DOKTORANDUPPSATS
ZOOLOGISKA INSTITUTIONEN
Stockholms Universitet S-106 91 Stockholm

THE BALTIC SEA ECOSYSTEM FROM A PORPOISE POINT OF VIEW

Författare: Ida Carlén

Ämne: Zoologisk ekologi

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Författarens namn: **Ida Carlén**

Handledare: **Anders Angerbjörn**

Forskningsämne: **Zoologisk ekologi**

Granskningskommitté: **Julia Carlström, Bodil Elmhagen, Anders Bignert**

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This essay is an attempt to predict the geographical areas important to the harbour porpoise (*Phocoena phocoena*) in the Baltic Sea. I will discuss what environmental factors may influence porpoise distribution, on what scale these parameters may be important and, based on this, what geographical areas in the Baltic Sea that may be of importance to porpoises. The foundation of this essay is a literature review, gathering knowledge on porpoises in general, their habitat and prey preferences and the environment of the Baltic Sea. Firstly, I look at the ecology of the harbour porpoise in general and the Baltic Sea harbour porpoise in particular, discussing what we know about its ecology from the current literature. Secondly, I discuss some key qualities of the Baltic Sea and the distribution of known prey species. Thirdly, I try to infer from the gathered knowledge what we can expect of the distribution and habitat preferences of the Baltic Sea harbour porpoise.

Harbour porpoise ecology

Short introduction to the harbour porpoise and its population structure in the Baltic region.

Here, emphasis will be put on life history and population structure of porpoises in the Baltic region, since population may have a real effect on the habitat use that is my main focus – different populations or subpopulations of porpoises may have different prey (Santos and Pierce, 2003) and react differently to qualities in their environment. They should therefore be considered separate entities when predicting distribution.

The harbour porpoise is a small odontocete, toothed whale, which inhabit temperate and cold shelf waters in the North Pacific, North Atlantic and the Black Sea. The harbour porpoise grows to about 160 cm in length and 65 kg in weight, size differing slightly between populations (Galatius and Gol'din, 2011). The dorsal side is dark grey while the ventral side is white, and there is a dark stripe from the corner of the mouth to the pectoral fin. The dorsal fin is low and triangular. The body shape is rather short and round, limiting heat loss in cool waters. Their small size, fast-paced reproduction and inability to store large amounts of energy means that harbour porpoises are dependent on feeding frequently (Koopman et al., 2002; MacLeod et al., 2007b; Read, 1999). This would imply that porpoises are quite tightly bound to their food source and their distribution should largely match that of their preferred prey. However, it also seems porpoises can be quite opportunistic in their choice of prey, foraging on whatever species are readily available at the moment.

The harbour porpoise is, despite its small size, a highly mobile animal. Satellite studies show that porpoises have an average swim rate of approximately 0.6-2.3 km/h, can swim distances of up to 58 km/day and have quite large home ranges (Read and Westgate, 1997; Sveegaard et al., 2011). This

has implications for reproduction and population structure as well as for foraging behaviour and environmental preferences.

Life history

The harbour porpoise is the only cetacean which is found throughout the year in the Baltic Sea (Berggren and Arrhenius, 1995; Kinze, 1995). Females are often slightly larger than males and reach sexual maturity at older age, from just over 3 to almost 5 years in Danish and German waters compared to approximately 3 years for males (BMBF, 1997; Møhl-Hansen, 1954; Sørensen and Kinze, 1994). In the Swedish Kattegat and Skagerrak Seas, the age at sexual maturity for females is approximately four years (Hedlund, 2008). Porpoises are among the odontocetes with the shortest life span, and rarely live longer than 12 years (Lockyer and Kinze, 2003; Read and Hohn, 1995). Females give birth to one calf almost every year, which means they are pregnant and lactating simultaneously for most of their lives (Read and Hohn, 1995). Gestation is approximately 10.5 months (Börjesson and Read, 2003) and calves suckle for 6-9 months (Koschinski, 2002; Lockyer, 2003), although they do start eating fish at a few months of age (Smith and Read, 1992).

Reproduction appears to take place approximately one month later in the German Baltic Sea than in the German North Sea, since the occurrence of calves in incidental sightings in the Baltic has its peak in August compared to July in the North Sea (Siebert m.fl. 2006). In Danish waters the mean birth date was estimated to 30 June (Sørensen och Kinze 1994). Mean conception date varies from 25 July in the Kattegat and Skagerrak Seas to 18 August in the Baltic Sea and mean gestation time is approximately 10.4 months (Börjesson and Read, 2003). The proportion of calves in sightings seem to be smaller in the German Baltic Sea compared to the German North Sea (Siebert m.fl. 2006). It has also been concluded from incidental sightings that the average group size seem to be larger in the Baltic Sea (2.5, SD=1.7) than in the North Sea (2.2, SD=3.2). In the North Sea the majority of sightings consisted of single individuals, while in the Baltic Sea most of the sightings were of two animals (Siebert et al., 2006). This is consistent with work in progress (Carlén, unpublished data) where spatial modelling of group size indicates somewhat larger group sizes in the Baltic Sea than in adjacent waters.

Sound production

Harbour porpoises use high frequency, narrow bandwidth echolocation clicks (Au et al., 1999; Møhl and Andersen, 1973) to orientate themselves in their environment, to locate prey and possibly also to communicate (Amundin, 1991; Verfuss et al., 2002). Clicks are approximately 100 µs in duration and occur in bursts or click trains with ranges in inter-click intervals from 150 ms in "search mode" down to 3 ms when closing in on a target (Linnenschmidt m.fl. 2013). This decrease of inter-click intervals to a "buzz" is often considered evidence of potential foraging (Linnenschmidt et al., 2013; Miller, 2010; Wright, 2013).

The peak frequency of porpoise clicks is approximately 130 kHz (Au et al., 1999) and the source level in wild porpoises has been reported to be up to 205 dB *re* 1 µPa pp @ 1m, which would mean that a porpoise can detect an adult herring at distances up to 40 m (Villadsgaard et al., 2007), although Linnenschmidt et al. (2013) discuss "scanning distances" of up to 102 m. It has been shown that porpoises use their biosonar almost continuously, although some diurnal variation and occasional quiet periods do occur (Carlström, 2005; Linnenschmidt et al., 2013; Todd et al., 2009; Wright, 2013).

Population structure

Currently, three subspecies of harbour porpoise are recognized; one in the Atlantic (*P. phocena phocoena*, L., 1758), one in the Pacific (*P. phocoena vomerina*, Gill, 1865) and one in the Black Sea (*P. phocoena relicta*, Abel, 1905). The Black Sea harbour porpoise is genetically distinct and has been genetically and geographically separated from the Eastern Atlantic populations for thousands of years (Viaud-Martínez et al., 2007). This division into sub-species is supported by morphometric studies (Amano and Miyazaki, 1992; Galatius and Gol'din, 2011).

The population structure of the harbour porpoise in the Baltic region has been much debated during the last decades. A majority of studies based on metric and non-metric skull characters (Börjesson and Berggren, 1997; Huggenberger et al., 2002), mitochondrial DNA (Tiedemann et al., 1996; Wang and Berggren, 1997), micro-satellite DNA (Andersen et al., 2001, 1997, 1995), contaminant patterns (Berggren et al., 1999) and tooth ultrastructure (Lockyer, 1999) seem to agree that there are significant differences between harbour porpoises in the North Sea and the Baltic Sea region. There is evidence that there has been very little gene-flow between the Baltic Sea and adjacent waters since the colonization by harbor porpoises of the Baltic Sea during the Littorina period (Tiedemann et al., 1996). More recently, the focus of many publications has been on resolving the more small-scale differentiation between possible sub-populations within the Baltic Region (Figure 1), investigating the existence of two or more stocks and the location of possible barriers to gene flow between those stocks. Huggenberger et al. (2002) found morphometric differences in skulls between two Baltic units, one in the "transition area" between the North Sea and the Proper Baltic Sea consisting of Skagerrak, Kattegat, Belt Sea, Öresund, Kiel Bight, Lübeck Bight and Fehmarn Belt, and one in the central Baltic Sea including the Arkona basin and waters off the Swedish east coast. Galatius et al (2012) found significantly different skull shapes between North Sea, Belt Sea and Baltic Sea porpoises. The difference found is not a general continuous shape trend going from the North Sea to the Baltic Sea, which could have been explained by isolation by distance. Instead the authors argue that there may be a greater reliance on benthic prey species in the Belt Sea sub-population, and that the different shapes detected may be an adaptation to different environments. A small but significant separation was also found by Wiemann et al. (2010) using mitochondrial and microsatellite genetic anayses, between porpoises from the Belt Sea and porpoises from the Inner Baltic Sea, and the authors argue that although the two units may not strictly be demographically independent they should, according to the precautionary principle, be treated as separate management units (Wiemann et al., 2010). This split seemed to be located within the Belt Sea. Wiemann et al. (2010) also detected a clear split between porpoises in the Belt Sea/Kattegat and porpoises in the Skagerrak/North Sea. This split was suggested to be located in the middle of Kattegat, which is consistent with the results of Sveegaard (Sveegaard, 2011) where spatial analysis of satellite tracking data shows that the best-fitting border between the North Sea-Skagerrak population and the Belt Sea-Kattegat population was suggested to be a diagonal line going from the eastern tip of Djursland in Denmark to a point between the islands Orust and Tjörn on the Swedish coast, straight through Kattegat.

The borders between populations are not fully resolved, however, there seems to be strong evidence of a border between the North Sea /Skagerrak/Northern Kattegat population and the Southern Kattegat /Belt Sea population going through Kattegat (Sveegaard, 2011; Wiemann et al., 2010). The border between the Southern Kattegat/Belt Sea population and the Inner Baltic population is more

difficult to localize. Galatius et al (2012) compared three different delimitations (Fehmarn belt and the Limhamn underwater ridge, the Darss and Limhamn underwater ridges and a line between the German/Polish border and the southeast corner of Sweden) and found that all three were significant, however the Fehmarn Belt and Limhamn underwater ridge gave greater morphological distances and more successful reclassification of individuals. On the other hand, Huggenberger et al. (2002) and Wiemann et al. (2010) agree that the Darss underwater ridge constitutes part of the border between the Belt Sea and the Baltic Sea populations. However none of these two studies tested the same options for delimitation as Galatius et al. (2012) which makes it difficult to compare the results. In addition, no limits between populations are ever exact. Firstly since mobile animals like porpoises will always move irrespective of the borders we try to impose on them, and secondly because it is very likely that populations do mix in the area around the split.
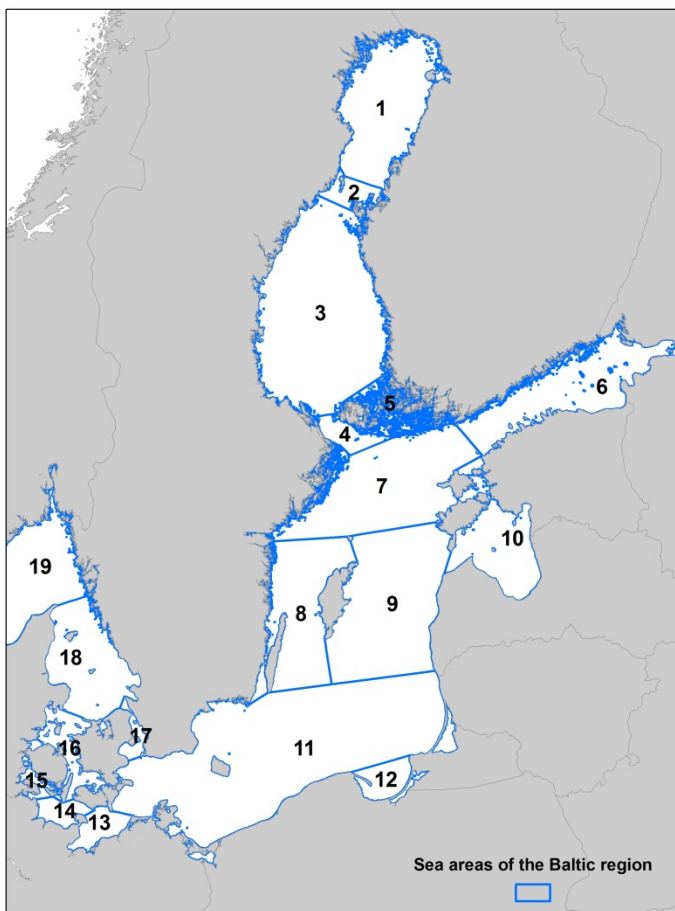

Figure 1. The Baltic Sea region. In this essay, the Baltic region is defined as the combination of the following sea areas: 1. Bothnian Bay, 2. The Quark, 3. Bothnian Sea, 4. Åland Sea, 5. Archipelago Sea, 6. Gulf of Finland, 7. Northern Baltic Proper, 8. Western Gotland Basin, 9. Eastern Gotland Basin, 10. Gulf of Riga, 11. Southern Baltic Proper, 12. Gdansk Basin, 13. Mecklenburg Bight, 14. Kiel Bight, 15. Little Belt, 16. Great Belt, 17. The Sound, 18. Kattegat, 19. Skagerrak). The Belt Sea is often referred to as the combination of areas 13-16, and the Baltic Proper as areas 7, 8, 9 and 11 combined. The Arkona Basin is situated west of Bornholm in the Southern Baltic Proper, and the Bornholm Basin is situated east of Bornholm. The Inner Baltic Sea is areas 1-11. Shape file from the Helcom map and data service, http://maps.helcom.fi/website/mapservice/index.html.

Comparisons among the above studies are difficult since samples often have been lumped together in different ways, presupposing certain, but different among studies, locations of limits between

stocks. However, in conclusion, most recent studies support the presence of three populations or sub-populations of harbour porpoises in the Baltic Region: one in northern Kattegat-Skagerrak, extending out into the North Sea, one in southern Kattegat and the Belt Sea, and one in the inner Baltic Sea (see Figure 1). Although the borders between populations are not resolved, these three can be considered separate sub-populations, which will be referred to in the following discussions on habitat use.

The differences between populations found in the above studies are very small on an evolutionary scale, however these differences, especially if they exist in foraging strategies and migration habits, are very likely enough to prevent recolonisation of for example the inner Baltic Sea in case the resident population was to become extinct. The small differences are not surprising in light of the fact that the Baltic Sea in its present form is only about 8000 years old (Bonsdorff, 2006), and so the separation of a Baltic population cannot be older than that. Also, there are no absolute physical barriers to gene flow, and porpoises are mobile and capable of moving long distances. Seasonal movements have been recorded in Little Belt where porpoises have been hunted since the 1300's, the last hunt occurring during the Second World War (Lockyer and Kinze, 2003). The migrating animals were thought to come from the Baltic Sea, moving to ice-free waters during the winter (Angerbjörn et al., 2006; Koschinski, 2002 and references therein) although the assumption of extensive seasonal migration has been challenged by new data from historical sources (Kinze, 2008). An inner Baltic Sea population of porpoises would have to migrate to some extent to avoid the ice. However, migration does not have to mean genetic exchange, since there is some proof of philopatry and the habit especially in females to return to certain breeding areas (Kinze, 1990). The results above, showing differentiation between populations, seem to support this theory. Other indications that there is a separate non-migratory subpopulation present in the Baltic Proper is for example the fact that bycatch have occurred in the Baltic Proper year-round (Berggren, 1994) and that there have been large-scale mortalities during the 1900's when porpoises have been trapped in the ice in the Baltic Proper during hard winters (Johansen, 1929; Ropelewski, 1957; Tomilin, 1957).

The barriers to dispersion, and thereby to gene flow, that caused the separation of porpoise populations in the Baltic region may be of different types. In the marine environment, there is of course the absolute physical obstacles of continents and islands, but also ocean frontal systems, currents and vertical stratification may act as barriers in the oceanic environment (Longhurst, 2010). Additionally, changes in bottom substrate and bathymetry (Gaines et al., 2007), as well as underwater ridges (Fontaine et al., 2007; Wiemann et al., 2010), may disrupt dispersion and thereby gene flow. Fontaine et al (2007) also conclude that across the entire harbour porpoise range in European waters, primary production and sea surface temperature seem to govern the gene flow and form the barriers that created population differentiation on the larger scale. The abrupt rather than continuous changes in environmental conditions at underwater ridges (Zettler et al., 2007) may explain the fact that there seem to be several sub-populations of harbour porpoises in the Baltic Region rather than one population where genetic differentiation is explained by isolation-by-distance.

Conservation status and population size
The reason for the decline of the Baltic Sea harbour porpoise (Berggren and Arrhenius, 1995; Määttänen, 1990; Skóra et al., 1988) and the lack of recovery (Gillespie et al., 2005) is believed to

have several reasons, including lethal bycatch in fisheries, environmental contaminants (Berggren et al., 1999) and heavy shipping (Koschinski, 2002). The number of porpoises in the Baltic Sea today is basically unknown, the latest surveys made in 1995 and 2002 gave point estimates of 599 (200-3300) and 93 (10-460) porpoise groups, respectively (Berggren et al., 2004; Hiby and Lovell, 1996). The very large confidence intervals are a result of the fact that the method used, visual line transect surveys, are largely unsuited for low-density populations such as the Baltic Sea harbour porpoise, giving very few observations to base calculations on.

The Baltic Sea subpopulation is classified as critically endangered by the IUCN (Hammond et al., 2008) based on the number of individuals estimated from the survey made in 1995 (Hiby and Lovell, 1996) and the derived number of mature animals (Taylor et al., 2007). The harbour porpoise is also listed in annex II and IV of the EU Habitats Directive (92/43/EEC), protected in the national legislation of Sweden, Finland, Estonia, Latvia and Poland, and listed in the national redlists of Sweden, Poland, Denmark, Estonia, Latvia, and Germany.

Environmental preferences

The harbour porpoise is mainly a coastal species, occurring predominantly in continental shelf waters between 20-200 m depth (Embling et al., 2010; Isojunno et al., 2012; Marubini et al., 2009; Watts and Gaskin, 1985), although the frequency of use tapers off at depths over approximately 100 m. In some regions porpoises regularly use areas more shallow than 20 m, for example in inner Danish waters where females with calves have been observed in several sites more shallow than 20 m (Kinze, 1990). It is generally believed that shallow waters are important as calving and nursing grounds (Hammond et al., 1995; Kinze, 1990). For example the area around the islands of Sylt and Amrum in the German North Sea have higher ratios of calves than the rest of the North Sea (Sonntag et al., 1999). However, the mechanisms behind this possible preference are currently unknown.

The distribution of porpoises within its depth range generally seem to be correlated to zones with oceanographic features giving higher-than-average production or aggregation of prey for other reasons, such as upwelling, eddies and high currents (Embling et al., 2010; Gilles et al., 2011; Johnston et al., 2005; Marubini et al., 2009; Skov and Thomsen, 2008; Skov et al., 2003), although porpoises have been suggested to avoid turbulence in shallow waters (Watts and Gaskin, 1985). Upwelling was suggested to be an especially important factor in porpoise presence at Horns Reef (Skov and Thomsen, 2008) and is very likely so because of higher productivity than surrounding areas. Tidal range has also been found to influence distribution of porpoises in the waters around Scotland (Booth et al., 2013).

Foraging ecology

The relatively small body size of harbour porpoises mean that heat-loss to the surrounding cool water is high and the capacity for energy storage is limited, which in its turn implies that harbour porpoises need constant access to prey (Brodie, 1995; Kastelein et al., 1997; Koopman et al., 2002). Also their challenging reproductive strategy is energy demanding (Read and Hohn, 1995; Recchia and Read, 1989). Studies suggest that porpoises need to eat between 4-9.5% of their body weight per

day (Kastelein et al., 1997; Lockyer et al., 2003). The energy density of prey may vary between seasons, for example the energy density of herring has been shown to vary by up to 250%. Prey availability may also change with prey species behaviour, which may for example shift between seasons (Sveegaard et al., 2012). All these factors would possibly limit porpoise distribution to areas with high primary productivity (Galatius and Gol'din, 2011).

To date, information on porpoise feeding ecology has mainly been deduced from analyses of stomach content, stable isotope analyses and studies of diving behaviour. Based on the diversity of prey and the geographic variation in prey items, it is generally believed that harbour porpoises are opportunistic predators feeding mainly on small schooling fish (Börjesson et al., 2003) such as cod, herring, sprat, gobiids and sandeel. Prey size is often less than 300 mm, and even though porpoises are sometimes seen in large aggregations (often where prey density is high), they are believed to hunt individually (Read, 1999). Foraging mainly takes place in the upper 200 m of the water column (Bjørge, 2003), which is supported by the deepest dive recorded for a porpoise at 226 m (Westgate et al., 1995), but since studies have always been restricted by the local bathymetry the maximum dive depth of harbour porpoises is currently unknown. There are, however, several pieces of evidence suggesting that porpoises feed at the sea floor, such as the large part of benthic prey species together with the fact that porpoises frequently get caught in bottom-set gillnets. Additionally, the characteristics of the harbour porpoise echolocation system seem to be adapted to be used for finding prey in or near the bottom sediments (Goodson and Sturtivant, 1996; R. A. Kastelein et al., 1997). Studies where time-depth recorders are attached to the dorsal fins of porpoises show that a common type of dive is the so called flat-bottomed or U-shaped dive, where the porpoise dives to a certain depth, spends about a third of the dive time there and then rises to the surface. These dives are interpreted as being foraging dives to the sea floor (Otani et al., 1998; Westgate et al., 1995). Wright (Wright, 2013) found that this type of dive is less common in deep waters, indicating that porpoises do not feed at the bottom as often in deeper areas, and the main prey of many porpoise populations also includes pelagic species.

Galatius and Gol'din (2011) suggest that the lack of profound shape differences in skulls between populations in their study may be due to that porpoises are mainly opportunistic feeders, not specializing in one type of prey species. There is evidence, however, of differences in skull shapes between porpoises in Danish waters and adjacent areas. According to Galatius et al (2012), the shape of the rostrum of Baltic porpoises is more similar to Atlantic porpoises than to IDW porpoises, where the latter is inclined more to the ventral side, presumably adapted for bottom feeding. This could suggest that Belt Sea porpoises feed more on benthic species than their conspecifics.

In the general northeast Atlantic area the main prey items for harbour porpoises are pelagic herring and more benthic gadids (Källquist, 1974; Lindroth, 1962; Rae, 1965), with herring being replaced by capelin (*Mallotus villotus*) to the far north (Aarefjord et al., 1995). Fontaine et al. (2007) suggest that porpoises in deep waters along the northern Norwegian coast prey mainly on pelagic species on a lower trophic level than porpoises further south in Swedish and Danish waters which feed more on bottom-dwelling and coastal species of higher trophic levels. Aarefjord et al (1995) also found that the main part of harbour porpoise prey in Scandinavian waters were benthic species such as gadids and gobiids, except in the northern parts of Norway where pelagic prey species such as herring and capelin dominated. This can be interpreted as the bottom being out of reach in these northernmost

areas where the depth is up to 400 m. There is evidence that Baltic porpoises are maybe more similar to the northern populations in this respect, feeding extensively on pelagic prey (Lindroth, 1962) despite the fact that the Baltic Sea is rather shallow.

Berggren (1996) reports the main prey of porpoises bycaught and stranded in the Skagerrak and Kattegat Seas during 1988-93 to be herring and sprat. In the same area, Börjesson et al. (2003) found that the most important prey species were herring (*Clupea harrengus*), gobies (Gobiidae), whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*), sprat (*Sprattus sprattus*) and hagfish (*Myxine glutinosa*), with sprat and gobies being more important to juvenile porpoises, and hagfish being a more common prey in adults. Sveegaard et al (Signe Sveegaard et al., 2012) conclude that the main prey of porpoises in the Sound between Sweden and Denmark was cod and herring, with cod being the most important species during summer and herring and cod equally important during winter. Other occurring prey species in this study were other gadoids such as whiting, but also gobiids, sandeel and sprat. In the Baltic Sea, Aarefjord (1995) found herring and cod to be the two main prey species. Another extensive study on prey species in the Baltic sea was made in the 1960's by Lindroth (1962), examining stomach contents from 50 animals collected in the Baltic Sea during 1960-61, finding evidence of sprat, herring, cod, gobies and sandeels being consumed, with sprat being the most important species both in presence and numbers. Gobids (transparent goby, *Aphya minuta*) was the second most important in numbers, and herring the second most dominating in terms of presence. Gobids were, however, the most important prey species in the German Baltic Sea (Benke et al., 1998; Benke and Siebert, 1996), making up 50% of the total prey weight, followed by herring (23%) and cod (15%). Sveegaard et al (2012) also report an apparent decline in prey species diversity from the North Sea towards the Baltic Sea, possibly as an effect of the decrease in salinity and the resulting decrease in the number of species, based on the results from several studies (Aarefjord et al., 1995; Börjesson et al., 2003; Lick, 1995, 1994). Sveegaard et al. (2012) found a positive correlation between porpoise and herring distribution in Kattegat, Skagerrak and the north-eastern North Sea, and conclude that porpoise migration may be influenced by herring movements.

It has been suggested that porpoises are rather stationary, adapting their foraging strategy to local environmental conditions that may change over the year despite the potential to move rather extensively (Fontaine et al., 2007). There is also large variation in prey preferences between individuals (Jansen et al., 2012; Santos and Pierce, 2003). The trophic level that porpoises feed on seem to have decreased gradually over time, likely due to changes in ecosystems limiting the higher trophic level prey available to porpoises (Jansen et al., 2012). In UK waters a preference for herring (*Clupea harengus*) in earlier studies has given way to other prey species, indicating that porpoises have switched to other food sources following the decline in herring abundance in this area (Santos and Pierce, 2003). In Scottish waters there is concern that climate change and a subsequent decline in sandeel abundance has led to an increase in emaciation in porpoises (MacLeod et al., 2007a, 2007b). However, this study has a small sample size and doubts have been raised about the reliability of results (Thompson et al., 2007).

Approximately 80% of the fish biomass in the Baltic sea consists of the piscivorous cod and the planktivores herring and sprat (Elmgren, 1984; Thurow, 1984). As seen above, this is quite well reflected in the Baltic Sea porpoise diet which is largely dominated by these three species. This supports the hypothesis of the porpoise as an opportunistic feeder.

Some studies have found differences in preferred prey between juveniles and adult porpoises (Benke and Siebert, 1996; Santos, 1998), generally suggesting that juveniles are limited in their diving depth and the size of prey and that calves and juvenile porpoises consume more benthic species of smaller size. Logically, gobies seem to be an important prey item for juvenile porpoises (Aarefjord et al., 1995; Benke and Siebert, 1996). A study of porpoise feeding ecology in North Sea waters, based on stable isotope analyses, concludes that juvenile porpoises tend to forage closer to shore, while adults seem to feed more offshore. Females in this study also took prey on a higher trophic level than males, and the prey of female porpoises were more coastal, similar to young porpoises feeding to a large extent on small gobies (Jansen et al., 2012). Also, Börjesson et al (2003) found that female porpoises in the Kattegat and Skagerrak Seas fed more frequently on Atlantic hagfish (*Myxine glutinosa*) than did males, and it could be hypothesised that hagfish is a relatively easy prey for females with calves, since they are rather stationary. Otherwise, there are few studies indicating that sex has an influence on diet (Santos and Pierce, 2003).

Prey species ecology
Herring is a largely pelagic species which feeds predominantly on zooplankton, although large individuals also prey on nektobenthos such as small crustaceans (Casini et al., 2004). The herring follow the diel vertical migration of its prey, aggregating in surface waters at dawn to feed on zooplankton before starting to descend to deeper darker waters, forming schools in deep waters during the day. At dusk they start spreading out, spending the night dispersed in surface waters to aggregate again at dawn.

Baltic Sea Herring (*Clupea harengus membras*) is a subspecies of the Atlantic herring, and do not grow to the same adult size as herring in the Kattegat/Skagerrak (Curry-Lindahl, 1985). The porpoises in the Baltic also seem to prey upon smaller individuals of herring than porpoises in Kattegat/Skagerrak. The sizes preferred by porpoises in both areas were the size of mature or maturing herring in the respective area. Depending on season, mature herring often have higher energy content than juvenile fish (Börjesson et al., 2003), although it varies considerably over the year, with considerably higher energy density before than after spawning (Pedersen and Hislop, 2001). Baltic herring generally has a lower fat content than Atlantic herring. Baltic herring mostly spawns during spring, although there are autumn spawning populations throughout the region. Spawning takes place over relatively shallow bottoms of sand, gravel and stone where the eggs stick to vegetation and rocks (Kullander and Delling, 2012). Juvenile herring live closer to the coast, but since porpoises seem to prefer mature herring they are likely searching for their prey in the pelagial or possibly at spawning sites where aggregation of herring would likely be a convenient food source. Spawning herring has been observed at Norra Midsjöbanken in June (Tomas Didrikas, pers. comm.), indicating that spawning does take place on offshore banks.

The Sound and the Danish Belt Seas are important autumn and wintering grounds (Sept-Feb) for a subpopulation of herring that spawns around the island of Rügen and Odra bank, Germany, in early spring (Nielsen et al., 2001). This Baltic Sea spring spawning herring moves north to feed in the north-eastern North Sea during late spring and early summer, to then migrate back through Skagerrak in late summer to arrive in Danish waters in autumn. Herring are also known to be present on Södra Midsjöbanken in autumn (J. Netzel, pers. comm. In Andrulewicz & Wielgat 1999).

Sprat is similar to herring in that it is mainly pelagic although it feeds exclusively on zooplankton, following the diel vertical migration of its prey, and seem to continue feeding throughout the day in contrast to herring which feeds primarily at dawn and dusk (Cardinale et al., 2003). Sprat is slightly more coastal than herring but still pelagic, avoiding cold surface waters and wintering in large shoals in deep waters. Spawning takes place in open waters both near the coast and out at sea (Kullander and Delling, 2012).

The two main populations of cod in the Baltic Sea are the eastern Baltic stock, east of the island of Bornholm, and the western stock in the Arkona basin west of Bornholm and in inner Danish waters (Nissling and Westin, 1997). Historically there have been three spawning grounds in this area; the Bornholm and Gotland basins and the Gdansk deep, however only the Bornholm basin has given successful spawning in years of severe oxygen depletion. Nursery areas are situated in more shallow waters around the coasts (Bagge et al., 1994). Spawning takes place from January to May with a peak in March in the western Baltic, while in the eastern Baltic the spawning period is more extended and the peak in June-August. The Sound between Denmark and Sweden has a separate cod subpopulation. This population is more abundant and have higher age diversity than other subpopulations in the Kattegat and Baltic Sea (Svedäng, 2010), probably due to low fishing pressure in the narrow Sound. In the Baltic, spawning takes place during summer in the Baltic Proper and the Danish straights, and the species is present throughout the region as far north as the Bothnian Bay. Cod is a predominantly demersal species, living close to the bottom but occasionally venturing up into the water column, feeding on bottom fauna and other fish (Kullander and Delling, 2012). Younger individuals prey upon crustaceans such as *Mysis* sp. and *Pontoporeia* sp. and the polychaete *Bylgides sarsi*, while older cod eat more herring, sprat and the benthic crustacean *Saduria entomon* (Bagge et al., 1994). Cod generally seem to prefer water temperatures from 2-10°C (Muus and Dahlström, 1985).

Whiting (*Merlangius merlangus*) is present in the southwestern Baltic Sea. It moves in shoals over sandy or muddy bottoms. Whiting feeds on mainly fish but also eats crustaceans and other evertebrats (Kullander and Delling, 2012). It has a long breeding period, starting in February-March depending on latitude, and ending in June. It often occurs near the surface, particularly at night (Finn Larsen pers. Comm. in Linnenschmidt 2013).

Flat fish often lie buried in the bottom sediments during the day, and are more active, swimming in the water column at night (Verheijen and De Groot, 1967). Flatfish present in the Baltic Sea are for example turbot (*Scopthalmus maximus*), dab (*Limanda limanda*), flounder (*Platichtys flesus*) and plaice (*Pleuronectes platessa*). These species are mostly present on sandy or muddy bottoms but also harder substrates such as gravel or stone.

Two species of sandeel occur in the Baltic Sea; small sandeel, *Ammodytes tobianus*, and greater sandeel, *Hyperoplus lanceolatus*. Sandeel have a distinct seasonal and diurnal pattern, staying mostly buried in the bottom sediments, preferably sand, during autumn and winter and being more pelagic during spring and summer, especially during the day. Smaller sandeel and young individuals of greater sandeel eat zooplankton, while older greater sandeel eat fish. Porpoises are likely able to find sandeel buried in the sand, however from Scottish waters it seems porpoises feed on sandeel to a larger extent during their pelagic period than in the autumn and winter (Santos, 1998).

Modelling porpoise distribution

According to foraging theory, prey distribution should have an important influence on the distribution of predators (Boyce and McDonald, 1999). This should be especially true for marine predators that can maintain a higher body temperature than their surroundings, and that are therefore not dependent on physical conditions to the same extent as their prey (Redfern et al., 2006; Torres et al., 2008). Additionally, as stated above, the small size of the harbour porpoise implies a need to feed regularly and often (Koopman et al., 2002; MacLeod et al., 2007b; Read, 2002, 1999), and the distribution of porpoises should therefore be closely related to environmental factors governing prey distribution. However, it can also be argued that in the marine environment, the predator cannot know exactly where the prey is at any given point in time, and will therefore have to rely on experience, possibly learned behaviours, likely coupled to certain physical conditions, to find prey patches. This would mean that using prey distribution to model and predict predator presence may not be the most effective procedure on all scales, and that using the underlying environmental parameters may actually give more stable predictions of predator distribution. Many studies of marine pelagic systems have failed to find clear correlations between predator and prey distributions (Fauchald, 2009; Greene et al., 1994; Russell et al., 1992), however this lack of correlation may be an issue of temporal and/or spatial scale, or of using a measure of prey distribution which is not relevant for the point of view of the predator (Benoit-Bird et al., 2013). Therefore it is important, when modelling the distribution of porpoises, to ensure that the scale applied is appropriate, and that the measures of prey density, if available at all, describes the prey availability in a way that is relevant for the predator, taking into account the patchiness of the prey distribution. The size and density of prey patches does influence the gains and costs of foraging (Tiselius et al., 1993) and are therefore important factors governing predator distribution.

Finding the relevant temporal and spatial scale when modelling marine apex predators is a challenging issue, and one that has large impact on the results. Highly mobile species such as porpoises are often aggregated on the short temporal scale, but in relation to physical conditions they may be more evenly distributed on a longer timescale (Robinson et al., 2011). Hierarchical patch dynamic theory suggests that patches of suitable habitat are nested within each other in a hierarchical system of different scales that govern the distribution of animals (Wu and Loucks, 1995), where animals search for prey in "behavioural cascades", increasing turning rates with increasingly smaller scales (Russell m.fl. 1992). This has been confirmed in fur seal (*Callorhinus ursinus*) in the Bering sea (Benoit-Bird et al., 2013). These ideas indicate that careful consideration of the scale is vital in modelling marine predators, since a highly aggregated distribution may be more difficult to model and predict than a more uniform one, and the choice of scale may influence the quality of the model. Also, the small-scale pattern may be hidden by the large-scale pattern of distribution (Fauchald et al., 2000), which in turn may be expected to remain the same for longer periods of time than the smaller-scale pattern (sensu Haury et al., 1978), which means predictions on spatial distribution in the larger scale may be more useful for species conservation measures.

Several studies have shown that the correlation between predator and prey do increase with spatial scale (Fauchald et al., 2000; Heinemann et al., 1989; Hunt, 1990; Schneider and Piatt, 1986), which has been taken as a sign that prey avoid their predators on the small spatial scale but that they do not succeed to do so on a larger geographical scale (Rose and Leggett, 1990). Guinet et al. (2001) conclude that different environmental variables may be significantly correlated with the presence of

marine predators on different scales. This has been shown by Bailey and Thompson (2009) who modelled five groups of marine mammals using three different spatial scales, and found that animal distribution was correlated to different environmental variables on different scales. Skov & Thomsen (2008) found that oceanographic processes such as fronts and upwelling occurring on a scale of approximately 10 km were the most relevant when describing porpoise presence on Horns Reef in the Danish North Sea, and they did this on a 500x500 m grid. Other studies have used spatial resolutions from 400 m (Edrén et al., 2010) up to 18.5 km (Hamazaki, 2002). However, in reality the choice of spatial scale is often not only influenced by what is the optimal scale for your response data but also by the environmental data available and by the extent of the study area. A larger study area often leads to using a lower resolution and a coarser grid, presumably looking for larger scale patterns in distribution.

It has been shown that pelagic schooling fish often aggregate in areas with specific oceanographic properties, such as upwelling, fronts or tidal currents on a larger spatial scale (Maravelias et al., 1996; Swartzman et al., 1994), and as mentioned above, porpoises gather in such areas presumably to benefit from the aggregation of prey. On the smaller scale both spatially and temporally, changes in local tidal currents have been shown to influence porpoise presence (Skov and Thomsen, 2008). Hence, finding the right parameters to describe these key oceanographic conditions from the porpoise point of view may go a long way to model and predict porpoise distribution. On the one hand, due to the fact that these oceanographic parameters may change rather rapidly, pooling data over longer time periods should be avoided. On the other hand, if the aim is a more general prediction of porpoise distribution, modeling using temporal averaged environmental variables may be beneficial.

Also, despite the fine-scale details, since porpoises move tens of kilometres every day, their distribution should be correlated to environmental variables measurable on the same scale (Sveegaard et al., 2012).

The Baltic Sea

The environment of the Baltic Sea

The history of the Baltic Sea

The Baltic Region has been subject to glaciation during several ice ages in the last glacial cycle. The last ice started melting about 15000-17000 years ago, and the ice was completely gone approximately 10000 years ago.

The Baltic ice lake, 12600–10300 yr BP, was developed in front of the receding edge of the melting ice. This water body consisted largely of fresh water and had no major link to the sea to the west. It evolved into the Yoldia Sea, 10300–9500 yr BP, which had a rather wide straight open to the west, leading to salt water inflow and hence a brackish or in some areas even saline phase. During the Ancylus Lake, 9500–8000 yr BP, the straights to the west closed and the Baltic was once again primarily fresh water (Björck, 1995). The Mastogloia Sea 8000-7500 yr BP acted as a transition into what is known as the Littorina Sea, 7500-4000 yr BP. The Littorina Sea is characterized by almost marine conditions, with saline water coming in through wide straights in Öresund and the Great Belt. This in combination with the warmer climate and increased nutrient availability led to significant ecological changes in the Baltic Sea environment, including higher primary production and a new species-rich fish community dominated by cod, flounder, plaice, mackerel and herring. Since the "peak" Littorina time, salinities in the Baltic Sea has decreased by approximately 4 psu (Sommer et al., 2008).

From subfossil remains from early human settlements, it seems the harbour porpoise entered the Öresund area between 9600-7000 yr BP, expanding to the western parts of what is now the Baltic Proper and the Gulf of Bothnia during 7000-5700 yr BP and had spread into the entire Baltic Littorina Sea during 5700-4000 yr BP, probably drawing on the new rich fish community. After 4000 yr BP porpoise remains are again basically absent from the eastern parts of the Baltic, indicating that the decrease in salinity and accompanying environmental changes may have limited the range of the species (Sommer et al., 2008). It seems likely that the very low abundance and limited geographical distribution of porpoises that we see in the Baltic Sea today is a result of an initial change in environmental conditions with the addition of anthropogenic impacts such as hunting, bycatch in fisheries and environmental degradation occurring primarily since the 1900's. The basic environmental conditions such as salinity would then be expected to have at least some influence on harbour porpoise distribution, and could possibly be used successfully as explanatory variables when modelling the distribution of porpoises in the Baltic Sea.

Oceanography

The Baltic Region consists of a series of basins (the deepest points are in Kattegat 124 m, in the Belt Sea 80 m, and in the Inner Baltic Sea 459 m). The basins are separated by shallow underwater ridges from 18 to 50 m depth. The limited inflow of saline water over these underwater ridges is estimated at approximately 475 km^3/year, and the fresh water input from the catchment area is approximately 660 km^3/year. Hence, a salinity gradient is created going from fully marine conditions in the Skagerrak, through brackish in the Baltic Proper with a surface salinity of about 6-8‰ to almost fresh water with a surface salinity of approximately 1‰ in the northern parts of the Bothnian Bay. Due to the profound underwater bathymetric structure, the boundaries between basins may constitute

relatively abrupt rather than continuous changes in salinity and other environmental conditions (Zettler et al., 2007).

There are virtually no tides in the Baltic Sea (Lass and Matthäus, 2008). In the absence of tidal driven phenomena it may well be that porpoise prey and therefore porpoises gather in areas with currents and upwelling induced by other factors than tides, even though these currents are weaker than they are in areas affected by tides. Upwelling, coastal jets and eddies have all been detected in the Baltic Sea. Upwelling and downwelling are wind-driven and occur predominantly on the western and eastern shores during the prevailing winds. If the wind is coming from the southwest, this triggers upwelling along the western shores and downwelling along the eastern coast, and if the wind comes from the northeast this changes to the opposite. Coastal jets can transport water over long distances along the coast. Eddies have been observed in the deeper basins of the Baltic, forming during the winter and early spring when the thermocline is prominent (Lass and Matthäus, 2008).

In the Baltic Sea, a thermocline forms in spring at about 25-30 m depth, and is present until late autumn. There is also a permanent halocline in the Baltic. It is situated at approximately 40 m depth in the Arkona basin and increases to 60-80 m depth in the Eastern Gotland basin (Conley et al., 2009; Lass and Matthäus, 2008). This discontinuity layer prevents mixing of layers and input of oxygen to deeper waters, which has created hypoxia and even anoxia in deeper areas of the Baltic Proper since the early Littorina Sea around 8000 yr BP (Conley et al., 2009). In combination with the eutrophication of the Baltic Sea, hypoxia has worsened during the last decades. The oxygen levels in the Baltic are also affected by saltwater inflow through the Danish straights which occur mainly during winter (October – February). Major saltwater inflows through the Öresund and the Great belt are needed to lessen the areas affected by hypoxia in the deeper areas of the Baltic Proper, replacing oxygen deprived waters with new saline oxygen rich waters. However, the inflow of saline water into the Baltic Sea also strengthens the stratification which in its turn instead increases the areas suffering from hypoxia (Conley et al., 2009, 2002; Lass and Matthäus, 2008). The halocline and underwater sills prevents saline water from the North Sea to propagate into the more shallow gulfs of Riga and Finland, where instead surface waters from the central Baltic sinks down to form bottom water.

There is evidence of an at least semi-permanent gyre southwest of the offshore bank Södra Midsjöbanken in the Baltic Proper (Naturvårdsverket, 2006; Voss et al., 1999), to which cod larvae from the Bornholm deep spawning ground are transported by currents (Voss et al., 1999). It is likely that this gyre also gather other organisms such as zooplankton and thereby herring and sprat, which would make it a potential feeding ground for porpoises. There may also be other gyres in the Baltic which have not been found.

Geology and morphology/bathymetry

The large scale bathymetry of the Baltic Sea is largely an effect of the bedrock morphology. However, the region has undergone several glaciations, and this has affected the seabed sediments in several ways. In the northern parts of the Baltic Sea land rise is still significant, with an uplift of up to 9 mm per year. Periods of erosion and sedimentation has given a very diverse seabed morphology. In the southern parts of the region, in the more shallow areas and along the southern and eastern coasts of the Arkona and Bornholm basins, sandy bottoms are common, being replaced by mud and some hard clay in deeper areas. In the Western and Eastern Gotland basins, soft bottoms become more

dominating, however with sand and hard bottom substrates in more shallow areas where water movement remove fine grained sediments. The Bay of Riga is dominated by sand in shallow areas along the coast and mud in deeper areas. The Gulf of Finland has a diverse mix of substrates including bare bedrock along the northern coast. The Bothnian Sea bottoms consist of mud and hard clay in deep areas, and hard bottom complex in more shallow areas. This continues into the Bothnian Bay although there are also some sandy bottoms here.

Offshore banks are defined by the Environmental Protection Agency (2006) as areas more shallow than 30 m not connected to land and surrounded by deeper waters. Offshore banks are considered ecologically important as refuges for coastal species since anthropogenic impacts of nutrient load and particle sedimentation are not as severe here as closer to the coast (Naturvårdsverket, 2010, 2006). It also seems that offshore banks attract fish, considering that some of them are important fishing grounds for commercial fisheries, often for species that are known prey for porpoises such as herring and cod (Andrulewicz and Wielgat, 1999). As mentioned above, it also seems spawning herring occur on some of the banks This may be due to nothing more than the underwater structure rising from the surrounding deeper areas, but may also be influenced by hydrological properties. For example, a Swedish study of offshore banks has shown that there are strong horizontal gradients in temperature and salinity over the banks, and that wind-driven intense but often short-lived currents occur over some banks (Naturvårdsverket, 2006). The water above the bank is often not stratified, and wave action removes sediments and ensures good oxygen conditions (Andrulewicz and Wielgat, 1999). There are a number of offshore banks in the Baltic Proper (see Figure 2), which may be important habitat for porpoises due to the possible aggregation of prey around these structures.
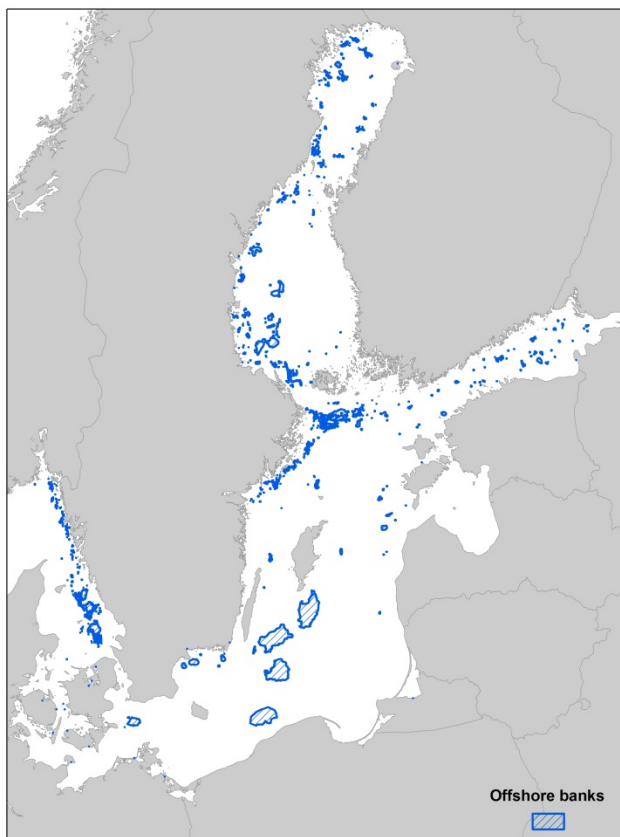

Figure 2: Offshore banks in the Baltic region

The Baltic ecosystem

In the last century, the Baltic Sea ecosystem has undergone considerable changes. In the beginning of the 20th century, the Baltic Sea was oligotrophic, dominated by marine mammals (seals and porpoises) as top predators and with small populations of cod, herring and sprat. During the 1930's seal populations were diminished by hunting, and the levels of fish biomass increased because of decreased predation pressure. As the hunting of seals continued, these populations were also subject to increased levels of environmental contaminants, causing reproduction problems, and were further diminished, while anthropogenic eutrophication led to high primary productivity. The result was a system dominated by cod as the most important top predator, and record cod catches in the middle of the 1980's. Meanwhile, eutrophication became a serious problem, causing hypoxia on deep bottoms, changing the benthic communities. Previously cod had fed mostly upon benthic crustaceans, but the disruption of benthic food webs led to cod switching prey to consume mostly clupeids (sprat and herring). After the 1970's, the Baltic Sea can be considered to be eutrophic. After the extremely high biomass of cod in the middle of the 1980's, the stock collapsed. This is considered to be due to a combination of a long period of stagnation of deep water with worsening hypoxia which reduced the reproductional success of cod, together with continuously high fishing pressure. The collapse of the cod population was immediately followed by a large increase of sprat, which was likely due to both the decrease in predation by cod but also to very good conditions for sprat reproduction, and in the middle of the 1990's the sprat stock was larger than ever before. Since then, the Baltic Sea ecosystem has been dominated by sprat and herring as the most important top predators (Österblom et al., 2007).

As previously mentioned, the dominating fish species in the Baltic Sea pelagic ecosystem are cod, herring and sprat. The zooplankton community consists mainly of calaniod copepods but also cladocerans and rotifers, and mysiids are the most common nektobenthos. Zooplankton have a diel vertical migration pattern, spending the day in deep waters and the dark hours closer to the surface. The salinity gradient results in a similar gradient in species composition where marine species are gradually replaced by freshwater species. The number of species which can survive the brackish conditions are not as numerous as the marine species, which means that the number of species present are lower in the Baltic Sea than in the North Sea. In the coastal areas of the Baltic Proper, habitat forming species such as bladderwrack (*Fucus vesiculosus*), eelgrass (*Zostera marina*) and blue mussels (*Mytilus edulis*) are considered important for the ecosystem. Underwater vegetation has been shown to be important as nurseries for juvenile fish of several species (Snickars et al., 2010, 2009). In deeper areas where bottoms are often muddy or sandy the burrowing mussel *Macoma baltica* and the crustacean *Saduria entomon* living on the sediment surface are examples of characteristic species.

Porpoise distribution in the Baltic Sea region

In this section, I attempt to make a prediction about what the porpoise distribution in the Baltic region should look like based on the facts gathered above. This is done through a rather straightforward overlay analysis. GIS layers were collected, describing environmental variables that from the above literature review can be deduced to have impact on the importance of an area as harbour porpoise habitat. Unfortunately not all relevant layers could be accessed, for example a layer showing the gyre close to Södra Midsjöbanken is missing in the analysis, even though the layer on current speed could be considered sufficient since increased current speeds are evident in the area where the gyre is supposedly located. Grid values were set to the value of one above certain threshold values and to zero below this limit. Using the ArcGIS raster calculator, all layers were then added together, giving areas likely to be important porpoise habitat higher values than areas of lower quality.

The offshore banks layer was made by selecting all areas more shallow than 31 m not connected to land, considering these areas as offshore banks according to the Swedish Environmental Protection Agency definition (2006). However, some Baltic Sea offshore banks were removed when using this strategy, for example Kriegers Flak and Slupsk bank were connected to land through tongues of water only slightly more shallow than 30 m. These offshore banks were manually added to the layer. Based on the theory that offshore banks act as important structures in the marine environment, attracting fish and serving as refuges also for other species, the banks themselves were given a value of one and the surrounding areas the value zero.

Three oceanographic/hydrographic variables were used in the analysis; temperature, salinity and current speed. For temperature and salinity the standard deviation over a year rather than the yearly mean was used, since the variation in these variables is likely to be more important than a specific range of temperature or salinity, given that areas where such variables show high variation can be more productive. For currents however, the mean current speed was used since high currents have been shown to influence porpoise presence (Edrén et al., 2010; Gilles et al., 2011), probably because currents influence sedimentation and food availability for fish, i.e. the porpoise prey. For all three of these variables, the threshold values were set to the mean, and all values above that were given the value of one for the following overlay analysis.

Predictions of cod and herring distribution in the Baltic Sea were also available for the analysis. These layers were modelled as catch per unit effort (CPUE) based on ICES BIAS and BITS data from 1999-2005 (Carlén and Isaeus, 2007). For herring, a model describing the distribution of small herring (<15 cm length) at the time of the survey in September-October was used in the analysis. For cod, predictions for the first and fourth quarter were available, and a mean of the two was used in the overlay analysis, to better complement the yearly averages of the other environmental variables. The cod predictions were made for cod >30 cm, since fish above that size is less common as prey for porpoises. The threshold value for prey layers in the overlay analysis was set to the mean plus one standard deviation. The reason for setting this threshold value is that the fish distribution predictions indicate rather large areas as important cod and herring habitat, and setting the threshold values to the mean would make the result from the overlay analysis less specific.

The ICES data that the prey species predictions are based upon are collected in a limited area. Therefore, to avoid extrapolation, the predictions of prey distribution were limited to certain depth intervals and certain areas. In the overlay analysis, this means that areas where one or more fish species predictions are absent will never achieve a value as high as areas where all fish distribution predictions are available. These areas are marked with striation in the map showing the result of the overlay analysis (Figure 3).

The result of the overlay analysis is shown in figure 3. The area between southern Sweden and the island of Rügen in Germany including the offshore bank Kriegers Flak, are indicated as being of high importance, as well as the mid-sea offshore banks Hoburgs bank, Norra and Södra Midsjöbanken and Slupsk bank. There are also areas along the coast of southern Finland, across Ålands hav and along the Swedish coast that may be of higher local importance. Areas in the Bothnian Bay and the Bothnian Sea are not considered relevant since the distribution of porpoises today is largely limited to the Baltic proper.
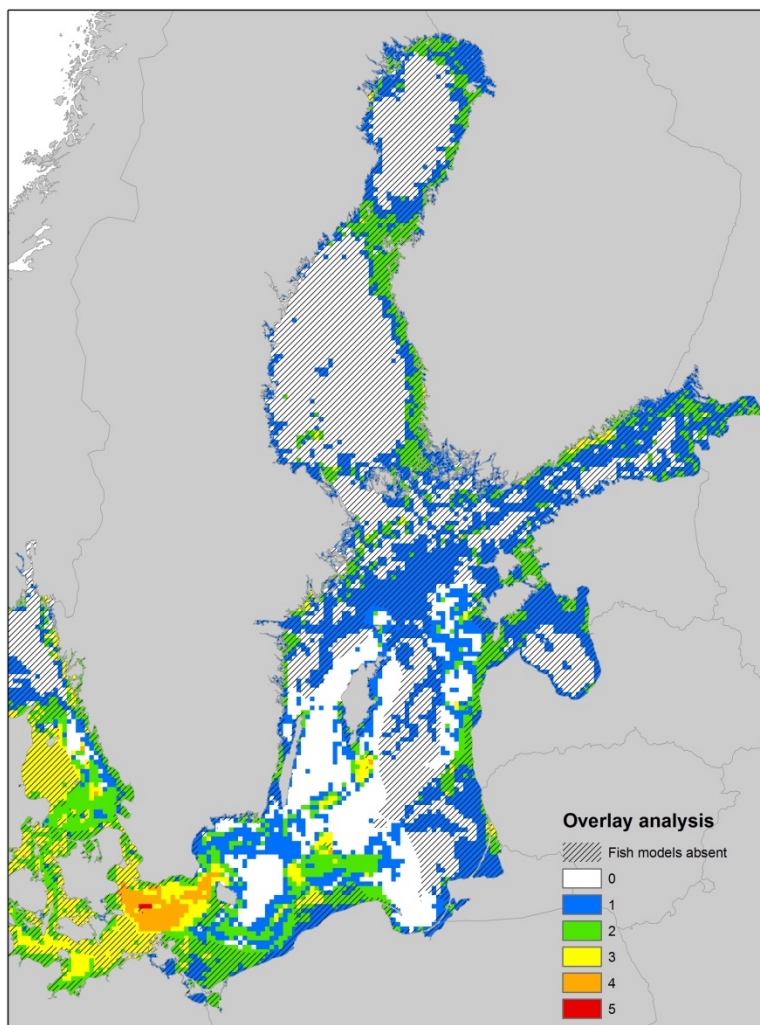

Figure 3: Result of the overlay analysis. Areas with high values are shown in red, orange and yellow and are thought to be of higher importance as habitat for porpoises than areas with low values shown in white, blue and green. Areas with striation indicate areas where one or more fish models are absent.

Conclusions

Highly mobile species such as porpoises are often aggregated on the short temporal scale, but may be more evenly distributed on a longer timescale (Haury et al., 1978; Robinson et al., 2011). Therefore, it can be argued that habitat modelling on a longer temporal scale would be more directly applicable in management situations, while shorter temporal scales in modelling would be important to understand what drives the fine-scale porpoise distribution.

Porpoises seem to prefer mature herring, which means they are likely searching for their prey offshore and possibly at spawning sites where aggregations of herring would likely be a convenient food source. Herring are known to be present on Södra Midsjöbanken in autumn (J. Netzel, pers. comm. In Andrulewicz & Wielgat 1999), which may make this offshore bank a feeding ground for porpoises. Sprat is slightly more coastal than herring but still pelagic, indicating that this food source may be found in similar environments as herring. Cod generally seem to prefer water temperatures from 2-10°C (Muus and Dahlström, 1985), and sandeel prefer sandy sediments. These fact suggest that basic environmental conditions such as salinity, temperature and bottom sediment are likely have some influence on harbour porpoise distribution, and could possibly be used successfully as explanatory variables when modelling the distribution of porpoises in the Baltic Sea.

To further increase knowledge on the harbour porpoise distribution in the Baltic Sea, and the environmental drivers for this, it is recommended as a next step that the environmental variables used in this overlay analysis are included in a statistical spatial model on porpoise distribution in the area.

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