.0	0	1
520	114	т2_5	Т2	5	07-Aug	22.5	4	1
521	115	т3_5	ТЗ	5	07-Aug	35.0	3	1
522	116	т4_5	Т4	5	07-Aug	75.0	3	1
523	117	т5_5	т5	5	07-Aug	105.0	5	1
524	118	т6_5	Т6	5	07-Aug	135.0	4	1
525	119	т7_5	т7	5	07-Aug	165.0	6	1
526	120	т8_5	Т8	5	07-Aug	225.0	2	1