Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0073.R2
Manuscript Type:	Article
Date Submitted by the Author:	07-Sep-2015
Complete List of Authors:	Volkenandt, Mareike; Université de Pierre and Marie Curie, Laboratoire d'Ecogéochimie des Environnements Benthiques UMR 8222 O'Connor, Ian; Marine Freshwater Research Centre, Galway-Mayo Institute of Technology Guarini, Jean-Marc; Université de Pierre et Marie Curie, Laboratoire d'Ecogéochimie des Environnements Benthique UMR 8222 Berrow, Simon; Irish Whale and Dolphin Group, ; Marine Freshwater Research Centre, Galway-Mayo Institute of Technology O'Donnell, Ciaran; Marine Institute,
Keyword:	fin whale (<i>Balaenoptera physalus</i>), foraging distance, herring (<i>Clupea harengus</i>), minke whale (<i>Balaenoptera acutorostrata</i>), sprat (<i>Sprattus sprattus</i>)

SCHOLARONE™
Manuscripts

Title:

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

Authors (order and email contact):

Mareike Volkenandt ^{1,2} (Volkenandt.Mareike@gmail.com)

Ian O'Connor ¹ (Ian.OConnor@gmit.ie)

Jean-Marc Guarini ² (jean-marc.guarini@upmc.fr)

Simon Berrow ^{1,3} (Simon.Berrow@gmit.ie)

Ciaran O'Donnell ⁴ (Ciaran.O'Donnell@Marine.ie)

Affiliations:

1. Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland
2. Laboratoire d'Ecogéochimie des Environnements Benthique / UMR 8222, Université Pierre et Marie Curie, Avenue du Fontaulé, 66650 Banyuls sur Mer, France
3. Irish Whale and Dolphin Group, Merchants Quay, Kilrush, Ireland
4. Marine Institute, Rinnville, Oranmore, Ireland

Corresponding author: Mareike Volkenandt, Email: Volkenandt.Mareike@gmail.com

Laboratoire d'Ecogéochimie des Environnements Benthique / UMR 8222, Université Pierre et Marie Curie, Avenue du Fontaulé, 66650 Banyuls sur Mer, France;

Phone: +33 4 68 88 73 94, Fax: + 33 4 68 88 73 95

Abstract

Baleen whales can be regularly observed in the Celtic Sea, however little is known about their local foraging behaviour. The study objective was to determine whether or not baleen whales selectively prey upon particular forage fish species 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 (*Balaenoptera physalus*, *Balaenoptera acutorostrata* and *Megaptera novaeangliae*) were carried out simultaneously from 2007 to 2013 during dedicated fisheries acoustic surveys assessing the abundance and distribution of forage fish. Probabilities of spatial overlap 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 dominantly observed in areas with herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), while areas with mackerel (*Scomber scombrus*) were not targeted. A 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. By linking baleen whale distribution to high-density herring and sprat areas it was possible to identify the Celtic Sea as a prey hot spot for baleen whales during autumn.

Keywords

fin whale (*Balaenoptera physalus*); foraging distance; herring (*Clupea harengus*); minke whale (*Balaenoptera acutorostrata*); sprat (*Sprattus sprattus*)

Introduction

Baleen whales undergo annual long-distance migrations from mating and calving 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 2015; 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 as top predators within the assessment of an ecosystem, and baleen whale impacts on prey population dynamics should be explored within 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 whales (*Balaenoptera physalus*) (Whooley et al. 2011; Ryan et al. *in press*),

suggesting some seasonal site fidelity within and between years. Understanding the habitat utilisation of baleen whales, based on local, small-scale behaviour traits including prey selectivity, foraging thresholds and foraging duration, can help to characterize links across trophic levels in the Celtic Sea. Such an understanding of trophic chains and the respective indication of conflicts due to resource competition can assist ecosystem-based fisheries management.

Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*) and Atlantic mackerel (*Scomber 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 based on stable isotope analysis 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 coincidentally passing the Celtic Sea during migration? Or is the Celtic Sea plateau a prey hot spot where baleen whales are associated with herring, sprat and mackerel?

Referring to seven years of synoptically observed predator and prey distributions, 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, sprat and mackerel. Further, where spatial overlap occurred, we calculated the average biomass and average length of forage fish in proximity to the whale sighting. With this approach, we sought to explore the habitat use of baleen whales in relation to commercially exploited forage fish in the Celtic Sea, and to provide baseline information for ecosystem management considerations.

Materials 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 southern Irish 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 horizontal segments 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 echotracess that were positively identified as herring or sprat were analysed in this study (O'Donnell et al. 2013).

EDSU values for herring and sprat were transformed into fish abundance per square metre. The average fish length (L , in cm) for each species from the closest geographical trawl to the respective EDSU was used to calculate the target strength (TS), which indicates the species-specific strength of the acoustic echo (Simmonds and MacLennan 2005). At 38 kHz the TS used for herring and sprat was:

$$TS = 20 \log L - 71.2dB.$$

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 for herring with $TS = 20 \log L - 69.7dB$ was used instead (Saunders et al. 2012). No abundance was estimated in 2010 for sprat, however the echotracess were used for the presence/absence analysis. Abundance was multiplied by the average fish weight, taken from the nearest trawl to obtain fish biomass (B , in kg m^{-2}) (Simmonds and MacLennan 2005). EDSU

values for mackerel were used as 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 from the bow 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 Beaufort 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. Here sightings were used as the unit to describe the presence of a whale, irrespective of group size per sighting; however most individuals were solitary and the largest group contained 10 individuals, which was recorded only once.

Analysis of spatial overlap and fish biomass within proximity

Fish biomass within the area around the observed whale sighting can identify a biomass target and foraging threshold of baleen whales. Therefore whale sightings were aligned with the acoustic dataset from the respective year, and fish biomass was calculated for circular areas (B_{area} , in kg m^{-2}) with different radii ($R=2, 4, 6, 8, 10, 14, 16, 18, 20, 25$ and 30 km) centred on the whale sighting. Biomass was averaged for each transect within the circle (B_t , in kg m^{-2}) and weighted with the EDSU distance of 1852 m and transect length (l_t , in meters):

$$B_t = \frac{\sum B \times 1852}{l_t}$$

To obtain B_{area} , average B_t was weighted with l_t and the total transect length within the circle (l_{area} , in meters); then the respective biomass estimate was applied to the surface area:

$$B_{area} = \pi \times R^2 \times \sum^{transect} \frac{B_t \times l_t}{l_{area}}$$

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 spatial overlap 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 from random were tested with a two-sided probability test of success (function `prob.test`, “stats” package, R software). 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 certain prey sizes. The total length values recorded from the fishing trawls during the survey were averaged:

- $\overline{TL}_{obs}$: average fish length from the trawl geographically closest to the whale observation; here called “observations”;

- $\overline{TL}_{sim}$: average fish length from the trawl geographically closest to the simulated whale location; here called “simulations”;
- $\overline{TL}_{full}$: average fish length from all trawls 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 Honestly Significant Difference test.

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

Results

Spatial overlap between baleen whales and forage fish

A total of 113 baleen whale sightings was recorded from 2007 to 2013 (Table 1). 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 of a sighting close to herring and sprat was similar over the distances. The highest proportions of spatial overlap were found when fish species were combined as forage fish (Figure 1). Proportions obtained from simulated random whale sightings showed the same pattern of increasing spatial overlap with radius (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 of 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 highest significant proportion of spatial overlap was 0.83 with a distance of 8 km of a sighting. In other words 94 of 113 whale sightings were recorded in proximity to forage fish (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 occur 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

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), applied over the area this represented 200 to 40,200 tonnes of fish. 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. Correspondingly, herring biomass close to fin whale sightings was high with 0.3 to 3.5 kg m⁻² in 2008, 2011 and 2012 (Figure 3). Likewise minke whales were seen in those herring-rich areas between 2010 and 2012 (Figure 3). 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 of each whale sighting

Average fish length for herring and sprat was calculated for fish within 8 km of a whale sighting and each simulated sighting location; and then compared to the total average fish length of the survey for each year. No significant differences in average length between the three groups were found (Figure 5). In more detail, no significant difference was detected for $\overline{TL}_{sim}$ compared to $\overline{TL}_{full}$ for either herring or 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).

Discussion

Over 80% of the baleen whale sightings were recorded in close proximity to herring and sprat (56% and 52% respectively). No significant spatial overlap was found for mackerel and baleen whales. The highest proportion of significant spatial overlap of prey and predator occurred within a distance of 8 km. Fin and minke whales were sighted in areas with 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. No significant difference in the fish length distribution in proximity to whales (to 8 km) and fish that were encountered without a simultaneous baleen whale sighting was found.

In the literature prey density distribution and environmental descriptors like sea surface temperature are used as explanatory factors in multivariate regression analysis to analyse whale distribution on feeding grounds (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 cases, no or only weak

spatial overlap of prey and baleen whales was found, which could be due to mis-matches in spatial and temporal resolution in the data (Laidre et al. 2010; Nøttestad et al. 2014). Annual surveys provide a snapshot of the ecosystem in time and hence spatial overlap of both moving predator and prey could easily be missed. With the prior understanding of herring distribution in the Celtic Sea in October, we expect that baleen whale distribution would follow the patchy distribution of its prey (Volkenandt et al. 2015) and 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). Here the spatial and temporal overlap of predator and prey was enforced by taking raw sighting data, i.e., the sighting coordinates and prey abundances in the surrounding, rather than taking sightings per survey unit or per grid cell. The acoustic survey for Celtic Sea herring provided a valuable opportunistic platform for obtaining high-quality fish distribution and abundance information with synoptic observations of baleen whale occurrence and allowed to identify the Celtic Sea plateau as a prey hot spot for baleen whales in autumn.

Spatial overlap of baleen whales and forage fish

With the analysis of increasing radii centred on a whale sighting, the spatial resolution of overlapping predator and prey distributions was identified. Overlap with fish farther than 8 km from the sighting statistically resembled a coincidental spatial overlap. Within the concept of prey detection and foraging on a local 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, dolphins and other baleen whales (Watkins and Schevill 1979; Anderwald et al. 2011), could be received within this distance and attract baleen whales to the prey source. Once detected and encountered by the whale, fish schools can be tracked and preyed on, while energetic costs for a new search effort and relocation can be reduced. 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 speeds 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). A distance of less than 10 km appears to be a profitable and easily reachable distance for foraging by staying close—but not too close—to prey.

Whale sightings were predominantly recorded in close proximity to fish, but not all whale sightings corresponded 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. 2015). Most feeding activities of baleen whales happen below the sea surface and are therefore less likely to be observed from a ship (Watkins and Schevill 1979), which could have further reduced the proportion of recorded feeding events during the surveys.

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 and the neighbouring North Sea and North Atlantic (Haug et al. 1997; Olsen and Holst 2001; Pierce et al. 2004; Ryan et al. 2014). Proximity of baleen whales to mackerel was not significantly different to a coincidental encounter in the Celtic Sea. Mackerel has been found as prey together with other species in one out of 15 minke whale stomachs (Olsen and Holst 2001) and has been mentioned as prey for humpback whales (Clapham 2009). Their infrequency in stomach contents of baleen whales together with the non-significant spatial overlap in the Celtic Sea, indicates that mackerel itself is not a main prey target, but may be consumed while preying on mixed fish schools in the region during autumn. Direct observations of mackerel made over successive years during the survey found this species to form low-density and widely dispersed layers as compared to the larger, high-density localised schools formed by herring

and sprat. Mackerel are fast swimmers, due to the larger body size compared to the clupeids. Hence foraging on mackerel could require a higher effort and could be less rewarding energetically compared to foraging on herring and sprat, which at this time of the year can be considered a more optimal prey.

Another explanation why more baleen whales were observed in areas with herring and sprat than mackerel could be due to a higher detectability of the clupeid species. Sounds and visual cues produced by the flow of air bubbles out of the swimbladder in herring and sprat could have facilitated the detection of clupeid species for baleen whales and other predators, which can further intensify the cues, e.g., foraging seabird flocks (Wahlberg and Westerberg 2003; Wilson et al. 2004; Hahn and Thomas 2008). Mackerel do not possess a swimbladder and could therefore be more difficult to detect for predators. More research is required to explore how baleen whales are attracted to prey, and to define the role of prey accessibility (i.e., foraging effort and cost) and prey detectability (e.g., cues by the prey species itself or foraging predators) within the foraging strategy of baleen whales.

Fish biomass and average length within an 8-km foraging distance

Within ecosystem-based fishery management, the uncertainty in baleen whale energetic requirement and consumption rate estimates complicates a comparison of fisheries exploitation and baleen whale consumption of the same resources. Smith et al. (2015) calculated daily consumption rates with relatively large confidence intervals for baleen whales for the Northeast US continental shelf. If their estimated average daily consumption of an individual fin whale (981 kg), minke whale (165 kg) and humpback whale (621 kg; Smith et al. 2015) can be applied to the Celtic Sea region, then baleen whales encountered sufficiently high prey abundances to forage over several days within the same patch. On average, fin and minke whales stayed in areas with $0.001 - 0.2 \text{ kg m}^{-2}$ (200

– 40,200 tonnes) of forage fish within an 8-km radius. Biomass observations were extrapolated over a circular area to obtain these estimates, but it has to be noted that forage fish did not form a continuous prey field and that biomass was built from several separated fish schools of different densities (Volkenandt et al. 2015). Baleen whales require high-density schools within prey patches to obtain a high energetic return of metabolically expensive bulk filter-feeding strategies (Goldbogen et al. 2008; 2011).

Herring and sprat biomass determined by the acoustic survey for the research area increased over time. Herring biomass was sufficiently high in all years to enable foraging with a high energetic net return. Fin whales did not target sprat in the years of low sprat stock biomass encountered during the survey. At the start of the time series, sprat biomass could have been too low, and school density and school size could have been insufficient to provide an efficient energetic return for fin whale foraging. Energetic costs for foraging and diving are related to body size in baleen whales (Goldbogen et al. 2012); hence, the lower sprat biomass in early years could have been satisfactory for the smaller minke whale (which was recorded in areas with sprat in all years), but not for the larger fin whale. The absence in low-sprat biomass areas and the presence of fin whales in high-prey biomass areas support the theory of a suggested prey biomass and foraging threshold for baleen whales (Piatt and Methven 1992; Goldbogen et al. 2011; Feyrer and Duffus 2015; Friedlaender et al. 2015).

A comparison of average fish length in proximity to baleen whales and the overall fish length distribution showed no significant differences and any prey size selection was not apparent. This suggests that baleen whales consumed forage fish of all lengths in the Celtic Sea. The numerous pairwise comparisons in the analyses increased the chance of making a type I error, being the incorrect rejection of the null hypothesis. Therefore additional data, e.g., otoliths from stomach contents of stranded whales, would be needed to improve the power of the analysis on prey size selectivity; however such data are difficult to obtain. To date, the only available data on baleen

whale diets (based on stable isotope analyses) in the Celtic Sea indicated a selectivity for smaller fish (sprat and juvenile herring) followed by larger herring (age 2 to 4) (Ryan et al. 2014). These two groups represent the dominant size classes of the forage fish community in the Celtic Sea (HAWG 2014). Based on our spatial analysis and the available stable isotope results, we suggest that baleen whales non-selectively target herring and sprat in autumn in the Celtic Sea.

Optimal foraging theory predicts that prey abundance, prey depletion over time, and energetic costs of travelling to a new area define the net energetic gain for baleen whales (Charnov 1976; Pyke et al. 1977). A negative energy balance, e.g., via prey depletion and an increased effort for foraging (due to less dense fish schools occurring after the spawning period) could result in the decision of baleen whales to leave the Celtic Sea plateau. Hence, more information on arrival and departure of baleen whales is needed to define baleen whale residence time in the Celtic Sea. Whale tagging experiments could help to provide further valuable information on residence time, habitat use and foraging ecology during different months in the Celtic Sea. Limited to the autumn time, the acoustic herring survey used as platform of opportunity provided concurrent important information on predator and prey in the Celtic Sea. By linking baleen whale distribution to high-density herring and sprat areas, the Celtic Sea was identified as hot spot for baleen whales. This is a first and necessary initial step for future studies on baleen whale foraging on small pelagic fish in the Celtic Sea. For true ecosystem-based management, predator, prey and their interactions have to be accounted for (Link and Browman 2014). Hence, after acknowledging the Celtic Sea as a prey hot spot and the importance of forage fish biomass for baleen whale foraging, further research on predator populations and their foraging decisions is necessary to evaluate predation impacts on commercially exploited fish stocks.

Acknowledgements

We are grateful to the chief scientists, crew and scientific crew of the CSHAS'07 to CSHAS'13 surveys from the Marine Institute for data collection. We thank the Irish Whale and Dolphin Group for the use of the cetacean data set and Dave Wall, Paula Ní Ríogaín, Enda McKeogh and David Williams for collecting the marine mammal data during the Celtic Sea Herring Acoustic Survey. Biological and acoustic data used in this study belong to the Marine Institute (Rinville, Ireland) and were used under the Data Agreements 2011/252, 2013/045, 2014/118 and 2014/161. M. Volkenandt was funded through a MARES Grant. MARES is a joint doctorate programme selected under Erasmus Mundus coordinated by Ghent University (FPA 2011 – 0016). Thanks to Cólín Minto, Conor Ryan and two anonymous reviewers, whose comments greatly improved this manuscript.

References

- Anderwald, P., Evans, P.G., Gyax, 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(2):129–136.
- Clapham, P. 2001. Why do baleen whales migrate? *Mar. Mammal Sci.* 17(2):432–436.
- Clapham, P. 2009. Humpback Whale. In *Encyclopedia of Marine Mammals Edited by W.F. Perrin, B. Würsig and J.G.M. Thewissen*. Academic Press, pp 582 – 585.
- Corkeron, P.J. and Connor, R.C. 1999. Why do baleen whales migrate? *Mar. Mammal Sci.* 15(4):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(1):90–104. doi:10.1093/icesjms/fst087.
- Feyrer, L.J. and Duffus, D.A. 2015. Threshold foraging by gray whales in response to fine scale variations in mysid density. *Mar. Mammal Sci.* 31(2):560–578. doi:10.1111/mms.12178.
- 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.

Friedlaender, A.S., Goldbogen, J.A., Hazen, E.L., Calambokidis, J. and Southall, B.L. 2015. Feeding performance by sympatric blue and fin whales exploiting a common prey resource. *Mar. Mammal Sci.* 31(1):345–354. doi:10.1111/mms.12134.

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., 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., 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(2):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(3):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). International Council for the Exploration of the Sea, ICES, Copenhagen, Denmark.

- 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(1):149–156. doi:10.1017/S0025315407054884.
- 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(1):9–18. doi:dx.doi.org/10.1139/cjz-2013-0161.
- 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(2):187–195. doi:10.3354/esr00570.
- 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. Manage. Special Issue 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. 71(5):345–354. 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, Ireland.

- 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(3):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(2):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(2):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, Marine Institute, Rinnville, Oranmore, Ireland.
- 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. Manage. 3(2):179–184.
- 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(3):313–318. doi:10.1578/AM.35.3.2009.313.
- 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(6):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(6):1241–1244.
doi:[dx.doi.org/10.1017/S0025315404010732h](https://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(1):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.* 52:137–154.

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(7):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(1):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. *in press*. 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(6):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 8(10):e76507. 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. 2015. Consumption by marine mammals on the Northeast US continental shelf. Ecol. Appl. 25(2):373–389. 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. Proc. Nat. Acad. Sci. USA 111(2):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(2):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(3):271–275. doi:10.1016/S0990-7440(03)00017-2.

Watkins, W. A. and Schevill, W.E. 1979. Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. J. Mamma. 60(1):155–163.

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(4):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(3):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 watch effort and baleen whale sightings from 2007 to 2013.

	total	2007	2008	2009	2010	2011	2012	2013
hours of effort	626	96	79	78	88	78	110	97
baleen whale sightings per hour	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	0	0	1	0	0	0
unidentified baleen whale	20	2	0	5	4	0	2	7

Table 2. Numbers of events of spatial overlap between baleen whales and all forage fish, herring, sprat and mackerel for increasing radii (in km) centred on the whale sighting. Total numbers of observed (obs.) and simulated (sim.) whale sightings are given as “n”. Statistically significant differences between observed and simulated sighting locations ($p < 0.05$) are highlighted in bold.

all forage fish					herring			sprat			mackerel		
	obs.	sim.	<i>p</i>	obs.	sim.	<i>p</i>	obs.	sim.	<i>p</i>	obs.	sim.	<i>p</i>	
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 all forage fish, herring, sprat and mackerel. 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 distributions in the Celtic Sea from 2007 to 2013. Whale sightings with fish within 8 km of the sighting are indicated (black squares), while no spatial overlap is indicated by a cross. Fish biomass (coloured points) has been calculated from the acoustic survey (grey points). No biomass was calculated for sprat in 2010 or mackerel in any year; values were considered as presence only (light blue points).

Figure 3 Frequency distributions of calculated herring and sprat biomass within 8 km of each whale sighting ($n=133$), by year and whale species.

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

Figure 5 Average fish length for herring and sprat within 8 km of the observed and simulated sightings 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 were available for sprat in 2012.

Figures

Figure 1 The proportion of positive spatial overlap of a whale sighting and the presence of fish is shown for all forage fish, herring, sprat and mackerel. 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 distributions in the Celtic Sea from 2007 to 2013.

Whale sightings with fish within 8 km of the sighting are indicated (black squares), while no spatial overlap is indicated by a cross. Fish biomass (coloured points) has been calculated from the acoustic

Figure 1 consists of eight stacked bar charts arranged in a 4x2 grid. The rows represent four whale species: Fin whale, Minke whale, Humpback whale, and Unid. whale. The columns represent two prey species: Herring and Sprat. The y-axis for all charts is 'Number of whale sightings' (0 to 10). The x-axis is 'Fish biomass (kg m⁻²)' with categories: 0.001-0.01, 0.01-0.03, 0.03-0.05, 0.05-0.1, 0.1-0.2, 0.2-0.3, 0.3-0.5, 0.5-0.8, 1-3.5. The legend at the bottom indicates the years: 2007 (blue), 2008 (orange), 2009 (green), 2010 (purple), 2011 (yellow), 2012 (brown), and 2013 (pink). The bars are stacked by year, with 2007 at the bottom and 2013 at the top. The Fin whale charts show the highest number of sightings, particularly in the 0.2-0.3 kg m⁻² range for Herring and 0.01-0.03 kg m⁻² for Sprat. The Minke whale charts show sightings across most biomass ranges. The Humpback whale charts show very few sightings, mostly in the 0.01-0.03 kg m⁻² range. The Unid. whale charts show sightings across most biomass ranges, with a peak in the 0.01-0.03 kg m⁻² range for Sprat.

28

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

Figure 5 Average fish length for herring and sprat within 8 km of the observed and simulated sightings 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 were available for sprat in 2012.