



Summer abundance and group size of
harbour porpoise, *Phocoena phocoena*, in
the outer southern Moray Firth

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Abstract

Information on harbour porpoise, *Phocoena phocoena*, populations in the Moray Firth, in the northwest North Sea remains fairly limited to date. Long-term studies on *Phocoena phocoena* populations are likewise relatively sparse, with most studies focusing on shorter time frames. This study presents the observations of *Phocoena phocoena* in the Moray Firth from dedicated cetacean surveys undertaken from 2001 to 2014, during May to October inclusive. Yearly and seasonal trends in both abundance and group size were subsequently analysed and compared with other populations of *Phocoena phocoena*. 25661 kilometres of sampling effort was undertaken in sea states of one or less, during which 699 sightings and 2149 individuals were observed. Relative abundance, or individuals observed per kilometre of sampling effort, showed a peak during 2002 and 2003, before declining over the latter part of the study period. Both relative abundance and group size showed general increase over the course of the summer season. Unlike relative abundance group size did not decline over the course of the study but instead showed peaks during certain periods of the study. Observed trends in abundance and group size possibly represent distributional shifts observed in the North Sea and are likely caused by shifting prey stocks. The findings of the survey highlights the importance of long term surveys of *Phocoena phocoena* and provides important information on how this species has utilised this area of the North Sea over the last 14 years.

Introduction

The harbour porpoise, *Phocoena phocoena*, is the smallest cetacean in European waters (Reid *et al.*, 2003; MacLeod *et al.*, 2007) and the most abundant cetacean species in the UK (Walton, 1997; Pierpoint, 2001). Occupying a slightly lower trophic position than most other sympatric marine mammals, its diet largely consists of zooplanktivorous fish (Das *et al.*, 2003). As such it is recognised as a significant predator (Weijs *et al.*, 2009) and their long life span means that they are important indicators of ecosystem health (Covaci *et al.*, 2002; Weir *et al.*, 2007; Weijs *et al.*, 2009). Although listed as of “least concern” by the International Union for the Conservation of Nature (IUCN) (Hammond *et al.*, 2008), North Sea populations of *P. phocoena* face numerous threats to local distributions including incidental by-catch (Tregenza *et al.*, 1997; Vinther & Larsen, 2004), prey depletion (MacLeod *et al.*, 2007), pollution (Covaci *et al.*, 2002; Weijs *et al.*, 2009) and other anthropogenic effects such as noise pollution (Brandt *et al.*, 2011).

The Moray Firth is rich coastal ecosystem both in terms of its productivity and biodiversity (Robinson *et al.*, 2007). As part of the northwest North Sea (57°41'N, 2°00'W) this large embayment represents an important area for cetaceans, both in the UK and Europe (Wilson *et al.*, 1997; Robinson *et al.*, 2007, 2009; Cheney *et al.*, 2012). A total of 28 different cetacean species have been observed in the Moray Firth over the past 25 years, although the harbour porpoise *P. phocoena*, Atlantic bottlenose dolphin *Tursiops truncatus* and Minke whale *Balaenoptera acutorostrata* are the three most commonly observed species (Robinson *et al.*, 2007). Despite being observed as the most abundant of these three species in the Moray Firth, *P. phocoena* has received relatively little attention here (Robinson *et al.*, 2007), especially compared to resident *T. truncatus* populations (Wilson *et al.*, 1997, 1999; Hastie *et al.*, 2004; Bailey & Thompson, 2006; Cheney *et al.*, 2012).

Robinson *et al.* (2007) found there was significant variation in the mean summer abundance of *P. phocoena* in the Moray Firth from the years 2001 to 2005, with a peak during 2003. Other research using model-based density surfaces predict a shift in the summer distribution of *P. phocoena* away from the northwest North Sea from

1994 to 2005 (Hammond *et al.*, 2013) resulting in a possible decrease in abundance in this area. Robinson *et al.* (2007) also found abundance to be higher later in the summer season (Robinson pers. com), a finding supported by other studies conducted in other areas of the North Sea (Thompson *et al.*, 2004; Weir *et al.*, 2007). Group size of *P. phocoena* shows some variation between different areas of the North Sea, although most estimates of mean group size fall between approximately between 1-2.2 individuals (Heide-Jorgensen *et al.*, 1993; Hammond *et al.*, 2002, 2013; Weir *et al.*, 2007; Sveegaard *et al.*, 2011; Haelters *et al.*, 2015).

Building on the data gathered by Robinson *et al.* (2007), this study presents the summer occurrences of *P. phocoena* in the outer southern Moray-Firth during 14 years' worth of boat based surveys on cetaceans in the area, with the aim of establishing how the relative abundance and group size of *P. phocoena* varies over this period. Both yearly and monthly trends are examined, allowing two primary predictions to be investigated; firstly relative abundance and mean group size should decrease over the 14-year period. Secondly relative abundance and mean group size should increase over the course of the summer season. Although this study does not include estimates of absolute abundance, long term studies of relative abundance still give important indications of population size (Weir *et al.*, 2007). It has been hypothesised that depletion of prey stocks, namely sandeels (*Ammodytes spp.*) could affect *P. phocoena* distribution in the northwest North Sea. As such investigating long-term population trends in areas such as the Moray Firth could give important indications about the status of local populations and how best to protect all European populations of *P. phocoena*.

Materials and methods

The study area

Measuring approximately 5,230 km² (Robinson *et al.*, 2007), the Moray Firth is a highly variable embayment on the northeast coast of Scotland (figure 1) and is defined as the area of sea from Duncunby head in the north to Fraserburgh in the east and to Inverness in the west (Robinson *et al.*, 2007) (figure 1). It is recognised as an

important part of the northwest North Sea and shares the same large scale environmental determinants (Wright *et al.*, 1998). It is categorised into two main areas, the inner Moray Firth and the outer Moray Firth. The inner Moray Firth is defined as the area to the west of Helmsdale and Lossiemouth (figure 1), whereas the sea to the east is the outer Moray Firth (figure 1).

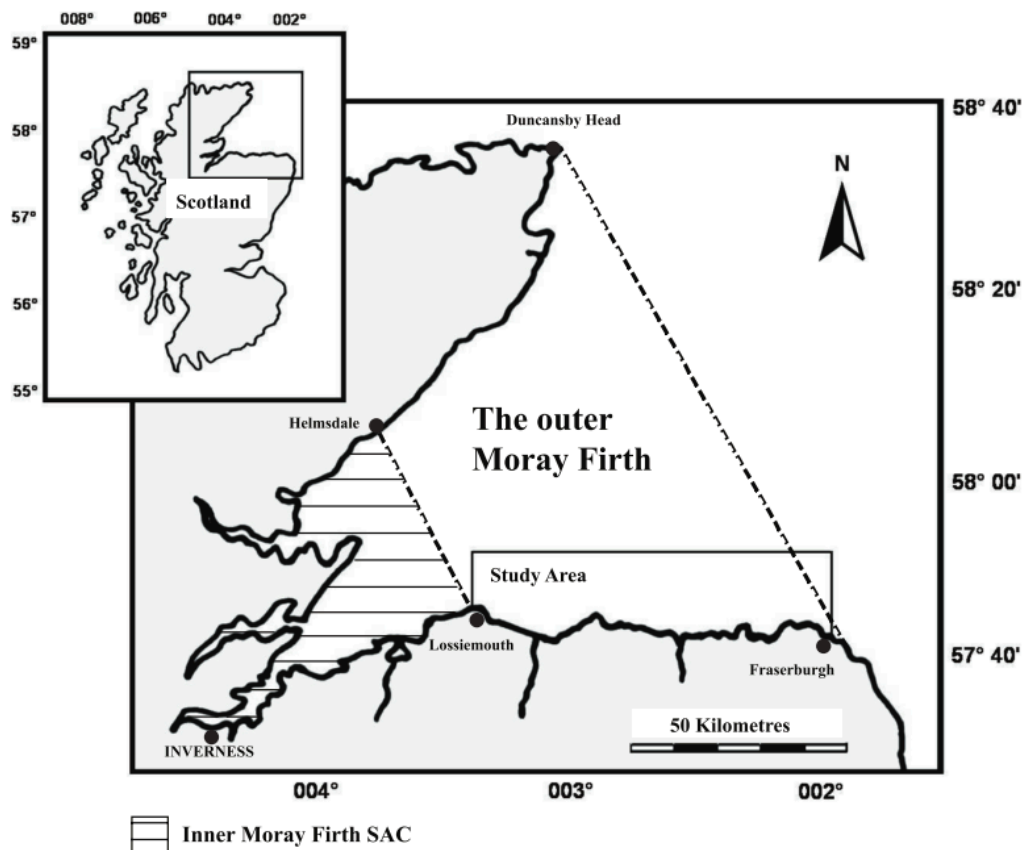


Figure 1 (from Robinson *et al.*, 2007). The Moray Firth, its location in Scotland and the different areas within it. The box marked study area denotes the area surveyed during this current study. The line-shaded area is the inner Moray Firth and is a special area of conservation (“Moray Firth Special Area of Conservation: Advice under Regulation 32 (2),” 2015).

The characteristics of these two areas differ greatly from one another. The inner Moray Firth is much shallower with the seabed sloping from the shore to about 50 m approximately 15 km out to sea. Twelve major rivers discharge in the Moray Firth and ten of these flow into the inner firth. This results in a comparatively lower salinity compared to the outer Moray Firth (Holmes *et al.*, 2004) which is more similar to the

North Sea. The seabed of the outer Moray Firth is somewhat more variable than inner firth, with a number of deeper areas such as the Southern Trench in the southwest (Holmes *et al.*, 2004). A large circulatory current, known as the Dooley current, circulates in a clockwise direction within the firth and brings in cooler mixed water from the north, causing strong horizontal gradients in surface or bottom temperatures (Reid *et al.*, 2003). The inner Moray Firth is a Special Area of Conservation (SAC), although the outer Moray Firth is under no such protection (Scottish Natural Heritage, 2015).

Data Collection

All the data for the current study was collected along an 83 km stretch of the southern coastline of the outer Moray Firth (figure 1) between the months of May and October, from 2001 to 2014. Data was collected using systematic observation inner coastal transects, transects parallel to the coast both as described by Robinson *et al.* (2007) or offshore “horseshoe” transects described by Hodgson (2014) (figure 2). This was carried out with two dedicated 5.4 m rigid inflatable boats (RIBs) equipped with Raymarine GPS/Sonar units and whilst searching the boats travelled at a constant speed between 10 – 18 km/h (7-10 knots). Each boat would have two experienced observers and up to 5 trained observers who used a continuous scanning method (Mann, 1999) to spot any cetaceans. 7x50 mm binoculars were also used to aid in long distance spotting. Once a sighting was made the boat was slowed (or circled back if required) to allow for species identification.

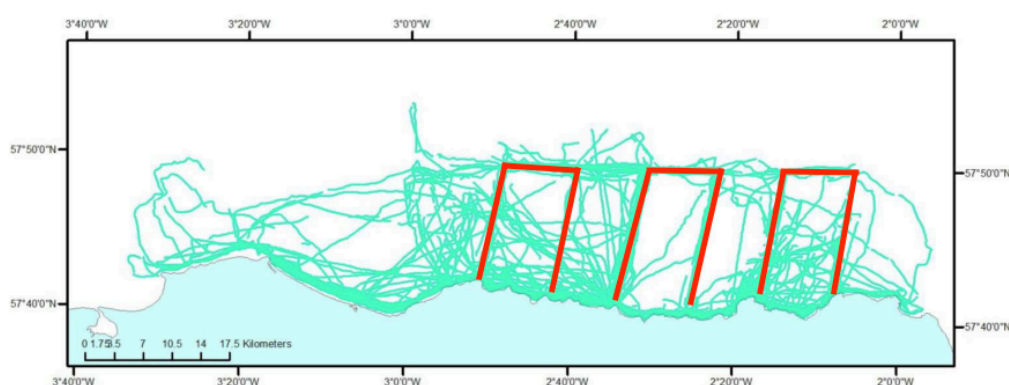


Figure 2 (from Hodgson, 2014; edited for the purposes of the current study). Green lines indicated sampling effort undertaken during surveying for Minke whale, *Balaenoptera acutorostrata*. Red lines indicate examples of “horseshoe” transects.

Due to the susceptibility of this method to adverse weather conditions, search efforts were either suspended or aborted should the sea state become greater 3 on the Beaufort scale or visibility drop to less than 1.5 km (Robinson *et al.*, 2007; Robinson, pers. com.) . Throughout the course of a survey the date, time, latitude, longitude, sea state, swell height and visibility were recorded. If *P. phocoena* was encountered the number of individuals was recorded along with the coordinates. A group was defined as any individuals in the immediate vicinity heading in the same direction or engaging in the same activity (Weir *et al.*, 2007) . This data was later compiled into a Microsoft excel spreadsheet.

Temperature data

Measurements of sea surface temperatures (in °C) in the study area were gathered from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Mean monthly sea surface temperature in the entire study area was calculated, which was then used in order to try and determine whether sea surface temperature was an explanatory variable for the abundance and group size of *P. phocoena*.

Data analysis

Due to the difficulty in assessing the number of porpoise in a sighting during rougher seas (Barlow, 1988; Barlow *et al.*, 1988; Palka, 1995), the data gathered from the entire study period was filtered to exclude sightings made during a sea state equal to or greater than 2 on the Beaufort scale. This was to reduce the effect of counting errors on the results and to better ensure that the observed abundances and group sizes were not over-estimates.

As with previous studies, to account for differences in sampling effort during different time periods in this study, the abundance of *P. phocoena* in a given period was divided by the amount of sampling effort for the same period (Heide-Jorgensen *et al.*, 1993; Pierpoint, 2001; Hammond *et al.*, 2002; Robinson *et al.*, 2007; Gilles *et al.*, 2009). Here the number of *P. phocoena* was divided by the number of kilometres of sampling effort for a given period, essentially the number of porpoise per kilometre. This value is henceforth referred to as the relative abundance.

Diagnostic tests revealed significantly different variances between both relative abundance and group size. Hence Kruskal-Wallis one-way analysis of variance tests were selected to test for significant differences between different pooled months and years during the survey. Relative abundance was log-transformed to allow for more effective analysis of the results, although the outcome of the diagnostics tests did not change and Kruskal-Wallis tests were still used. Linear regressions were used to analyse the relationship of temperature with log relative abundance and average group size. Log Relative abundance was then plotted as a time series to help identify patterns. To allow for decompositions of this data, missing values for winter months or months where no sampling could be undertaken were interpolated using `auto.arima` and Kalman smooth modelling within R using the `zoo` (Zeileis & Grothendieck, 2005) and `forecast` (Hyndman, 2008) packages. `Auto.arima` allowed an appropriate model to be fitted to the data, whilst Kalman smooth interpolated the missing data within the parameters of this model. This then allowed for a moving average using a 12-month span to be calculated, in order to generate a trend line. All other analysis was likewise completed in R version 3.1.2; with all graphics constructed using R base graphics (R Core Team, 2014) or the `ggplot2` package (Wickham, 2009), along with the `lattice`, `plyr` and `Rmisc` packages (Sarkar, 2008; Wickham, 2011; Hope, 2013) .

Results

Over the course of the study, 1125 sightings of *P. phocoena* were made. When filtered to exclude sampling done in a sea state above 1, 25661 km of surveying effort was undertaken (table 1), during which 2149 individual *P. phocoena* were recorded from 699 sightings (table 1). The mean group size was 3.074 and the relative abundance was 0.084 individuals per kilometre. The greatest number of group encounters within a single year was 94 in 2002 (table 1), although this was the third highest number of individuals in a year, the highest being 325 in 2013 (table 1). The greatest sampling effort was also undertaken in 2013. Conversely the lowest sampling effort was undertaken in 2001, which also had the lowest number of encounters and individuals (9 and 33 respectively). Most of the sampling during the study was undertaken in July (table 2), with the least being undertaken during May

(table 2). More encounters occurred in July than any other month (table 2), although more individuals were encountered during September (table 2). The largest group size of *P. phocoena* recorded in the the entire survey was 40 and observed in July (recorded during 2003) (table 2). In May however the largest observed group was only 7 individuals (recorded during 2001) (table 2). The least number of encounters and individuals were also recorded during May (table 2).

Table 1. The sampling effort as well as the number of *Phocoena phocoena* encounters and individuals recorded, over 14 years from 2001 to 2014 inclusive.

Year	Total sampling effort (km)	Total number of encounters	Total number of individuals	Relative Abundance (individuals km ⁻¹)
2001	541	9	33	0.061
2002	1441	94	289	0.201
2003	1166	80	318	0.273
2004	1390	40	86	0.062
2005	1024	37	71	0.069
2006	2108	90	181	0.086
2007	1498	27	74	0.049
2008	1057	42	167	0.158
2009	2606	41	107	0.041
2010	2326	51	137	0.059
2011	2101	36	96	0.046
2012	2626	62	222	0.085
2013	3964	70	325	0.082
2014	1814	20	43	0.024
All	25661	699	2149	0.084

Table 2. The sampling effort, number of encounters, number of individuals and largest group size of *Phocoena phocoena* of pooled monthly periods of the 14-year study.

Pooled Month	Total sampling effort (km)	Total number of encounters	Total number of individuals	Relative Abundance (individuals km ⁻¹)	Largest group size
May	850	18	40	0.047	7
June	5321	130	262	0.049	21
July	6684	228	542	0.081	40
August	5352	154	543	0.101	25
September	5476	123	573	0.105	32
October	1978	46	189	0.096	25
All	25661	699	2149	0.084	40

Relative abundance

Mean relative abundance in a given year showed considerable variation throughout the study, but seemed to show a general decline, especially over the latter part of the survey. It was greatest at 0.201 and 0.273 during 2002 and 2003 respectively (figure 3). The following years showed drastically lower mean relative abundance, although there was another slight peak in 2006 (figure 3). Relative abundance was much higher in 2008, but was again lower in 2009 (figure 3). It then stayed relatively low, peaking again slightly during 2012 and 2013 but was only 0.024 during 2014, the lowest of any year in the entire survey (figure 3). A Kruskal-Wallis test showed there to be significant differences in the mean relative abundance for each year of the survey ($K = 171.81$, $df = 13$, $p < 0.0001$).

Many years in the survey were characterised by considerable variation month to month (figure 4), especially 2003 and 2005. Likewise the moving average shows considerable variation, ranging from 0.02 to 0.26 (figure 4). The trend line shows the greatest peak during 2002 and 2003 (figure 4), with the log relative

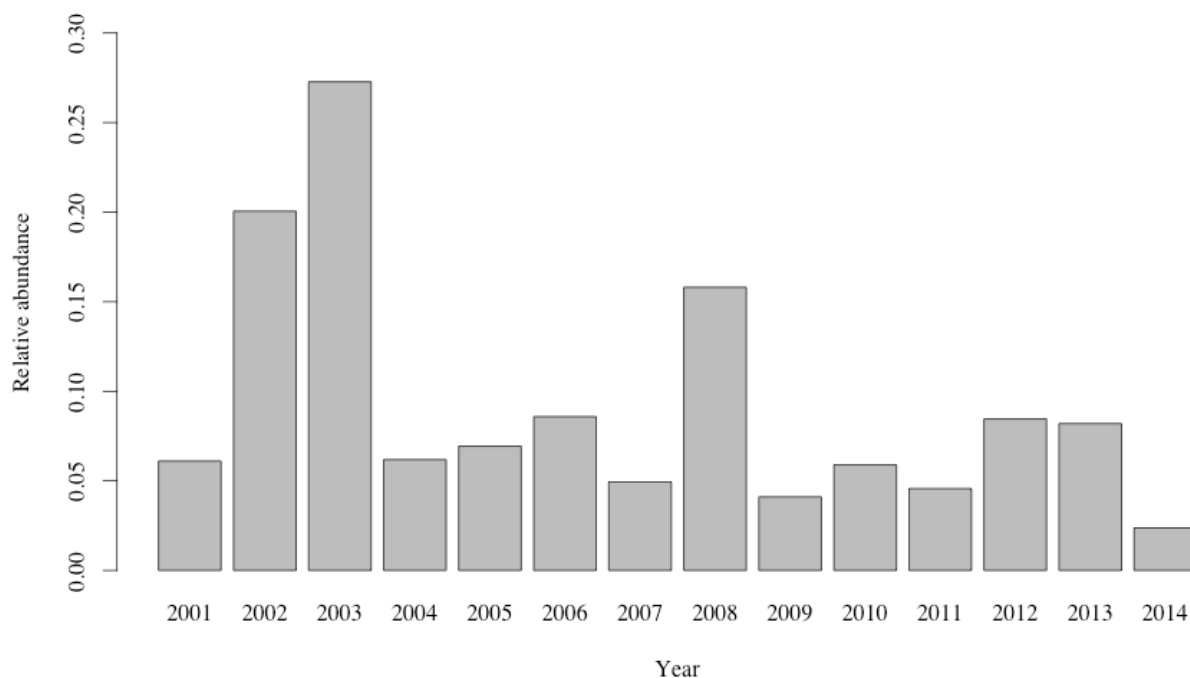


Figure 3. The total relative abundance, or number of *Phocoena phocoena* per kilometre of sampling effort for each year from 2001 to 2014.

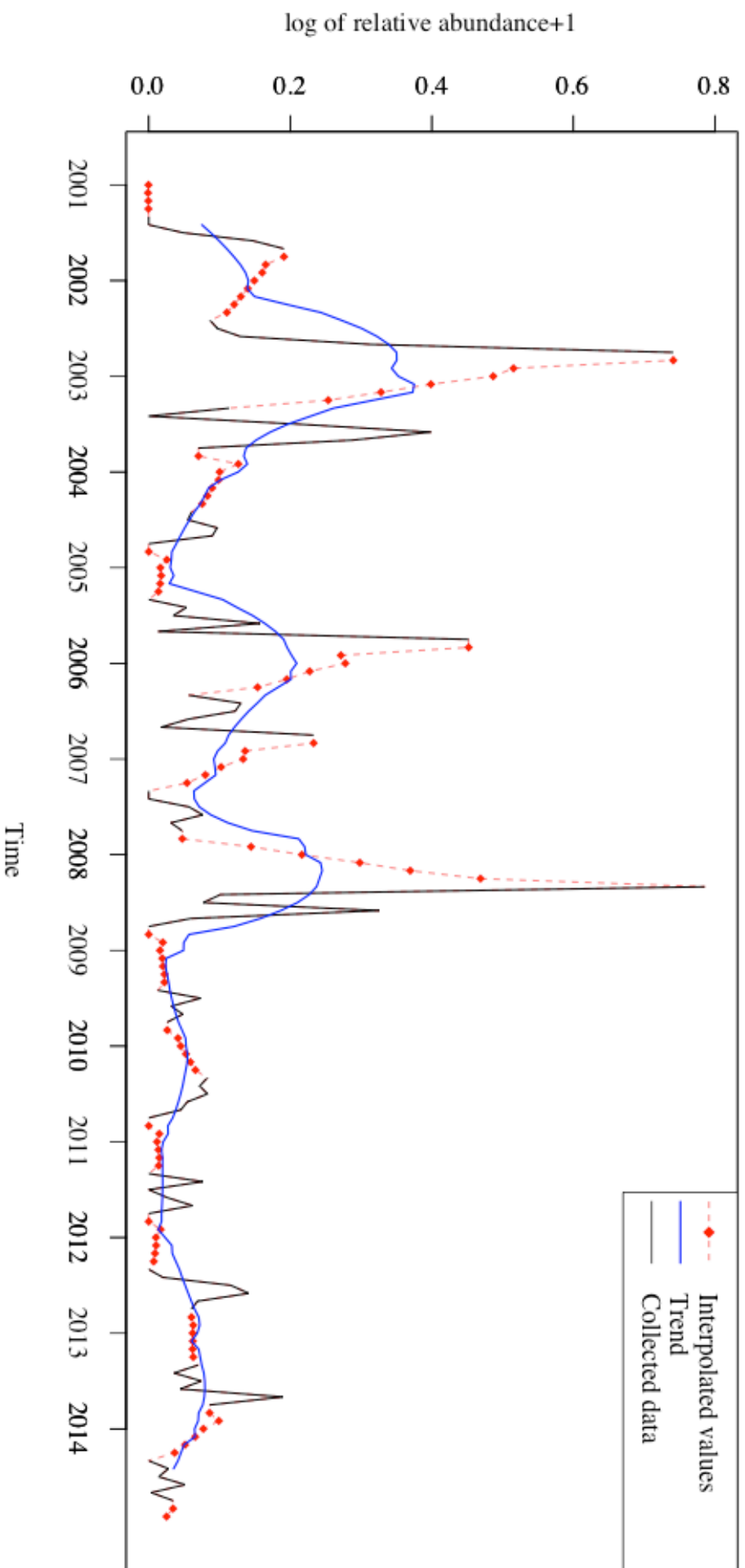


Figure 4. Time series of the relative abundance of *Phocoena phocoena* for individual months from 2001 to 2014 inclusive. Relative abundance was log transformed to allow for easier comparison between smaller values. Interpolated values were calculated and used to fill in winter months or months where sampling wasn't able to be undertaken. The trend represents a moving average calculated using a 12 month span.

abundance for October 2002 being the second highest for the entire survey at 0.741 (figure 4). The trend then showed a decline into 2004 and early 2005. Log relative abundance then rose and peaked again at 0.451 (figure 4) in October 2005, resulting in a larger peak in the trend during 2005 and early 2006 than shown in figure 4. The trend then showed another decline over the remainder of 2006 and 2007, before showing a steep increase into early 2008. Log relative abundance then peaked at 0.785 in May 2008 (figure 4), before declining sharply into the start of 2009. The trend then remained comparatively low for the rest of the study, showing a slight peak in 2010, as well as a slightly larger peak in 2012 and 2013.

In terms of seasonal trends, relative abundance generally showed an increase as the study period progressed. May and June showed the lowest mean relative abundance at 0.047 and 0.049 respectively (figure 5). For July this figure was 0.081 (figure 5), approximately 65% higher than June. Mean relative abundance then peaked at 0.101 and 0.104 in August and September respectively (figure 5). There was a slight decrease in October compared to August or September with the mean relative abundance for this month being 0.095 (figure 5). Kruskal-Wallis analysis showed there to be a significant difference between the mean relative abundance of each pooled month ($K = 142.37$, $df = 5$, $p = <0.0001$).

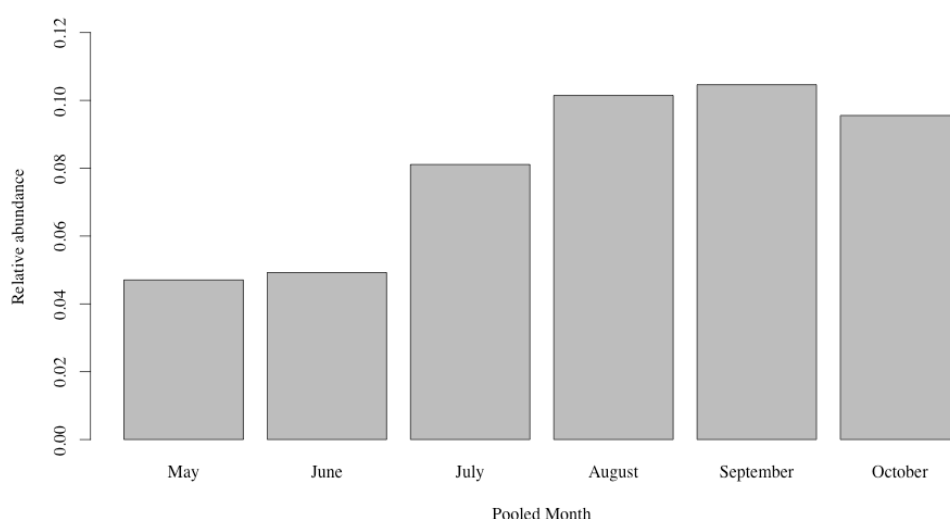


Figure 5. The total relative abundance of *Phocoena phocoena* for the six different months of sampling undertaken throughout the survey. Pooled month refers to the combined values of that specific month from each year of the entire survey.

Group size

Average group size showed a similar pattern to relative abundance when considered by pooled months, showing a general increase as the summer season goes on. Mean group size early in the season was comparatively low at 2.22 in May, reaching its lowest in the summer season during June at 2.01 (figure 6). In July there was a slight increase in mean group size to 2.37, marginally higher than in May. Average group size showed a substantial increase during the latter part of the season reaching 3.52 in August and reaching its highest during September at 4.65 (figure 6). It was slightly lower in October at 4.10 (Figure 6). A Kruskal-Wallis test showed the differences between the mean average group size for each pooled month to be significant ($K = 52.87$, $df = 5$, $p < 0.0001$).

Rather than showing a decline, group size showed considerable variation over the course of the study with a series of “peaks”. The first three months of each year showed less variation between different years and typically showed mean group sizes around two (figure 7). During certain periods of the study mean group size then tended to increase as the summer season drew on. The first of these periods was during 2002 and 2003, coinciding the first peak in relative abundance. Mean group size was approximately two during June and July 2002, before increasing to approximately 3.2 in August and September, before

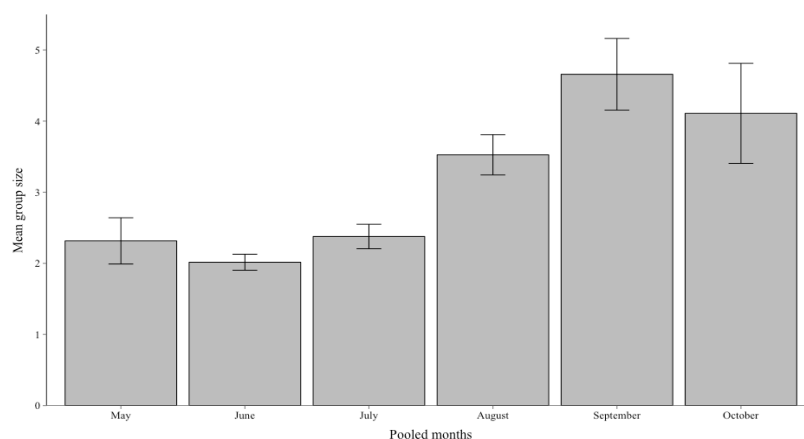


Figure 6. The mean group size of *Phocoena phocoena* for the six different months of sampling undertaken throughout the survey. Pooled month refers to the combined values of that specific month from each year of the entire survey.

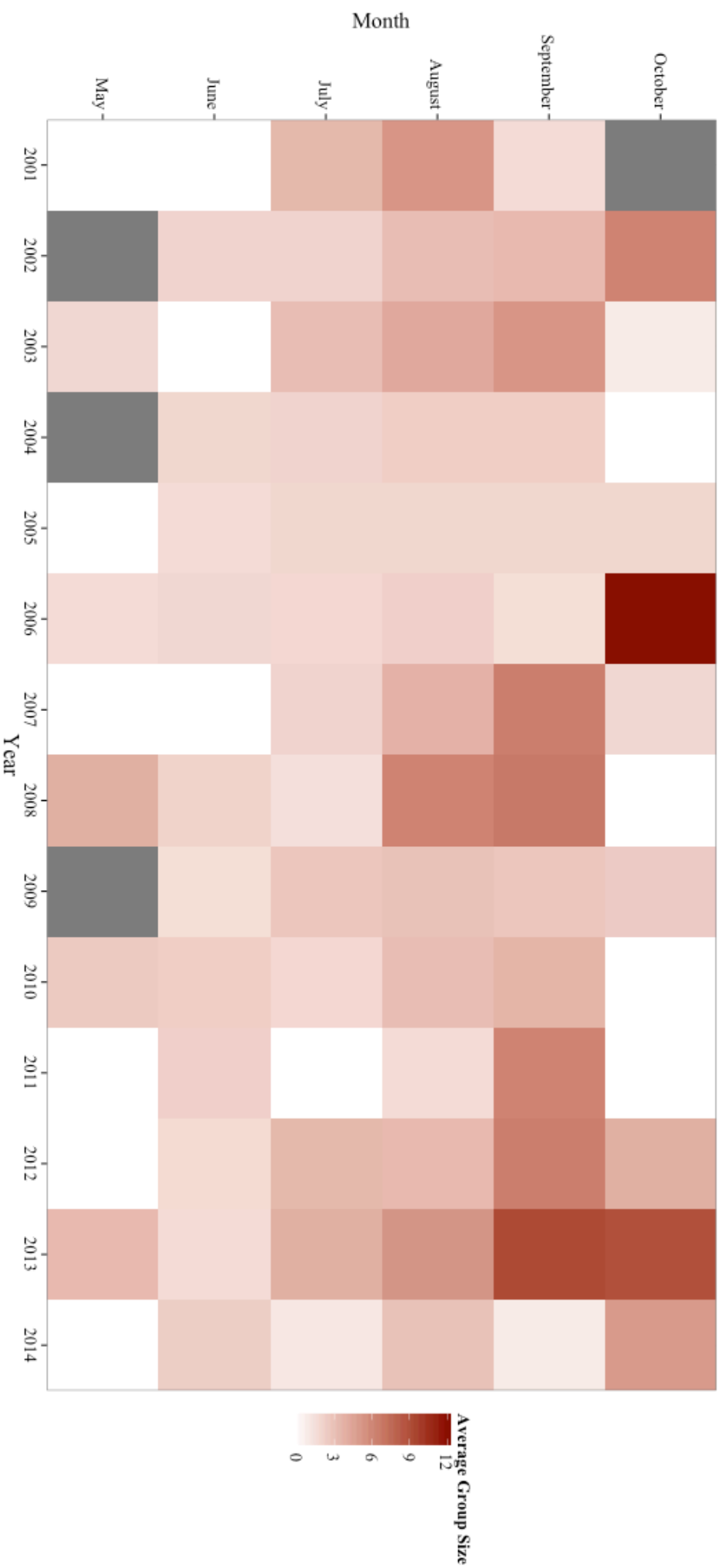


Figure 7. Average group size of *Phocoena phocoena* per month from 2001 to 2014. Average group size represents the mean group size for a given month. White tiles represent “true zero” values where no animals were encountered whilst grey tiles represent months where no sampling was able to be undertaken.

reaching a peak of around six in October. Subsequently during July, August and September 2003 mean group size increased from 3.19 to 5.25 (figure 7). However during 2004 and 2005 there was no such increase with mean group size remaining around 1.3 for the entire year (figure 7). 2006 showed a similar pattern apart from October which had a mean group size of 12, the highest at any point in the study. A peak in group size was also observed during the next two years with increases in September in 2007 as well August and September 2008 (figure 7). Like 2004 and 2005, there were no considerable increases during 2009 and 2010, with mean group size remaining fairly low (figure 7). A slight rise was observed during 2011 and 2012, although there was a more pronounced rise during 2013 with mean group size increasing from 1.75 in June to 9.06 in September (figure 7). 2014 showed fairly variation apart from a small peak in October. A Kruskal-Wallis showed the differences between the mean group size per year to significant ($K = 35.69$, $df = 13$, $p = 0.0006$).

Temperature

A significant amount of variation in group size ($t = 2.835$, $p = 0.00569$) and relative abundance after log transformation ($t = 2.056$, $p = 0.0432$) was dependant on sea surface temperature when plotted as linear regressions (figure 8). However both showed an extremely weak correlation ($R^2 = 0.096$ for average group size and $R^2 = 0.053$ for relative abundance).

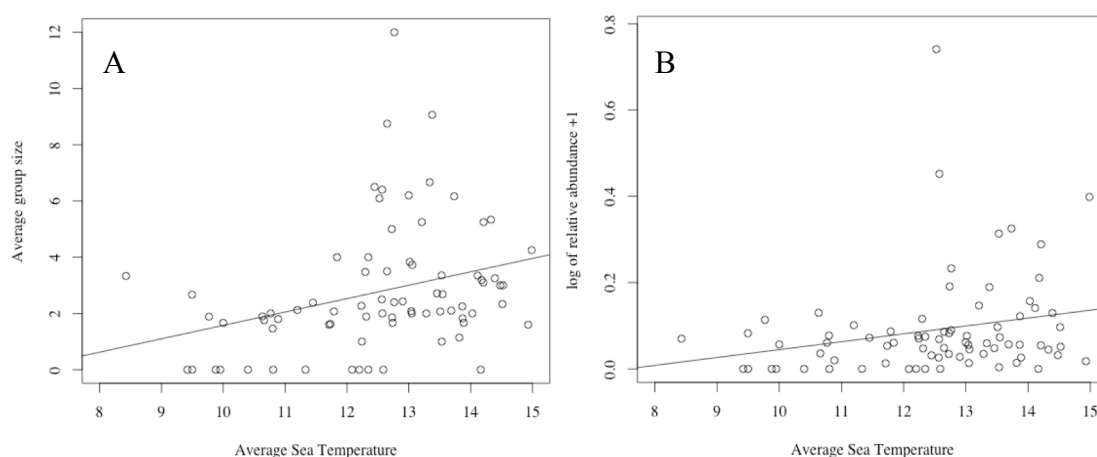


Figure 8. The relationship of average sea temperature with average group size (panel A) and relative abundance (panel B).

Discussion

Sampling methods, viability of Arima modelling and potential anomalous results

Although sampling *P. phocoena* during surveys for other cetacean species allows for a more extensive dataset, it produce biased estimates of relative abundance. As previously stated this study uses data collected on inshore coastal transects which are primarily undertaken to sample bottlenose dolphins, *Tursiops truncatus*. *P. phocoena* and *T. truncatus* are recorded as having violent interspecific interactions (Ross & Wilson, 1996; Patterson *et al.*, 1998; Spitz *et al.*, 2006), with *P. phocoena* avoiding areas where *T. truncatus* is present (Thompson *et al.*, 2004). This could result in downwards biased results of relative abundance, since disproportionately low numbers of *P. phocoena* could be observed per unit effort whilst on inshore transects compared to other survey types. However results from inshore transects are included, since the majority of this sampling type was undertaken during rougher sea states and all results taken above a sea state of 1 were subsequently excluded from analysis, meaning that the effect of *T. truncatus* presence on *P. phocoena* abundance was probably minimal.

The viability of the interpolation used to generate missing data for the time series is also considered here. Although the interpolated winter values represent a considerable part of the time series, no conclusions were based off these values alone and they are included to allow the calculation of a moving average to analyse seasonal patterns during specific years.

The highest relative abundance (1.194) for any single month in the survey was observed during May 2008, a result which had a considerable effect on mean relative abundance for this period. It is likely an anomalous result, as just four individuals were found in three kilometres of sampling. Such low sampling effort was unlikely to be enough to attain an accurate representation of the actual relative abundance during this period. Henceforth this period of the study is disregarded during subsequent discussion.

Trends in Relative Abundance

As previously stated there is a lack of abundance data for *P. phocoena* in the Moray Firth. Previous reports of *P. phocoena* abundance here have been published (Whaley

& Robinson, 2004; Robinson *et al.*, 2007) although both use parts of the dataset of this study, preventing any comparison of results. *P. phocoena* was investigated in the adjacent waters of the Aberdeenshire coast (Weir *et al.*, 2007) from 1999 to 2001. Direct comparisons of relative abundance are difficult however, as sampling effort was quantified by minutes rather than distance in kilometres. Relative abundance can be calculated as approximately 0.16 individuals kilometre⁻¹ (Weir *et al.*, 2007), nearly twice the mean relative abundance for this study (0.084) and nearly three times higher than relative abundance during 2001 (0.06). This increased abundance could be part of a peak however as yearly fluctuations in abundance, similar to that found in this study, could be present in the Aberdeenshire coast. Four-fold fluctuations in sightings over consecutive years have also been reported in northwest Scotland (Marubini *et al.*, 2009). Yearly differences are not mentioned in the study (Weir *et al.*, 2007) and the shorter time frame may not capture such variation. The proximity of the Aberdeenshire coast and the Moray Firth (separated by 50 km of coastline) suggests that populations could utilise and move between these sites, offering an explanation to observed differences in relative abundance during similar time periods.

Seasonal trends of relative abundance also mirrored those found in the current study, with relative abundance off the Aberdeenshire coast reaching a peak during August and September and trailing off into October (Weir *et al.*, 2007). Mackerel move inshore during summer months (Weir *et al.*, 2007) and the increased abundance later in the summer season could represent *P. phocoena* exploiting this. Baltic Sea populations have been shown similar trends, with peaks in abundance during July and August (Verfuß *et al.*, 2007). German North Sea populations show slight variation on this pattern with abundance peaking during May and June (Gilles *et al.*, 2009), whereas Dutch populations have been shown to peak during the winter (Camphuysen, 2004). As with the Aberdeenshire and Moray Firth, populations it is hypothesised that these trends represent *P. phocoena* moving to the coast from offshore water to exploit different prey (Brodie, 1995; Trippel *et al.*, 1999).

Even greater relative abundances for *P. phocoena* have been recorded further afield in Europe, with 0.39 individuals kilometre⁻¹ observed around the German island of Sylt during July 1992 (Heide-Jorgensen *et al.*, 1993). Comparatively the highest abundance observed in the current study was 0.27 during 2003. The area around these

islands was subsequently identified as a possible calving ground for *P. phocoena* (Sonntag *et al.*, 1999) possibly explaining the high density of individuals in this area. The survey by Heide-Jorgensen *et al.* (1993) also recorded a degree of variability amongst Baltic Sea populations of *P. phocoena*, with yearly relative abundance decreasing in two sites from 0.21 to 0.14 and 0.07 to 0.01 from 1991 to 1992 respectively. The fact that this study took place nearly a decade after however, means direct comparison of these trends is not applicable. The North Sea site around was only surveyed during 1992, meaning that no variation could be observed. The study also didn't account for any seasonal variation in relative abundance with sampling only taking place during a single month at each site (Heide-Jorgensen *et al.*, 1993). More recent estimates of relative abundance mirror from the German-Danish Baltic mirror the lower end of these estimates at 0.01 individuals km⁻¹. In comparison the lowest value for the Moray Firth was 0.02 in 2014 and this was the only time that relative abundance for a yearly period fell below 0.04, suggesting the presence of a larger population than in this area of the Baltic. In the context of a wider geographical scale, relative abundance of *P. phocoena* in California, Oregon and Washington using ship-based surveys have been estimated at 0.275 individuals km⁻¹ (Barlow, 1988), similar to the highest yearly relative abundance observed in this study. Further aerial studies estimated relative abundance to be 0.11 and 0.10 in 1984 and 1985 respectively (Barlow *et al.*, 1988). This value was closer to the mean relative abundance observed during this study, although the aerial observations were thought to be biased downwards due to adverse weather conditions (Barlow *et al.*, 1988), suggesting that the overall relative abundance of this Pacific population was higher than that of the Moray Firth.

As hypothesised a general decline in relative abundance was noted during over the course this study. Distribution shifts could be a cause of the reduced abundances observed during this study (figure 3 & 4) (Camphuysen, 2004; Hammond *et al.*, 2013). The results of SCANS I (undertaken in 1994) and SCANS II (undertaken in 2005) suggest a general decline in the abundance of *P. phocoena* in Scottish waters over the 11 year period. The decline observed from 2001 to the beginning of 2005 could reflect Hammond *et al.*'s observation. Furthermore from 2009 onwards relative abundance persists at relatively low levels showing no more large peaks (figure 3 & 4), a slump which could possibly represent a continuation of the overall trend

described by Hammond *et al.* (2013) since 2005. The 11 year gap between the SCANS surveys could easily overlook short term “rebounds” in abundance however, such as the peak in relative abundance observed in this study during 2002/2003 (figure 3 & 4, the 2008 peak is disregarded as discussed previously). Many years also show dramatic variation month to month with sharp peaks. These peaks in abundance, as well as the reduced abundance in the latter part of the study are unlikely to be due to population fluctuations (Hammond *et al.*, 2013). Incidental by-catch is thought to be above sustainable levels in some European waters (Tregenza *et al.*, 1997; Berggren *et al.*, 2002; Vinther & Larsen, 2004) and could be a cause of decline in Scottish waters, although a reduction in gillnet fishing, the most detrimental method in terms of by-catch, has been observed in Scottish fisheries (Gill, 1999) and the speed of the changes is uncharacteristic with a long-lived species (Camphuysen, 2004; Hammond *et al.*, 2013). *P. phocoena* relies on specific prey items at locations and times of year (Das *et al.*, 2003; Santos *et al.*, 2004) and it is probably that fluctuations in prey stocks are driving observed distribution trends in the North Sea (Camphuysen, 2004; Robinson *et al.*, 2007; Hammond *et al.*, 2013), as well as the trends observed in this study. Temperature rise in the North Sea has been cited as a primary cause of prey fluctuations (Perry *et al.*, 2005; Dulvy *et al.*, 2008), with sandeel, a primary diet component of *P. phocoena*, exhibiting a reduction in recruitment with increased sea temperature (Frederiksen *et al.*, 2004). Contrary to what this might suggest about *P. phocoena* abundance, this study found there to be a significant positive correlation between relative abundance and sea surface temperature (figure 8). This was a weak relationship however and it likely represents the seasonal trend observed in relative abundance during the study.

Trends in Group Size

The seasonal trend in group size observed in this study generally matched the hypothesis that mean group size would increase over the course of the season (figure 6) with a significant difference between mean group size for each pooled month. Studies on seasonal trends in group size are scarce especially in the North Sea, although a similar trend amongst western Atlantic populations has been observed (Neave & Wright, 1968). More recent studies however haven't found a significant difference in group size during different months (Weir *et al.*, 2007; Dahlheim &

White, 2010). *P. phocoena* have been shown to reproduce during late July or August and the increased mean group size during this period in the Moray Firth could represent the presence of breeding aggregations.

At 3.074, the mean group size for the entire duration of this study was also higher than corresponding values for many other areas in Europe which range from 1.13 individuals to 2.82 individuals (Pierpoint, 2001; Johnston *et al.*, 2005; Weir *et al.*, 2007; Gilles *et al.*, 2009; Hammond *et al.*, 2013; Haelters *et al.*, 2015). Mean group size did fluctuate from year to year, however they were still fairly high compared to other areas and mean group size in the Moray Firth was greater than the rest of the northwest North Sea (approximately 1.8 vs. 1.42) despite this year showing some of the smallest mean group sizes (figure 7). The peaks observed in group size seemed to also be loosely associated with periods of higher abundance (figure 4 & 7). Group size of *P. phocoena* has been shown to rise in prey rich areas (Weir & O'Brien, 2000) and it is possible that, like relative abundance, the peaks in mean group size observed during 2002/2003, 2007, and 2012/2013 (figure 7) represent *P. phocoena* populations responding to changing prey stocks in the Moray Firth. The increased mean group size suggests a possible importance of the Moray Firth, either as a breeding or feeding area.

Conclusions

In general the findings of this survey suggest that the predictions made regarding relative abundance were somewhat accurate. Although lower at the start of the study, relative abundance peaked during 2002 and 2003, before declining and remaining at fairly low levels for the rest of the study. This could reflect large scale distribution shifts observed in the North Sea (Hammond *et al.*, 2013), likely caused by shifting prey stocks (Camphuysen, 2004; Hammond *et al.*, 2013). As predicted, relative abundance of *P. phocoena* increased over the course of the summer season, likewise probably reflecting the exploitation of specific prey inhabiting the Moray Firth later in the summer season. Seasonal trends in group size also matched predictions, showing an increase as the season progressed. This possibly represented *P. phocoena* gathering to reproduce or feed. Group size did not show a decline over the course of the study,

but was instead categorised by a series of peaks, which seemed to be associated with relative abundance.

The observed seasonal trends in relative abundance and group size suggest that the Moray Firth is of increased importance to *P. phocoena* later in the summer season, whilst observed trends in relative abundance suggest that the area was of more importance around 2002. Such trends could be a cause for concern, possibly suggesting a decline in habitat quality in the Moray Firth. This study also give us important information how *P. phocoena* utilises an area over long temporal periods and supplies clues as to possible distribution shifts, such as those identified by Hammond et al. (2013). The observed variation in group size and relative abundance during this study highlight the importance of undertaking sampling at multiple time periods in order to obtain an effective snapshot of a population. The presented findings help us to identify areas currently important to *P. phocoena*, helping us to direct conservation efforts more effectively. If the observed trends are a result of shifting populations, then further study should aim at how the individuals using the Moray Firth move between here and other areas in the North Sea, possibly through the use of methods of satellite tagging, further helping us to identify how the Moray Firth utilise the wider North Sea area.

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