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Appraisal of a novel fishery of whelks (*Buccinum undatum*) in Danish waters

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A B S T R A C T

In 2016, a fishery for whelks (*Buccinum undatum*) was initiated in the Danish part of Kattegat and the Belt Sea. Until then the whelk had been a pristine resource in Danish fisheries. The inner Danish waters are not covered by EU regulations and very little is known about the whelk population characteristics in the area. Thus, the Danish whelk fishery is at present carried out without any administrative regulations or specific biological knowledge. This work gives novel information about the Danish whelk populations in the Southern Kattegat and Belt Sea. The stock size (shell length > 40 mm) in Kattegat was estimated to be in the range of 230,250–921,000 tons. The overall meat percentage in the three studied fishing zones ranged from 58.2–65.6%. The size at maturity (sexes pooled) ranged from 62.9–70.3 mm corresponding to 4–4.5 years of age. The average shell length of the studied populations ranged from 64.1–73.2 mm and the asymptotic shell length was estimated to be 77.6–83.1 mm. Test fishery showed the CPUE quickly to decrease in a southern direction in the Belt Sea due to the prevailing salinity gradient. Commercial fishermen achieved an average CPUE of 1.3 kg pot−1 in the Southern Kattegat (January 2017–November 2018). Although the three zones studied are adjacent, significant differences were found in several of the measured parameters. This underlines the need of local monitoring of population characteristics in order to advice authorities on possible regulation of whelk fishery. The ongoing whelk fishery in the Southern Kattegat has at present an intensity not believed to cause recruitment overfishing. However, the Danish fishing authority is encouraged to implement a minimum conservation reference sizes (MCRS) based on locally determined size of maturity (SOM).

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1. Introduction

Due to reduced stocks and quota many Danish coastal fishermen strive to survive economically (Autzen and Delaney, 2021) and introduction of alternative species such as the common whelk (*Buccinum undatum* Linnaeus, 1758) are highly needed. Until 2016, common whelks from the inner Danish waters was only landed in 2010 as a by-catch of 87 kg (Danish Fishery Agency, 2021). Thus the common whelk in inner Danish waters can be considered a pristine resource for the Danish fishery. In 2015, the European Maritime and Fisheries Fund (EMFF) and the Danish Fisheries Agency funded a project to launch and consolidate a commercial Danish whelk fishery. Unlike previous Danish projects on whelk fishery our project did not only focus on the fishery itself, but included the whole production line from fishing to export and thereby consolidated the ongoing Danish whelk fishery. During the two years project period, the yearly landings of whelks from inner Danish waters reached more than 340 tons (Danish Fishery Agency, 2021).

The common whelk *B. undatum* is a boreal neogastropod, common in continental shelf waters throughout the North Atlantic (Golikov, 1968; Taylor and Taylor, 1977). In European waters, the whelk can reach shell lengths of 110–125 mm and an age of 11–13 years (Kideys, 1996; Shelmerdine et al., 2007). The whelk can tolerate salinities down to approximately 20% (Staaland, 1972) and in Danish waters the species is found in the North Sea, Skagerrak, Kattegat and through the belts into the westernmost part of the Baltic Sea (Koie and Kristiansen, 2000). In its geographical range, whelks experience temperatures in the range of 0–22 °C (Smith et al., 2013) and 29 °C has been reported lethal (Gowanloch, 1927). Adult whelks are not migratory (Shelmerdine et al., 2007) as illustrated by Hancock (1963) who showed that over a 3 years period only a single marked whelk was recaptured outside an 8 km² area, where 3099 whelks had been marked and released.
The densities of whelks are highly variable in different geographical regions and has been reported in the range of 0.05 up to 2.12 m\(^{-2}\) (Petersen, 1911; Petersen and Boysen Jensen, 1911; Hancock, 1963; Gros and Santarelli, 1986; Himmelman, 1988; McQuinn et al., 1988; Jalbert et al., 1989; Kideys, 1993; Legault and Himmelman, 1993; Valentinsson et al., 1999; de Voogs and van der Meer, 2010; Emmerson, 2018). In the Swedish part of Kattegat the density of whelks has been estimated to 0.05–0.24 m\(^{-2}\) (Valentinsson et al., 1999).

The age at which whelks become sexually mature differs in different geographical areas and has been found in the range of 2–9 years, with a median value of about 5 years (Gendron, 1992; McIntyre et al., 2015; Valentinsson et al., 1999; Lawler, 2010; Heude-Berthelin et al., 2011; Magnúsdóttir et al., 2011; Borsetti et al., 2021; Hollyman et al., 2018a). In general, whelks spawn at temperatures of 4–10 °C (Smith et al., 2013). Spawning in Swedish (and Danish) waters takes place in the period October to December (Valentinsson, 2002a), and in French waters, 90% of whelks showed ripe gonads in October (Heude-Berthelin et al., 2011). In boreal region, gonad maturation in general occurs in the spring and summer whereas spawning occurs during the winter (Kideys et al., 1993; Valentinsson et al., 1999; Borsetti et al., 2020). The absence of planktonic trochophere and veliger larval stages together with the adult whelk’s not migratory lifestyle can easily result in establishment of subpopulations. This is supported by the findings of genetically and morphologically differences in populations down to a small spatial scale (Gendron, 1992; Valentinsson, 2002b; Weetman et al., 2006; Shelmertine et al., 2007; Pálsson et al., 2014; Goodall et al., 2021). The life history of the common whelk, is characterized by initially rapid growth, late sexual maturity, relatively low fecundity, absence of pelagic larval stages, and a long live span. This, together with the non-migratory trait and the whelk’s high catchability, all points to an increased risk of recruitment overfishing (Himmelman and Hamel, 1993; Weetman et al., 2006). The sign of recruitment overfishing is risk of recruitment overfishing (Himmelman and Hamel, 1993; Valentinsson, 2002b; Weetman et al., 2006; Shelmerdine et al., 2011). In boreal region, gonad maturation in general occurs in the spring and summer whereas spawning occurs during the winter (Kideys et al., 1993; Valentinsson et al., 1999; de Voogs and van der Meer, 2010; Emmerson, 2018). In the Southern Kattegat the densities of whelks are highly variable in different geographical regions and has been reported in the range of 0.05 up to 2.12 m\(^{-2}\) (Petersen, 1911; Petersen and Boysen Jensen, 1911; Hancock, 1963; Gros and Santarelli, 1986; Himmelman, 1988; McQuinn et al., 1988; Jalbert et al., 1989; Kideys, 1993; Legault and Himmelman, 1993; Valentinsson et al., 1999; de Voogs and van der Meer, 2010; Emmerson, 2018). In the Swedish part of Kattegat the density of whelks has been estimated to 0.05–0.24 m\(^{-2}\) (Valentinsson et al., 1999).

Concerning a possible regulation of the novel Danish whelk fishery, knowledge on population parameters at a local scale is highly needed. Therefore, a second project (also funded by the European Maritime and Fisheries Fund (EMFF) and the Danish Fisheries Agency) was launched in 2016 aiming to provide the Danish Fisheries Agency advice on management of the Danish whelk fishery. Apart from the studies by Petersen (1911) and Petersen and Boysen Jensen (1911), the present work represents the first study appraising the whelk populations in the inner Danish waters. The major objectives of the work were firstly to obtain general knowledge on the population characteristics of whelks in the Danish Southern Kattegat, where most of the novel Danish whelk fishery takes place and secondly to provide some advice for the Danish Fisheries Agency.

2. Methods

2.1. Area of study

All sampling in the present work was done within three of the officially designated fishing zones in the Southern Kattegat. The three zones studied are the zones where most of the commercial whelk fishery has been initiated. More specifically the three zones are by the Danish Fisheries Agency numbered 107, 108 and 109 (Fig. 1). The positions (WGS84) within the three zones where pots were deployed in the present work were 56°03.250N 11°18.317E; 56°07.150N 11°53.000E and 56°08.650N 12°24.433E, respectively. The water depth at the three locations were approximately 20 m. In the remaining text, the positions will be referred to as zone 107, 108 and 109, respectively.

2.2. Animals and biometric measurements

In each zone, whelks were caught late October–early November 2017 using 20 professional stand up pots consisting of a 20 l high density polyethylene (HDPE) pot with pre-drilled drainage holes (24 mm), a concrete weight cast (10 kg) inside the pot and a rope handle (attachment line) with a plastic spinner. The top entrance was netted with a drawstring opener/closer. The bait was half a brown crab (Cancer pagurus) and 100 g of lesser spotted dogfish (Scyliorhinus canicula). Pots were rigged on longlines with 30 m between each pot. The drainage holes also served as escape ways for whelks with a shell width below 24 mm. On retrieval of the pots, whelks were passed through a riddle (i.e., whelks with shell length < 40 mm were discarded). From all catches, 100 whelks were chosen randomly and transported to the Marine Biological Section, Helsingør, Denmark. At the laboratory, the whelks were passed through a riddle (i.e., whelks with shell width below 24 mm were discarded). From all catches, 100 whelks were chosen randomly and transported to the Marine Biological Section, Helsingør, Denmark. At the laboratory, the whelks were immediately frozen (\(\mp 18^\circ C\)) until analysis.

2.3. Measurements and biometric relationships

For all whelks the shell length, shell weight, meat weight and fresh weight (i.e., whole animal weight) was measured. All weights were measured as wet weights. The biometric relationships between shell length, shell weight, meat weight and fresh
weight were fitted by either linear regression or non-linear regression. All relationships were first tested for linearity by the procedure recommended by Boldina and Beninger (2016) to test if the best linear unbiased estimator (BLUE) conditions were fulfilled. If BLUE conditions were not fulfilled, the relationships were fitted by 2-parameter non-linear models: (1) power, (2) logarithmic and (3) quadratic. The model with the best fit and the least Akaike information criterion corrected for small sample sizes (AICc) was chosen.

2.4. Age and growth

The age was estimated from the number of dark striae on the operculum. It was assumed that the dark striae represent yearly growth (Santarelli and Gros, 1985; Ilanoa et al., 2004). The method has been frequently used in age determination of whelks (e.g., Narvarte, 2006; Shelmerdine et al., 2007; Heude-Berthelin et al., 2011). The operculum was carefully removed from each whelk and cleaned from tissue. The operculum was left to dry on paper towel for 24 h before the striae on the inner side of the operculum were counted. It should be noted that Hollyman et al. (2018a,b) introduced an improved age determination using whelk paper towelfor 24 h before the striae on the inner side of the operculum were counted. If the best linear unbiased estimator (BLUE) conditions were fulfilled, if the best linear unbiased estimator (BLUE) conditions were fulfilled, the relationship between age and shell length was fitted by 2-parameter non-linear models: (1) power, (2) logarithmic and (3) quadratic. The model with the best fit and the least AICc was chosen. For all models the asymptotic pertzand (3) von Bertalanffy model were fitted by (1) logistic, (2) Gom- (2018a,b) introduced an improved age determination using whelk paper towelfor 24 h before the striae on the inner side of the operculum were counted. It should be noted that Hollyman et al. (2018a,b) introduced an improved age determination using whelk paper towelfor 24 h before the striae on the inner side of the operculum were counted. If the best linear unbiased estimator (BLUE) conditions were fulfilled, the relationship between age and shell length was fitted by 2-parameter non-linear models: (1) power, (2) logarithmic and (3) quadratic. The model with the best fit and the least AICc was chosen. For all models the asymptotic pertzand (3) von Bertalanffy model were fitted by (1) logistic, (2) Gom-

2.5. Sex and sexual maturity

All whelks were removed from their shells and the sex was determined. The reproductive status of females was evaluated by visual inspection of the maturity of the gonads (Lawler, 2010; Couillard and Brulotte, 2020). The reproductive status of males was evaluated by penis length and males with a penis length greater than or equal to half of the shell length were considered mature (Gendron, 1992; Kaie, 1969; Santarelli and Gros, 1985). In the present work, whelks were collected October–early November, which is just prior to spawning (Valentinsson, 2002a; Heude-Berthelin et al., 2011) and optimal for evaluation of gonad maturity (Haig et al., 2015).

The maturity as a function of shell length was determined by binomial logistic regression (i.e., logit model):

\[ P = \frac{1}{1 + \exp^{-a - bS}} \]

where \( P \) is the possibility of a whelk with the shell length \( S \) (mm) to be sexually mature, \( a \) and \( b \) = coefficients for intercept with the y-axis and the slope of the logistic curve.

The size of maturity (SOM) was defined as the shell length where the probability for sexual maturity was 0.5 (SL50).

2.6. Size distribution, age distribution and mortality

The distributions of shell length, fresh weight, meat weight and age were expressed as frequency and fitted with non-linear regressions (3-parameters Gaussian or 3-parameters log normal, depending on best fit and least AICc). The instantaneous mortality \( Z \) was estimated by linear regression of the semi-logarithmic transformed age size key structure (right hand segment) using the equation:

\[ \ln(N_t) = \ln(N_0) - Zt \]

where \( N_t \) = number of whelks alive at the time \( t \) (years), \( N_0 \) = the hypothetical number of whelks at the time 0 years, \( Z \) = the instantaneous mortality rate and \( t \) = age (years). Finite mortality \( = 1 - \exp(Z) \).

2.7. Population size and density

Population sizes were estimated by classic mark-recapture experiments. In zone 108 and 109, the experiments were done August 2018 and in zone 107, the experiment was made in May 2018. The water depth for all experiments were approximately 20 m. Each mark-recapture experiment was made by deploying a longline with 20 pots 30 m apart (pots and baits as described in 2.2). After 2 days, the pots were retrieved and all whelks were counted and marked with broad lobster rubber bands around the shells. The pots were deployed and the marked whelks were released evenly in a distance of app. 20 m on both sides along the longline. The pots were retrieved again after 2 days. The number of unmarked and marked whelks in the retrieved pots were counted.

The population size \( \hat{N} \) was estimated by Chapman estimator, which as compared to the Lincoln-Petersen estimator gives an almost unbiased estimate (Chapman, 1951):

\[ \hat{N} = \frac{(M + 1) (C + 1)}{(R + 1)} - 1 \]

where \( M \) = number of individuals marked in the first sample, \( C \) = total number of individuals captured in the second sample and \( R \) = number of marked individuals in second sample.

Following Seber (1986) confidence intervals (CI) for \( \hat{N} \) was calculated either as binominal distributed (if \( R/C > 0.10 \)), normal distributed (if \( R/C < 0.10 \) and \( R > 50 \)) or Poisson distributed (if \( R/C < 0.10 \) and \( R < 50 \)).

Besides the number of pots used in the mark-recapture experiments the area from which the pots can attract whelks must be known in order to estimate the population density. At water depths similar to the southern Kattegat, Himmelman (1988) found the attraction area to be 111 m² at low water currents and 585 m² at high water currents. In the present work, the population densities were estimated using both attraction areas.

2.8. Test fishery

To get a first impression of the salinity dependent distribution of whelks in the Southern inner Danish waters, a small test fishery was done in August 2018. At 24 localities in the southern Kattegat and extending southwards into both Øresund and The Great Belt (see Fig. 6) 10 pots (pots and baits as described in 2.2) where deployed and retrieved after 24 h and the catch per unit effort (CPUE) was determined.

2.9. Commercial fishery

The CPUE at the fishing grounds for the period January 2017–November 2018 was achieved from the logbooks of two fishermen as a part of the first EMFF project.

2.10. Statistical analysis

SigmaPlot 14.0 (Systat Software) was used to test data for normality and homoscedasticity and then to perform statistical analysis. Mean values and estimated parameters were compared by one-way ANOVA followed by a post hoc Holm–Sidak test (if data were normal distributed and variances were homogeneous) or by Kruskal–Wallis test followed by post hoc Tukey test (if data were non-normal distributed and/or variances were non-homogeneous). The effect size of differences in mean values and regression estimators was calculated using Cohen’s D and evaluated by the convention given by Sawilowsky (2009). Mean values are given with ± 1 SD and estimated parameter with ± 1 SE, respectively. In all tests the significance level were set at \( \alpha = 0.05 \).
Fig. 2. Allometric relationships for the whelk (Buccinum undatum) in zone 107, 108 and 109 in the southern Kattegat, Denmark. The relation between shell length and fresh weight (left panel), shell length and meat weight (middle panel) and shell weight and meat weight (right panel). In all graphs, the allometric equation is given together with $R^2$.

### Table 1
Biometrics of whelks (mean values ± SD) collected in the three zones in the Southern Kattegat, Denmark. All weights are given as wet weights.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Shell length (mm)</th>
<th>Fresh weight (g)</th>
<th>Meat weight (g)</th>
<th>Shell weight (g)</th>
<th>Meat content (%)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>107</td>
<td>64.7 ± 8.6</td>
<td>27.0 ± 10.5</td>
<td>17.8 ± 7.3</td>
<td>9.1 ± 3.4</td>
<td>65.6 ± 4.3</td>
<td>100</td>
</tr>
<tr>
<td>108</td>
<td>64.1 ± 9.8</td>
<td>26.5 ± 11.4</td>
<td>16.4 ± 7.8</td>
<td>10.1 ± 3.8</td>
<td>60.8 ± 4.8</td>
<td>100</td>
</tr>
<tr>
<td>109</td>
<td>73.2 ± 7.3</td>
<td>42.1 ± 12.0</td>
<td>24.5 ± 7.2</td>
<td>17.6 ± 5.9</td>
<td>58.2 ± 6.4</td>
<td>100</td>
</tr>
</tbody>
</table>

3. Results

3.1. Measurements and biometric relationships

The average shell length (mm), fresh weight (g), meat weight (g) and shell weight (g) in the three zones are shown in Table 1. There was no significant difference in any mean values between zone 107 and 108. However, all mean values for zone 109 were significantly different as compared to both 107 and 108 ($p < 0.001$) with effect sizes in the range of large to very large ($D = 0.92–1.77$). The average meat percent was significantly different between all zones ($p < 0.001$) with effect sizes ranging from small to very large ($D = 0.46–1.36$). The biometric relationships between meat weight and shell weight at all zones and meat weight and shell length in zone 109 fulfilled the BLUE condition (Fig. 2) indicating isometric relationships. For all other relationships, the 2-parameter power function had the best fit with the least AICc (Fig. 2) indicating allometric relationships. The allometric exponents for fresh weight as a function of shell length were significantly different between zone 107 and 109 ($p = 0.008$) but the difference had a small effect size ($D = 0.40$). For the relation between meat weight and shell weight the slope in zone 109 was significantly different from both zone 107 and 108 ($p < 0.001$) and both effect sizes were very large ($D = 1.16–1.26$).

3.2. Age and growth

The opercula of all whelks caught at the three zones had between two and eight striae (i.e., age = 2–8 years). The best model for shell length as a function of age was the Gompertz model for zone 107 and 108 and the van Bertalanffy model for zone 109 (Fig. 3). The estimated asymptotic shell length ($L_\infty$) at zone 107, 108 and 109 was 77.6 ± 5.02, 78.2 ± 3.72 and 83.1 ± 6.46 mm, respectively. The asymptotic shell lengths were not significantly different ($p = 0.718$). The estimated growth coefficients in zone 107, 108 and 109 were 2.28 ± 0.78, 1.84 ± 0.51 and 0.53 ± 0.19 and not significantly different ($p = 0.402$).

3.3. Sex and sexual maturity

In zone 107, 108 and 109, females comprised 41, 52 and 47% of the populations, out of which 38, 15 and 55% were sexual mature, respectively. Of the males in zone 107, 108 and 109, the percentage of sexually maturity was 68, 40 and 96%, respectively. The estimated size at maturity (SOM = SL50) pooled for both sexes in zone 107, 108 and 109 was 62.9, 70.3 and 63.4 mm (Fig. 4), corresponding to 4–4.5 years of age (Fig. 3, zone 107 and 108). The SL50 for females in zone 107, 108 and 109 was 68.6, 71.8 and 71.3 mm, respectively (data not shown). The SL50 for males at zone 107 and 108 was 60.5 and 70.1 mm (data not shown). Male SL50 in zone 109 could not be fitted because all males (except two; shell lengths 74.7 and 73.7 mm) were mature. In zone 109 the smallest sexual mature male had a shell length of 62.9 mm and the male SL50 in this zone can only be estimated to be <62.9 mm.

3.4. Size distribution, age distribution and mortality

The size distributions of shell length, fresh weight, meat weight and shell weight for zone 107, 108 and 109 are shown in Fig. 5.
For zone 107, the Gaussian model was best in fitting shell length, fresh weight and meat weight and the log-normal was best in fitting the shell weight distribution. For zone 108, the Gaussian model was best in fitting shell length, fresh weight and shell weight and the log-normal was best in fitting the meat weight distribution. For zone 109, the log-normal model was best in fitting all distributions. No significant differences in peak values were observed between zone 107 and 108 (0.058 < \( p < 0.333 \)). The peak values for all distributions in zone 109 were significantly different from 107 and 108 (\( p < 0.001 \)) with effect sizes in the range of medium to huge (\( D = 0.7–2.0 \)). No peak values were significantly different from the measured mean values (Table 1) (0.289 < \( p < 0.950 \)) showing that the distributions were symmetrical. The age distribution (Fig. 6) was best fitted by the Gaussian model in zone 107 and 109 and by the log-normal model in zone 108. The age peak value for zone 107, 108 and 109 was 4.6, 3.3 and 4.0 years, respectively and all peaks significantly different (\( p < 0.001 \)) with effect sizes from large to very large (\( D = 0.81–1.44 \)). The model fit of the yearly instantaneous mortality rates in zone 107, 108 and 109 were estimated to \(-1.13 ± 0.19\), \(-0.72 ± 0.05\) and \(-0.95 ± 0.11\), respectively (Fig. 7). The estimated instantaneous mortality rates were not significantly different (\( p = 0.068 \)).

### 3.5. Population size and density

The estimated population size in zone 107, 108 and 109 was 14,107, 15,342 and 6,320 whelks, respectively (Table 2). The confidence interval in zone 107 and 109 was calculated using normal approximation (107: \( R/C = 0.14 \) and 109: \( R/C = 0.23 \)). The confidence interval for zone 108 was calculated as binomial (\( R/C = 0.04 \) and \( R = 57 \)). The population density of whelks in zone 107, 108 and 109 using 111 m\(^2\) as attraction area could within the 95% confidence limits be estimated to \( 5.7 < \hat{N} < 7.3 \) ind m\(^{-2}\), \( 5.3 < \hat{N} < 10.3 \) ind m\(^{-2}\) and \( 2.4 < \hat{N} < 3.6 \) ind m\(^{-2}\), respectively (Table 2). Using an attraction area of 585 m\(^2\) the population densities at zone 107, 108 and 109 were estimated to be within \( 1.1 < \hat{N} < 1.4 \) ind m\(^{-2}\), \( 1.0 < \hat{N} < 2.0 \) ind m\(^{-2}\) and \( 0.5 < \hat{N} < 0.7 \) ind m\(^{-2}\), respectively (Table 2). Based on the 95% confidence limits, zone 109 had a significantly different population density as compared

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**Table 2**

Mark-recapture experiments, population sizes and densities in the three zones in the Southern Kattegat, Denmark.

<table>
<thead>
<tr>
<th>Zone</th>
<th>107</th>
<th>108</th>
<th>109</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mark-recapture parameters</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marked 1st sample (M)</td>
<td>2026</td>
<td>627</td>
<td>1456</td>
</tr>
<tr>
<td>Total captured 2nd sample (C)</td>
<td>1384</td>
<td>1273</td>
<td>1140</td>
</tr>
<tr>
<td>Marked captured 2nd sample (R)</td>
<td>198</td>
<td>57</td>
<td>262</td>
</tr>
<tr>
<td>Number of pots</td>
<td>19</td>
<td>40</td>
<td>19</td>
</tr>
<tr>
<td>Population</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \hat{N} ) (ind.)</td>
<td>14,107</td>
<td>15,342</td>
<td>6,320</td>
</tr>
<tr>
<td>Lower 95% CI (ind.)</td>
<td>16,186</td>
<td>22,821</td>
<td>8,013</td>
</tr>
<tr>
<td>Upper 95% CI (ind.)</td>
<td>12,587</td>
<td>11,720</td>
<td>5,238</td>
</tr>
<tr>
<td>Population density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pot attraction area = 111 m(^2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \hat{N} ) (ind m(^{-2}))</td>
<td>6.69</td>
<td>6.94</td>
<td>3.00</td>
</tr>
<tr>
<td>Lower 95% CI (ind m(^{-2}))</td>
<td>5.91</td>
<td>6.06</td>
<td>2.70</td>
</tr>
<tr>
<td>Upper 95% CI (ind m(^{-2}))</td>
<td>7.69</td>
<td>8.19</td>
<td>3.36</td>
</tr>
<tr>
<td>Pot attraction area = 585 m(^2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \hat{N} ) (ind m(^{-2}))</td>
<td>1.27</td>
<td>1.32</td>
<td>0.57</td>
</tr>
<tr>
<td>Lower 95% CI (ind m(^{-2}))</td>
<td>1.12</td>
<td>1.15</td>
<td>0.51</td>
</tr>
<tr>
<td>Upper 95% CI (ind m(^{-2}))</td>
<td>1.46</td>
<td>1.55</td>
<td>0.64</td>
</tr>
</tbody>
</table>

---

Fig. 3. Non-linear regressions of the whelk (Buccinum undatum) shell length as a function of age within zone 107, 108 and 109 in the southern Kattegat, Denmark. Horizontal dashed lines show the estimated size at maturity (SL\(_{50}\)). In all graphs, the regression equation is given together with R\(^2\).

Fig. 4. Proportion of mature whelks (Buccinum undatum) as a function of shell length, for zone 107, 108 and 109 in the southern Kattegat, Denmark. The logit curves are presented with 95% confidence intervals. In all graphs, estimated size at onset of maturity (SL\(_{50}\), open circles) is shown together with R\(^2\) of the logit curve fits.
3.6. Test fishery

In the test fishery, the CPUE was seen to decrease quickly in a southern direction in both Øresund and the Great Belt (Fig. 8). The CPUE in Øresund decreased from 4.4 to 0 kg pot⁻¹ over app. 30 km and in the Great Belt, the CPUE decreased from 2 to 0.002 kg pot⁻¹ over app. 100 km.

3.7. Commercial landings

The CPUE achieved by the two commercial fishermen are seen in Fig. 9. The fishermen started their novel whelk fishery in zone 108 but when the CPUE decreased below 1 kg pot⁻¹ they moved the fishery to zone 215 (see Fig. 1). The 2017 and 2018 mean CPUE was 1.77 ± 0.72 and 2.08 ± 0.57 kg pot⁻¹, respectively. The average CPUE achieved in the two years was significantly different \( (p = 0.001) \) but with a small size effect \( (D = 0.48) \). In 2017 the fishermen made 206 landings and landed in total 174,538 kg (mean = 851.4 ± 351.1 kg landing⁻¹) and in 2018 they made 127 landings amounting to 101,840 kg (mean = 801.9 ± 341.6 kg landing⁻¹). At each fishing occasion, the fishermen deployed on average 508 ± 139 pots. The lowest and highest number of pots at any single deployment was 100 and 1600, respectively.

4. Discussion

The present work reports for the first time population characteristics for whelk populations in the inner Danish waters. Besides a significant difference in age peak values in zone 107 and 108 (4.6 and 3.3 year, respectively) the two zones shared all other population characteristics. In contrast, zone 109 only shared the growth coefficient with zone 107 and 108 and the allometric exponent for fresh weight as a function of shell length with zone 108. From this, the whelk population in zone 109 clearly had different population characteristics as compared to the two other zones. The smallest whelk (>40 mm) in zone 109 had a shell length of 53.9 mm. In zone 107 and 108, the smallest whelks were 42.2 and 44.3 mm, respectively. The proportion of whelks in zone 107 and 108 smaller than 53.9 mm comprised 11% and 17%, respectively. Thus, zone 109 seemed to suffer from low recruitment. This was also supported by the fact that although no difference in instantaneous mortality rates was seen, the estimated population size and density in zone 109 was less than half of the population sizes estimated for zone 107 and 108. However, it should be noted that the CPUE in the three zones obtained in the test fishery was of equal size, which could be due to higher catchability of the larger whelks in zone 109 or simply a stochastic phenomenon. In addition, 55% of females and 96% of the males were sexual mature in zone 109. Why the recruitment in zone 109 appears very low is unknown, but it is very unlikely due to overfishing, because in zone 109 no commercial landings took place in 2017 and only
8798 kg were landed in 2018 (Danish Fishery Agency, 2021). It is also unknown whether the difference is due to presence of a single weak cohort as no whelks <40 mm were included in the present work. Shrives et al. (2015) found that a decrease in CPUE of whelks >44 mm was accompanied by a decrease in CPUE of whelks <44 mm. This supports the apparent lack of recruitment in zone 109. Overall, the difference between zone 109 and the 2 other zones emphasizes that whelk populations on a small geographical scale (∼25 km) can have very different population characteristics and adds evidence to the importance of evaluating the effect of fishery on whelk populations at a local scale.

Concerning the biometric relationships, the meat weight as a function of shell weight showed isometric growth in all three zones (Fig. 2). Except the relation between meat weight and shell length in zone 109, all other relationships showed allometric growth (Fig. 2). The allometric exponent for the relation between fresh weight and shell length showed hyperallometry in zone 107 and hypoallometry in zone 109 (Fig. 2). This, together with the meat percentage (Table 1), indicates that the whelks in zone 107 had the highest condition and zone 109 had the lowest. The above indicate that the shell morphology in zone 109 was different from the two other zones. This finding could be due to either a higher presence of predators in zone 109 (cf. Thomas and Himmelman, 1988) or fine-scaled spatial patterns resulting in differences in shell morphology (Borsetti et al., 2018; Magnúsdóttir et al., 2018). The mean shell length found in the three zones (Table 1 and Fig. 5A) is in accordance with the mean shell length found in Swedish waters, the Southwest Irish Sea, Iceland, Faroe Island, and the Eastern Scotian shelf (Valentinsson et al., 1999; Fahy et al., 2005; Magnúsdóttir et al., 2011; Ashfaq et al., 2019). All mean fresh weights in the present work were higher than reported for whelks of similar shell lengths in Iceland and the Faroe Islands (Magnúsdóttir et al., 2011). This could tentatively be a result of different thermal effect on growth of shell and soft parts as temperature is known to affect growth parameters (Emmerson et al., 2020; Borsetti et al., 2021).

The maximum shell lengths (L∞ = 77.6–83.1 mm), estimated from the relation between shell length and age in the present work were lower than what has been estimated for whelk populations of the Southern and Southwest Irish Sea and Isle of Man (L∞ > 100 mm) (Fahy et al., 1995, 2000; Kideys, 1996) and off Shetland (Henderson and Simpson, 2006). However, the maximum shell lengths in the present work are within the range of whelk populations found in a survey of landings from ten English ports and off Shetland together with the South and South-eastern coast of England (L∞ > 62.62–157.52 mm) (Lawler, 2010; Shelmerdine et al., 2007; Hancock and Simpson, 2006) and in accordance with the L∞ found at similar depth in the Northern part of Kattegat (Valentinsson et al., 1999). In addition, it should be noted that the Gompertz growth model was best describing the growth in zone 107 and 108 (cf. (Hollyman et al., 2018b)). In general, the growth exponent (k) estimated in the present work (k = 0.53–2.28) were larger than reported by others (k = 0.08 - 1.02) (Hancock, 1963; Fahy et al., 1995; Kideys, 1996; Fahy et al., 2000; Henderson and Simpson, 2006; Shelmerdine et al., 2007; Heude-Berthelin et al., 2011). From the relation between shell length and age it can be noted that a whelk with shell length 70 mm from zone 107, 108 and 109 will be about 5, 4 and 3 years old, respectively. However, the whelks in Kattegat are in general not getting as large as at many other localities but they seem to grow faster. It should be noted that Hollyman et al. (2018b) showed that age determination using the operculum method tends to
give smaller asymptotic shell lengths \( L_\infty \) and higher growth exponents (k) as compared to the statoloth method. If this bias applies to the present work and the referred literature all using the operculum method is not known. Using the statoloth method Emmerson et al. (2020) found \( L_\infty \) and growth exponent (k) for whelk populations in the Irish Sea to be in the range of 59.9–116.8 mm and 0.44–1.04, respectively. Borsetti et al. (2021) also used the statoloth method and found \( L_\infty \) = 72.3 mm and a growth exponent of 0.59 for whelks in U.S. Mid-Atlantic waters. Although the estimates made by Emmerson (2018) and Borsetti et al. (2021) are more precise the general picture is not changed.

The shell length of whelks when reaching sexual maturity \( (S_{L_{\infty}} = \text{SOM}) \) varies between geographic regions. In the waters off the British canal islands and in the Normand-Breton bight the SOM has been measured to 45–50 mm (Santarelli and Gros, 1985). However, in 20 out of 22 English whelk-fishing areas the size of maturity \( (\text{SOM}) \) has been found to be larger than the 45 mm MCRS (Bell and Walker, 1998; Lawler, 2010; McIntyre et al., 2015; Emmerson et al., 2017). In fact, in nine studies covering 23 English, 1 French, 10 Canadian, 8 Icelandic, 2 Faroese and 2 Swedish whelk populations only two English populations had SOM equal or near to the EU MCRS (Gendron, 1992; Bell and Walker, 1998; Valentisson et al., 1999; Lawler, 2010; Heude-Berthelin et al., 2011; Magnusdottir et al., 2011; McIntyre et al., 2015; Emmerson et al., 2017; Ashfaq et al., 2019). In addition, it should be noted that one of the two English populations reported to have SOM equal to or close to MCRRS, were studied by two research groups (Bell and Walker, 1998; McIntyre et al., 2015) and the population with \( \text{SOM} \approx \text{MCRS} \) found by one research group was by the other group found to have \( \text{SOM} > \text{MCRS} \) and vice versa. Considering this, it must be concluded that, apart from the study by Santarelli and Gros (1985), all studied whelk populations including the present work have \( \text{SOM} > \text{MCRS} \). This conclusion is also in full accordance with a meta-analysis made by Borsetti et al. (2018) who reached the conclusion that 90% of males and 92.3% of females had \( \text{SOM} > \text{MCRS} \). The above made McIntyre et al. (2015) to encourage the English fisheries authority to implement a MCRS based on local determined SOMs instead of a single national (i.e., European) MCRS. Similar encouragements have been put forward concerning the whelk fishery in the Irish Sea, off the island of Jersey, the Shetland Islands and in Canada (Fahy et al., 1995, 2003; Morel and Bossy, 2004; Shelerdine et al., 2007; Ashfaq et al., 2019). The above scientific recommendations led local fishery authorities at the Shetland Islands, the Isle of Man and in Canada to increase the MCRS to locally determined SOMs (Shelerdine et al., 2007; Henderson and Simpson, 2006; DFDS, 2009; Emmerson et al., 2017). In addition, the whelk fishery off Isle of Man and the Shetland Islands is regulated by boat licenses, number of pots per boat and periodically closure of fishery (Statutory document no. 279/94, 1994; SSMO regulations, 2018).

Valentinsson et al. (1999) estimated SOM in the Swedish part of Kattegat to be 57–71 mm. In the present work, the SOM was 62.9–69.9 mm, which is in full accordance with the above study. The age of maturity (4–4.5 years) found in the present work is within the range found by others (Lawler, 2010; Heude-Berthelin et al., 2011; Magnusdottir et al., 2011; Borsetti et al., 2021). However, in the study by Valentinsson et al. (1999) the age of maturity for whelks in the Kattegat was estimated to 7–9 years, this is in the high end of what have been found by others and considerable higher than the 4–4.5 years found in the present work. Typically, the SOM does not vary more than 5% between male and female, but with a tendency for females to have higher SOM (Heude-Berthelin et al., 2011; Lawler, 2010). Accordingly, the female SOM in zone 107 was 2% higher than that of the males, but in zone 108 the female SOM was 12% higher than the male SOM.

In the zone 107, 108 and 109 the percentages of recaptured whelks in the mark-recapture experiments were in the range 9.8–18.0% (Table 2), which is regarded acceptable and in good accordance with the 2.9 – 15.4% recapture achieved in other studies (e.g., Hancock, 1963; Robson, 2014; Turtle, 2014; Robinson, 2015; Bolger, 2016). The densities of whelks in the studied zones were estimated using attraction areas of both 111 and 585 m$^2$ (cf. Himmelman, 1988). The density estimates in the present work makes an attraction area of 585 m$^2$ the most plausible, when compared with literature (Hancock, 1963; Gros and Santarelli, 1986; Himmelman, 1988; McQuinn et al., 1988; Jalbert et al., 1989; Kideys, 1993; Legault and Himmelman, 1993; Valentinsson et al., 1999; Emmerson, 2018). Using an attraction area of 585 m$^2$ the estimated densities were in the range of 0.5–2.0 ind m$^{-2}$, which are within the range of densities (0.05–2.12 m$^{-2}$) reported in literature (Hancock, 1963; Gros and Santarelli, 1986; Himmelman, 1988; McQuinn et al., 1988; Jalbert et al., 1989; Kideys, 1993; Legault and Himmelman, 1993; Valentinsson et al., 1999; de Voors and van der Meer, 2010; Emmerson, 2018). Valentinsson et al. (1999) also used an attraction area of 585 m$^2$ and reported an estimated population density of 0.05–0.24 ind m$^{-2}$ in the Swedish coastal area of Kattegat, which is a factor 10 lower than densities estimated in the present work. The discrepancy is most likely not due to a dramatic increase in whelk density during the 18 years elapsed between the two studies. We believe the difference has to do with the difference in methodology and study area. Valentinsson et al. (1999) based their density estimate on a depletion experiment conducted in a small (0.27 km$^2$) semi-enclosed bay at the northern Kattegat coast of Sweden whereas...
the present estimates were based on mark-recapture experiments offshore at whelk fishing grounds. Whether the different methodologies have influenced the respective density estimates are unknown, but to us it seems more reliable to base density estimates on experiments performed in the Kattegat proper and at the whelk fishery sites. This especially because whelk densities are known to be different in different geographical areas.

The above density estimates also influence the estimates of the total stock of whelk in Kattegat reached by Valentinsson et al. (1999) and in the present work. Based on the average CPUE and the total bottom area between 10 and 30 m depth in the Kattegat (app. 15,000 km²) Valentinsson et al. (1999) estimated the stock of whelks in Kattegat to be 45,000–225,000 tons. In the present work, using the same bottom area, the average density estimates and the average fresh weight (30.7 g) we estimate the total stock of whelks (> 40 mm) in Kattegat to be in the range of 230,250–921,000 tons. Thus, the total stock of whelks in the Kattegat seems to be much larger than earlier anticipated.

The test fishery made in the present work showed that commercial whelk fishery in the Inner Danish waters is only possible in Kattegat and the northern part of the Great Belt area. The salinity of the Inner Danish waters decreases in a North to South direction. The test fishery clearly showed that due to the decreasing salinity, no whelks were caught off Copenhagen and in the Great Belt virtually no whelks were caught off the Southern part of the island Langeland.

The CPUEs of the Danish commercial fishermen were in the range of 1.77 and 2.08 kg pot⁻¹ and in full accordance with CPUEs reported from European waters (1.3–3.3 kg pot⁻¹) (Valentinsson et al., 1999; Morel and Bossy, 2004; Shrives et al., 2015). The novelty of the Danish whelk fishery is evident from the reported landings. When the CPUE in October 2017 dropped below 1 kg pot⁻¹, the fishermen stopped fishing in zone 108 and moved to zone 215. However, the drop in CPUE was not due to overfishing in zone 108 but merely reflecting the seasonal change in the catchability of the whelks.

The area in zone 108 having water depths > 10 m can be estimated to app. 350 km². Using the average fresh weight (24.1 g) and density range (1.5 < N < 1.55 ind m⁻²), the total stock (>40 mm) is estimated to be in the range 9700–13,074 tons. In 2017, the commercial fishery landed approximately 175 tons whelks from zone 108. The 2017 landings from zone 108 is equivalent to 1.3–1.8% of the total estimated stock. For comparison, with the natural early instantaneous mortality rate in zone 108 was estimated to −0.215, which is in full accordance with the natural mortality rates found in Southwest Irish Sea by Fahy et al. (2005). Thus, the fishery only marginally contributed to the overall whelk mortality in zone 108.

5. Conclusions

According to the results of the present work, the estimated stock of whelks in Kattegat may be larger than previously estimated. The present work showed clear biometric differences between adjacent fishing zones, confirming that any regulation of whelk fisheries must be based on knowledge of population parameters determined at a local scale. At present the magnitude of the commercial Danish whelk fishery in the Southern Kattegat was not found to point towards overfishing. However, it could be argued that a precautionary approach (cf. FAO, 1996) would be to implement MCRS according to locally determined SOMs. Therefore, in addition to monitoring the CPUE separately for each zone we highly recommend the Danish Fisheries Agency to implement MCRS according to the locally determined SOMs, which for the three zones studied was found to be 17.9–24.9 mm larger than the EU regulated MCRS.

CRediT authorship contribution statement

**Bent Vismann:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing–original draft, Writing–review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Johan Wedel Nielsen:** Conceptualization, Investigation, Methodology, Resources. **Jacob Linnemann Rønfeldt:** Conceptualization, Investigation, Methodology, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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