Combining hydroacoustic seabed survey and grab sampling techniques to assess “local” sandeel population abundance

Simon P. R. Greenstreet, Gayle J. Holland, Emma J. Guirey, Eric Armstrong, Helen M. Fraser, and Iain M. Gibb


Sandeels (Ammodytes marinus) are a critical prey of many top predators in the North Sea, and have also been the target of a major industrial fishery. To quantify resource allocation between competing predators, and between natural predators and fishers, and to assess the impact of each source of mortality on sandeel population dynamics, estimates of the absolute abundance of sandeels at the spatial scale at which these interactions take place are required. In this study, hydroacoustic seabed survey and nocturnal grab surveys are combined to examine variation in the abundance of sandeels at a sandbank complex off southeast Scotland. Grab surveys provide point estimates of sandeel density and sediment composition data, which are used to define sandeel sediment preference categories. The total area of each sandeel sediment preference category is determined by hydroacoustic seabed survey. Sandeel population abundance recovered immediately following the closure of the sandeel fishery. However, simply closing the fishery was not sufficient to maintain the size of the local sandeel stock; the population is also highly dependent on good recruitment. We demonstrate how this combination of techniques might be used to examine variation in overwintering mortality rates in sandeels.

Keywords: grab surveys, local stock assessment, RoxAnn, seabed classification, sediment preference.

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Introduction

Over recent decades, sandeels (Ammodytes marinus) have been the target of the largest single-species fishery operating in the North Sea (Gislason and Kirkegaard, 1998). Many marine top predators are also heavily dependent on sandeels as prey, be they fish (Hislop et al., 1991; Greenstreet et al., 1998; Greenstreet, 2006), marine mammals (Hammond et al., 1994; Tollit et al., 1997; Brown et al., 2001; Santos and Pierce, 2003), or seabirds (Furness and Tasker, 2000). This potential for competition between fisheries and marine top predators has raised concerns (Ormerod, 2003), which managers seeking to implement an ecosystem approach to management need to address (Garcia and Cochrane, 2005). Sandeels in the North Sea are assessed annually, but the assessments cover the whole region. However, rather than there being a single homogenous stock, several discrete populations are thought to be present (Proctor et al., 1998; Pedersen et al., 1999; Boulcott et al., 2007; Christensen et al., 2008). Fishing effort for sandeels is patchily distributed, so even if the regional sandeel stock assessment suggests a “healthy” situation, local sandeel populations could still be depleted (Frank and Brickman, 2001), causing problems for local predators. For example, many sandeel fishing grounds are close to major seabird breeding colonies, and the distributions of industrial fishing activity and seabirds at sea tend to coincide (Wright and Begg, 1997).

One sandeel subpopulation is situated off the southeast Scottish coast; its core concentration is located on a complex of sandbanks that includes the Wee Bankie, Marr Bank, and Berwick’s Bank (Proctor et al., 1998; Pedersen et al., 1999). Particle-tracking studies, using three-dimensional hydrodynamic models (Magen, 2000; Baistrocchi, 2003; Christensen et al., 2008), and studies of population maturity-at-age (Boulcott et al., 2007) have confirmed the relatively closed, self-sustaining nature of the sandeel population on those sandbanks. The sandbanks lie 40–80 km east of important seabird colonies in and around the Firth of Forth, such as the Bass Rock and the Isle of May. Many of the seabirds at those colonies depend on sandeels during the breeding season (Wanless et al., 1998; Daunt et al., 2008), so when a sandeel fishery commenced there in the early 1990s, concerns were raised almost immediately over the potential threat the fishery posed to seabird food supplies. In 2000, to mitigate any potential threat to seabirds breeding at Scottish southeast coast colonies, including those in the Firth of Forth, the entire area west of longitude 1°W between latitudes 55°30’ and 58°00’N was closed to sandeel fishing (Greenstreet et al., 2006; Daunt et al., 2008).

Assessing the consequences of variation in sandeel abundance on their predators’ population dynamics may require sandeel abundance to be assessed at times that are critical to the predators in question. Determining the effect of variation in sandeel abundance on kittiwake (Rissa tridactyla) breeding success, for example, required sandeel abundance to be assessed during the breeding season of the seabirds in late spring/early summer (Daunt et al., 2008). Sandeels are most active at that time of year, moving freely between the seabed and the water column.
daily (Winslade, 1974a, b, c; Freeman et al., 2004). This presents a challenge to assessing their population abundance; estimates based on acoustic surveys will not include sandeels buried in the sediment (Freeman et al., 2004), whereas bottom trawl surveys will miss sandeels in the water column higher than the trawl headline (Greenstreet et al., 2006). Variation in a survey index might be interpreted as variation in population abundance, when it may actually reflect only variation in sandeel emergence behaviour (Greenstreet et al., 2006). Modelling sandeel emergence behaviour and applying such models to indices of sandeel abundance in both the water column and the sediment, for example, indices derived from acoustic and bottom trawl survey data, may provide a solution (Greenstreet et al., 2006). However, that approach needs a lot of data, and is therefore costly. Moreover, acoustic survey estimates depend on the sandeel target strength (Greenstreet et al., 2006). Strictly speaking, therefore, such estimation approaches provide measures of relative rather than absolute abundance. Finally, parsing of the total abundance estimates between different age components depends on the sampling of fish in pelagic trawl samples (used in support of the acoustic survey), and in bottom trawls, so may be biased as a result of size-related variation in catchability (Fraser et al., 2007).

Although perhaps not ideal, if constraints on survey timing can be relaxed, or in other circumstances are less critical, then sampling sandeels at a time of year when they are inactive and buried in the sediment can alleviate these problems. During autumn and winter, except for a brief midwinter emergence to spawn (Bergstad et al., 2001), sandeels lie dormant, buried in the sediment (Winslade, 1974a, b, c), so surveys that focus on estimating density in the sediment then can provide abundance estimates for the entire local population. Such logic underpins recent dredge surveys on the Dogger Bank (Mackinson et al., 2005) and in the southern North Sea (ICES, 2008), which provided information in support of precautionary sandeel fisheries management (ICES, 2008). However, such surveys only provided estimates of density at each station sampled. Unless such density estimates can be raised by the area occupied, they only provide indices of relative rather than absolute abundance. Furthermore, issues of catchability arise (Mackinson et al., 2005), and if sandeel catchability in dredges is size-dependent (see Fraser et al., 2007), then the density estimates of different sandeel age classes would not be directly comparable.

Grab surveys provide an alternative to dredges. Their disadvantage compared with dredges lies in the small total area sampled during a survey, and the resultant relatively small total catch of sandeels on which to base estimates of population size and age composition. However, comparison of sandeel density estimates from grab and dredge samples collected at the same location, and collected as close together in time as possible, suggests that catchability rates in grabs are between one and two orders of magnitude higher than in a dredge (HMF, unpublished data). Surveying at night reduces the chance of sandeels detecting the descending grab visually, and although they may be sensitive to the shock wave in the water column ahead of the grab, the escape response generally appears to be triggered by direct shock to the sediment (SPRG, pers. obs.). By the time the grab has landed, it would be too late for sandeels inside the grabbed area to escape into the water column. The only escape route left open would be through the sediment, and the time available for this before the grab closes around the sediment would be short.

Catchability in grabs may therefore be close to 100%, so the density estimates they provide may indeed be a close indication of absolute abundance. Another advantage of grab surveys is that not only do they provide a large number of point estimates of sandeel density, they also provide information on the sediment characteristics of the seabed at each location sampled. Recent work, in the laboratory (Wright et al., 2000) and in the natural environment (Holland et al., 2005), has focused on identifying the sediment characteristics that define the seabed habitat preferred by sandeels. Both approaches produced similar results, indicating that sandeels preferred sediments with a high percentage of medium-to-coarse-grained sand (particle size 0.25–2 mm), and avoided sediment containing >4% silt (particle size <0.063 mm) and >20% fine sand (particle size 0.063–0.25 mm).

Here we draw on the work of Holland et al. (2005) to define four sandeel sediment preference categories. The nocturnal grab surveys analysed previously by Holland et al. (2005) provided estimates of sandeel density within each of these sandeel sediment preference categories each time the area was surveyed. We then used the hydroacoustic seabed classification system RoxAnn to derive estimates of the area of each sandeel sediment preference category within the entire 5243 km2 Wee Bankie/Marr Bank/ Berwick’s Bank study area off the Firth of Forth in southeast Scotland. Combining these strands of information produced estimates of the absolute abundance of sandeels in the study area at each period of sampling. As examples of the application of this approach, we used grab-survey data collected in October of 1998–2003 to assess the impact of the sandeel fishery closure on the abundance and biomass of the local sandeel population off the Firth of Forth. We then compared estimates of 1-group sandeel abundance determined from grab surveys carried out in March of 2000–2003 with corresponding estimates of 0-group sandeel abundance determined in the previous October to assess 0-group sandeel overwintering mortality.

**Sandeel sediment preference categories**

Holland et al. (2005) analysed 2885 grab-samples from within the study area (Figure 1) to determine sandeel preferences for particular seabed sediment types in terms of its sediment particle size composition. A full description of the methods employed and the rationale underlying their sampling scheme is provided in that paper. They defined eight particle size classes (see Table 2 of Holland et al., 2005), and performed an odds ratio analysis to identify sandeel preferences for sediment particle size. As the percentage of fine sand, coarse silt, medium silt, and fine silt (particles <0.25 mm in diameter) increased, sandeels increasingly avoided the habitat. Conversely, as the percentage of coarse sand and medium sand (particles ranging from 0.25 to <2.0 mm) increased, sandeel showed increased preference for the habitat (Figure 2 of Holland et al., 2005). We therefore merged the fine sand and three silt grades, and the two coarser sand grades, to define two particle size classes, "silt and fine sand" and "coarse sand", and examined the combined effect of these two size grades of sediment particles on the percentage of grab samples with sandeels present. Based on the results obtained, four sandeel sediment preference categories were defined (Figure 2). Having accounted for the influence of the proportion of silt and fine sand and of coarse sand on the proportion of grab-samples with sandeels present, variation in the proportion of gravel had no additional power to discriminate between samples containing sandeels and those that did not.
Sandeel density in each sandeel sediment preference category

Marine abundance data are rarely normally distributed; variance is generally large, with the data frequently strongly skewed, containing a large proportion of zeroes and a few exceptionally high abundance values (Dennis and Patil, 1988). These characteristics impose low precision on the sample mean, even when sampling effort is high (Grosslein, 1971). The few exceptionally large catches may account for a large proportion of all individuals sampled in the survey, so having a disproportionate effect on the sample mean and substantially inflating the variance. Despite such values introducing considerable uncertainty, they do reflect spatial variation in the distributions of the organisms in question, so cannot be ignored (McConnaughey and Conquest, 1992). A solution to the problem is to model the underlying abundance distribution and to use the model’s properties to derive more precise estimators of population parameters (Pennington, 1983, 1996; Smith, 1990; Lo et al., 1992; Stefánsson, 1996). The delta-distribution assumes that survey samples consist of a known proportion of zero values, and that the remaining positive non-zero values fit a lognormal distribution (Aitchison and Brown, 1957). For marine abundance data, the distribution of non-zero values is frequently approximated by a lognormal distribution (Myers and Pepin, 1990). Consequently, the delta-distribution has been applied widely, to a range of different types of marine survey abundance data (Pennington and Berrien, 1984; Sherman et al., 1984; Conquest et al., 1996).

Nocturnal grab surveys were carried out in October of 1998–2003 and in March of 2000–2004 (Figure 1). Full details regarding the survey design, sampling protocols, sample processing, and data analysis are provided by Holland et al. (2005). Variation in sandeel abundance in the grab survey data displayed all the characteristics described above; the data were strongly skewed with a large proportion of samples containing no sandeels, whereas a few samples contained exceptionally large numbers of sandeels (Tables 1 and 2). A delta-distribution was therefore applied to the grab-sample data to derive more-precise estimates of mean sandeel density in each sandeel sediment preference category during each survey, and to determine 95% confidence limits either side of these mean values. In the October surveys, 0-group and 1+ sandeels were analysed separately (Table 1), whereas in the March surveys, only 1-group sandeels were analysed (Table 2). Where six or more non-zero samples were available, goodness-of-fit to the lognormal distribution was assessed, and always there was no evidence to suggest that the lognormal distribution assumption was inappropriate (Tables 1 and 2). In several instances, particularly for the unsuitable sediment preference category, only one non-zero sample was obtained. On every occasion that this was found, the non-zero sample contained just one sandeel. Under those circumstances, the delta-distribution could not be applied, so a simple arithmetic mean density was assumed instead (Tables 1 and 2).

Area of each sandeel sediment preference category

RoxAnn (Sonarvision Ltd, Aberdeen, UK) is a remote-sensing hydroacoustic seabed classification system that interfaces with ship-based echosounding and global positioning systems. RoxAnn functions by integrating the tail of the first seabed echo to provide a measure of seabed roughness, E1.
whole of the second seabed echo to derive a measure of seabed hardness, $E_2$ (Brown et al., 2005). Three surveys were carried out in July 1999, June 2000, and June 2001 covering an area of $\sim 5200 \text{ km}^2$ immediately east of the Firth of Forth and the Tay estuary in southeast Scotland (Figure 1). Individual cruise tracks and other details regarding the hydroacoustic surveys can be found in Greenstreet et al. (2006). RoxAnn data were collected using a 38-kHz transducer connected to a Simrad EK500 echo-sounder with a pulse length of 1 ms and a beam angle of $8^\circ$.

Raw RoxAnn data obtained from each ping from the echosounder were averaged over intervals of 10–15 s. Following accepted practice (Brown et al., 2005), these raw data were screened to discard all anomalous records. All latitude and longitude positional data were converted to a Universal Transverse Mercator 30N (UTM30N) projection using the PROJECT module in the Idrisi (Clark Laboratories, USA) Geographic Information System software package. This standardizes the distance units on both east and north axes. RoxAnn $E_1$, $E_2$, and depth data were binned into 1 km$^2$ spatial units (from now on referred to as pixels). The same six east–west orientated transects were surveyed in each year (see Greenstreet et al., 2006), allowing between-year variation in the performance of the RoxAnn hardware to be examined in those pixels surveyed each year. The correlations obtained were close, indicating consistent RoxAnn performance across all three years; $r^2$ values for pairwise comparisons ranged from 0.87 to 0.92 for $E_1$, and from 0.82 to 0.86 for $E_2$. Linear regression therefore provided inter-year calibration relationships, and these were used to covert the $E_1$ and $E_2$ data collected in July 1999 and June 2001 to values equivalent to June 2000 (Table 3). In that way, the data collected in all 3 years could be combined for analysis. Average $E_1$, $E_2$, and depth values were determined for each 1 km$^2$ pixel covered by RoxAnn survey (Figure 1).

Following standard practice (e.g. Greenstreet et al., 1997b; Brown et al., 2005), $E_1$, $E_2$, and depth data recorded along the survey track were interpolated to estimate values in each non-surveyed pixel. A kriging interpolation routine (Clark, 1979; Cressie, 1991) was employed using the GRID/DATA/KRIGING function provided in the Surfer (Golden Software, USA) mapping software package. Experimental variograms were first constructed for each of the three datasets, using Surfer’s GRID/DATA/VARIOGRAMS function, to identify the most suitable kriging model and appropriate parameter values (Table 4; Greenstreet et al., 1997b). For further analysis, the interpolated grid data were imported into the Idrisi GIS software, and all pixels considered to lie outside the surveyed area, i.e. land area, sea area east of the main study area, or sea area within the study area, but too far outside the survey transects and so requiring excessive extrapolation, were blanked out using a Boolean overlay (Figure 3). As Surfer effectively uses pixel corners as grid-nodes, whereas Idrisi references each pixel’s centre point, slightly different grid geometry was required in the two software packages to ensure that the geographic referencing in each was identical.

False colour composite image (FCCI) analysis was used to assimilate the information from the three separate RoxAnn $E_1$, $E_2$, and depth datasets, to produce a single image (Greenstreet et al., 1997b). Using the COMPOSITE routine in Idrisi, each

Figure 2. Categorization of the seabed sediment into four sandeel sediment preference categories, depending on the relationship between the percentages of silt and fine sand and of coarse sand in the sediment and the proportion of samples with sandeels recorded present.

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Table 1. Delta-distribution estimators of the mean (\(\mu\)) and \(\pm 95\%\) confidence limits (\(\pm 95\%\ CL\)) around the mean estimator, number of 0-group and 1+ group sandeels sampled per grab taken from each of four sandeel sediment preference categories in October surveys carried out each year between 1998 and 2003.

<table>
<thead>
<tr>
<th>Year</th>
<th>Sediment category</th>
<th>m</th>
<th>c</th>
<th>(\pm 95%\ CL)</th>
<th>(P_{\text{delta}})</th>
<th>(w) (g)</th>
</tr>
</thead>
<tbody>
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</tr>
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The total number of grab samples (\(n\)) and the number of non-zero samples (\(m\)) collected from each sediment category in each year is indicated, along with the mean individual sandeel weight (\(\mu\)) of a sandeel of each age category in each year. Where goodness-of-fit of non-zero data to the lognormal distribution was assessed, the results are shown (\(P_{\text{delta}}\)). Italicized data indicate situations where the delta-distribution could not be applied because only one non-zero grab sample was obtained, necessitating the use of simple arithmetic mean densities and assumed zero 95% CLs (see text for detail).

Table 2. Delta-distribution estimators of the mean (\(\mu\)) and \(\pm 95\%\) confidence limits (\(\pm 95\%\ CL\)) around the mean estimator, number of 1+ group sandeels sampled per grab taken from each of four sandeel sediment preference categories in March surveys carried out each year between 2000 and 2003.

<table>
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<tr>
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<th>c</th>
<th>(\pm 95%\ CL)</th>
<th>(P_{\text{delta}})</th>
<th>(w) (g)</th>
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<td>0.0000</td>
<td>0.0000</td>
<td>0.00</td>
</tr>
</tbody>
</table>

The total number of grab samples (\(n\)) and the number of non-zero samples (\(m\)) collected from each sediment category in each year is indicated, along with the mean individual sandeel weight (\(\mu\)) of a sandeel of each age category in each year. Where goodness-of-fit of non-zero data to the lognormal distribution was assessed, the results are shown (\(P_{\text{delta}}\)). Italicized data indicate situations where the delta-distribution could not be applied because only one non-zero grab sample was obtained, necessitating the use of simple arithmetic mean densities and assumed zero 95% CLs (see text for detail).

Table 3. Calibration equations used to convert July 1999 and June 2001 E1 and E2 data to June 2000 equivalent values.

<table>
<thead>
<tr>
<th>Equation</th>
<th>(r^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(E1_{2000} = 1.1400E1_{1999} + 0.0440)</td>
<td>0.920</td>
</tr>
<tr>
<td>(E2_{2000} = 0.8616E2_{1999} + 0.1134)</td>
<td>0.870</td>
</tr>
<tr>
<td>(E2_{2000} = 1.0863E2_{1999} + 0.0163)</td>
<td>0.857</td>
</tr>
<tr>
<td>(E2_{2000} = 1.1752E2_{2001} + 0.0161)</td>
<td>0.843</td>
</tr>
</tbody>
</table>

Table 4. Variography models and parameter values used to interpolate RoxAnn E1, E2, and depth data.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model</th>
<th>Number of lags</th>
<th>Maximum lag distance</th>
<th>Nugget</th>
<th>Scale</th>
<th>Length (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1</td>
<td>Spherical</td>
<td>25</td>
<td>10 000 m</td>
<td>0.0016</td>
<td>0.024</td>
<td>7 000</td>
</tr>
<tr>
<td>E2</td>
<td>Spherical</td>
<td>25</td>
<td>10 000 m</td>
<td>0.0023</td>
<td>0.050</td>
<td>6 500</td>
</tr>
<tr>
<td>Depth</td>
<td>Spherical</td>
<td>25</td>
<td>10 000 m</td>
<td>0.0000</td>
<td>0.000</td>
<td>10 000</td>
</tr>
</tbody>
</table>

The composite colour image was then produced by combining the three individual colours (Figure 4a). The resulting FCCI was dataset was assigned to one of three colour bands: blue, green, and red. To ensure equal weighting of each dataset, and to utilize the full range of colour within each colour band, the data in each of the three sets were first stretched, so that the minimum value in each set was given a value of 1 and the maximum value assigned a new value of 255. All data values in between the minimum and maximum values were assigned an appropriate value between 1 and 255, following a simple proportional linear stretch routine. The composite colour image was then produced by combining the three individual colours (Figure 4a). The resulting FCCI was
then subjected to an unsupervised cluster analysis (Greenstreet et al., 1997b), using Idrisi’s CLUSTER routine, to produce the final seabed classification map (Figure 4b). Unsupervised cluster analysis of FCCIs identifies “natural” discontinuities in the three colour-band signatures of each pixel in the image. Pixels with similar colour-band signatures are clustered together into groups. Overlap in the general colour signatures of each cluster of pixels, if not entirely eliminated, is reduced in this way to a negligible level. The proportion of grab-samples assigned to each sandeel sediment preference category collected from each of the RoxAnn seabed classes was determined. Knowing the area of each RoxAnn seabed class (using the AREA function in Idrisi), these proportions were then used to estimate the actual area of each sandeel sediment preference category in each RoxAnn seabed class (Table 5). Summing across all RoxAnn seabed classes provided estimates of the total area of each sandeel sediment preference category in the whole study area (Table 5).

For this FCCI and unsupervised cluster analysis, we used depth as the third variable, along with RoxAnn E1 and E2 data. However, rather than being a characteristic of the seabed, depth is more a measure of the height of the overlying water column. Depth may be a factor determining where sandeels choose to settle, but sandeels are known also to occupy areas at depths greater than those found within our study area (Wright et al., 1998). Sandeels tend to occupy areas on the sloping edges of sandbanks (i.e. gradients ≠ 0). Maintenance of oxygen concentration in the sediment interstitial water is also important (Quinn and Schneider, 1991), and sandeels prefer well-flushed sediments (Macer, 1966; Meyer et al., 1979; Pinto et al., 1984; Wright et al., 2000). Slopes facing into the current might be expected to have the highest flushing rates. To focus our analyses on characteristics of the seabed, rather than of the overlying water column, that might influence buried sandeel density, the depth image was further analysed using the Idrisi function SURFACE ANALYSIS/TOPOGRAPHIC VARIABLES, to produce alternatives to depth that could be used as the third dataset in the FCCI analysis. Three images were derived: a slope image, the differences in depth between individual pixels; an aspect image, the angular

Figure 3. Maps of RoxAnn E1, E2, and depth showing estimated values for each 1 km² pixel following a kriging interpolation of the data recorded along the survey track. Blacked-out areas indicate pixels considered to lie outside the surveyed area.
bearing of the slope; and a barrier image, the extent to which the combination of the slope and its aspect presented a barrier to a mean tidal current along a $350^\circ/170^\circ$ axis. Two further FCCIs were derived, one with slope and the other with barrier assigned to the red band, and both with RoxAnn E1 and E2 assigned to the blue and green bands, respectively. Unsupervised cluster analysis was then applied to derive two alternative seabed classification maps, but these varied little from the original map shown in Figure 4b derived using just the basic depth data for the red band. Consequently, choice of the third variable assigned to the red band in the FCCI analysis had little effect on final estimates of the total area of each sandeel sediment preference category in the study area (Table 5).

“Local” sandeel abundance in the whole study area

The total number of each age class ($g$) of sandeels in the study area in each year ($Y$) can now be determined. The delta-distribution estimators of the mean sandeel catch per grab sample ($c_{P,g,Y}$; Tables 1 and 2) in each of the four sandeel sediment preference categories ($P$) were standardized to densities per square kilometre. The area sampled by a grab is $0.0961 \times 10^{-6}$ km$^2$. Multiplying these density estimates by the area of each sandeel sediment preference category ($A_P$) in the study area (Table 5), then summing across all four sandeel sediment preference categories, provided the required study-area abundance estimates ($N_{g,Y}$):

$$N_{g,Y} = \sum_{P=1}^{P=4} 10^6 c_{P,g,Y} A_P / 0.0961.$$

The 95% confidence intervals around these abundance estimates could be derived by first adding and then subtracting the appropriate confidence limit values (Tables 1 and 2) from the mean density estimates (Pennington, 1983, 1996; Pennington and Berrien, 1984).

Patterns of annual variation in the estimated October 0-group and 1+ sandeel between 1998 and 2003 were almost identical regardless of whether the depth, slope, or barrier images were used as the red band in the FCCI analysis (Figure 5). The 0-group sandeel production was particularly good in 1999 and 2000, and particularly poor in 1998 and 2001. The abundance of 1+ sandeels was low in 1998 and 1999, the last 2 years that the sandeel fishery in the area was open (Greenstreet et al., 2006). In fact, fishing activity in the area was comparatively low in 1999, but 1+ sandeel abundance was low because of removals by the fishery in 1998 and failure of the stock to recover as a consequence of the poor recruitment in 1998. Following the two high recruitment-production years, 1+ sandeel abundance recovered to high levels in 2000 and 2001, the first 2 years of the sandeel fishing moratorium. However, relatively poor recruitment production thereafter resulted in a steady decline in 1+ sandeel abundance through 2002 and 2003. These estimates suggest that, even when fishing mortality was low (a low-level scientific fishery has been maintained throughout the period of the sandeel fishery closure), maintenance of sandeel population size in the area depended on relatively high levels of recruitment. Converting the abundance trends to trends in biomass (Figure 5), by multiplying the abundance data by sandeel individual mean weights for each year and age class (Table 1), allowed the October grab-survey biomass trends to be compared with modelled early summer
biomass, based on a combination of acoustic and bottom trawl surveys carried out in the same study area between late May and early July each year (Greenstreet et al., 2006). Our estimates of 1+ sandeel biomass presented here are approximately half, and our estimates of 0-group sandeel biomass approximately double, those given in the previous study.

Sandeels aged 1 in March belong to the same cohort as 0-group sandeels carried out in March of 2000–2004 therefore provided estimates giving rise to greater mortality rates (Figure 6a). Much of the residual variation could be explained further by variation in average water temperature at the seabed in the areas utilized by sandeels buried in the sediment (Figure 6b), with higher water temperatures over winter tending to elevate overwintering 0-group sandeel mortality rates. Choice of variable assigned to the red band in the FCCI analysis had little impact on these results (Table 6).

### Discussion

Assessing the abundance of organisms is perhaps the most critical aspect of any study of ecological processes. In studies of predator–prey interactions, knowledge of predator abundance is essential if total prey losses through predation are to be assessed (Hislop et al., 1991; Mills and Shenk, 1992; Wanless et al., 1998; Daunt et al., 2008). Likewise, without knowing the abundance of prey organisms, these predation losses cannot be converted to prey mortality rates (Sterner, 1986; Greenstreet et al., 1997a; Hebblewhite, 2005). Such interactions are summarized, for example, by the classical Lotka–Volterra type differential equations for interacting predator

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**Table 5.** Number of grab samples collected from each of the RoxAnn seabed classes identified by unsupervised cluster analysis of FCCIs derived assigning RoxAnn E1 and E2 data to the blue and green bands, respectively, and either depth, slope, or barrier to the red band.

<table>
<thead>
<tr>
<th>Red band</th>
<th>RoxAnn class</th>
<th>Number of grabs</th>
<th>Proportion of grabs</th>
<th>Area (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td></td>
<td>Prime Subprime</td>
<td>Suitable Unsuitable</td>
<td>Cluster area (km)</td>
</tr>
<tr>
<td>1</td>
<td>941</td>
<td>0.0988 0.1977</td>
<td>0.3337 0.3698</td>
<td>2326</td>
</tr>
<tr>
<td>2</td>
<td>1728</td>
<td>0.2471 0.2471</td>
<td>0.3228 0.1730</td>
<td>1077</td>
</tr>
<tr>
<td>3</td>
<td>29</td>
<td>0.0000 0.0000</td>
<td>0.0000 1.0000</td>
<td>751</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>0.0000 0.0000</td>
<td>0.0000 1.0000</td>
<td>342</td>
</tr>
<tr>
<td>5</td>
<td>56</td>
<td>0.7500 0.0179</td>
<td>0.0536 0.1786</td>
<td>271</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>– – – –</td>
<td>– – 104</td>
<td>0.0</td>
</tr>
<tr>
<td>7</td>
<td>122</td>
<td>0.1967 0.3033</td>
<td>0.3361 0.1639</td>
<td>113</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>– – – –</td>
<td>– – 104</td>
<td>0.0</td>
</tr>
<tr>
<td>9</td>
<td>1</td>
<td>0.0000 0.0000</td>
<td>0.0000 1.0000</td>
<td>87</td>
</tr>
<tr>
<td>Total</td>
<td>2885</td>
<td>721.5 765.0</td>
<td>1187.0 2569.5</td>
<td></td>
</tr>
</tbody>
</table>

| Slope    |              | Prime Subprime  | Suitable Unsuitable| Cluster area (km) |
| 1        | 15           | 0.0000 0.0000   | 0.0000 1.0000      | 608      |
| 2        | 1870         | 0.2235 0.2187   | 0.3460 0.2118      | 2257     |
| 3        | 256          | 0.1406 0.0898   | 0.2344 0.5352      | 1140     |
| 4        | 426          | 0.2019 0.2864   | 0.3310 0.1808      | 466      |
| 5        | 36           | 0.1944 0.3889   | 0.1111 0.3056      | 291      |
| 6        | 282          | 0.1383 0.2943   | 0.2872 0.2801      | 274      |
| 7        | 0            | – – – –         | – – 207            | 0.0      |
| Total    | 2885         | 853.4 923.3     | 1313.4 2530.4      |          |

| Barrier   |              | Prime Subprime  | Suitable Unsuitable| Cluster area (km) |
| 1        | 19           | 0.0000 0.0000   | 0.0000 1.0000      | 687      |
| 2        | 1567         | 0.1768 0.1966   | 0.3644 0.2623      | 2252     |
| 3        | 123          | 0.0894 0.1301   | 0.1463 0.6341      | 851      |
| 4        | 452          | 0.1858 0.2544   | 0.3296 0.2301      | 435      |
| 5        | 474          | 0.2975 0.3017   | 0.2827 0.1181      | 307      |
| 6        | 244          | 0.2992 0.2828   | 0.2500 0.1680      | 300      |
| 7        | 6            | 0.0000 0.0000   | 0.0000 1.0000      | 245      |
| 8        | 0            | – – – –         | – – 166            | 0.0      |
| Total    | 2885         | 736.1 841.5     | 1250.3 2415.2      |          |

The proportion of grab-samples assigned to each of four sandeel sediment preference categories within each RoxAnn seabed class is indicated along with the total area of each RoxAnn seabed class. These data are used to estimate the total area of each sandeel sediment preference category in each RoxAnn seabed class and, by summing across RoxAnn seabed classes, in the whole study area (emboldened font). Given the rationale underlying the original sampling design (Holland et al., 2005), unsampled RoxAnn seabed classes are assumed to consist entirely of unsuitable sediment category (italicized font).
and prey species (May, 1976). Quantitative analysis of trophodynamic rates in foodwebs simply expands this process to include all species in the assemblage with significant predator–prey interactions (Pimm, 1982; Bax, 1991; DeAngelis, 1992; Greenstreet et al., 1997a; Blanchard et al., 2002; Araujo et al., 2005). For this form of foodweb modelling, estimates of the absolute abundance of all included species are required. However, most surveys of marine fish taxa only provide indices of relative abundance. They do not provide estimates of absolute abundance because the efficiency of the survey gear used is almost always less than one; survey gears (trawls, dredges, etc.) only catch a proportion of the fish present in the path of the gear (Harley and Myers, 2001; Fraser et al., 2007). Trawl efficiency varies between species and between different sized individuals of the same species (Fraser et al., 2007). Moreover, gear efficiency can also vary with time of day, season, and depth (Michalsen et al., 1996; Casey and Myers, 1998; Harley and Myers, 2001; Benoit and Swain, 2003). The relative abundance indices provided by groundfish surveys are therefore not directly comparable, presenting problems with using such data to parameterize foodweb models.

Figure 5. Variation in the abundance and biomass of 0-group and 1+ sandeels estimated to be present in the study area in October each year between 1998 and 2003. Three trend lines are shown in each plot (with jitter of 0.25 years introduced to separate them), showing estimates derived from three seabed classification maps depending on which variable was assigned to the red band in the FCCI analysis (see text and Table 5). Error bars show the 95% confidence intervals.

Table 6. Estimates of 0-group sandeel overwinter mortality rate ($M$) derived by applying the mortality rate equation (see text) to the numbers of 0-group sandeels present in October ($N_t$) and the numbers of 1-group sandeels present in March ($N_{t+D}$) each winter, where $D$ is the period in days between the two surveys.

<table>
<thead>
<tr>
<th>Red band</th>
<th>Winter</th>
<th>$N_t \times 10^6$</th>
<th>$N_{t+D} \times 10^6$</th>
<th>$N$ dying $\times 10^6$</th>
<th>$D$ (d)</th>
<th>Daily $M$</th>
<th>Annual $M$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td>1999/2000</td>
<td>116.175</td>
<td>37.141</td>
<td>79.033</td>
<td>161</td>
<td>0.00708</td>
<td>2.592</td>
</tr>
<tr>
<td></td>
<td>2000/2001</td>
<td>104.424</td>
<td>54.470</td>
<td>46.954</td>
<td>136</td>
<td>0.00457</td>
<td>1.668</td>
</tr>
<tr>
<td></td>
<td>2001/2002</td>
<td>14.023</td>
<td>13.316</td>
<td>0.707</td>
<td>164</td>
<td>0.00321</td>
<td>0.115</td>
</tr>
<tr>
<td>Slope</td>
<td>1999/2000</td>
<td>136.758</td>
<td>43.809</td>
<td>92.949</td>
<td>161</td>
<td>0.00707</td>
<td>2.588</td>
</tr>
<tr>
<td></td>
<td>2000/2001</td>
<td>119.821</td>
<td>63.558</td>
<td>56.263</td>
<td>136</td>
<td>0.00466</td>
<td>1.702</td>
</tr>
<tr>
<td></td>
<td>2001/2002</td>
<td>16.640</td>
<td>15.796</td>
<td>0.844</td>
<td>164</td>
<td>0.00322</td>
<td>0.116</td>
</tr>
<tr>
<td></td>
<td>2002/2003</td>
<td>46.678</td>
<td>14.765</td>
<td>31.913</td>
<td>178</td>
<td>0.00647</td>
<td>2.360</td>
</tr>
<tr>
<td>Barrier</td>
<td>1999/2000</td>
<td>120.338</td>
<td>38.435</td>
<td>81.903</td>
<td>161</td>
<td>0.00709</td>
<td>2.595</td>
</tr>
<tr>
<td></td>
<td>2000/2001</td>
<td>105.000</td>
<td>57.217</td>
<td>47.783</td>
<td>136</td>
<td>0.00446</td>
<td>1.629</td>
</tr>
<tr>
<td></td>
<td>2001/2002</td>
<td>14.539</td>
<td>13.812</td>
<td>0.727</td>
<td>164</td>
<td>0.00311</td>
<td>0.114</td>
</tr>
<tr>
<td></td>
<td>2002/2003</td>
<td>40.749</td>
<td>12.902</td>
<td>27.846</td>
<td>178</td>
<td>0.00646</td>
<td>2.358</td>
</tr>
</tbody>
</table>

Mortality is expressed as both a daily and an annual rate.
Sandeels play a key role in the North Sea foodweb. Sitting in a mid-trophic position, sandeels are major predators of zooplankton and the principal prey of many top predators (Greenstreet et al., 1997a; Heath, 2005). For many top predators, surveys provide estimates of absolute population abundance. When combined with information on diet and rates of food consumption, estimates of actual daily or annual consumption of particular prey can therefore be made (Wanless et al., 1998; Brown et al., 2001; Daunt et al., 2008). However, without corresponding estimates of the absolute abundance of sandeels, it is difficult to put such predation losses into context; to assess whether, when, and where sandeel availability might start to limit predator populations or to determine when, if at all, such predation mortality might actually influence sandeel population dynamics. Such information is critical if foodweb models are ever to fulfil their potential in the provision of scientific advice in support of management, for example, in the management of the industrial fisheries for sandeels.

The Wee Bankie/Mart Bank/Berwick’s Bank complex of sandbanks supported a significant sandeel fishery up to 2000, when the entire coastal area off southeast Scotland was closed to sandeel fishing (Greenstreet et al., 2006). Colonies in the Firth of Forth support internationally important numbers of seabirds, several of which depend on sandeels as their main prey during the breeding season (Wanless et al., 1998; Rindorf et al., 2000; Daunt et al., 2008). Because of the high potential for competition between marine top predators and the fishery, considerable effort has been expended in assessing the demands made on this resource by each competitor (Wanless et al., 1998; Greenstreet, 2006; Daunt et al., 2008), but to determine the extent to which the sandeel resource is limiting also requires information on the local abundance of sandeels. Efforts to address this issue have, until now, focused on modelling the effect of the timing and extent of the spring plankton bloom on sandeel emergence behaviour, then using the model to interpret data from acoustic and demersal trawl surveys to derive estimates of absolute population abundance in June each year (Greenstreet et al., 2006). This approach depends, however, on the assumption that acoustic surveys provide reliable estimates of the absolute abundance of sandeels in the water column, and this in turn depends on the sandeel acoustic TS assumed in the analysis of acoustic data.

Because of the way that a grab captures sandeels buried in the sediment, particularly at night when visual warning of the descending grab is diminished, we consider the density estimates obtained from grab surveys to be much closer to estimates of absolute density than those obtained using any other survey method. Our estimates of 1+ sandeels from the grab surveys suggest that the Greenstreet et al. (2006) acoustic/demersal trawl/modelling approach may have overestimated sandeel biomass by a factor of 2. However, this is within the range anticipated given the level of uncertainty surrounding estimates of sandeel acoustic TS (Armstrong, 1986). Had Greenstreet et al. (2006) used a TS at the higher end of the range observed experimentally, their estimates of total biomass would have halved, almost exactly in line with the biomass estimates derived here from the October grab surveys. Of course, in making this comparison, we are ignoring the possibility that mortality may have reduced 1+ sandeel abundance between the June and October surveys.

In contrast, the relative trend in our October grab-survey estimates of 0-group sandeel biomass bore less resemblance to relative variation in total modelled 0-group biomass in June based on the acoustic and bottom trawl surveys. However, the October grab 0-group biomass estimates more closely resembled the relative variation in the biomass of 0-group sandeels already buried in the sediment by the time of the acoustic and bottom trawl surveys. Greenstreet et al. (2006) speculated that 0-group sandeels still needing to feed actively in the water column later in the season would be likely to experience considerable natural mortality. Our analyses appear to confirm this possibility. It would seem that sandeels still active in the water column in late June, or later, may contribute little to the biomass present in the study area in October. October grab 0-group sandeel biomass estimates were approximately three times higher than the June/July estimates obtained by applying the emergence behaviour model to the acoustic and bottom trawl survey data. Again, this discrepancy can be explained by uncertainty regarding actual 0-group sandeel acoustic TS. TS is generally inversely proportional to fish length; smaller fish have

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**Figure 6.** (a) Density-dependence effect (the effect of 0-group sandeel population abundance in October, $N_0$) on overwintering 0-group sandeel mortality rate ($M$), (b) Relationship between average water temperature ($T$) at the seabed in areas where seabed sediment was likely to be occupied by sandeels, and residuals from the fitted relationship in (a).
higher TS because their greater surface-to-volume ratio provides more reflection of sound per unit biomass (MacLennan and Simmonds, 1991). A 0-group sandeel TS of approximately –46 dB kg⁻¹ would be sufficient to explain the difference between the biomass estimates derived from the acoustic/bottom trawl and grab surveys.

In using grab surveys to assess local sandeel population abundance, two factors are critical. First, reliable estimates of the area of the different types of sediment used by sandeels are necessary; second, reliable estimators of the mean density of sandeels in each sediment type are required. Using the analyses of Holland et al. (2005) as a starting point, we identified four categories of seabed sediment depending on the proportions of coarse sand and of fine sand and silt present in the sediment. We then scored these in respect of their value to sandeels: in rank order prime sediment, sub-prime sediment, suitable sediment, and unsuitable sediment. Our principal tasks therefore were to determine the total area of each sandeel sediment preference category present in the study area, and then to estimate the mean density of sandeels in each sandeel sediment preference category in each year. To address the former task, we used unsupervised cluster analysis of the FCCIs to produce seabed classification maps, whereas in many habitat-mapping exercises, supervised cluster analysis has probably been used more frequently (Magorrian et al., 1995; Donnan and Davies, 1996; Davies et al., 1997; Sotheran et al., 1997; Foster-Smith and Sotheran 2003; Foster-Smith et al., 2004; Brown et al., 2005).

The supervised cluster analysis approach utilizes ground-truth samples early on in the analysis to identify a priori a particular suite of habitat types; for example, rock, mud, and sand, or in our case, prime, subprime, suitable, and unsuitable sandeel sediment. Therefore, at particular locations, the sites where ground-truth samples were collected, the actual habitat type is known. Pixel values at those known sites are then examined to establish blue, green, and red band signatures associated with each habitat type. Each pixel across the whole area is then assigned to a habitat category according to which signature its three band values most resemble. This approach has the advantage of producing maps with specific habitat classifications; in other words, the maps show areas of rock, mud, sand, etc., or prime, subprime, suitable, and unsuitable sandeel sediment. Initially, this might appear to fulfil our requirements exactly, but because the signatures associated with each habitat type often overlapped considerably, and because of spatial scale mismatches (at 60 m, each acoustic ping ensonifies an area of ~350 m², compared with a Day grab sample which identifies the habitat type in 0.1 m² of seabed), error rates in assigning individual pixels to particular habitat types may be as high as 70–80% (Brown et al., 2005; SPRG, pers. obs.). In the absence of additional ground-truth sampling, it is often not possible even to assess the extent of such error. Essentially, regions classified as prime, subprime, or suitable sandeel sediment would also contain areas of unsuitable sediment, and vice versa. With no way to assess the extent of such errors, the actual area of each of the sandeel sediment preference categories, the information needed to convert estimates of sandeel density to estimates of local abundance, would remain unknown, rendering the maps produced unusable as a basis for grab-survey-based sandeel abundance assessments.

Unsupervised cluster analysis, although less common, has been used in several instances as the basis for seabed habitat classification (Greenstreet et al., 1997b; Sotheran et al., 1997; Pinn et al., 1998). Unsupervised cluster analysis makes no use of ground-truth samples during the analytical process. Instead, once the seabed classification has been done, ground-truth samples are referred to so as to determine, in a probabilistic way, what each seabed class actually consists of. Therefore, in our case, if each ground-truth sample can be assigned to a particular sediment category, e.g., our four sandeel sediment preference categories, then for each of the mapped seabed classes, the probability that any single grab sample might hit a particular sandeel sediment preference category can be determined. Unlike the supervised cluster analysis approach, which attempts to assign a specific sediment category to each mapped seabed class, the unsupervised cluster analysis method provides an estimate of the proportional sediment category composition within each mapped seabed class. This is equivalent to estimating the proportion of the area within each mapped seabed class that consists of a particular category of seabed sediment, e.g., prime, subprime, suitable, and unsuitable sediment for sandeels. As such, this provides precisely the information necessary to convert estimates of sandeel density obtained from grab-surveys to estimates of local population abundance. However, the disadvantage of the approach is that the seabed classification maps produced do not represent the exact spatial distributions of the sediment categories of interest.

Our overall estimates of local sandeel population abundance were relatively unaffected by the choice of variable assigned to the colour band in the FCCI analyses. Essentially, all three maps produced quite similar estimates of the total area of each of the sandeel sediment preference categories.

We applied the delta-distribution model to grab-sample sandeel abundance data to derive estimators of mean density. The difficulties involved in analysing marine abundance data and the need for such an approach have been discussed widely in the scientific literature, and we have already touched on the subject above. However, use of the delta-distribution in this way is not universally approved. Syrjala (2000) in particular noted that the delta-distribution estimator of the mean was “not robust to seemingly small departures from the assumed delta-distribution”. We examined goodness-of-fit to the lognormal distribution in 36 instances where six or more non-zero abundance samples were obtained and no significant departures from a lognormal distribution were observed. However, the question posed by Syrjala’s (2000) analysis is whether the test was sufficiently powerful to detect actual departures from the expected distribution, particularly in those instances where the number of samples available was small. To examine this possibility, we fitted a Poisson distribution to the non-zero October 0-group sandeel abundance data collected from prime and subprime samples in each year, and in 5 of the 12 tests demonstrated a significant departure from the expected distribution. In 11 of the 12 tests, the lognormal distribution provided the better fit to the data (higher p-values: lognormal p = 0.441 ± s.e. 0.059; Poisson p = 0.135 ± s.e. 0.043). In circumstances where goodness-of-fit tests fail to detect real departures of the distribution of non-zero abundance data from the assumed lognormal distribution, positively biased estimates of mean density tend to result (Syrjala, 2000). In respect of 1+ sandeels, where because of their lower densities (compared with 0-group sandeels) such problems are likely to be most acute, we have shown that alternative methods for estimating the absolute abundance of sandeels in our study area produce biomass estimates that are higher than those derived from grab surveys. Therefore, even if our grab-survey estimates of population abundance are positively biased, alternative approaches may be worse.
The trends in sandeel abundance in the Wee Bankie/Marr Bank/Berwick’s Bank study area off the Scottish southeast coast revealed by October grab surveys closely resembled those obtained from combined acoustic and bottom trawl surveys carried out in June. The conclusions to be drawn regarding the effectiveness of the closure of the sandeel fishery off southeast Scotland are therefore essentially the same as those drawn in the previous study (Greenstreet et al., 2006). The closure resulted in an immediate recovery of the local sandeel population attributable mainly to a reduction in fishing mortality and high recruitment in the year before the moratorium, followed by a second year of high recruitment in the first year of the closure. However, the sandeel stock in the area subsequently steadily declined. In the absence of adequate recruitment, simply reducing fishing mortality was insufficient to maintain local sandeel abundance. The sandeel population off the Scottish southeast coast appears, therefore, to be heavily dependent on recruitment.

We have demonstrated how appropriately scheduled grab surveys might be used to examine overwintering mortality in sandeels. The data we present here suggest that both initial high 0-group density at the start of winter and warmer water temperature at the seabed have an adverse effect on 0-group overwinter survival. High densities of sandeels in the sediment may lead to reductions in oxygen concentration, with potentially lethal effects (Behrens and Steffensen, 2007; Behrens et al., 2007). Sandeels have to survive winter on the energy reserves laid down in spring and early summer. Warmer water would elevate their metabolic rates, causing their energy reserves to be used up faster and potentially exhausting them before they have an opportunity to feed again (Schurmann and Steffensen, 1997; Clarke and Johnston, 1999). Both effects are therefore plausible, but we have too few years of data to comment on this with certainty.

Grab surveys combined with hydroacoustic survey techniques potentially offer a relatively cheap method of assessing local sandeel population abundance. Similar approaches have been adopted to assess the abundance of other marine organisms that have a particularly intimate association with the seabed and exhibit strong preferences for specific sediment habitats (Moore et al., 2009; Smith et al., 2009; Tremblay et al., 2009). Each of the grab surveys analysed in this study required approximately half the research vessel time needed to complete a combined acoustic and bottom trawl survey (e.g. Greenstreet et al., 2006). However, grab surveys depend on the availability of adequate seabed classification maps that allow estimates of density to be converted to estimates of abundance. Such maps could be developed over the course of several of the grab surveys themselves. However, in an ideal situation, it is extremely beneficial if they are available before starting serious abundance survey work on sandeels, so that they can be used to aid the design of efficient stratified sampling schemes. The grab-survey design we used was informed by earlier seabed classification work carried out by the Danish RV “Dana” (Holland et al., 2005). The production of such maps before the commencement of grab-survey work can itself represent a substantial additional investment of RV time, although hydroacoustic seabed classification mapping could also be carried out while the vessel is involved in other activities (Mackinson et al., 2004), as we have demonstrated here. Furthermore, considering the problems involved in generating reliable estimators of mean density, it is questionable whether survey effort in the grab surveys reported here was adequate. Additional sampling might, for example, have increased the power of goodness-of-fit tests to assess the fit of non-zero data to the lognormal distribution. However, with the benefit of hindsight, additional samples could also have been collected simply by altering the survey design, without necessarily increasing the amount of RV time required.

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