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Estimating the abundance of benthic invertebrates from trap-catch data

Jan Geert Hiddink ${ }^{1}$
Matt Coleman ${ }^{1}$
Stephen Brouwer ${ }^{2}$
Isobel Bloor ${ }^{1}$
Stuart Jenkins ${ }^{1}$

1. School of Ocean Sciences, Bangor University, United Kingdom, j.hiddink@bangor.ac.uk
2. Saggitus Environmental Science Limited, New Zealand

## Short running title: Analysis of trap-distance experiments

IJMS


#### Abstract

Trap fisheries targeting invertebrates are economically important but many of the target species lack 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 distances. With declining spacing, the sphere of attraction will increasingly overlap, leading to reductions in catches, allowing for the estimation of the density that is catchable by traps on the seabed. Here we review the analytical methods adopted across a range of studies and find that no consensus on robust methods exists. We propose an analytical method that assumes the trapping area is circular and that the chance of catching an individual declines linearly with distance from the trap. We apply this method to estimate the density and the trapping radius of crabs and gastropods from real and simulated datasets. The method estimated a trapping radius of between 4 and 86 metres, and densities that are up to 2.5 times less and 13 times greater than estimates provided in the original sources, illustrating the sensitivity to methodology. In conclusion, we provide and test a standardized method to estimate the density of benthic invertebrates.


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## Introduction

Trap, pot and creel fisheries targeting crustaceans and gastropods are economically important worldwide, with growth of wild capture crustacean fisheries outpacing all other major species groups since 1990. Global landings have nearly doubled from $4.4 \%$ of total landed biomass to $7.8 \%$ and they account for $21.3 \%$ of global marine fisheries value (Boenish et al. 2022). The socio-economic importance of wild capture crustacean and gastropod fisheries is further evident at local scales. For example, in the UK whelk Buccinum undatum, brown crab Cancer pagurus and European lobster Hommarus gammarus landings are worth $\sim £ 77$ Million annually at the first point of sale (Marine Management Organisation 2022). However, many of the target species of these fisheries, including 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 production while minimizing environmental impacts (Emmerson et al. 2022; Hilborn et al. 2020; Lart 2019). In the European union, managers are predominantly reliant on fisheries dependent data to assess stock status in trap fisheries (ICES 2021; Marine Institue and Bord lascaigh Mhara 2022; Mesquita et al. 2023) despite recognition of the potential limitations of such approaches in provision of management advice (Emmerson et al. 2022; Maunder and Piner 2014). Fisheries independent approaches to determining stock abundance for crustaceans and gastropods are relatively limited. In using traps to generate estimates of stock abundance one of the key pieces of information that is currently missing is understanding of the area of the sea floor fished.

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

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

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

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.

## Review of methods and terminology

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

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

The horizontal shape of the area from which animals were assumed to be caught was either circular or 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 are carried out. To date, such experiments have not been undertaken.

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

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

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.

## 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.
- Trapping area: $A=\pi r^{2}$
- Density of the target species: $H$.
- Capture probability for animals at the trap: $P$. 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 at distance $x$ from the trap: $p_{x}$. This is assumed to decline linearly with distance from the trap, from $p_{x=0}=P$ directly at the trap, to $p_{x \geq r}=0$.
- The density catchable by traps: $h=H P$. 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 $p_{x} H$ over $A$.
- Half the distance between traps in the experiment: $d$

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

The key assumptions of this framework are that:

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 (1988) released a large number of tagged whelks Buccinum undatum at 6 distances from a baited trap (refreshed every 24 hours) and recorded their recovery in the trap over a period of 15 days. Using the full period leads to an exponential decline in catch rates with distance, but using a period of 48 hours, which is a much more realistic period of soak time in most coastal fisheries, leads to a linear decline in capture probability (Figure 2). Observations of marked snow crabs Chionoecetes opilio (Brethes et al. 1985) and brown crab Cancer pagurus (Ungfors 2008) show similar patterns that do not clearly deviate from a linear decline. It is worth noting that each of these studies does show large variations that could justify other shapes (concave and convex curves), but such shapes would not allow a mathematical solution of the equations.
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. 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
predictable or uniform (Himmelman 1988; Lapointe and Sainte-Marie 1992). The area of attraction has been estimated by a number of different shapes, described by either a circle (Bell et al. 2001), rectangle (Melville-Smith 1986) or an ellipse (Gros and Santarelli 1986). In locations of less intense tidal current flow, the area of attraction might average out as circular over the course of the tidal cycle, even if it is not circular at any given point in time. Given the complexity of bait plume dispersal and lack of current data we therefore assume that circular is a good assumption for convenience and mathematical solvability. Catch from overlapping trapping areas are divided equally between traps.
We assume that animals in an area where trapping areas overlap will move towards the closest trap.
4) The likelihood of traps capturing the target species is not affected by the presence of previously caught animals in a trap.
Trap saturation caused predominantly by inter- and intraspecific interactions is known to affect catches in trap fisheries (Fogarty and Addison 1997). For example Emmerson et al (2022) showed that interaction with European lobster Homarus gammarus led to a reduction in catch rates of targeted brown crab Cancer pagurus while Rayner and McGaw (2019) documented that trap saturation by nontarget invasive green crab Carcinus maenas had a negative impact on American lobster Homarus americanus catches. Trap saturation seems to be particularly common in lobster fisheries (e.g. Clark et al. 2018; Watson and Jury 2013) which can result in a lack of a correlation between lobster catches and lobster abundance (Courchene and Stokesbury 2011; Watson and Jury 2013).

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

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 $P\left(p_{x=0}\right)$ 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:

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.

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):

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

If $d>r$, there is no overlap between the two cones and the Overlapping volume $=0$. The catch of a trap that is competing with $n$ traps with overlapping trapping areas ( $n=1$ at the end of a line, and $n=$ 2 in the middle of a line) is therefore:

Catch $=$ Cone volume $-n$ Overlapping volume
(equation 3)

When fishing at close trap spacings, or where attraction areas are large, interactions may extend beyond just adjacent traps (i.e. the overlaps may themselves be overlapping), but given that we assume that all animals move to the closest trap, this does not affect our estimates of $h$ and $r$.

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, which provides estimates of the parameters of interest, catchable density $h$ and trapping radius $r$. Even though a Poisson error distribution may have been more appropriate for the count data that underly the catch rates, a non-linear ordinary least-squares regression does not allow other error structures than Gaussian. Given that the distribution of the residuals did not deviate from a normal distribution on visual inspection, using non-linear ordinary least-squares regression seems appropriate here. R code using both non-linear regression and Bayesian statistics and an example dataset are provided in the Supplementary Material of this paper. The non-linear regression is more straightforward to use and is recommended for users that are not familiar with Rstan (Stan Development Team 2020).

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

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

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

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. The method estimated a catchable density (the product of the density and the probability of capture for animals right next to the trap) between 15.3 individuals per $100 \mathrm{~m}^{-2}$ for Portumnus latipes, 0.052 individuals per $100 \mathrm{~m}^{-2}$ for Cancer pagurus to 0.043 individuals per $100 \mathrm{~m}^{-2}$ for Scylla serata. These estimates of $h$ are between 0.4 to 13 times relative to the estimates provided in the original sources, which illustrates that these estimates are highly sensitive to the method used (Table 2). Although the studies on Cancer porter (Aedo and Arancibia 2003) and Portumnus latipes (Cores et al. 2019) reported 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 original estimates suggests that they did not in fact use the same analysis and points to the lack of clarity across studies in general.

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

The estimates of $h$ and $r$ generated using the $n l s$ 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).

## 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
most datasets and fitted them well. Although other shapes are plausible (e.g. an exponential decline in $p_{x}$ with distance, elliptical trapping areas), they would make it much more difficult to mathematically solve the equations and estimate the parameters. This would introduce several further parameters to estimate, which would be difficult on the datasets that only have a few data points.

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 randomly in space at a density of $0.03125 \mathrm{~m}^{-2}$, 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 areas that ranged from perfectly circular to extremely elliptical, expressed by the eccentricity ranging from 0 to 0.99 . Figure 4 shows that the estimate of density $h$ is not biased by the shape of the trapping area until the shape parameter is $>0.85$ (which represents ellipses that are about 3 times as long as wide), above which point the density is increasingly underestimated. We therefore consider our choice of a circular attraction area a reasonable trade-off between capturing the complexity of the relationship versus the ability to usefully estimate the desired parameters.

## Discussion

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

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).

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

1) 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.
2) For the traps that are furthest apart, $d$ needs to be much larger than $r$ to allow a robust estimate of the trapping area and maximum catch rates.
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).
4) Shorter soak times are better, because they avoid trap saturation and are more likely to lead to a linear decline in $p_{x}$ with distance. This is particularly important in lobster fisheries, where trap saturation seems to be prevalent than in other fisheries (Clark et al. 2018; Watson and Jury 2013)
5) A critical issue to consider is that the efficiency of traps (just like all forms of fishing gear whether used commercially or in scientific sampling) will always be lower than $100 \%$, i.e. $\mathrm{P}<1$. In order to estimate actual densities of target species on the seabed, that is estimate the absolute density $H$ from the catchable density $h$, an estimate of $P$ is required. Mark-recapture experiments are probably the most effective means of achieving this (e.g. Ungfors et al. 2007).

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.

The failure of the model fitting for Chionocetes japonicus because catches declined with trap spacing (Figure 3 H ) 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 $h$.

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

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

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 $18-27 \mathrm{~m}$. 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
would be obtained at a trap spacing of $171.6 \mathrm{~m}(2 \mathrm{xr}, 95 \% \mathrm{Cl}: 88.5-252.2 \mathrm{~m})$. Obtaining these higher catch rates using such a large trap spacing would require the use of much longer mainlines. The open access nature of the fishery means there high competition between vessesl, with limited ground and therefore vessles may need to deploy all their pots over a smaller area due to a lack of available suitable ground. Increasing trap spacing could potentially increase catch rates. However, there would be operational implications because while the catch per trap could go up substantially, the catch per unit of line would decline by almost $50 \%$. Lower catch per trap may therefore be outweighed by higher overall catch per unit of 'fishing effort', as lower trap catch rates may be offset by the ability to lift more traps, leading to an overall higher catch per fishing day. However, if ground availability and the length of the mainline that can be deployed are not a limiting factor, this presents the opportunity to reduce trap numbers whilst maintaining the desired overall catch. Wider trap spacing could reduce ecosystem impacts related to seabed abrasion (Gall et al. 2020) and reduce bait use, and could reduce costs and $\mathrm{CO}_{2}$ emissions (but could increase the entanglement of marine mammals). In regions where trap limits are imposed this presents the opportunity to maintain the viability of the fishery by developing single trap deployment zones, e.g. coinciding with priority marine features or limited gear/limited access areas.

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

## Conclusions

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

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## Data and Code Availability Statement

The code created and an example dataset are available in the supplementary material, using both frequentist and Bayesian methods. Most datasets were extracted from the literature and are therefore freely available, and the only new dataset is available in the supplementary material. Man Government. We thank the observers and crew of the Altair 6 for their assistance and hard work on the Jasus survey. We thank Mike Bell and other reviewers for reviewing an earlier version of this manuscript.

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## Tables

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

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



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 | Units | Original study | This study |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Catchable density $h$ ( $100 \mathrm{~m}^{-2}$ ) | Catchable <br> density $h$ <br> ( $100 \mathrm{~m}^{-2}$ ) | p-value $h$ | Trapping radius $r$ (m) | p-value <br> $r$ | 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) Cancer porter (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) Buccinum undatum (Gros and Santarelli 1986) | Weight <br> (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) Chionoecetes japonicus, (Sinoda and Kobayasi 1969) | Relative numbers | Not given | Failed to fit because catches decline with spacing |  |  |  |  |

## Figures

a

b


C


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 2 d ; (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 18 m in within 48 h . 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.


## Eccentricity

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 50 m 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". $10^{\prime \prime}$ 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) Cancer porter (Aedo and Arancibia 2003) | The Fathom Plus trap was used as the experimental fishing gear and measured $87 \mathrm{~cm} \times 69 \mathrm{~cm} \times 29 \mathrm{~cm}$ (length, width and depth, respectively), and had a highdensity polyethylene structure and framework, mesh openings of 4.5 $\mathrm{cm} \times 1.8 \mathrm{~cm}$ (length and width) and upward-tilted tunnels on both sides of the trap which lead into it through a semicircular opening of $16.7 \mathrm{~cm} \times 8.6 \mathrm{~cm}$ (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 |

$\left.\begin{array}{lll} & \begin{array}{l}\text { After } 10 \text { min, each stake was } \\ \text { visited and crabs found feeding }\end{array} \\ \text { on the bait, on the surface or } \\ \text { buried beneath the bait, were } \\ \text { caught by hand. This procedure }\end{array}\right]$

|  | Probability of capture $=0.5$ when closer than 1 m 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 1 m per time step. If we assume crabs move at around 200 m a day (Ungfors et al. 2007), this would represent about a 24 h soak time. |
| :---: | :---: | :---: | :---: | :---: |
| G) Scylla serata, (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 ( $900 \times 600 \mathrm{~mm}$ ), covered with 38 ram 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 $200 \times 80 \mathrm{~mm}$ ) at opposite ends. | Traps organised in rectangular grids. | 50 m spacing - 49 traps in a $7 \times 7$ grid (2 replications); <br> 100 m spacing - 63 traps in a $7 \times 9$ grid (8 replications); <br> 200m spacing -20 traps in a $5 \times 4$ grid (8 replications). | 24 hours |
| H) Chionoecetes japonicus, (Sinoda and Kobayasi 1969) | The pudding-shaped trap used is about 80 cm in diameter on the upper surface and about 120 cm on the lower, and 75 cm high, it has an opening 40 cm in diameter on the top. Iron rods about $9-12 \mathrm{~mm}$ 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 46 mm mesh excluded to balance the dataset. | 13 traps were set at 33 m intervals, <br> 27 traps at 50 m , <br> 10 traps at 67 m . | Generally 24 h . |

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.

| Study | Units | Catchable density $h$ ( $100 \mathrm{~m}^{-2}$ ) | h lower Cl | h upper Cl | Trappin radius (m) | r lower Cl | r upper Cl | Estimated maximum catch 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 Arancibia 2003) | Numbers | 6.2179 | 2.8754 | 15.4498 | 32.8 | 19.5 | 51.7 | 69.96 |
| C) Portumnus latipes (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) Buccinum undatum (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) Scylla serata, (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. 

```
##################################
######### functions ##############
##################################
# 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.l=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 yet
                                ({1/3 * pi * r^2 * h}
                            -Neighbour.1* {(h/(3*r))*{r^3 * acos(x.1/r)
2*r*x.1*
                            -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 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.l)[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& &. > > 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 = (e-10),trace = TRUE)
fit
}
plot.hr<- function(dataset,fit,label="A",ylab) {
```

    h=coefficients (fit) [1]
    \(r=c o e f f i c i e n t s(f i t)[2]\)
    dataset \(\$=r o w M e a n s(c b i n d(d a t a s e t \$ D i s t a n c e .1, d a t a s e t \$ D i s t a n c e .2), n a . r m=T) / 2\)
    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 * $r^{\wedge} 2$ * h\} - mid.string*\{(h/(3*r))*\{r^3 * acos(x/r) $\left.\left.2 * r^{*} x^{\star} \operatorname{sqrt}\left(r^{\wedge} 2-x^{\wedge} 2\right)+x^{\wedge} 3 * \log \left(\left\{r+\operatorname{sqrt}\left(r^{\wedge} 2-x^{\wedge} 2\right)\right\} / x\right) \quad\right\}\right\}, a d d=T, l w d=2$, from $=-1$, to $=$ max (dataset\$x,na.rm=T), col="black"
lines $\left(x=c(r, 250), y=c\left(1 / 3\right.\right.$ * pi * $r^{\wedge} 2$ * h,1/3 * pi * $r^{\wedge} 2$ * 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 * $\left.r^{\wedge} 2 * h\right\}-\operatorname{end} . \operatorname{string}{ }^{\wedge}\left\{(h /(3 * r)) *\left\{r^{\wedge} 3 * \operatorname{acos}(x / r)-\right.\right.$ $\left.\left.2 * r^{*} x^{*} \operatorname{sqrt}\left(r^{\wedge} 2-x^{\wedge} 2\right)+x^{\wedge} 3 * \log \left(\left\{r+\operatorname{sqrt}\left(r^{\wedge} 2-x^{\wedge} 2\right)\right\} / x\right) \quad\right\}\right\}, a d d=T, l w d=2, f r o m \quad=-1$, to = max (dataset $\$ \mathrm{x}, \mathrm{na} . \mathrm{rm}=\mathrm{T})$, col="grey")
lines $\left(x=c(r, 250), y=c\left(1 / 3 * p i * r^{\wedge} 2 * h, 1 / 3 * p i * r^{\wedge} 2 * h\right), c o l=" g r e y ", l w d=2\right)$
\}
legend(legend=substitute(paste(italic(label))),"topleft",bty="n")
\}
stat.table<-function(fit) \{
h=coefficients (fit) [1]
r=coefficients (fit) [2]
Asymptotic.distance $=2 * r$
Catchable.Density=h
max.catch.rate $=\left\{1 / 3\right.$ * pi * $r^{\wedge} 2$ * $\left.h\right\}$
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, $h=4.998 e-04, r=8.576 e+01)$
windows (width=18, height=14)
$\operatorname{par}(\operatorname{mfrow}=c(1,1), x a x s=" i ", y a x s=" i ", \operatorname{mar}=c(4,4,1,1), \operatorname{ma}=c(2,0,0,0), \operatorname{tck}=0.01, \operatorname{mgp}=c(2.25,1,0))$
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")

153 154
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

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

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

```
require(rstan)
require(rethinking)
##################################
######### functions ##############
##################################
# The first function fits the Bayesian model using rstan
# 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
Bayesian.estimate.h.r<- function(dataset=df,prior.h=c(10^-6,0.20),prior.r=c(1,200)) {
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
dataset$x1= dataset$x.1
#dataset=subset(dataset,x1<150)
Catch=dataset$Catch
x1 = dataset$x.1
Neighbour1 = dataset$Neighbour.1
Neighbour2 = dataset$Neighbour.2
data_list <- list(
    Catch = Catch,
    x1 = x1,
    N = length(Catch),
    Neighbour1=Neighbour1,
    Neighbour2=Neighbour2,
    priorh = prior.h
    priorr = prior.r
)
model_conditional<- '
data{
        int<lower=1> N;
        vector[N] Catch;
        vector[N] x1;
        vector[N] Neighbour1;
        vector[N] Neighbour2;
        vector[2] priorh;
        vector[2] priorr;
        }
parameters{
    real<lower=1e-06,upper=0.2> h;
    real<lower=.1,upper=300> r;
    real<lower=0> sigma;}
model{
    vector[N] mu;
    sigma ~ exponential( 1 );
    r ~ uniform(priorr[1],priorr[2] );
    h ~ uniform( priorh[1],priorh[2] );
    for ( i in 1:N ) {
        if (x1[i] < r) {
    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^2 - x1[i]^2))/x1[i])))) -
            (Neighbour2[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^2 - x1[i]^2))/x1[i]))))
    } else {mu[i] = ((pi() * r^2 * h)/3) ;}
    mu[i] = log(mu[i]);}
    Catch ~ lognormal( mu , sigma );}
generated quantities{
    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,
            data = data_list)
fit
}
####################################################################
### this second function plots that data and the fitted relationship
####################################################################
plot.hr<- function(dataset,fit,label="A",ylab) {
post <- extract.samples(fit)
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.l==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)
```



```
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)
2*r* x*sqrt(r^2-\mp@subsup{x}{}{\wedge}2)+ ( x^3* log({r+sqrt(r^2-\mp@subsup{x}{}{\wedge}2)}/x) }},add=T,lwd=2,from =-1, to =
max(dataset$x,na.rm=T),col="grey")
    lines(x=c(r,250),y=c(1/3 * pi * r^2 * h,1/3 * pi * r^2 * h),col="grey",lwd=2)
    }
    legend(legend=substitute(paste(italic(label))),"topleft",bty="n")
}
####################################################################
# this function makes a table of the estimated parameter values
####################################################################
stat.table<-function(fit){
post <- extract.samples(fit)
h=median(post$h)
r=median(post$r)
h.ci=quantile(post$h,c(0.025,0.975))
r.ci=quantile(post$r,c(0.025,0.975))
    Asymptotic.distance=2*r
    Catchable.Density=h
    max.catch.rate ={1/3 * pi * r^2 * h}
c(h, h.ci,r, r.ci,max.catch.rate)
}
####################################################################
# analysis starts here
####################################################################
#### IoM Cancer pagurus ####
#setwd("C:/Users/ossc06/OneDrive - Bangor University/Documents/Projects/17. IoM")
setwd("C:/Users/Jan Geert Hiddink/Documents/Projects/17. IoM")
IoM=read.csv("Crab Survey.csv")
IoM=aggregate(data=IoM, Catch~string.position+Distance+Treatment,FUN=mean) #it may be necessary
to take the means of data points
IoM=aggregate(data=IoM,Catch~string.position+Distance,FUN=mean) #it may be necessary
to take the means of data points
IoM$Distance.1=IoM$Distance
IoM$Distance.2=IoM$Distance
IoM$Distance.2[IoM$string.position==1]=NA
fit.IoM=Bayesian.estimate.h.r(dataset=IoM,prior.h=c(0.00001,0.05),prior.r=c(10,200))}##prior
need to be chosen to fit the dataset
##diagnostics
pairs(fit.IoM, pars=c("sigma","h","r"))
traceplot(fit.IoM, pars=c("sigma","h","r"))
windows(width=18,height=14)
par(mfrow=c (1, 1), xaxs="i",yaxs="i",mar=c (4,4,1,1),oma=c (2,0,0,0) ,tck=0.01,mgp=c (2. 25,1,0))
plot.hr(dataset=IoM,fit=fit.IoM,label="A) Cancer pagurus, IoM",ylab="Mean catch per pot
(numbers)")
mtext(side=1, expression(paste("Half the distance between traps",italic(' d '),"(m)")),outer=T)
legend (legend=c ("mid
string"),col=c("black","grey"),pch=19,"bottomright", cex=1.25,bty="n")
# run this is you want to plot a sample of the possible lines you can expect
#post=extract(fit.IoM)
#alpha=0.005
#mid.string.col=adjustcolor( "black",alpha.f = alpha)
#end.string.col=adjustcolor( "blue",alpha.f = alpha)
#for (x in 1:length(post$r)) {
# h=post$h[x]
# r=post$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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```
# 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) +
x^3* log({r+sqrt (r^2-\mp@subsup{x}{}{\wedge}2) }/x) }}, add=T,lwd=2, from =-1, to = r,col=mid.string.col)
# 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)
# 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)
# }
stat.table(fit.IoM)
names(stats)=c("Density (h)","h lower CI","h upper CI","Cone radius (r)","r lower CI","r upper
CI","Maximum catch rate")
stats
```

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\# The expected output using Supplementary data 1 using rstan.
4126
4137
4148
4159
41610
41711
41812
41913
$420 \quad 14$
$421 \quad 15$
42216
42317
42418
42519
42620
42721
42822
42923
$430 \quad 24$
43125
43226
43327
43428
43529
43630
43731
$438 \quad 32$
43933
$440 \quad 34$
44135
44236
$443 \quad 37$
44438
44539
44640
44741
$448 \quad 42$
44943
45044
45145
45246
45347
45448
45549
45650
45751
45852
45953
1
2
3
4
9
10
17
18
21
27
29
45
46
52
Treatment String Pot_No.
$\begin{array}{rrrr}0 . & \text { Date } & \text { Distance } & \text { Catch } \\ 1 & 05 \text {-Aug } & 15.0 & 1\end{array}$
T1_1 T1
$\begin{array}{ll}15.0 & 1 \\ 22.5 & 0\end{array}$
$\begin{array}{llll}1 & 05-A u g & 22.5 & 0 \\ 1 & 05-A u g & 35.0 & 1\end{array}$
Date Distance Catch string.position
2 T3_3
6
8
9

        3
        T1 -1
    T2 1
T3 -1
T2
T3 1 05-Aug
$\begin{array}{ll}1 & 05-A u g \\ 1 & 05-A u g\end{array}$
$35.0 \quad 1$
$\begin{array}{rrr}1 & 05-A u g & 105.0\end{array}$
$\begin{array}{llll}1 & 05-A u g & 135.0 & 5 \\ 1 & 05-A u g & 165.0 & 2\end{array}$
$135.0 \quad 5 \quad 1$
1
1 05-Aug 165.0 2
105 -Aug $225.0 \quad 0 \quad 1$
106 -Aug $\quad 15.0 \quad 2$
106 -Aug
$\begin{array}{ll}22.5 & 2 \\ 35.0 & 3\end{array}$
$\begin{array}{llll}1 & 06 \text {-Aug } & 35.0 & 3 \\ 1 & 06 \text {-Aug } & 75.0 & 6\end{array}$
106 -Aug $\quad 75.0 \quad 6$
106 -Aug 105.0 9
106 -Aug 135.0 7
1 06-Aug $165.0 \quad 6$
1 06-Aug $225.0 \quad 5$
107 -Aug $15.0 \quad 3$
$\begin{array}{llll}1 & 07 \text {-Aug } & 22.5 & 4\end{array}$
$\begin{array}{llll}1 & 07 \text {-Aug } & 35.0 & 1\end{array}$
$\begin{array}{llr}1 & 07 \text {-Aug } & 75.0 \\ 1 & 07 \text {-Aug } & 105.0\end{array}$
$\begin{array}{lll}1 & 07 \text {-Aug } & 105.0 \\ 1 & 07 \text {-Aug } & 135.0\end{array}$
1
1
$\begin{array}{ll}\text { T3-1 } & \text { T3 } \\ \text { T4 }-1 & \text { T4 }\end{array}$
$\mathrm{T} 5^{-1}$
T5
T6
T1
0 1 1
1
1
1
105 -Aug $\quad 75.0 \quad 2 \quad 1$
105 -Aug $105.0 \quad 2$
1
1
T7
T8
T1
T2
T3
T4
T5
T6
16
T 7
T7
T8
T8
T1
T2
T3
T4
T5
T6
T7
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T1
T1
T2
T3
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T8
T1T1
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T3
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T 4
T 5
T6
T7
T8
T1
T2
T3
T3
T4
T4
T5
T5-3
7
$107-A u g$
165.0
1 07-Aug
1 07-Aug
$225.0 \quad 9$
$\begin{array}{rrrr}1 & 07 \text {-Aug } & 225.0 & 9 \\ 2 & 05-A u g & 15.0 & 0\end{array}$
2 05-Aug
2 05-Aug $22.5 \quad 1$
$\begin{array}{llll}2 & 05-A u g & 35.0 & 1\end{array}$
$\begin{array}{llll}2 & 05-A u g & 105.0 & 4\end{array}$
205 -Aug $135.0 \quad 0$
205 -Aug 165.01
205 -Aug $225.0 \quad 2$
$\begin{array}{lll}2 & 06 \text {-Aug } & 15.0 \\ 2 & 06 \text {-Aug } & 22.5\end{array}$

| 2 | 06 -Aug |
| :--- | :--- |
| 2 | 22.5 |

    2 06-Aug 35.0
    2 06-Aug
            \(75.0 \quad 1\)
        2
        206 -Aug 105.0 6
        \(\sim \sim\)
        \(\begin{array}{llll}2 & 06 \text {-Aug } & 135.0 & 5 \\ 2 & 06 \text {-Aug } & 165.0 & 6\end{array}\)
        \(\sim \sim\)
    206 -Aug
            165.0
        225.0 -
        \(\begin{array}{rrrr}2 & 06 \text {-Aug } & 225.0 & 1 \\ 2 & 07 \text {-Aug } & 15.0 & 1\end{array}\)
        \(\begin{array}{rrrr}2 & 06 \text {-Aug } & 225.0 & 1 \\ 2 & 07 \text {-Aug } & 15.0 & 1\end{array}\)
        2
    2
$\begin{array}{lll}2 & 07-A u g & 15.0 \\ 2 & 07-A u g & 22.5\end{array}$
2
2 07-Aug
$\begin{array}{ll}22.5 & 3 \\ 35.0 & 3\end{array}$
2 07-Aug
2
2
2
$\begin{array}{lrrr}2 & 07 \text {-Aug } & 75.0 & 4\end{array}$
$\begin{array}{lrrr}2 & 07 \text {-Aug } & 75.0 & 4\end{array}$
2
2
207 -Aug $105.0 \quad 2$
$\begin{array}{llll}2 & 07-A u g & 135.0 & 2 \\ 2 & 07-A u g & 165.0 & 6\end{array}$
2
2
2
2
2
2
$\begin{array}{rrrr}2 & 07 \text {-Aug } & 225.0 & 2 \\ 3 & 05-A u g & 15.0 & 0\end{array}$
$\begin{array}{rrrr}2 & 07 \text {-Aug } & 225.0 & 2 \\ 3 & 05-A u g & 15.0 & 0\end{array}$
2
2
3 05-Aug
$15.0 \quad 0$
$\begin{array}{lll}3 & 05-A u g & 22.5 \\ 3 & 05-A u g & 35.0 \\ 3 & 05-A u g & 75.0\end{array}$
$\begin{array}{lll}3 & 05-A u g & 35.0 \\ 3 & 05-A u g & 75.0\end{array}$
$\begin{array}{rrrr}3 & 05-A u g & 75.0 & 1 \\ 3 & 05-A u g & 105.0 & 2\end{array}$
2
2
1
1
1
1
1

| 460 | 54 | T6_3 | T6 | 3 | 05-Aug | 135.0 | 1 | 2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 461 | 55 | T7_3 | T7 | 3 | 05-Aug | 165.0 | 5 | 2 |
| 462 | 56 | T8-3 | T8 | 3 | 05-Aug | 225.0 | 2 | 2 |
| 463 | 57 | T1_3 | T1 | 3 | 06-Aug | 15.0 | 0 | 2 |
| 464 | 58 | T2_3 | T2 | 3 | 06-Aug | 22.5 | 3 | 2 |
| 465 | 59 | T3-3 | T3 | 3 | 06-Aug | 35.0 | 2 | 2 |
| 466 | 60 | T4_3 | T4 | 3 | 06-Aug | 75.0 | 4 | 2 |
| 467 | 61 | T5-3 | T5 | 3 | 06-Aug | 105.0 | 3 | 2 |
| 468 | 62 | T6_3 | T6 | 3 | 06-Aug | 135.0 | 4 | 2 |
| 469 | 63 | T7-3 | T7 | 3 | 06-Aug | 165.0 | 11 | 2 |
| 470 | 64 | T8-3 | T8 | 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 | 1 | 2 |
| 473 | 67 | T3_3 | T3 | 3 | 07-Aug | 35.0 | 0 | 2 |
| 474 | 68 | T4_3 | T4 | 3 | 07-Aug | 75.0 | 4 | 2 |
| 475 | 69 | T5_3 | T5 | 3 | 07-Aug | 105.0 | 5 | 2 |
| 476 | 70 | T6_3 | T6 | 3 | 07-Aug | 135.0 | 2 | 2 |
| 477 | 71 | T7_3 | T7 | 3 | 07-Aug | 165.0 | 9 | 2 |
| 478 | 72 | T8_3 | T8 | 3 | 07-Aug | 225.0 | 3 | 2 |
| 479 | 73 | T1_4 | T1 | 4 | 05-Aug | 15.0 | 2 | 2 |
| 480 | 74 | T2_4 | T2 | 4 | 05-Aug | 22.5 | 0 | 2 |
| 481 | 75 | T3_4 | T3 | 4 | 05-Aug | 35.0 | 0 | 2 |
| 482 | 76 | T4_4 | T4 | 4 | 05-Aug | 75.0 | 4 | 2 |
| 483 | 77 | T5_4 | T5 | 4 | 05-Aug | 105.0 | 3 | 2 |
| 484 | 78 | T6_4 | T6 | 4 | 05-Aug | 135.0 | 1 | 2 |
| 485 | 79 | T7-4 | T7 | 4 | 05-Aug | 165.0 | 1 | 2 |
| 486 | 80 | T8-4 | T8 | 4 | 05-Aug | 225.0 | 0 | 2 |
| 487 | 81 | T1_4 | T1 | 4 | 06-Aug | 15.0 | 2 | 2 |
| 488 | 82 | T2-4 | T2 | 4 | 06-Aug | 22.5 | 0 | 2 |
| 489 | 83 | T3_4 | T3 | 4 | 06-Aug | 35.0 | 2 | 2 |
| 490 | 84 | T4_4 | T4 | 4 | 06-Aug | 75.0 | 4 | 2 |
| 491 | 85 | T5_4 | T5 | 4 | 06-Aug | 105.0 | 2 | 2 |
| 492 | 86 | T6_4 | T6 | 4 | 06-Aug | 135.0 | 4 | 2 |
| 493 | 87 | T7_4 | T7 | 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 | T3-4 | T3 | 4 | 07-Aug | 35.0 | 1 | 2 |
| 498 | 92 | T4_4 | T4 | 4 | 07-Aug | 75.0 | 4 | 2 |
| 499 | 93 | T5-4 | T5 | 4 | 07-Aug | 105.0 | 6 | 2 |
| 500 | 94 | T6-4 | T6 | 4 | 07-Aug | 135.0 | 5 | 2 |
| 501 | 95 | T7-4 | T7 | 4 | 07-Aug | 165.0 | 4 | 2 |
| 502 | 96 | T8-4 | T8 | 4 | 07-Aug | 225.0 | 2 | 2 |
| 503 | 97 | T1_5 | T1 | 5 | 05-Aug | 15.0 | 0 | 1 |
| 504 | 98 | T2_5 | T2 | 5 | 05-Aug | 22.5 | 0 | 1 |
| 505 | 99 | T3_5 | T3 | 5 | 05-Aug | 35.0 | 4 | 1 |
| 506 | 100 | T4_5 | T4 | 5 | 05-Aug | 75.0 | 2 | 1 |
| 507 | 101 | T5_5 | T5 | 5 | 05-Aug | 105.0 | 3 | 1 |
| 508 | 102 | T6_5 | T6 | 5 | 05-Aug | 135.0 | 1 | 1 |
| 509 | 103 | T7-5 | T7 | 5 | 05-Aug | 165.0 | 2 | 1 |
| 510 | 104 | T8-5 | T8 | 5 | 05-Aug | 225.0 | 5 | 1 |
| 511 | 105 | T1_5 | T1 | 5 | 06-Aug | 15.0 | 1 | 1 |
| 512 | 106 | T2_5 | T2 | 5 | 06-Aug | 22.5 | 0 | 1 |
| 513 | 107 | T3-5 | T3 | 5 | 06-Aug | 35.0 | 1 | 1 |
| 514 | 108 | T4_5 | T4 | 5 | 06-Aug | 75.0 | 1 | 1 |
| 515 | 109 | T5_5 | T5 | 5 | 06-Aug | 105.0 | 6 | 1 |


| 516 | 110 | T6 5 | T6 | 5 | 06-Aug | 135.0 | 4 | 1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 517 | 111 | T7-5 | T7 | 5 | 06-Aug | 165.0 | 6 | 1 |
| 518 | 112 | T8-5 | T8 | 5 | 06-Aug | 225.0 | 5 | 1 |
| 519 | 113 | T1_5 | T1 | 5 | 07-Aug | 15.0 | 0 | 1 |
| 520 | 114 | T2_5 | T2 | 5 | 07-Aug | 22.5 | 4 | 1 |
| 521 | 115 | T3_5 | T3 | 5 | 07-Aug | 35.0 | 3 | 1 |
| 522 | 116 | T4 5 | T4 | 5 | 07-Aug | 75.0 | 3 | 1 |
| 523 | 117 | T5_5 | T5 | 5 | 07-Aug | 105.0 | 5 | 1 |
| 524 | 118 | T6-5 | T6 | 5 | 07-Aug | 135.0 | 4 | 1 |
| 525 | 119 | T7_5 | T7 | 5 | 07-Aug | 165.0 | 6 | 1 |
| 526 | 120 | T8_5 | T8 | 5 | 07-Aug | 225.0 | 2 | 1 |


[^0]:    Keywords: stock assessment, Cancer pagurus, Buccinum undatum, pot, creel, static fishing gear

