

Depth preference in released juvenile turbot *Psetta maxima*

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Abstract

Hatchery-reared juvenile turbot *Psetta maxima* were tagged with Passive Integrated Transponder (PIT) tags and released at three different depths in a sandy bay in Denmark. About 2-7 % of the released fish were registered daily to monitor their distribution using a tag antenna mounted on a modified beam trawl, thus avoiding actually sampling the fish. The change in distribution of the three groups was adequately represented by a two-dimensional movement model. Movement along shore was described by a Brownian motion with group specific drift. Movement perpendicular to the shore line was described by a Cox-Ingersoll-Ross process with a group specific attraction point. All three groups exhibited similar depth preferences of 1.7 m. Immediately after the release, fish were concentrated around the release points but after one day, fish had moved to the preferred depth and subsequently maintained their position at this depth. Farmed turbot exhibited strong site fidelity and an innate behavior for selecting a preferred depth.

Keywords: Flatfish, migration modelling, site fidelity, PIT-tags, released fish

1. Introduction

Flatfish (Pleuronectiformes) juveniles are commonly concentrated in shallow waters indicating that water depth plays an important role in their distribution. These coastal nursery habitats provide good foraging opportunity, low predation risk, higher temperatures, and appropriate substrata (Kramer, 1991; Vanderveer et al., 1991; Burrows et al., 1994; Neuman and Able, 1998). Settlement of flatfish in shallow nursery areas is established after transport of larvae to these areas from the spawning grounds. Once settled, turbot *Psetta maxima*, brill *Scophthalmus rhombus*, and flounder *Platichthys flesus* exhibit highly restricted depth distribution (0-3 m) during the early juvenile stage (Gibson, 1994).

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Plaice *Pleuronectes platessa* (Burrows et al., 1994) and turbot (Sparrevojn et al., 2002) reveal strong site fidelity within their restricted shallow depth range. For plaice this site fidelity is largely maintained during the daytime (Gibson, 1973) whereas they move inshore during nighttime (Burrows et al., 2001). Released turbot in a microtidal area showed an alongshore displacement within the same depth with the directional movement related to the direction of local wind-driven currents (Sparrevojn et al., 2002). This restricted habitat use during the juvenile stage strongly influences the recruitment potential of the species (Gibson, 1994). If the size of the nursery area is reduced, for example because of negative impact from human activities, numbers of juvenile flatfishes would not compensate by increasing their densities, and the total stock would be reduced (Zijlstra, 1972).

Selecting the most suitable habitat for the release of farmed fish is an important determinant for the success of a release, which is measured by the survival of the released individuals and their contribution to the natural recruitment of the adult population. The suitable habitat is thus a combination of location and sufficient area of the preferred depth of the species. However, it may not always be possible to release fish at their ideal depth due to either limited access by land, for example, where fish were released directly from a truck on board a ferry in deeper depths (≥ 6 m; Støttrup et al., 2002) or without access to smaller vessels, for example, where the fish were released directly from the shore line using waders (≤ 1 m; Sparrevojn et al., 2002). Differences in environmental conditions with depth may affect diet, diel and tidal migration patterns in tidal areas (Burrows, 1994) and growth (Rountree and Able, 1992; Sparrevojn and Støttrup, 2008). If the farmed fish are unable to make their way to the optimal depths, the success of the release may be negatively impacted.

A simple way to describe small-scale movement of fish is to apply diffusion theory, where each individual fish displays Brownian motion and moves independently of conspecifics. A one-dimensional model was applied successfully to released turbot to describe alongshore movement or displacement which was related to directional wind-driven currents (Sparrevojn et al., 2002). In this study, we wished to go one step further and quantify fish movement in two directions, thus enabling the study of depth preference in juvenile turbot. The Cox-Ingersoll-Ross process limits movement variability when the fish are close to the shore which, along with an incorporated preference parameter, drives them away from the shore. When the fish are far from the shore, they are modelled to move more freely but with a long term depth preference. These qualities make the process suitable for modelling movement perpendicular to the coast.

A field experiment was conducted to examine whether naïve turbot exhibit depth preference. For quantification, a two-dimensional model was developed to describe this small-scale movement, including the speed with which the turbot sought their preferred depth, and whether or not they maintained their position subsequently (site fidelity).

2. Materials and Methods

2.1. Location and experimental design

Begtrup Vig is a small bay near Aarhus, Denmark (Fig. 1). Because of its sandy bottom, limited exposure to wind and isobaths parallel to the coast it was chosen as the site for this experiment. Reared one-year old turbot (average size: 14.2 cm, range: 11-19

cm), were purchased from a commercial fish farm and were tagged with individually identifiable PIT tags (Length: 23 mm, diameter: 3.65 mm, weight 0.6 g). A total of 694 fish were divided into three groups and released (231 fish released at depth of 1 m, 231 at 3 m, 232 at 5 m) at 20:30 h ($t = 0$).

Starting the day after release and continuing for five consecutive days, the release area was trawled in multiple directions with a modified 2 m beam trawl (without net) and mounted with a PIT tag antenna (Sparrevohn et al., 2014, width: 186 cm) and a dive computer. Two 8.8 kg blocks were mounted on the trawl to keep it on the seabed. On the first day, the equipment was calibrated in the morning, and subsequently trawls were performed in the afternoon. On the following days the area was trawled during the entire day.

Positional data were registered by the Humminbird navigational system on the boat at each directional change. Depth data were registered by both the Humminbird and the dive computer. Additionally the dive computer recorded temperature data.

2.2. Model and data handling

The model is setup to mimic the location and the experiment. The movement model is two-dimensional and the two movement directions are modeled independently, which is based on the observation that the bathymetry curves are parallel to the shore line in the study area. The movement along the shore is assumed to follow a Brownian motion with drift and diffusion. For the movement perpendicular to the shore line a Cox-Ingersoll-Ross is assumed. A Cox-Ingersoll-Ross process has an attraction point (here used to model preferred depth) and its diffusion part decreases when the distance to the shore line becomes small, which realistically ensures that the fish only move in the water. The observations are modeled by taking the scanner tracks into account, and modeling the probability of individuals being within or outside these scanned tracks. Let $X_i(t)$ and $Y_i(t)$ denote the position parallel (x) and perpendicular (y) to the shore of the i th fish at time $t > 0$ measured in days. Assuming that the fish are independent, and that the movement in the x and y direction is independent for each fish, then the movement of each fish in the x direction is modelled by a Brownian motion

$$dX_i(t) = \alpha_{x,g(i)}dt + \sigma_x dB_i(t) \quad (1)$$

with $X_i(0) = r_{x,g(i)}$, while the movement of the fish in the y direction is modelled by a Cox-Ingersoll-Ross process

$$dY_i(t) = -\alpha_y(Y_i(t) - \mu_{g(i)})dt + \sqrt{Y_i(t)}\sigma_y dB_i(t) \quad (2)$$

with $Y_i(0) = r_{y,g(i)}$. Here $g(i)$ is a factor mapping the number of the fish to the corresponding release group, $a_{x,g(i)} \in \mathbb{R}$, $\alpha_y, \mu_{g(i)}, \sigma_x, \sigma_y > 0$ and $B_i(t)$ is a two dimensional standard Brownian motion where B_i is independent of B_j for all $i \neq j$. Finally, $(r_{x,g(i)}, r_{y,g(i)})$ is the point at which the group containing fish i is released.

The assumption of independence between the fish is supported by the lack of evidence for social behaviour amongst flatfish outside spawning season. The assumption of independence between the movement in the x and in the y direction relates to the depth curves being parallel to the coast. When this is the case, the depth related movement should not depend on the distance parallel to the coast from the release point and vice versa. Estimates were found by maximum likelihood (see Appendix A).

2.2.1. Implementation

The transition distribution for the process in equation 1 is known to be a normal distribution with mean $\alpha_{x,j}t$ and variance σ_x^2t , which is a straight forward calculation. Likewise the transition distribution for the process in equation 2 is known to be a transformation of a non-central chi-square distribution. The density of this distribution is approximated by solving the forward Kolmogorov equation (Fokker-Planck) with the finite volume method. A spatial resolution of $\Delta y = 0.5$ and a time resolution of 14.42886 minutes were chosen for the finite volume method.

The trawled area was approximated by creating a grid with a resolution of 1×1 m and summing the density at the midpoint of each cell, where the midpoint of the cell is no further from the line segment between two registered positions than half the width of the PIT tag antenna.

3. Results

During the sampling period a total of 120 observations were accomplished. Daily observations for each group ranged between 4 and 16, corresponding to 2-7% of the population (Table 1).

The full model with different depth preferences for each release group was fitted to the data, and was reduced to a model with equal depth preferences for all three groups without the fit being significantly reduced (likelihood ratio test with p value = 61.9%). The attraction parameter in the reduced model is estimated at 291.87 m from the coast, corresponding to a depth of 5.4 m, while the mode of the distribution perpendicular to the coast is estimated at 136.3 m from the coast corresponding to a depth of 1.7 m. The spread of the spatial distribution parallel to the coast of the fish was estimated to 202.34 m-day^{-1/2}. All the parameter estimates are shown in Table 2.

The trawled path was concentrated in the area 100 to 400 m from the coast and 0 to 400 m east by south of the release points (Fig. 2). The area was extended each day and covered 60 to 500 m from the coast and approximately 600 m on each side of the release points on the last day.

Perpendicular to the coast, the fish are estimated to follow the same distribution for all three release groups from day three (Fig. 3). Immediately after release, the highest probability mass of the depth distributions are found at the release points. After one day the modes of all three distributions are closer to the shore than 200 m, and from the third day the modes are at the estimated asymptotic mode. The estimated depth distribution of the fish is highly skewed; the fish are most likely to be at 1.7 m, with 95% of the fish between 1.3 m and 10 m, at a mean depth of 5.4 m.

4. Discussion

In this study, farmed juvenile turbot *Psetta maxima* showed strong habitat fidelity, highly specific depth preference and an ability to rapidly migrate to their preferred depth within a short space of time after their release. Several flatfish species demonstrate different depth distributions that also vary with different life stages (Macpherson and Duarte, 1991; Gibson, 1994; Allen and Balz, 1997; Armstrong, 1997). Juvenile turbot, brill *S. rhombus* and flounder *Platichthys flesus* exhibit highly restricted depth distribution (<3

m) during the early juvenile stage, whereas plaice (<5 m), sole (<10 m) and dab (<15 m) *Limanda limanda* have a broader depth preference (Riley et al., 1981; Gibson, 1994). These depths distributions describe the range for age-0 fish. Age-I fish tend to have a slightly deeper distribution. Up to 88 % and 90 % of age-I wild and released farmed turbot respectively were distributed in shallow (<4 m) coastal waters (Støttrup et al., 2002). However, many of these studies are mainly descriptive and the extent to which preferred depth distribution is the result of active choice or external factors has not been widely investigated. This inshore depth distribution may not be the result of random inshore migration. In field experiments transplanted juvenile plaice exhibited active selection for preferred depths (Gibson et al., 2011). This is the first study conducted pursuing active depth selection in turbot juveniles that targeted a depth of 1.7 m. These results indicate an innate behaviour, possibly evolved to maintain their position in shallow nursery habitats characterised by ample food resources and low predation pressure, which may be important determinants for a successful release of farmed fish.

In the coast of North Zealand, Denmark, the typical restricted distribution to shallow coastal waters was reversed and juvenile turbot exhibited a broader depth distribution, although only a smaller percentage of the age-class were distributed in waters deeper than 4 m (Sparrevojn and Støttrup, 2008). The observed broader depth distribution coincided with the highest abundance of natural turbot, the lowest growth rates in juvenile turbot and the lowest occurrence of fish in the diet of these juveniles (Sparrevojn and Støttrup, 2008). This indicated that although the natural supply of pre-settled turbot was high, the environmental conditions were generally unfavourable for growth. The broader depth distribution of turbot was interpreted as being either a response to searching a larger area for food in the absence of gobies, or a mechanism to avoid competition with other individuals when fish abundance is high, as predicted by MacCall's (1990) habitat basin model. The difference in behavioural strategy may thus represent evolutionary 'bet-hedging' as described by Philippi and Seger (1989), where a trade-off is made between shallow water preference in nursery habitats with ample food resources and low predation pressure and deeper water habitats when the shallow habitats are less suitable to provide food and avoid competition or predators.

Wild metamorphosing flatfish select and subsequently maintain their position in their juvenile habitat, but the environmental cues for this behaviour are largely unknown (Gibson, 1997). After settling, the type of juvenile habitat they maintain affects their encounters with prey and predators and the abiotic factors they may be exposed to as well as the selective pressures that shape their phenotype (Gibson, 1994). The strong site fidelity exhibited by flatfish species (Gibson et al., 2002; Burrows et al., 2004) suggests that depth preference may be a genetic trait evolved to maintain their position in nursery areas where food resources are ample and predators less frequent. A positive relationship between fish length and water depth, such as the case for plaice *Pleuronectes platessa* (Gibson et al., 2002, 2011) and sole *Solea solea* (Dorel et al., 1991), also may be applicable for turbot. If habitat preference was the result of natal experience (Davis and Stamps, 2004), released farmed fish would be at a disadvantage relative to their wild counterparts and would affect their post-release survival. In a previous study, the farmed turbot showed site fidelity and were displaced alongshore within the same depth due to wind-driven currents in a non-tidal area (Sparrevojn et al., 2002). The farmed turbot used in this experiment were raised on zooplankton to metamorphosis in large, outdoor, concrete tanks, 2.5 m deep. After metamorphoses they were transferred to indoor four square meter tanks, and

fed commercial dry feed until release (<http://www.maximus-fry.dk/weaning.html>; accessed July 11, 2014). The rearing tanks were generally < 1m deep (JG Støttrup, personal observations). Thus the farmed fish had not been adapted to the 1.7 m preferred depth shown for the released fish in this study. These results indicate an innate behaviour, not requiring previous habitat experience to select preferred depths in an area suitable as nursery area.

The model used in this study was developed further from a dispersal model that described one-dimensional small-scale migration, post-release mortality and gear efficiency (Sparrevohn et al., 2002). The constructed model in this study included a second dimension and described the experimental results well. It included release group specific depth preference, the primary goal, as well as, land avoidance. The estimated distribution of the three release groups turned out to be very similar as early as from the second day and onwards of the experiment, which indicated that they all have the same depth preference. When planning future similar experiments this fast adaptation should be taken into account. Also, having more samples within the first 24 hours will give more precise estimates of the distribution. It may be possible to further develop this model to examine post release mortality in naïve and conditioned fish released at different depths to monitor whether releases at different depths affects vulnerability of fish to predation.

The success of a release can be measured by the survival of the released individuals and their contribution to the natural recruitment of the adult population. Survival is linked to growth and predation risk and a high quality habitat provides good conditions for foraging as well as refuge and low predation risk (Gibson, 1994). In many cases survival may be low due to high post-release mortality, i.e. high mortality the first days or weeks after the release. This is linked to the behaviour of farmed fish and the process of adaptation to the natural environment. Naïve turbot are highly susceptible to avian predation when released directly from the hatchery without preconditioning (Sparrevohn et al., 2002; Sparrevohn and Støttrup, 2007). High post-release mortality was also observed for Japanese flounder *Paralichthys olivaceus* (Furuta et al., 1997). Foraging behaviour in naïve turbot differed to that of their wild counterparts; naïve farmed turbot fed on smaller prey items (Sparrevohn and Støttrup, 2007) and showed initially a lower proportion of attacks when presented live prey (Ellis et al., 2002). Thus, although naïve turbot may exhibit behavioural traits that may enhance initial mortality, they do exhibit an ability to select and maintain their position in a suitable nursery habitat. These results therefore indicate that choice of release site is important for a successful release, since survival is not only a function of limits/deficits in farmed fish but rather the interaction of a suitable good quality habitat and post-release behaviour in farmed fish.

Apart from habitat quality, habitat size is correlated to the size of the adult population for a number of flatfish species such as turbot, brill, plaice, sole, flounder and dab (Gibson, 1994). Because of the highly restricted depth range during the early juvenile stage of turbot, brill, and flounder, recruitment depends on the magnitude of suitable shallow habitat. This is an important aspect in management of coastal areas where human activities may negatively impact habitat quality or the magnitude of suitable habitats. The findings of highly selective depth distribution and site fidelity in juveniles may be further important for the development of local populations that may be restricted to specific local juvenile nursery areas and this information is important for developing management strategies for Marine Protected Areas or coastal habitats.

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Appendix A. Likelihood function

Let $\nu_{j,t}$ denote the transition density for the process in eq. 1 and 2 from time 0 to time t for the j th group. Then the likelihood function for a single fish is:

$$f_t(\theta | x_{i,t}, y_{i,t}) = q\nu_{g(i),t}(x_i, y_i)$$

when the fish is observed, and

$$f_t(\theta | x_{i,t}, y_{i,t}) = 1 - qp_{g(i),t}$$

otherwise, where p_t is the probability of being in the swept area and q is the detection rate. As an approximation we ignore re-catches and hence by the independence assumption the negative log-likelihood for fish in release group j simplifies to

$$\begin{aligned} \ell_j(\theta | t, \mathbf{x}_t, \mathbf{y}_t) &= (n_j - n_{j,t}) \log(1 - 1p_{g(i),t}) \\ &+ \sum_{i \in G_{j,t}} \log(q\nu_{j,t}(x_i, y_i)), \end{aligned}$$

where $n_{j,t}$ is the number of fish from group j observed and n_j is the number of fish released in group j . The sum is taken over the set $G_{j,t}$ consisting of the observed individuals from group j at day t . The full negative log-likelihood is then simply

$$\ell(\theta | \mathbf{x}, \mathbf{y}) = \sum_{t=1}^5 \sum_{j=1}^3 \ell_j(\theta | t, \mathbf{x}_t, \mathbf{y}_t)$$

The detection rate was fixed at $q = 1$.

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| Release group | 1 m | 3 m | 5 m | Total |
|--------------------|-----|-----|-----|-------|
| Released | 231 | 231 | 232 | 694 |
| Total observations | 42 | 47 | 31 | 120 |
| Observations day 1 | 9 | 5 | 5 | 19 |
| Observations day 2 | 7 | 16 | 6 | 29 |
| Observations day 3 | 8 | 10 | 6 | 24 |
| Observations day 4 | 9 | 12 | 9 | 30 |
| Observations day 5 | 9 | 4 | 5 | 18 |

Table 1: Number of turbot released and observed daily for each release group.

| Parameter names | Estimate | Standard error |
|-----------------|----------|----------------|
| $\alpha_{x,1}$ | -25.943 | 35.675 |
| $\alpha_{x,3}$ | 47.334 | 23.197 |
| $\alpha_{x,5}$ | 84.077 | 26.295 |
| μ | 291.87 | 44.911 |
| σ_x | 202.34 | 25.150 |
| σ_y | 23.746 | 14.916 |
| α_y | 1.8123 | 2.3518 |
| Mode | 136.30 | 27.244 |

Table 2: Daily advection ($\alpha_{x,i}$) and standard deviation (σ_x) in the x direction, long-term mean (μ) and mode of the y distribution, adjustment speed and diffusion coefficient in the y direction from the reduced movement model.

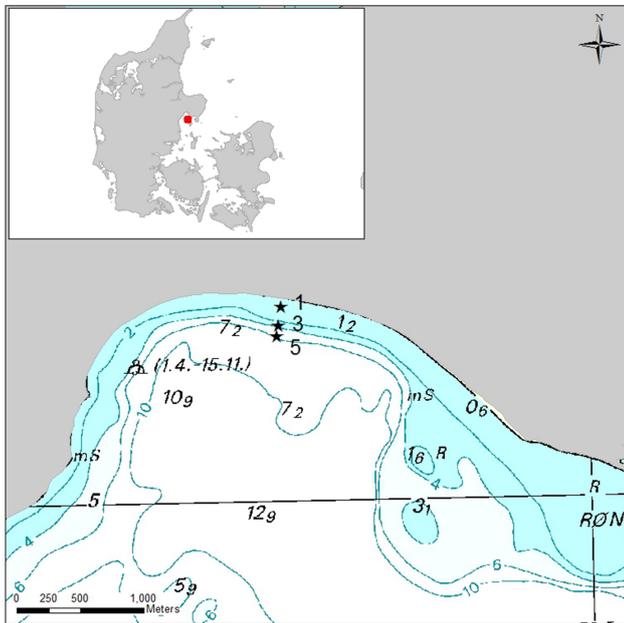


Figure 1: Map showing the location of the turbot releases at Begtrup Vig, Denmark. Release points at 1, 3 and 5 m depth are marked with a *. Depth curves of 2, 4, 6, 8 and 10 meters are also shown on the sea chart.

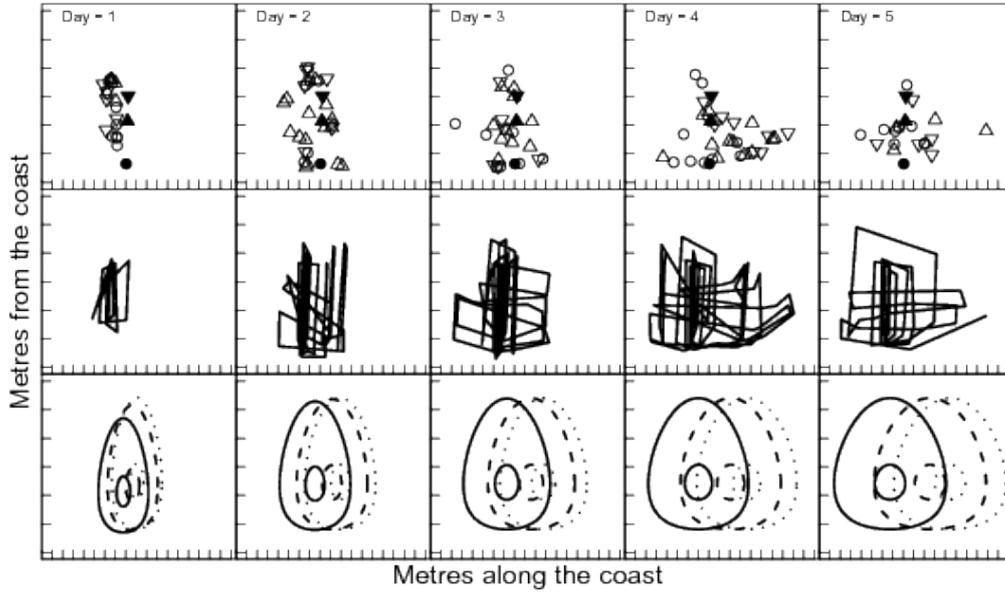


Figure 2: Trawled path (black line, middle row), release points (filled shapes, top row), position of observations (hollow shapes, top row) and 5 % and 50 % probability regions for the spatial distribution of the fish as estimated (bottom row). The group released at 1 m is indicated by \circ and a solid line, the group released at 3 m is indicated by Δ and a dashed line while the group released at 5 m is indicated by ∇ and a dotted line. The distance between tick marks represents 100 m.

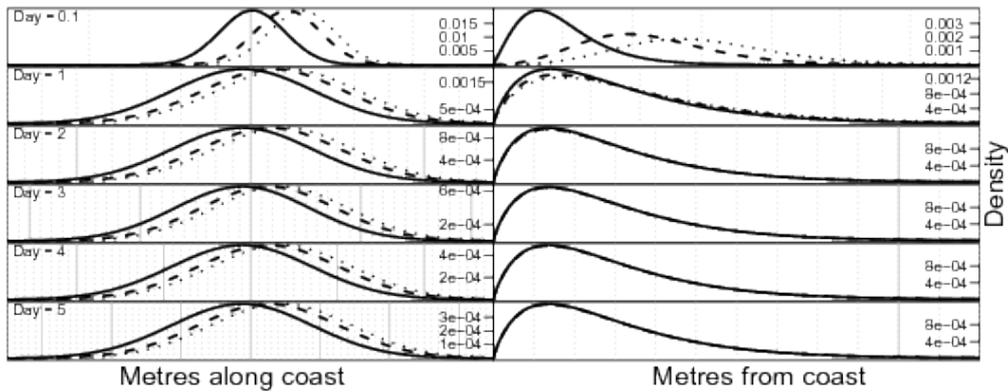


Figure 3: Marginal densities of the x and y distributions at $t = 0.1, 1, 2, 3, 4, 5$ days after release. The group released at 1 m is indicated by a solid line, the group released at 3 m is indicated by a dashed line while the group released at 5 m is indicated by a dotted line. The distance between vertical dotted grey lines represents 100 m. Distance between vertical solid grey lines represents 1000 m.