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Title:

Fine-scale spatial association between baleen whales and forage fish in the Celtic Sea

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Abstract

The Celtic Sea is a productive area, which attracts large baleen whales to feed, however little is known about their foraging behaviour. The study aim was to know whether or not baleen whales actively target forage fish or, on the contrary, is predation on the Celtic Sea plateau driven by random encounters between prey and predator? Concurrent sighting surveys for fin, minke and humpback whales (*B. pysalus*, *B. acutorostrata* and *M. novaeangliae*) were carried out simultaneously during a dedicated fisheries acoustic survey assessing the abundance and distribution of forage fish from 2007 to 2013. Probabilities of spatial overlap on a resolution up to 30 km between baleen whales and forage fish were analysed and compared to the probability of a random encounter. For estimations of foraging threshold and prey selectivity, average fish biomass and fish length were calculated when baleen whales and forage fish co-occurred. Whales were found to actively searched in areas with herring (*C. harengus*) and sprat (*S. sprattus*), while areas with mackerel (*S. scombrus*) were not targeted. A foraging distance and prey detection range of up to 8 km was found, which enables baleen whales to track their prey to minimise search effort. Fish densities within the defined foraging distance ranged from 0.001 to 3 kg m^{-2} and were correlated to total fish abundance. No prey size selectivity according to fish length was found. Selectivity and active foraging behaviour in whale predation modify the forage fish mortality and should be considered in an ecosystem-based management of the Celtic Sea resources.

Keywords

Fin whale (*Balenoptera physalus*); foraging; foraging distance; Herring (*Clupea harengus*); Minke whale (*Balenoptera acutorostrata*); Sprat (*Sprattus sprattus*)

Introduction

Baleen whales undergo annual long distance migrations from mating grounds to nutrient rich feeding grounds at high latitudes to feed on zooplankton and small pelagic fish (Corkeron and Connor 1999; Clapham 2001; Kennedy et al. 2013). Within a conceptual foraging model, large migrations of several thousands of kilometres can be seen as the first spatial scale of foraging strategies (Kenney et al. 2001; Hazen et al. 2009). The spatial meso-scale is within hundreds of kilometres to select a prey hot spot (an area with potentially high prey densities), while individual foraging events take place on the scale of less than 10 km (Kenney et al. 2001; Hazen et al. 2009). As prey abundance decreases in space and time, it can become advantageous for an animal to leave and to explore new areas, if the potential value of the new area promises a net energetic gain (Charnov 1976; Pyke et al. 1977). Tagging and mark/recapture studies have shown that baleen whales visit several prey hot spots within the same region, but also leave an area to discover new hot spots which involves longer travelling distances (Watkins et al. 1996; Zerbini et al. 2006; Witteveen et al. 2008; Olsen et al. 2009; Silva et al. 2013; Feyrer and Duffus 2014; Kennedy et al. 2014). Prior knowledge due to matrilineal learning and site fidelity (the recurring search within a certain area) can help baleen whales to accept or reject possible areas before visiting, thereby attempting to prevent a negative energy balance (Pyke et al. 1977; Kenney et al. 2001).

Baleen whales can shape an ecosystem on multiple levels for instance by acting as nutrient vectors and apex predators (Roman et al. 2014; Willis 2014). Therefore baleen whales should be given attention within the assessment of an ecosystem as top predator and baleen whale impacts on prey population dynamics should be explored within an ecosystem-based fishery management (Engelhard et al. 2014, Link and Browman 2014; Travis et al. 2014). Results from photo-id surveys within the Celtic Sea have demonstrated inter-annual resighting of both humpback (*Megaptera novaeangliae*) and fin whale (*Balaenoptera pysalus*) (Whooley et al. 2011; Ryan et al. 2015), suggesting some seasonal site fidelity within and between years. A predation impact assessment requires an understanding on local, small-scale baleen whale foraging decisions including prey selectivity, foraging thresholds, foraging duration and habitat utilisation.

Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*) and Atlantic mackerel (*Scromber scombrus*) are abundant pelagic fish species in the Celtic Sea which support large scale fisheries (Marine Institute 2013). Small pelagic fish are defined as forage fish because of their dense schooling behaviour and position in the trophic food web as common prey for higher trophic levels (Engelhard et al. 2014; Pikitch et al. 2014). The only reported in-situ diet analysis of baleen whales in the Celtic Sea showed a preference by fin and humpback whales for sprat and juvenile herring (Ryan et al. 2014). Are whales intermittently preying on forage fish while coincidently passing the Celtic Sea during migration? Or is the Celtic Sea plateau a prey hot spot where baleen whales directly and reliably target herring, sprat and mackerel?

Referring to seven years of synoptic observed predator and prey distribution, we analysed the spatial overlap of fin, minke (*Balaenoptera acutorostrata*) and humpback whales, which are the most common baleen whales recorded in the Celtic Sea, with the presence of herring and sprat. Further, where spatial overlap occurred, we calculated the average biomass and average fish length of forage fish in proximity to the whale sighting. The results provide information on:

1. prey selectivity and habitat use of baleen whales, which can help to understand and quantify foraging decisions;

2. potential predation of forage fish stocks, which can contribute to mortality rate estimations in stock assessments;

3. trophic chain characterization in the Celtic Sea to improve ecosystem modelling allowing for different set-ups e.g. increase of prey or predator abundances and different bottom-up or top-down scenarios.

Material and Methods

Fish data acquisition

Acoustic data were collected from 2007 to 2013 during the annual Celtic Sea Acoustic Herring Survey which occurs over 21 consecutive days each October in the Celtic Sea along the Irish South coast. A calibrated Simrad EK60 echosounder recorded acoustic data continuously along pre-determined transect lines with four frequencies (18, 38, 120 and 200 kHz). NASC (Nautical Area Scattering Coefficient) data were obtained and integrated over the local depth and 1.85 km intervals into effort blocks known as elementary distance sampling units (EDSUs). Echograms were identified to species level based on species-specific acoustic signals and echotrace recognition, and ground-truthed with directed fishing tows (O'Donnell et al. 2013). Only herring and sprat echotraces positively identified were analysed in this study (O'Donnell et al. 2013). The average fish length (L, in cm) per species from the closest geographical trawl to the respective EDSU was used to calculate the target strength (TS) per fish species at 38 kHz with $TS = 20\ \log L - 71.2dB$ for herring[1] and sprat.

No 38 kHz frequency data were available from 2010 due to a technical defect, so the 18 kHz signal and an adjusted TS/length relationship was used instead (Saunders et al. 2012). No abundance was estimated in 2010 for sprat, however the echotraces were used for the presence/absence analysis. NASC values for herring and sprat were transformed into fish abundance per square metre and multiplied with the average fish weight taken from the closest haul to obtain fish biomass per square meter (B, in kg m^{-2}) (Simmonds and MacLennan 2005). NASC values for mackerel were used as

[1] For the year 2010: $TS = 20\ \log L - 69.7dB$ for 18kHz and only for herring

indication for presence only and no biomass was calculated. No distribution data for mackerel were available for 2010 and 2012.

Simultaneous baleen whale observations

During the survey, one observer kept a daylight watch recording marine mammal sightings from the crow's nest (18 m above sea level) or from the bridge (11 m above sea level). All sightings in an area up to 90 degrees to either side of the vessel were recorded. The field of view was constantly scanned during watch hours by eye and through binoculars. For each sighting the following data were recorded: time, location, species, distance, bearing, number of animals and behaviour. Only fin, humpback and minke whale sightings recorded up to a maximum sea state of 5 were used in this analysis. Whale sightings that could not be identified to species level (i.e. no body but the blow was seen) were recorded as unidentified large whale sightings. A total of 113 baleen whale sightings were recorded from 2007 to 2013 (Table 1). Here sightings were used as unit to describe the presence of a whale, irrespective of group size per sighting. Generally most individuals were solitary, but groups of up to 10 individuals were recorded within one sighting.

Analysis of spatial co-occurrence and fish biomass within proximity

Whale sightings were aligned with the acoustic data set from the respective year and fish biomass (B_{area} in kg m^{-2}) was calculated for a circular area with different radii (R with 2, 4, 6, 8, 10, 14, 16, 18, 20, 25 and 30 km) centred to the whale sighting. Fish biomass within the area around the observed whale sighting can identify a biomass target and foraging threshold of baleen whales. To calculate B_{area} the average acoustic density over each transect (B_t) was weighted by the transect length (l), summed and applied to the surface area:

$$B_{area} = \pi \times R^2 \sum^{transect} B_t \times l / \sum l$$

with R and l in meters and B_t as:

$$B_t = \sum {B \times 1852}/{l}$$

For each whale sighting, the presence of fish (defined as $B_{area} > 0$) was recorded for each radius and target fish species. The proportion of positive co-occurrence between whale sighting and fish was calculated for a total of 113 sightings over seven years. To test if any spatial overlap of baleen whale and pelagic fish species was coincidental, whale sightings were replaced by random points on the ship transect. Presence/absence analysis for each radius was repeated 200 times for the simulated random whale presences. The probabilities of a positive fish biomass per whale location (observed vs. simulated sighting) being significantly different to random were tested with a two-sided probability test of success (R function prob.test, "stats" package). When the test of disparity of probabilities was significant ($p < 0.05$), the null-hypothesis was rejected, meaning that spatial co-occurrence was not coincidental.

Analysis on size selection by baleen whales

Average fish length ($\overline{TL}$) and standard deviation were calculated for fish proximal to a whale sighting to explore if whales preferentially associate with or select certain prey sizes. The total length values recorded from the fishing trawls during the survey were averaged:

- $\overline{TL}_{obs}$: average length of the trawl geographically closest to the whale observation; here called "observations";

- $\overline{TL}_{sim}$: average length of the trawl geographically closest to the simulated whale location; here called "simulations";
- $\overline{TL}_{full}$: average length of all trawl in the study area; here called "full survey";

$\overline{TL}_{obs}$ provided information on the size distribution close to a whale sighting and thus could indicated a possible prey size selection by baleen whales. $\overline{TL}_{sim}$ represented a random selection from the stock and therefore should be similar to $\overline{TL}_{full}$. $\overline{TL}_{obs}$, $\overline{TL}_{sim}$ and $\overline{TL}_{full}$ were calculated for each survey year and compared using a Tukey's test.

All analyses were carried out using the open source statistical software "R" (http://cran.r-project.org).

Results

Spatial co-occurrence of baleen whales and forage fish

The proportion of positive co-occurrence was calculated for a circular area centred on a whale sighting with increasing distances (2 to 30 km). With increasing distance, the proportion of spatial overlap increased (Figure 1). The proportion of spatial overlap with herring and sprat was very similar, however when all fish species were combined, the spatial overlap of whale sightings within proximity to fish was highest (Figure 1). Proportions obtained from simulated random whale sightings showed the same pattern of increasing spatial overlap with distance (Figure 1). However, a comparison of proportions of overlap showed significant differences between observed and simulated data up to a distance of 8 km (Figure 1, Table 2). Within 8 km to a sighting, the null-hypothesis could be rejected suggesting that occurrence of a whale sighting in proximity to herring and sprat did not occur by chance (Table 2). For distances larger than 8 km, no difference between observed and simulated co-occurrence events was detected ($p > 0.05$, Table 2), implying that any spatial overlap of predator and prey over larger distances was coincidental. The proportion of co-occurrence was highest with 0.83 within an 8 km radius, thus 94 of 113 whale sightings were seen in proximity to potential prey (Table 2). The spatial overlap between mackerel and whale sighting was not significant for any distances ($p > 0.05$, Table 2). In the Celtic Sea, baleen whales appeared to actively search in the proximity to forage fish without differentiation between herring and sprat, while mackerel did not appear to be targeted (Figure 2).

Fish biomass within foraging distance

Because mackerel may not be a target species for baleen whales in the Celtic Sea, only the acoustic biomass of herring and sprat was calculated within the circular area with an 8 km radius. Sightings of the three whale species were in proximity to fish biomass of 0.001 to 0.2 kg m^{-2} (Figure 3), representing 0.2 to 4 tonnes of fish within an 8 km radius. In years of high herring biomass recorded during the acoustic survey (2010 to 2012, Figure 4) whales were more frequently observed in areas with high herring biomass densities (Figure 3). In some years single, large herring schools were recorded (Figure 2) and whales were seen in proximity to those schools, explaining the higher fish biomass for 2008, 2011 and 2012 for fin whales and for minke whales between 2010 and 2012. Total sprat biomass was much lower compared to the total herring biomass recorded during all surveys (Figure 4). Sprat was targeted by fin whales only in the years with higher sprat biomass survey estimates, while minke whales were observed in proximity to sprat irrespective of sprat biomass, i.e. during all years (Figure 3 and 4).

Fish size in proximity to the whale sightings

Average fish length for herring and sprat was calculated for fish within 8 km to the whale sighting and the simulated data, and then compared to the total average fish length of the survey per year. No significant difference was detected for $\overline{TL}_{sim}$compared to $\overline{TL}_{full}$ for neither herring nor sprat (*p* = 0.68 and *p* = 0.78 respectively; Figure 5). $\overline{TL}_{obs}$ in proximity to the observed whale sightings followed the distribution of the surveys, without general significant differences to $\overline{TL}_{full}$ (*p* = 0.99 for herring and *p* = 0.53 for sprat). Only in selected years, $\overline{TL}_{obs}$ for herring was smaller (2008) and larger (2013) compared to the herring $\overline{TL}_{full}$ from the survey (Figure 5).

Discussion

Over 80% of the baleen whale sightings were recorded in close proximity to herring and sprat (56% and 52% respectively), which are therefore likely to be actively search out by whales. No significant spatial overlap was found for mackerel and baleen whales; hence mackerel does not appear to be actively targeted by baleen whales in the Celtic Sea. Direct observations of mackerel made over successive years during the survey found this species to form low density scattering and widely dispersed layers as compared to the larger, higher density localised schools formed by herring and sprat. The highest proportion of significant spatial overlap of prey and predator occurred within a distance of 8 km. Fish biomass within the 8 km radius ranged between 0.2 and 4 tonnes (or 0.001 – 0.2 kg m^{-2}). Fin and minke whales were actively targeting localised areas with the high herring density in years where acoustic densities of herring were correspondingly high. Sprat was targeted in all years by minke whales; however only in years with high sprat biomass survey estimates was sprat also targeted by fin whales. This suggests a density-driven relationship of predator-prey co-occurrence which is different for different whale species. No significant difference in the length distribution of fish was found between herring and sprat in proximity to whales (to 8 km) and fish that were encountered without a simultaneous baleen whale sighting. This suggests that, based on spatial proximity that fin, humpback and minke whales engage in feeding without an explicit prey size selection while in the Celtic Sea.

Spatial co-occurrence of baleen whales and forage fish

A set of circular areas with increasing radii around a whale sighting were tested to find the spatial resolution of overlapping distribution. Overlap with fish further than 8 km to the sighting statistically resembled a coincidental spatial overlap. However whale sightings were predominantly recorded in close proximity to fish. However, not all whale sightings in proximity to fish correspond to actual observed foraging behaviour. In fact, foraging was only observed in 20 out of the 113 sightings. Diving and foraging have a high metabolic cost (Goldbogen et al. 2006, 2008) and single foraging dives are often separated by several minutes of rest close to the surface (Goldbogen et al. 2013). Considering that both the whale and the prey target are mobile, foraging events can occur on the scale of several kilometres (Kenney et al. 2001; Hazen et al. 2009; Friedlaender et al. 2014). Minke and humpback whales have swimming speeds of 3 to 6 km h^{-1} and could cover 2 to 8 km within 30 minutes to 2 hours respectively, while fin whales have faster swimming speed of up to 20 km h^{-1} thus could swim 8 km in less than 30 minutes (Markussen et al. 1992; McDonald et al. 1995; Goldbogen et al. 2006; Kennedy et al. 2013; Silva et al. 2013; Risch et al. 2014).

Within the concept of prey detection and foraging on a local small-scale (Kenney et al. 2001), a maximum distance between predator and prey of less than 10 km could be the limit of baleen whale detection range. Visual and acoustic cues originating from forage fish and other predators like foraging seabirds and dolphins (Anderwald et al. 2011), could be received within this distance and attract baleen whales to the prey source. Additionally, fish schools can be detected, tracked and preyed on, while energetic costs for a new search effort and relocation may be reduced. A distance of less than 10 km appears to be a profitable, easy reachable distance for foraging by staying close - but not too close - to prey. Significant spatial overlap of baleen whales with prey was found for herring and sprat, which are known prey items of baleen whales in the region (Ryan et al. 2014), the North Atlantic and the North Sea (Haug et al. 1997; Olsen and Holst 2001; Pierce et al. 2004). Mackerel was not targeted by baleen whales in the Celtic Sea even though it has been found as prey together with other species in one minke whale stomach and been mentioned as prey for humpback whales (Olsen and Holst 2001; Clapham 2002). Their infrequences in stomach contents of baleen whales together with the non-significant spatial overlap in the Celtic Sea, indicates that mackerel itself is not a prey target, but may be consumed while preying on mixed fish schools. Unlike mackerel, herring and sprat contain a swimbladder, which can produce sounds and can give visual cues (Wahlberg and Westerberg 2003; Wilson et al. 2004; Hahn and Thomas 2008) which could facilitate the detection of Clupeids species for baleen whales. At the time of sampling, in October, mackerel are more dispersed, forming scattered foraging layers as opposed to dense schools, which are known for herring and sprat. Hence foraging on mackerel could be less rewarding energetically compared to the high density of herring and sprat schools.

Prey density distribution and environmental descriptors like sea surface temperature have been used as explaining factors for whale distribution on feeding grounds using multivariate models (e.g. generalized additive models, GAMs) (e.g. Friedlaender et al. 2006; Ingram et al. 2007; Hazen et al. 2009; Laidre et al. 2010; Anderwald et al. 2012; Nøttestad et al. 2014). In some studies, no or only weak spatial overlap of forage fish and baleen whales was found, which could be due to non-matching spatial and temporal resolution in the data (Laidre et al. 2010; Nøttestad et al. 2014). Here the acoustic survey for the Celtic Sea herring provided a valuable opportunistic platform of obtaining high-quality fish distribution and abundance information with synoptic baleen whale occurrence. Herring is known to be randomly distributed in patches with a strong attraction to coastal spawning grounds but without being influenced by temperature or salinity in the region (Volkenandt et al.

2015). Following a random, patchy, prey distribution, we suggest that baleen whale distribution would be less influenced by a continuous variable like temperature, which has less variability in this area compared to that encountered by baleen whales during migration (Piatt et al. 1989). Based on high-resolution spatial distribution data of predator and prey with high level of synchrony, a general comparison between distances of observed and simulated baleen whale sightings to prey abundance as single variable has highlighted the importance of the Celtic Sea plateau as a prey hot spot for baleen whales.

Fish biomass and average length within an 8 km foraging distance

Fish densities of herring and sprat within an 8 km radius to the whale sighting were variable and skewed to lower fish densities. To calculate fish densities, biomass observations with a 1.85 km resolution were extrapolated over the circular area. Hence low biomass densities can still represent a single large school surrounded by zero values due to the patchy distribution of forage fish schools (Volkenandt et al. 2015). With calculated daily consumption rates for baleen whales (Fin whales 981 kg; Minke whales 165 kg and Humpback whales 621 kg with respective large confidence intervals, see Smith et al. 2014) the observed low fish densities equalling 0.2 to 4 tonnes over the 8 km radius could still sustain an energetic return on foraging. Sprat was targeted by fin whales in years when total stock biomass as determined by the acoustic survey data was also high, supporting a suggested prey biomass- and foraging threshold for baleen whales (Piatt and Methven 1992; Goldbogen et al. 2011; Feyrer and Duffus 2014; Friedlaender et al. 2014), especially for fin whales but less for minke whales.

No significant differences were found between average fish length in proximity to baleen whales and the overall fish length distribution. Hence baleen whales approach forage fish that are abundant in the environment without apparent prey size selection. Exceptions occurred in 2008 and 2013 for herring which could be due to a high abundance of one-year old herring in 2008 and the respective higher abundance five years later (Figure 6); however no selectivity could be found for other years even with a higher abundance of young herring. An in-depth analysis of length-frequencies and year class abundances is necessary to explore possible selectivity by prey size. We suggest that baleen whales non-selectively target herring and sprat according to their availability in the Celtic Sea based on spatial correlation, which does not necessarily imply actual foraging. To date the only available dietary data originating from stable isotope analysis in the Celtic Sea indicated a selectivity for smaller sized fish (sprat and juvenile herring) followed by larger size herring (age 2 to 4) by baleen whales (Ryan et al. 2014), which could support the deviation to the overall abundant prey sizes in certain years.

Ecosystem implication

The current study showed that baleen whales actively search for forage fish in the Celtic Sea, which can be identified as a prey hot spot. This is a first and necessary initial step for future studies on baleen whale foraging on small pelagic fish in the Celtic Sea. After the spatial link between predator and prey, predation will have to be further specified. Geographic memories and site fidelity could be directing foraging decisions of baleen whales on larger spatial scales, while acoustic and visual cues together with prey densities and energetic net gain could be local drivers on a small-spatial scale (Kenney et al. 2001). Residency, and hence predation pressure on forage fish, could be linked to the net-energetic gain. Optimal foraging depends on the time spent in a patch as the net-energetic gain decreases with the removal of prey (Charnov 1976; Pyke et al. 1977). A negative energy balance, e.g. via prey depletion and an increase effort for foraging (due to less dense fish schools occurring after the spawning period) could result in the decision to leave the Celtic Sea plateau to travel to more distant, zooplankton rich foraging areas along the Celtic Sea shelf edge (Ryan et al. 2014). Tagging experiments could provide further valuable information on habitat use and foraging ecology of baleen whales in the Celtic Sea and if whales remain longer in patches of high fish densities (Goldbogen et al. 2013).

While no prey size selectivity was evident, predation can influence the natural mortality estimates of all age classes. Notably, when fish species were treated separately, spatial overlap occurred for 56% and 52% of the whale sightings for herring and sprat respectively, while the percentage was increased to 80%, when species were combined to resemble a forage fish community. Herring is well-studied in the Celtic Sea, but much less is known about sprat. In a changing ecosystem with increasing herring and sprat total stock biomass, the inter-species specific fish population dynamics will become important together with the impact it could have on baleen whale foraging decisions. Here, sprat became a more attractive target for fin whales with increased biomass . Within an ecosystem-based management, predator, prey and their interactions have to be accounted for (Link and Browman 2014). Hence, after acknowledging the importance of the Celtic Sea as a prey hotspot for baleen whales, further research on predator population and their foraging decisions as well as on prey population dynamics is necessary.

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References

Anderwald, P., Evans, P.G., Gygax, L. and Hoelzel, A.R. 2011. Role of feeding strategies in seabird - minke whale associations. Mar. Ecol. Prog. Ser. 424:219–227. doi:10.3354/meps08947.

Anderwald, P., Evans, P.G., Dyer, R., Dale, A., Peter, J. and Hoelzel, A.R. 2012. Spatial scale and environmental determinants in minke whale habitat use and foraging. Mar. Ecol. Prog. Ser. 450:259–274. doi:10.3354/meps09573.

Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9:129–136.

Clapham, P. 2001. Why do baleen whales migrate? Mar. Mammal Sci. 17:432–436.

Clapham, P. 2002. Humpback Whale. *In* Encyclopedia of Marine Mammals *Edited by* W.F. Perrin, B. Würsig and J.G.M. Thewissen. Academic Press, pp 589 – 592.

Corkeron, P.J. and Connor, R.C. 1999. Why do baleen whales migrate? Mar. Mammal Sci. 15:1228–1245.

Engelhard, G.H., Peck, M.A., Rindorf, A., Smout, S., van Deurs, M., Raab, K., Andersen, K.H, Garthe, S., Lauerburg, R.A.M., Scott, F., Brunel, T., Aarts, G., van Kooten, T. and Dickey-Collas, M. 2014. Forage fish, their fisheries, and their predators: who drives whom? ICES J. Mar. Sci. 71:90–104. doi:10.1093/icesjms/fst087.

Feyrer, L.J. and Duffus, D.A. 2014. Threshold foraging by gray whales in response to fine scale variations in mysid density. Mar. Mammal Sci. doi:10.1111/mms.12178.

Friedlaender, A.S., Goldbogen, J.A., Hazen, E.L., Calambokidis, J. and Southall, B.L. 2014. Feeding performance by sympatric blue and fin whales exploiting a common prey resource. Mar. Mammal Sci. doi:10.1111/mms.12134.

Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D. and Read, A.J. 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Mar. Ecol. Prog. Ser. 317:297–310. doi:10.3354/meps317297.

Goldbogen, J.A., Calambokidis, J., Croll, D.A., Harvey, J.T., Newton, K.M., Oleson, E.M., Schorr, G. and Shadwick, R.E. 2008. Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. J. Exp. Biol. 211:3712–3719. doi:10.1242/jeb.023366.

Goldbogen, J.A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G. and Shadwick, R.E. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. J. Exp. Biol. 214:131–146. doi:10.1242/jeb.048157.

Goldbogen, J.A., Calambokidis, J., Shadwick, R.E., Oleson, E.M., McDonald, M.A. and Hildebrand, J.A. 2006. Kinematics of foraging dives and lunge-feeding in fin whales. J. Exp. Biol. 209:1231–1244. doi:10.1242/jeb.02135.

Goldbogen, J.A., Friedlaender, A.S., Calambokidis, J., McKenna, M.F., Simon, M. and Nowacek, D.P. 2013. Integrative approaches to the study of baleen whale diving behavior, feeding performance, and foraging ecology. BioScience 63:90–100. doi:10.1525/bio.2013.63.2.5.

Hahn, T.R. and Thomas, G. 2008. Modeling the sound levels produced by bubble release of individual herring. J. Acoust. Soc. Am. 124:1849–1857. doi:10.1121/1.2951593.

Haug, T., Lindstrøm, U., Nilssen, K. and Skaug, H.J. 1997. On the variation in size and composition of minke whale *Balaenoptera acutorostrata* forestomach contents. J. Northwest Atl. Fish. Sci. 22:105–114.

HAWG (2014) Report of the herring assessment working group for the area south of 62°N (HAWG). Sec. 04 Herring in the Celtic Sea (Division VIIa South of 52°30'N and VIIg, h, j).

Hazen, E.L., Friedlaender, A.S., Thompson, M.A., Ware, C.R., Weinrich, M.T., Halpin, P.N. and Wiley, D.N. 2009. Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. Mar. Ecol. Prog. Ser. 395:75–89. doi:10.3354/meps08108.

Ingram, S.N., Walshe, L., Johnston, D. and Rogan, E. 2007. Habitat partitioning and the influence of benthic topography and oceanography on the distribution of fin and minke whales in the Bay of Fundy, Canada. J. Mar. Biol. Assoc. UK. 87:149–156. doi:10.1017/S0025315407054884.

Kennedy, A.S., Zerbini, A.N., Rone, B.K. and Clapham, P.J. 2014. Individual variation in movements of satellite-tracked humpback whales *Megaptera novaeangliae* in the eastern Aleutian Islands and Bering Sea. Endanger. Species Res. 23:187– 195. doi:10.3354/esr00570.

Kennedy, A.S., Zerbini, A.N., Vasquez, O.V., Gandilhon, N., Clapham, P.J. and Adam, O. 2013. Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean. Can. J. Zool. 92:9–18. doi:dx.doi.org/10.1139/cjz-2013-0161.

Kenney, R.D., Mayo, C.A. and Winn, H.E. 2001. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. J. Cetacean Res. Manag. 2:251–260.

Laidre, K.L., Heide-Jørgensen, M.P., Heagerty, P., Cossio, A., Bergström, B. and Simon, M. 2010. Spatial associations between large baleen whales and their prey in West Greenland. Mar. Ecol. Prog. Ser. 402:269–284. doi:10.3354/meps08423.

Link, J.S. and Browman, H.I. 2014. Integrating what? Levels of marine ecosystem-based assessment and management. ICES J. Mar. Sci. doi:10.1093/icesjms/fsu026.

Marine Institute 2013. The Stock Book 2013: Annual Review of Fish Stocks in 2013 with Management Advice for 2014. Marine Institute, Rinville, Oranmore

Markussen, N.H., Ryg, M. and Lydersen, C. 1992. Food consumption of the NE Atlantic minke whale (*Balaenoptera acutorostrata*) population estimated with a simulation model. ICES J. Mar. Sci. 49:317–323.

McDonald, M.A., Hildebrand, J.A. and Webb, S.C. 1995. Blue and fin whales observed on a seafloor array in the Northeast Pacific. J.Acous. Soc. Am. 98:712–721.

Nøttestad, L., Sivle, L.D., Krafft, B.A., Langård, L., Anthonypillai, V., Bernasconi, M., Langøy, H. and Axelsen, B.E. 2014. Ecological aspects of fin whale and humpback whale distribution during summer in the Norwegian Sea. Mar. Ecol. 35:221–232. doi:10.1111/maec.12075.

O'Donnell, C., Nolan, C., Mullins, E., Lyons, K., Volkenandt, M., Keogh, N., McAvoy, S. and Williams, D. 2013. Celtic Sea Herring Acoustic Survey Cruise Report 2013. FSS Survey Series: 2013/2014.

Olsen E., Budgell W.P., Head, E., Kleivane, L., Nøttestad, L., Prieto, R., Silva, M.A., Skov, H., Víkingsson, G.A. and Waring, G. 2009. First satellite-tracked long-distance movement of a sei whale (*Balaenoptera borealis*) in the North Atlantic. Aquat. Mamm. 35:313–318. doi:10.1578/AM.35.3.2009.313.

Olsen, E. and Holst, J.C. 2001. A note on common minke whale (*Balaenoptera acutorostrata*) diets in the Norwegian Sea and the North Sea. J. Cetacean Res. Manag. 3:179–184.

Piatt, J.F. and Methven, D.A. 1992. Threshold foraging behavior of baleen whales. Mar. Ecol. Prog. Ser. 84:205–210.

Piatt, J.F., Methven, D.A., Burger, A.E., McLagan, R.L., Mercer, V. and Creelman, E. 1989. Baleen whales and their prey in a coastal environment. Can. J. Zool. 67:1523–1530.

Pierce, G.J., Santos, M.B., Reid, R.J., Patterson, I.A.P. and Ross, H.M. 2004. Diet of minke whales *Balaenoptera acutorostrata* in Scottish (UK) waters with notes on strandings of this species in

Scotland 1992-2002. J. Mar. Biol. Assoc. UK 84:1241–1244. doi:dx.doi.org/10.1017/S0025315404010732h.

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Heppell, S.S., Houde, E.D., Mangel, M., Plagányi. E., Sainsbury, K., Steneck, R.S., Geers, T.M., Gownaris, N. and Munch, S.B. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish. 15:43–64. doi: 10.1111/faf.12004.

Pyke, G.H., Pulliam, H.R. and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 137–154.

Risch, D., Siebert, U. and Van Parijs, S.M. 2014. Individual calling behaviour and movements of North Atlantic minke whales (*Balaenoptera acutorostrata*). Behaviour 151:1335–1360. doi:10.1163/1568539X-00003187.

Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J.B., Nicol, S., Pershing, A. and Smetacek, V. 2014. Whales as marine ecosystem engineers. Front. Ecol. Environ. 12:377–385. doi:10.1890/130220.

Ryan C., Berrow S.D., McHugh B., O'Donnell, C., Trueman, C.N. and O'Connor, I. 2014. Prey preferences of sympatric fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales revealed by stable isotope mixing models. Mar. Mammal Sci. 30:242–258. doi:10.1111/mms.12034.

Ryan, C., Whooley, P., Berrow, S.D., Barnes, C., Massett, N., Strietman, W.J., Broms, F., Stevick, P.T., Fernald, T.W. and Schmidt, C. 2015. A longitudinal study of humpback whales in Irish waters. J. Mar. Biol. Assoc. U.K. doi:10.1017/S0025315414002033.

Saunders, R., O'Donnell, C., Korneliussen, R.J., Fässler, S.M.M., Clarke, M.W., Egan, A. and Reid, D. 2012. Utility of 18-kHz acoustic data for abundance estimation of Atlantic herring (*Clupea harengus*). ICES J. Mar. Sci. 69:1086–1098. doi:10.1093/icesjms/fss059.

Silva, M.A., Prieto, R., Jonsen, I., Baumgartner, M.F. and Santos, R.S. 2013. North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: Building up energy reserves for the journey? PLOS one. doi:10.1371/journal.pone.0076507.

Simmonds, J. and MacLennan, D.N. 2005. Fisheries Acoustics: Theory and Practice. 2nd Edition. Blackwell Science, Oxford, U.K.

Smith, L.A., Link, J.S., Cadrin, S.X. and Palka, D.L. 2014. Consumption by marine mammals on the Northeast US continental shelf. Ecol. Appl. doi:10.1890/13-1656.1.

Travis, J., Coleman, F.C., Auster, P.J., Cury, P.M., Estes, J.A., Orensanz, J., Peterson, C.H., Power, M.E., Steneck, R.S. and Wootton, J.T. 2014. Integrating the invisible fabric of nature into fisheries management. PNAS 111:581–584. doi:10.1073/pnas.1305853111.

Volkenandt, M., Berrow, S., O'Connor, I., Guarini, J.M. and O'Donnell, C. 2015. Prespawning herring distribution in the Irish Celtic Sea between 2005 and 2012. ICES J. Mar. Sci. 72:498–507. doi:10.1093/icesjms/fsu143.

Wahlberg, M. and Westerberg, H. 2003. Sounds produced by herring (*Clupea harengus*) bubble release. Aquat. Living Resour. 16:271–275. doi:10.1016/S0990-7440(03)00017-2.

Watkins, W.A., Sigurjónsson, .J, Wartzok, D., Maiefski, R.R., Howey, P.W. and Daher, M.A. 1996. Fin whale tracked by satellite off Iceland. Mar. Mammal Sci. 12:564–569.

Whooley, P., Berrow, S. and Barnes, C. 2011. Photo-identification of fin whales (*Balaenoptera physalus* L.) off the south coast of Ireland. Mar. Biodivers. Rec. 4:1–7. doi:10.1017/S1755267210001119.

Willis, J. 2014. Whales maintained a high abundance of krill; both are ecosystem engineers in the Southern Ocean. Mar. Ecol. Prog. Ser. 513:51–69. doi:10.3354/meps10922.

Wilson, B., Batty, R.S. and Dill, L.M. 2004. Pacific and Atlantic herring produce burst pulse sounds. Proc. R. Soc. Lond.: Biol. Sci. 271:S95–S97. doi:10.1098/rsbl.2003.0107.

Witteveen, B.H., Foy, R.J., Wynne, K.M. and Tremblay, Y. 2008. Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. Mar. Mammal Sci. 24:516–534. doi:10.1111/j.1748-7692.2008.00193.x.

Zerbini, A.N., Andriolo, A., Heide-Jørgensen, M.P., Pizzorno, J.L., Maia, Y.G., VanBlaricom, G.R., DeMaster, D.P., Simões-Lopes, P.C., Moreira, S. and Bethlem, C. 2006. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. Mar. Ecol. Prog. Ser. 313:295–304.

Tables

Table 1. Overview of cetacean watch effort (in hours) and sightings per unit effort (n per hour) from 2007 to 2013 with the respective number of sightings of baleen whales on species level.

	total	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**
Hours of effort	626	96	79	78	88	78	110	97
Sightings per unit effort	0.18	0.15	0.18	0.22	0.10	0.36	0.15	0.15
Total baleen whale sightings	113	14	14	17	9	28	16	15
Fin whale	61	3	9	4	3	24	12	6
Minke whale	30	8	5	8	1	4	2	2
Humpback whale	2	1			1			
Unident. baleen whale	20	2	0	5	4	0	2	7

Table 2. Number of events of spatial co-occurrence between baleen whales and forage fish, herring, sprat and mackerel for increasing radii (in km) centred to the whale. The total number of observed (obs.) and simulated (sim.) whale sightings are given as "n". Significant differences of probabilities between observation and simulation were calculated, p-value rounded to two decimals and significant events are highlighted in bold ($p < 0.05$).

		forage fish			**herring**			**sprat**			**mackerel**		
		obs.	sim.	*p*	obs.	sim.	*p*	obs.	sim.	*p*	obs.	sim.	*p*
n		113	22600		113	22600		104	20800		88	17600	
radius (km)	2	**43**	**4630**	**<0.01**	**25**	**2671**	**<0.01**	**14**	**1473**	**0.03**	4	501	0.54
	4	**60**	**8206**	**0.02**	33	4928	0.17	**33**	**2895**	**<0.01**	8	978	0.26
	6	**80**	**11086**	**0.01**	**50**	**6779**	**0.03**	**48**	**4300**	**<0.01**	9	1541	0.76
	8	**94**	**14191**	**0.05**	**63**	**8797**	**0.03**	**54**	**6116**	**<0.01**	14	2197	0.49
	10	96	15966	0.21	68	10142	0.07	**57**	**7421**	**0.01**	18	2765	0.38
	14	98	18759	0.80	76	12607	0.23	65	10111	0.13	24	3960	0.47
	16	105	19890	0.74	79	13861	0.41	73	11479	0.13	28	4755	0.52
	18	105	20449	0.90	81	14581	0.52	76	12382	0.20	33	5287	0.33
	20	107	20963	0.93	84	15380	0.59	78	13325	0.33	40	5984	0.15
	25	110	21637	0.95	89	16868	0.76	82	14779	0.53	47	7354	0.20
	30	112	22077	0.97	95	18133	0.79	84	15840	0.74	49	8586	0.51

Figure legends

Figure 1 The proportion of positive spatial overlap of a whale sighting and the presence of fish is shown for herring, sprat and mackerel and their combination here defined as forage fish. Observed proportions of overlap are shown (closed lines) and compared to simulated data (dotted lines) with increasing distance to the whale sighting. Significant differences ($p < 0.05$) between the two models are shown. The black vertical line indicated the break in significance with distances larger than 8 km.

Figure 2 Visualisation of the fish and whale sighting distribution in the Celtic Sea from 2007 to 2013. Whale sightings with fish within 8 km to the sighting are indicated (black squares), while no spatial overlap is indicated with a cross. Fish biomass (coloured points) has been calculated based on the NASC values per EDSU from the acoustic survey (grey points). No biomass was calculated for sprat in 2010 and mackerel at any year; NASC values were seen as presence only (light blue point).

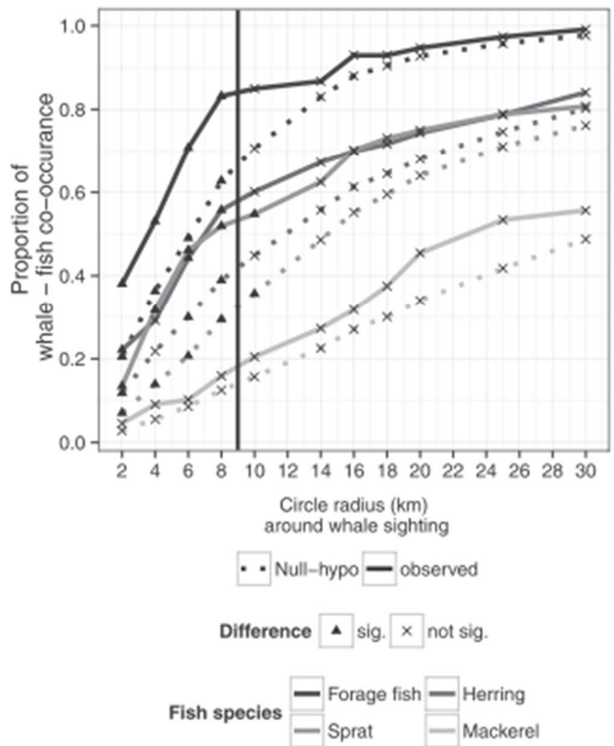
Figure 3 Calculated fish biomass by year for herring and sprat over the circular area of 8 km distance to the whale sighting is shown for respective whale species. (in colour in the online version)

Figure 4 Total herring and sprat biomass observed during the surveys in tonnes per thousand over the entire survey area. No biomass was estimated for sprat in 2010. Note different scales on the y-axis.

Figure 5 Average fish length for herring and sprat within 8 km to the observed and simulated sighting compared to the average length of fish recorded for the full survey. No whale sightings were recorded within proximity to sprat in 2008 and no data was available for sprat in 2012.

Figure 6 Herring abundance by age class and average length per age is given. Numbers were obtained from the Celtic Sea herring stock assessment (HAWG 2014).

Figures



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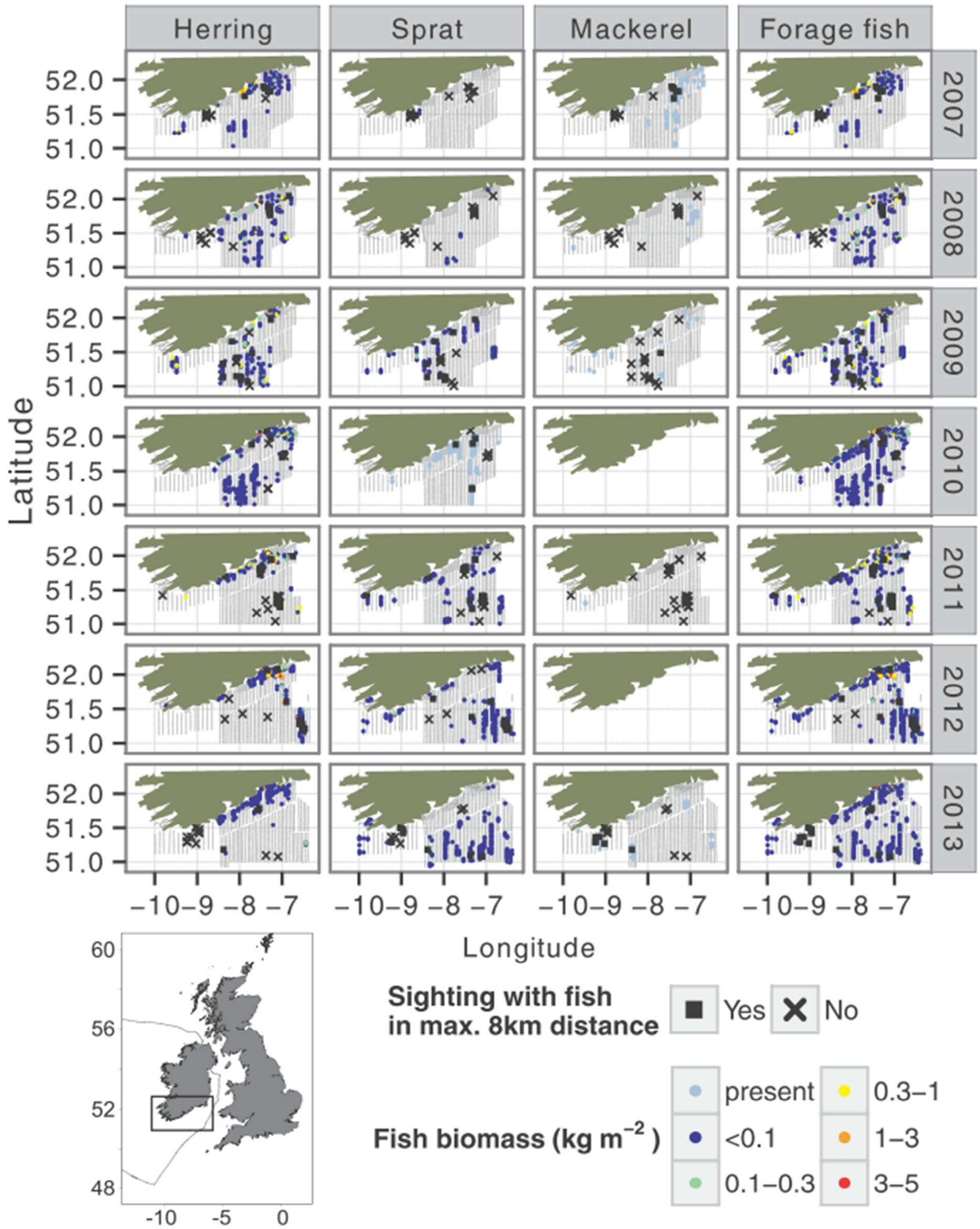

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No biomass was calculated for sprat in 2010 and mackerel at any year; NASC values were seen as presence only (light blue point).

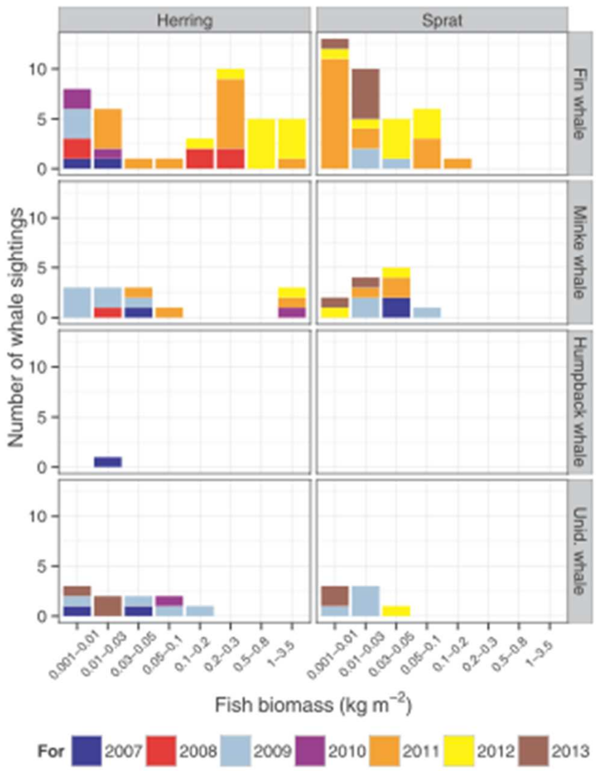


Figure 3 Calculated fish biomass by year for herring and sprat over the circular area of 8 km distance to the whale sighting is shown for respective whale species. (in colour in the online version)

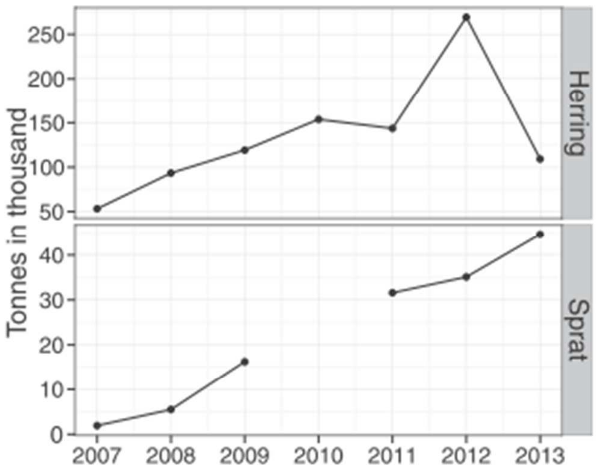


Figure 4 Total herring and sprat biomass observed during the surveys in tonnes per thousand over the entire survey area. No biomass was estimated for sprat in 2010. Note different scales on the y-axis.

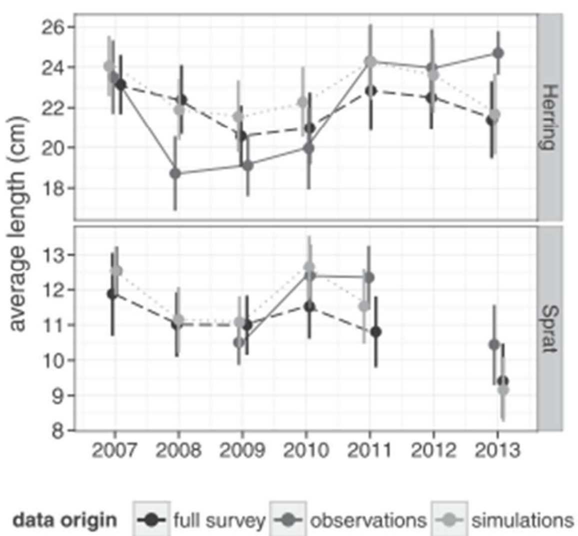


Figure 5 Average fish length for herring and sprat within 8 km to the observed and simulated sighting compared to the average length of fish recorded for the full survey. No whale sightings were recorded within proximity to Sprat in 2008 and no data was available for sprat in 2012.

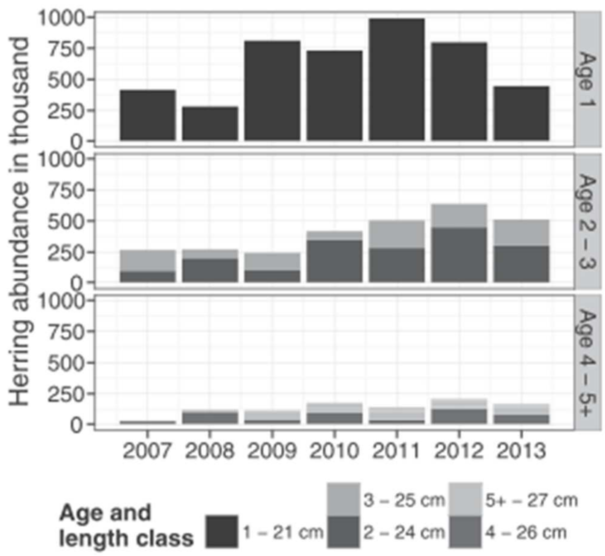
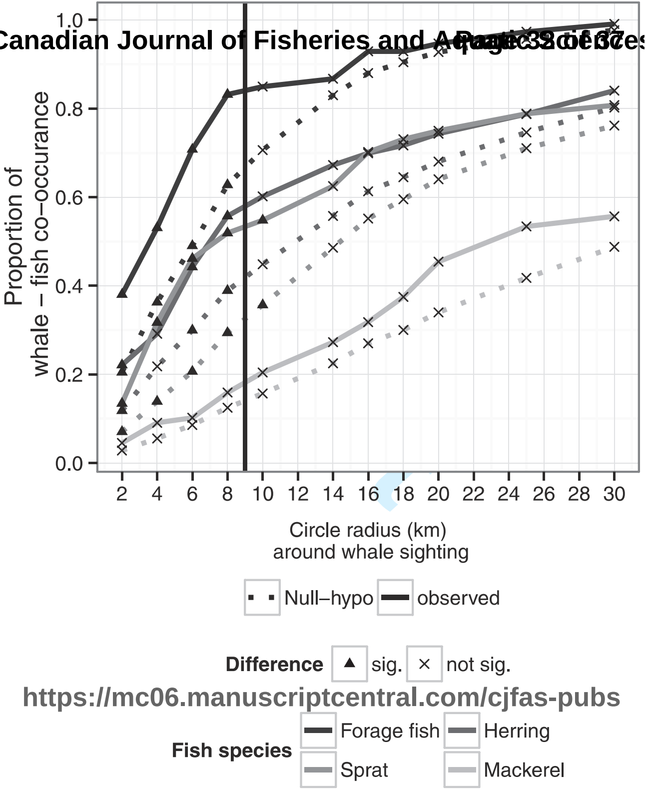
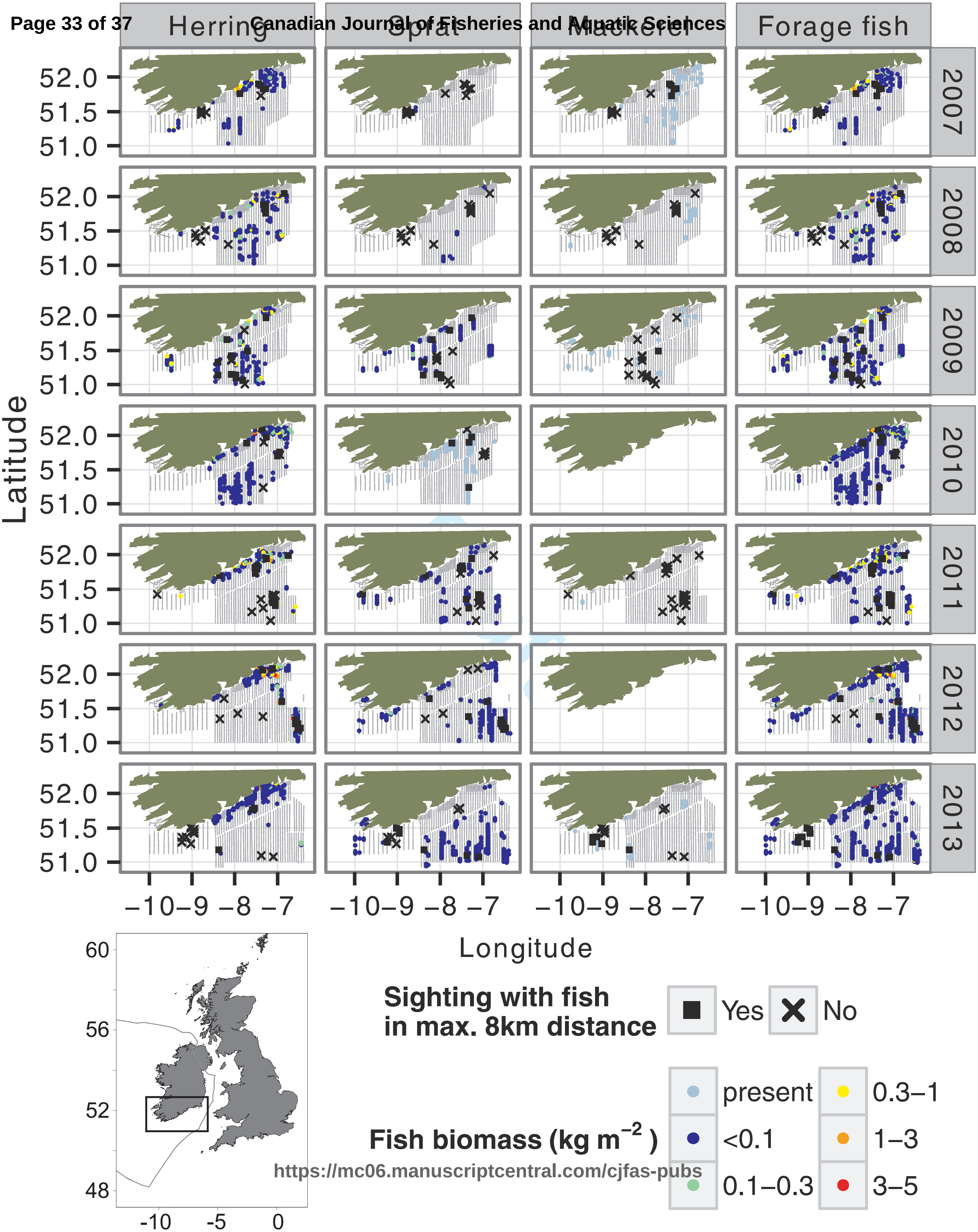
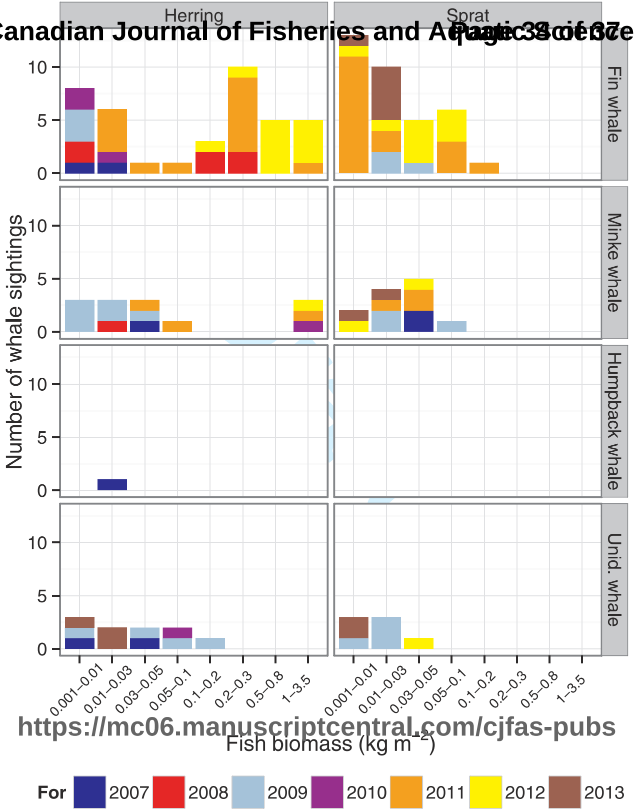


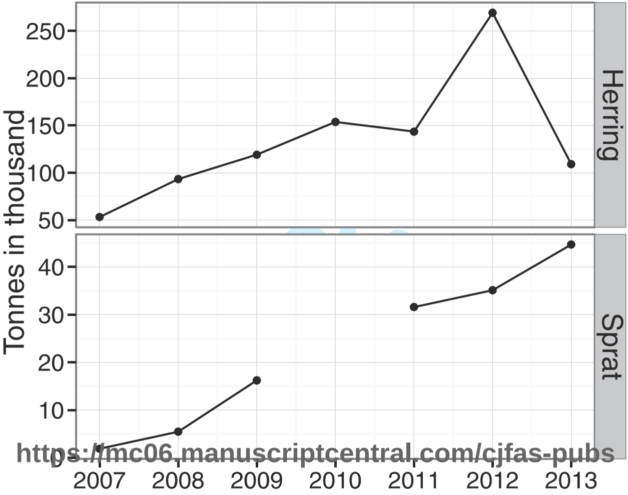
Figure 6 Herring abundance by age class and average length per age is given. Numbers were obtained from the Celtic Sea herring stock assessment (HAWG 2014).

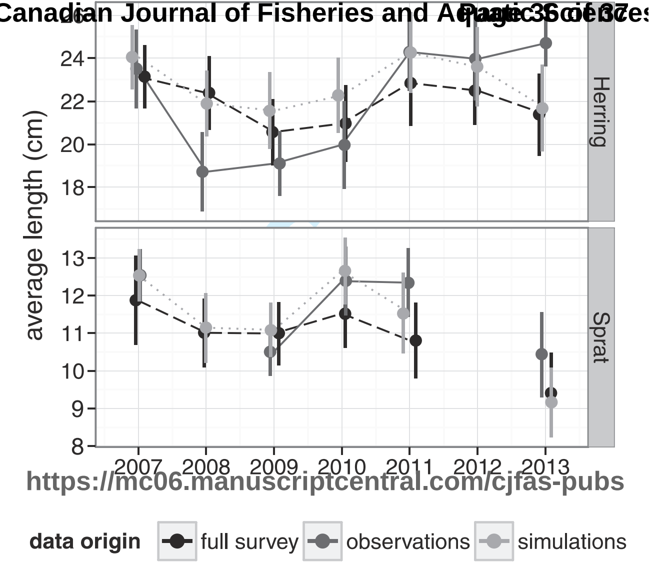

Proportion of
whale – fish co–occurance
1.0
0.8
0.6
0.4
0.2
0.0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Circle radius (km)
around whale sighting
Null–hypo
observed
Difference
sig.
not sig.
Fish species
Forage fish
Herring
Sprat
Mackerel

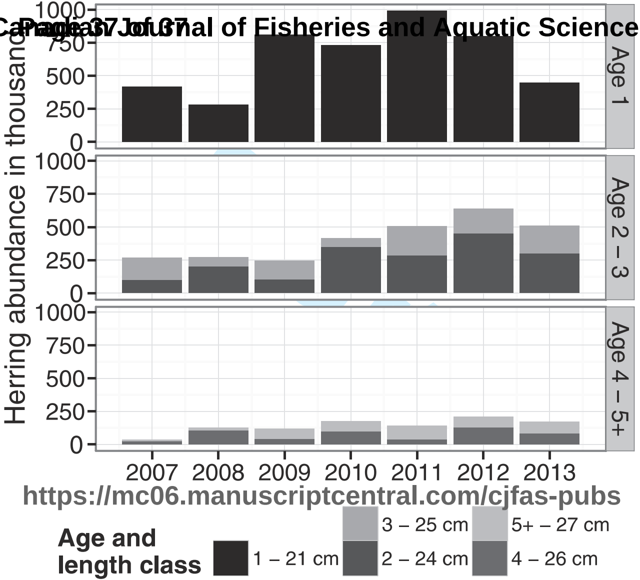

Herring
Sprat
Mackerel
Forage fish
2007
2008
2009
2010
2011
2012
2013
Latitude
52.0
51.5
51.0
Longitude
−10 −9 −8 −7
60
56
52
48
-10
-5
0
Sighting with fish in max. 8km distance
Yes
No
Fish biomass (kg m^{-2})
present
<0.1
0.1–0.3
0.3–1
1–3
3–5


Herring
Sprat
Fin whale
Minke whale
Humpback whale
Unid. whale
Number of whale sightings
0
5
10
0.001–0.01
0.01–0.03
0.03–0.05
0.05–0.1
0.1–0.2
0.2–0.3
0.5–0.8
1–3.5
Fish biomass (kg m^{-2})
For
2007
2008
2009
2010
2011
2012
2013

Canadian Journal of Fisheries and Aquatic Sciences




Herring
Sprat
average length (cm)
2007
2008
2009
2010
2011
2012
2013
data origin
full survey
observations
simulations


Herring abundance in thousands
Age 1
Age 2 – 3
Age 4 – 5+
0
250
500
750
1000
2007
2008
2009
2010
2011
2012
2013
Age and
length class
1 – 21 cm
3 – 25 cm
2 – 24 cm
5+ – 27 cm
4 – 26 cm