

Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters

M. J. KAISER,^{1*} M. GALANIDI,¹ D. A. SHOWLER,² A. J. ELLIOTT,¹ R. W. G. CALDOW,³
E. I. S. REES,¹ R. A. STILLMAN³ & W. J. SUTHERLAND²

¹*School of Ocean Sciences, University of Wales – Bangor, Menai Bridge, Anglesey, Wales, UK;*

²*School of Biological Sciences, University of East Anglia, Norwich, UK;*

³*Centre for Ecology and Hydrology, Winfrith, Dorset, UK.*

Offshore wind farms are proposed around the coast of the UK and elsewhere in Europe. These sites tend to be located in shallow coastal waters that often coincide with areas used by over-wintering Common Scoter *Melanitta nigra*. A large-scale study was undertaken to ascertain the relationship of the spatial distribution of Common Scoter in Liverpool Bay with prey abundance and environmental and anthropogenic variables that may affect foraging efficiency. The highest numbers of Common Scoter coincided with sites that had a high abundance and biomass of bivalve prey species. There was strong evidence that the maximum observed biomass of bivalves occurred at a mean depth of *c.* 14 m off the Lancashire coast and at *c.* 8 m off the north Wales coast. This coincided well with the distribution of Common Scoter at Shell Flat, but less well with the distribution of birds off North Wales. Common Scoters were observed in lowest numbers or were absent from areas in which anthropogenic disturbance (shipping activity) was relatively intense, even when these areas held a high prey biomass. Commercial fishing activities did not appear to contribute to this disturbance.

INTRODUCTION

Common Scoters *Melanitta nigra* are a migratory species of seaduck that are protected in Europe through the provisions of the European Commission's Birds Directive (79/409/EEC) and Habitats Directive (92/43/EEC). Within the UK, this species is considered endangered in terms of its resident breeding population (Underhill *et al.* 1998) and is protected under the Wildlife & Countryside Act of 1981 as amended and the Countryside & Rights of Way Act 2000 which controls hunting and provides protection against disturbance to breeding birds. Elsewhere in Europe, Common Scoters are not protected from hunting. Thus, Common Scoter are wary of human activity and man-made structures, boats and vehicles (Garthe & Hüppop 2004), the presence of which may exclude them from using potential feeding, roosting and breeding sites.

There is increasing interest in the use of renewable sources of energy to reduce reliance on fossil fuels and the negative effects of their associated emissions. At present, there are constructed, consented or proposed over 20 offshore wind farms around the coast of the UK of which 10 are in Liverpool Bay, Irish Sea, UK (one of which has been constructed already). Liverpool Bay is an important non-breeding site for Common Scoters. Birds are present in Liverpool Bay throughout the year with peak numbers occurring from October to March. The first full census of Liverpool Bay using aerial surveys during the winter of 2000/2001 recorded a peak count of *c.* 16 000 birds (Oliver *et al.* 2001) with current estimates for 2003 approaching 29 000 birds (P. Cranswick unpublished data). At these population levels, Liverpool Bay ranks as one of the most important wintering sites for Common Scoter in the UK, and has been proposed as a marine Special Protection Area (SPA) for Common Scoter as defined under the provisions of the Birds Directive (Johnston *et al.* 2002). In Liverpool Bay, aggregations of Common Scoter are found primarily off Llanddulas (North Wales) and from an area off the

*Corresponding author.
Email: michel.kaiser@bangor.ac.uk

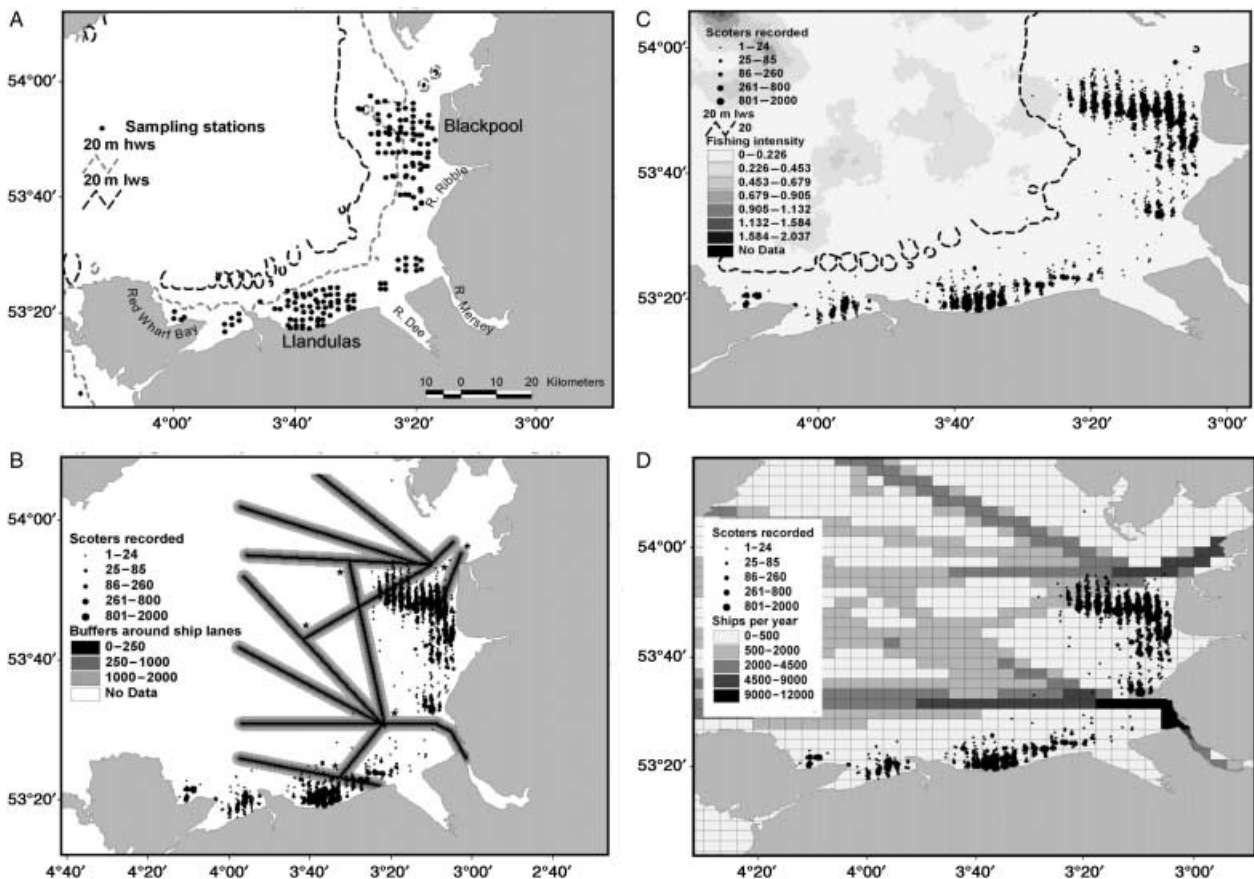


Figure 1. (A) Map indicating the position of Liverpool Bay within the Irish Sea UK, with the modelled bathymetries for spring and neap tides at high and low water at 5 m depth band intervals. Sites sampled for benthic prey species are shown as filled circles. (B) The distribution of fishing effort in Liverpool Bay derived from DEFRA overflight data and the sightings of Common Scoters for the winter seasons 2002/2003 and 2003/2004. (C) Sightings of Common Scoters as for (B), with proposed round 1 wind farm applications and the projected areas of intense shipping activity using the flush distance data from the present study, the less intense routes of shipping activity are bounded by stars at the start and end of the shipping lanes. (D) The number of ships > 300 t that passed through each 3.7×3.35 km area of the sea. The number of Common Scoters sighted during eight overflights for the period 2002/2004 is shown for reference in B, C and D.

mouth of the River Ribble up to Shell Flat, a shallow subtidal area off Blackpool, Lancashire, UK (Fig. 1).

Common Scoters are diving ducks that feed on prey species that live upon or within the upper few centimetres of the substratum. The diet of Common Scoter is thought to comprise mainly bivalve molluscs, other species are incorporated less frequently (e.g. crabs, small fishes and gastropods), and echinoderms seem to be included in the diet at such a low frequency that they are presumed to be ingested incidentally (Stott & Olson 1973, Bourne 1984, Ferns 1984, Stempniewicz 1986, Vaitkus & Bubinas 2001, present study). Common Scoters tend to be highly aggregated and, like other diving ducks, have been reported to severely deplete their food resources

over one season (Stempniewicz 1986, Guillemette *et al.* 1996, Guillemette 1998, Nehls & Ketzenberg 2002, although see Nilsson (1972) for evidence to the contrary). They may therefore exert considerable mortality to populations of certain prey types. The exact mechanism of feeding is unknown, although it is unlikely that they are visual feeders, particularly in Liverpool Bay where the water is especially turbid due to riverine discharge from the Rivers Dee, Mersey, Ribble and Conwy.

Common Scoter feed on benthic prey whose life-history strategies and productivity are intimately linked to the sedimentary and coastal environment (Snelgrove & Butman 1994). Sedimentary habitats are strongly influenced by near-bed hydrodynamic

stress and hence this can be an important determinant of benthic assemblage distribution (Warwick & Uncles 1980, Yates *et al.* 1993). Shear bed stress will have both positive and negative effects on benthic communities. At low shear stress values, increasing shear increases the supply of food and hence production of the benthos until a threshold where further increases in shear stress inhibit feeding (Hiddink *et al.* in press). Increasing levels of wave erosion increase mortality of the benthos (Hiddink *et al.* in press). These two factors are likely to interact close to the coastline and will have a strong influence on the production of the associated benthic communities. In addition, benthic communities are notoriously patchy in their distribution and the population sizes of benthic invertebrates fluctuate greatly from one year to the next (e.g. Rees *et al.* 1977, Beukema 1995). Thus food resources available for Common Scoters are unlikely to be uniformly distributed over the seabed and certain areas will yield higher rates of energy intake than others. Presumably, Common Scoter, like other diving ducks, distribute themselves over, or in close proximity to, areas that have a sufficient abundance of prey, to maintain their energetic requirements and are able to assess the rate of encounter with suitable prey as they probe through the sediment with their bill (Stott & Olson 1973, Phillips 1991). The consistency of the sediment is likely to affect foraging efficiency if selection of prey is by passive sifting. Sediments that contain a proportion of 'prey-sized' inedible particles may interfere with ingestion such that foraging efficiency is compromised. The profitability of prey will also be affected by the depth to which the birds need to dive to feed, which is a continuously changing variable in tidal areas. The deeper that benthic feeding birds need to dive, the longer they must take to travel to and from the seabed (Dewar 1924) and the greater the energy that they must expend acquiring prey (Lovvorn & Jones 1991). However, because buoyancy is the predominant force against which ducks have to work during dives (Stephenson *et al.* 1989), and the uplift generated by air in the lungs decreases as a function of depth and hence increasing pressure, the increasing relationship between depth and energy expenditure may be non-linear (Wilson *et al.* 1992).

A number of environmental and anthropogenic factors are likely to affect the distribution of the birds at the sea surface: the distribution and quality of the prey that may vary interannually and through the year; the depth of the water over the seabed that fluctuates tidally; the surface current speed which,

in Liverpool Bay, will move birds at the water surface at speeds of up to 1–2 m/s at peak tidal flow; the distribution and density of conspecifics; diurnal patterns in feeding behaviour; and the proximity to human activity and structures.

As in other species, the birds probably use visual cues such as the density of conspecifics to locate initial feeding sites before sampling other possible food patches (Nilsson 1972). Because swimming against a current is costly (Woakes & Butler 1983, Hawkins *et al.* 2000), surface currents may be important if birds are required to continually maintain their position over patches of prey by swimming against currents, or by relocating periodically by flying up-stream.

The development of offshore wind farms has the potential to influence scoter duck distribution through two mechanisms. First, these ducks may avoid areas of the sea populated by man-made structures and may thereby be prevented from accessing feeding areas. Secondly, the foundation base of the each turbine and associated cable laying activities may alter near-bed hydrography such that the sediment environment changes its suitability for important prey species. Understanding the relationship between the distribution of Common Scoter and the abundance of their potential prey may be critical when attempting to predict the response of scoter duck populations to loss of habitat due to the construction of structures such as wind farms. Understanding the likely consequences of wind farm developments requires knowledge of the other forms of disturbance that already occur which may include shipping, fishing and recreational yachting activities, hydrocarbon and aggregate extraction.

Previous studies of the relationship between Common Scoters and their prey have inferred diet by surveying general areas of seabed in the vicinity of known aggregations of birds (e.g. Degraer *et al.* 1999). However, in the present study, we were able to use aerial surveys of Common Scoter to generate a more accurate picture of the distribution of a regional population of birds in direct relation to quantitative samples of the benthic assemblage and environmental characteristics of the surveyed area. The specific aims of the present study were to:

- (1) study changes in seasonal habitat use by immature, male and female Common Scoter;
- (2) to make direct observations on the behaviour of Common Scoter in relation to environmental conditions, human disturbance and during foraging bouts;

- (3) ascertain whether the distribution of Common Scoter in Liverpool Bay was related to the distribution of key prey-types;
- (4) determine environmental factors that may predict either the distribution of Common Scoter or key prey-types; and
- (5) to ascertain to what extent existing anthropogenic activities influence or constrain the distribution of Common Scoter. These data provide the basis for predictive modelling of the population effects of likely wind farm construction in Liverpool Bay on the Common Scoter population. The predictive modelling is outside the scope of the present manuscript.

METHODS

Distribution and general behavioural observations

Aerial survey

Common Scoters were surveyed by staff of the Wildfowl and Wetlands Trust (WWT, Slimbridge, UK) from a light aircraft flown along transects in a north-south orientation during February and March 2004. Due to the limited number of observation dates in the winter season of 2003/2004, caused by weather constraints and factors beyond the control of the authors, observations from the previous winter season (August 2002 to April 2003) were also included to give a more detailed impression of the summed extent of the distribution of Common Scoter observed during these periods (data were extracted from a total of eight separate overflight surveys, Table 1). Counts of birds were made following the protocol outlined in Camphuysen *et al.* (2004). The aerial survey did not achieve 100% cover of the sea surface and we did not interpolate between these observations for the purpose of the present study; only the raw data were used. This approach is acceptable given that we are primarily interested in the relative abundance of Common Scoter at each observation point (highest abundance cf. lowest abundance cf. no Common Scoter). For each sighting of single or groups of Common Scoter, the time (GMT) and date were recorded. Given this information we were able to hindcast the depth of water at each observation point at the time of observation using tidal prediction models adapted from Liverpool Bay. Overflights occurred primarily from mid morning to early afternoon (i.e. in daylight) but the tidal state varied from one survey to another (Table 1) (Cranswick *et al.* 2004).

Table 1. The date and start time and end time of each overflight survey from which counts of Common Scoter were used in the present study. The time of approximate time of high water is also shown. All times are GMT.

Day	Month	Year	time start	time end	high water
16	Aug	2002	1040	1150	1700
17	Aug	2002	1210	1310	1800
19	Aug	2002	1030	1230	1900
15	Nov	2002	1100	1315	800
17	Nov	2002	1030	1345	900
6	Dec	2002	1100	1100	1200
7	Dec	2002	1050	1050	1300
10	Jan	2003	1100	1430	1600
11	Jan	2003	1100	1430	1700
7	Feb	2003	1040	1440	1400
8	Feb	2003	940	1240	1500
8	May	2003	1115	1230	1500
9	May	2003	1030	1115	1600
10	Feb	2004	1050	1340	1300
11	Feb	2004	1050	1410	1400
10	Mar	2004	1030	1430	1300
11	Mar	2004	1050	1350	1400

Behavioural observations

Preliminary land-based observations and a ship-based survey on board the RV Prince Madog were undertaken during October 2003. Suitable land-based observation points were identified and field methodologies tested. During this period, climatic conditions were good with light winds and calm to moderate seas. Study sites were selected on the basis of the preliminary survey, however, later the Blackpool site was not utilized as it was not possible to see Common Scoter in sufficient detail for the purposes of data collection. The localities used for the purposes of behavioural observations during the period of study were (from west to east); Red Wharf Bay; Conwy Bay observing from Llanfairfechan, Penmaenmawr and Llanddudno West Shore and the Great Orme; Colwyn Bay observing from Llandudno Little Orme, Penmaen Rhôs, Llanddulas and Abergele. Of these localities only in Colwyn Bay between Penmaen Rhôs (Ordnance Survey grid reference SH881788) east to Abergele (SH943788) were large numbers of scoter visible and close enough inshore to afford data collection opportunities. An especially good locality situated between these two points, Llanddulas (SH906786), was selected as the main survey locality where it was possible to observe consistently between 200 and 2000 Common Scoter. Observations were made from the area of the beach car park situated north of the A55 coast road.

Occasional observations during subsequent 2-week survey periods in each of December 2003, February 2004 and March 2004, were made at localities visited in October 2003. This was done to assess the presence/absence of Common Scoter and to identify any additional survey sites. Of the latter, only at Red Wharf Bay were significant numbers of scoter located close enough inshore (< 1.5 km) for observations to be undertaken, with an estimated 900–1000 birds present in February and March 2004.

Sex and age ratios

Sex and age data were collected during the course of direct observations and undertaken during each of four survey periods (October and December 2003, February and March 2004) to ascertain arrival dates and the proportions of male to female/juvenile Common Scoter wintering in Liverpool Bay. Observations were made using binoculars and a $\times 30$ magnification wide-angle telescope mounted on a tripod, both from the shore and at sea. During the first two survey periods (October/December) at each locality where scoter were encountered, at least 100 birds were assigned to one of two age/sex categories: (1) female/juvenile (i.e. first autumn) and (2) adult and subadult (i.e. 2nd winter) male. Due to the similarity in plumage of female and juvenile Common Scoter in the autumn and early winter (basically brown with pale cheeks) coupled with the observation distance (Common Scoter often > 800 m from the observer), it was not possible to distinguish between them. All such birds were placed in one category, i.e. female/1st autumn. Adult males are easily identified with all black plumage except for pale undersides to flight feathers. Sub-adult males (approaching their second winter) can only be reliably distinguished from adult male birds by their pale belly. Because this is only visible in flight, when wing-flapping on the sea surface with body raised or when roll-preening it was necessary to assign all adult and subadult males to a second category, i.e. adult and subadult males.

As winter progresses young males (first autumn entering their first winter) gradually attain an adult-like plumage with black feathers that appear from December onwards. During the February/March surveys, these could not be distinguished from adult/subadult males, except at relatively close range (< c. 600 m) in good light when the dark brown wings and brownish black rather than pure black upper parts were apparent. As observation conditions were rarely conducive for such determination, first winter males were placed in the 'adult

and subadult male' category in the post December 2003 surveys.

Orientation at the sea surface and flight direction

Common Scoter feed by day drifting with the tide, wind or current, flying back to regain their original position (Cramp & Simmons 1977). Repositioning or maintenance of position presumably can be achieved by swimming against the prevailing wind and/or current when wind speed and current velocity are low. Orientation and flight direction observations were undertaken to examine the possible influence of wind, tide and current on bird behaviour. During land-based observations from Llanddulas, each hour or half hour, a sample of 100 scoter sitting on the water were assigned one of four orientations (north, south, east or west) dependent upon which direction they were facing. If the required number of birds was not visible in the initial field of view of the telescope (looking out perpendicular to the coastline), the sea was scanned east or west (dependent upon position of the sun and location of birds) until the required number was counted.

From a fixed observation point with telescope mounted on a tripod at a fixed angle looking out perpendicular to the shoreline, for 10 min each hour or half hour, the direction of flight of all Common Scoter flying through the field of view was recorded. A dictaphone was used so that observation was continuous throughout the duration of each survey. All flying individuals were counted regardless of the flight distance, i.e. a short rise and ditch consisting of tens of metres, or a flight passing from one side of the field of view to the other. The flight direction was recorded as north, south, east or west. Circling birds landing in approximately the same position from which they rose were recorded as 'circling'. Wind direction (N,NE,E,SE) and wind speed (Beaufort Scale) were recorded at the end of each count.

Habitat use during rough sea state

Most observational data concerning winter ecology of Common Scoter, including aerial surveys conducted to determine their numbers and distribution at sea, not surprisingly stem from observations undertaken during periods of good weather. Therefore, on an *ad hoc* basis during periods of inclement weather additional land-based scoter observations were undertaken to ascertain if Common Scoter distribution was influenced by adverse weather conditions, e.g. utilization of sheltered bays. During periods of inclement weather, i.e. c. force 6 or above (wind speeds > 40 km/h),

localities along the North Wales coast from Red Wharf Bay to Abergele were assessed for presence/absence of Common Scoter by scanning with telescope and binoculars from land-based observation points. Basic behavioural activities, i.e. feeding, loafing and displaying, were noted when possible.

Existing potential sources of disturbance

Boat traffic disturbance and flush distance

There is little empirical data regarding the effects of disturbance to Common Scoter from boats, but it is known that they are intolerant of approaching vessels and are easily flushed from their feeding/loafing areas (Garthe & Hüppop 2004). The ship's radar was used in combination with field observations to assess flush distances of Common Scoter flocks at the approach of the RV Prince Madog. Flush distance is likely to relate to the size (height) of vessel structure above the water-line, hence our observations related only to vessels of the critical specifications of the RV Prince Madog (length overall 34.9 m, breadth moulded 8.5 m, height above waterline to the top of the main superstructure = 15.4 m (excluding the main whip aerial), 390 t (gross). A fuller investigation of the influence of this parameter on flush distance was beyond the scope of the present study.

Two observers (using binoculars) positioned on the ship's bridge located and counted the number of Common Scoter in a flock as they rose from the sea surface at the approach of the research vessel. From the radar, knowing the position of the ship and the point at which the birds rose from the sea surface, a flush distance and bearing was determined. The ship travelled on a steady course at a typical cruising speed of *c.* 10 knots whilst observations were made.

In addition to these direct observations, we used data of the relative intensity (highest to lowest) of shipping activity in Liverpool Bay collated by the Department of Trade and Industry (DTI) to examine the distribution of observed Common Scoter in relation to the main areas of shipping activity. Detailed information of fishing activities in Liverpool Bay were ascertained for the period 1987–2002 from enforcement agency overflight data of direct observations of fishing vessels expressed as sightings per unit effort of observation (SPUE) (see Dinmore *et al.* 2003 for a full explanation of methods of data calculation and interpretation). For the dti observations of commercial shipping activity we used two approaches.

First, we plotted the central navigational channels from the interpolated plots and used these to delineate Common Scoter exclusion zones based on the observations of Common Scoter flush distances. Using ArcView (Environmental Systems Research Institute) software we were able to assign observations of birds to areas that fell within these zones of shipping activity. Considering that the flush distance of birds was only ascertained for a vessel of the size of the RV Prince Madog, these data should be interpreted in this context only (birds may respond at longer or shorter distances to larger and smaller vessels, respectively).

Secondly, we used commercial shipping intensity data made available to us by Anatec UK Ltd through the COASTS database, and supplied as the number of ships (> 300 t) passing through each 3.7 × 3.35 km area of sea per year. The COASTS database holds only data for vessels greater than 300 t (gross). The RV Prince Madog from which the flush distances were measured (section 4) is 390 t (gross). Hence the data represent vessels from 300 t up to super-tankers >> 90 000 t (gross). Vessels were assigned to each grid cell from the reported route taken by the vessel (port of embarkation, port of destination). Vessel routes are assumed to take the shortest possible linear distance other than to conform to the regulations imposed by navigational channels and separation zones (e.g. off the northern tip of Anglesey). The numbers of vessels that docked or embarked from each of the major ports around the North Wales and Lancashire coastline were extracted per month for the year 2003/2004 to determine any seasonality in the amount of potential disturbance from commercial shipping activity.

Foraging activity and prey type demography

Dive duration

Common Scoter dive duration time (seconds), time and location of all field observation points were recorded. Common Scoter dive individually, or more often as a group when in a small flock. When in a flock they have a strong tendency to dive almost simultaneously, resurfacing together or staggered over a period of a few seconds (D.A. Showler, personal observations). When staggered, an estimated time ± 2 s was assigned to each individual. The observations were made using a telescope mounted on a tripod. The distance of birds offshore was estimated to the nearest 50 m, using known reference points, i.e.

surface marker buoys. Water depth was recorded using the ship's echosounder for sea-borne observations. For each land-based observation water depth and surface current velocity was hindcast using standard tidal models.

Spatial and temporal variation in prey-types

In order to quantify the distribution and quality of food types available in Liverpool Bay, it was necessary to undertake an extensive stratified survey that sampled areas of the sea where Common Scoter had been observed and also areas where Common Scoter were not observed. For the purposes of the present study, we divided Liverpool Bay into two main areas; the Lancashire coast that extended from just north of Shell Flat to the centre of the entrance to the River Mersey, and the North Wales coast that extended from Red Wharf Bay across to the centre of the entrance of the River Mersey. These two areas held distinct high density aggregations of Common Scoter. The outer limits of our survey area were set by the reported maximum dive depth for Common Scoter which is 20 m (Degraer *et al.* 1999). As depth directly affects energy expended on travelling to and from the seabed and while foraging on it, we calculated depth bathymetries at 5 m intervals for both spring and neap tides. When possible, a selection of our sample sites coincided with the intersection between these depth bathymetries and the aerial survey flight paths that would enable a direct analysis of the relationship between Common Scoter abundance and prey abundance at these sites. Additional survey sites were selected to ensure that the full gradient of depth zones was sampled across Liverpool Bay.

Three surveys were undertaken from the RV Prince Madog in August and December 2003 and April 2004 to span a full over-wintering season of Common Scoter in Liverpool Bay. During the initial survey in August 2003, 81 and 88 sites were sampled off the Lancashire and North Wales coast, respectively. At each site, two 0.1 m² day grab samples were taken and their contents sieved over a 1 mm mesh aboard ship. Bivalves were picked off the mesh by hand and frozen for later biomass analysis. All other residues and biota were preserved in 4% buffered formalin. Of these sites, a total of 32 sites were sampled additionally (total of four day grabs) for biota and sediment analyses. These sites were termed monitoring sites and were re-sampled with the same sampling effort in December 2003 and April 2004 to enable the rate of decline of prey types to be calculated (mortality rate). Twenty-four of the 32 monitoring

sites occurred in areas over which Common Scoter were not observed, or occurred in low numbers throughout the overflight surveys. These 24 sites provide important information on the natural seasonal changes in potential prey abundance in the absence of predation by Common Scoter. In addition to these sites, we sampled two transects of six sites, spaced at an interval of 200 m to gain an estimate of small-scale variability in terms of prey-types and their abundance. Four Day grab samples were collected at each of these sites.

Given the necessity to collect a large number of samples across as wide an area as possible, our ability to analyse all components of the benthos within samples was constrained by time and manpower. As a result, we undertook an extensive search of the literature to ascertain the main recorded prey types of Common Scoter. The literature review yielded eight quantitative analyses of the diets of Common Scoter. The results of these studies are summarized in Table 2. It is clear that in all studies, the importance of molluscs in general and bivalves in particular is pronounced. In every study the percentage value for the occurrence of molluscs exceeded 90% and that for bivalves exceeded 88%. Fox *et al.* (2003) concluded that the local distribution and abundance of scoters is likely to be strongly influenced by the local abundance and availability of bivalves. As a consequence of these findings we have assumed that bivalves are the only prey resources of any significance that are exploited by Common Scoter in Liverpool Bay, and these were the primary focus of our benthic faunal analyses.

The literature search yielded a list of in excess of 30 different species of bivalve that have been recorded in the diet of Common Scoter. Thus, we considered that it is unlikely that Common Scoter are species specific in their choice of prey, but that selection is more likely to be determined by prey abundance, morphology, digestibility, energy content, prey abundance and accessibility. As a result we considered mollusc prey to fall into three main prey morphologies; elongate prey (e.g. *Ensis*, *Pharus*, *Phaxas*), ovate brittle shelled (e.g. *Abra*, *Fabulina*, *Lutraria*) and ovate hard shelled (e.g. *Nucula*, *Donax*, *Chamelea*) and within each of these, to fall into a number of size classes. For each sample site, mollusc prey-types were defrosted and their maximum and minimum shell dimensions measured to the nearest mm using Vernier callipers. Mollusc flesh was removed from the shell and weighed wet, after blotting, to the nearest mg. Wet flesh was dried to a constant temperature at 60 °C in preweighed crucibles. Dry flesh was then

Table 2. Summary of the findings of the 8 quantitative studies of the diet of Common Scoter. N birds denotes the number of individual birds examined. Values represent the percentage of the diet comprising each prey type as assessed by the method listed in the last column. Methods: i) % of birds found to contain items of the taxa in question, ii) % of total number of items identified from all birds sampled, iii) % of volume of gut contents, iv) % of weight of gut contents.

Reference	Method	N birds	Mollusca	Bivalvia	Gastropoda	Crustacea	Annelida	Echinodermata	Pisces
Madsen 1954	i)	219	95.9	93.2	10.9	10.9	12.8	0	0
Nilsson 1972	ii)	13	100	100	0	0	0	0	0
Stott & Olson 1973	iii)	42	99	98	1	1	0	1	0
	i)		100	100	12	21*	0	0	0
Bourne 1984	i)	16	94	88	12	56*	0	6	0
Stempniewicz 1986	iv)	52	93.9	93.9	0	0	0	0	6.2
	i)		100	100	0	0	0	0	19.2
Goudie & Ankney 1986	iv)	15	100	> 95	< 5	0	0	0	0
Meissner & Brager 1990	iv)	157	100	100	0	0	0	0	0
Durinck <i>et al.</i> 1993	ii)	125	100	100	0	0	0	0	0

*Refers to barnacles probably ingested incidentally with mussels *Mytilus edulis*.

placed in a muffle furnace set at 450 °C for 12 h to determine the ash free dry weight content (AFDW) to the nearest mg.

The relationship of AFDW on depth was modelled as a Gaussian curve according to:

$$G = G_{\min} + (G_{\max} - G_{\min}) e^{-\frac{(S-S_m)^2}{V}}$$

where G is the depth dependent bivalve biomass modifier; G_{\min} is the minimal biomass; G_{\max} is the maximum biomass; S is depth (m); S_m is the depth at which the maximum biomass is attained; and V is the variance of the Gaussian curve.

RESULTS

Visual surveys and behavioural observations

The main aggregations of Common Scoter were observed off Blackpool (Shell Flat), the River Ribble, Formby (Lancashire), Rhyl to Colwyn Bay, Conwy Bay and Red Wharf Bay (North Wales) (Fig. 1). In October 2003, 102 Common Scoters were sexed/aged and supplemented with *ad hoc* observations of *c.* 3500–5000 Common Scoter sighted between Llanddulas to Rhyl. At this time the majority of birds were male with a ratio of 8.3 adult/subadult males: 1 female/1st autumn female. In December 2003, a total of 1744 birds were sexed/aged at four different sites. The sex ratio at all localities was 1.1 adult/subadult males to 1 female/1st autumn. In February 2004, a total of 519 birds were sexed and a sex

ratio of 3.3 males:1 female estimated at Llanddulas. Weather conditions were consistently poor at this time, hence the sex ratio may have been an underestimate. At Red Wharf Bay an estimated 900–1000 birds were present in February 2004. Those birds that were sexed/aged ($n = 81$) gave a ratio of 4.1 males: 1 female. In March 2004 a ratio of 5.0 males: 1 female was estimated at Llanddulas ($n = 163$) while at Red Wharf Bay a ratio of 3.2 males: 1 female was estimated ($n = 135$). Intensive sea-based observations indicated that Common Scoter were no longer present off the North Wales coast in May 2004.

The proportion of Common Scoter flying into or within 45° of the prevailing wind increased with increasing wind speed ($P = 0.012$, $r^2 = 0.83$, d.f. = 4 (force 1 mean = 27%, force 2 = 65%, force 3 = 71%, force 4 = 63%, force 5 = 91%, force 6 = 100%). On days with a fairly constant moderate wind there appeared to be a discernable change in flight activity with the change in current direction. More specifically, on 11 December 2003, a day-long synchronized flight count was undertaken from two points; the west end of Llanddulas beach car park and 3 km to the east of this position. Wind was a relatively constant westerly force 4 (veering NW at 14 : 00). With wind and sea surface current acting together, a greater proportion of birds flew in the opposing direction; west Llanddulas: $74.2 \pm 7.41\%$; east Llanddulas: $75.2 \pm 8.22\%$. In contrast, when the wind and sea surface current countered each other the proportion of birds that flew into the wind was significantly reduced; west Llanddulas: $55.4 \pm 5.45\%$ east Llanddulas: $47.0 \pm 5.51\%$.

Habitat use during rough conditions

Visual shore based surveys were undertaken on two separate dates. On the 14 December 2003 the wind was north-westerly variable force 6–7 (occasionally gusting 8) and the sea state very rough in areas exposed to the prevailing wind with no protective land-mass (e.g. off Colwyn Bay to Rhyl). Areas where previously no significant numbers of Common Scoter were observed in autumn/winter 2003/2004 but that afforded some shelter from prevailing wind/high seas, still held no Common Scoter (Red Wharf Bay and Colwyn Bay west – with shelter from the Great Orme). For areas that usually supported significant numbers of scoter but that afforded no shelter from the prevailing wind/high sea: *c.* 200 Common Scoter 1000–2000 m offshore were observed in Conwy Bay, occasional more distant birds being observed in flight. The majority of closer birds were loafing with some small groups displaying. No Common Scoters were observed feeding. At Llanddulas *c.* 2000–3000 Common Scoter were observed as in calmer weather. As for Conwy Bay, the majority were loafing although many were engaged in intermittent display and very occasionally diving.

On the second survey (24 February 2004), the wind was northerly force 6 and the sea-state rough with intermittent rain. All sites apart from Llandudno were surveyed and on this occasion the northern end of Red Wharf Bay provided some shelter from the prevailing wind. Although Conwy Bay was sheltered beneath the Great Orme, no Common Scoter were observed in this area while in the central region of Conwy Bay only *c.* 150 birds were observed some 3–4 km offshore. At Llanddulas approximately 1000 birds were observed in a similar distribution to calm weather periods, while at Red Wharf Bay approximately 1000 birds were observed from 800 to 1500 m offshore. Not surprisingly, it was more difficult to make accurate observations in rough weather conditions due to birds appearing and disappearing from view in the troughs of waves, with the added reduced visibility due to frequent rain.

Dive duration

Based on hindcast tidal model calculations, the mean depth of water beneath Common Scoter observed at Llanddulas, for birds observed from the shore, was almost half the depth of water beneath observed birds in Red Wharf Bay (RWB) (mean \pm sd Llanddulas 6.85 \pm 1.70 m, RWB 11.42 \pm 1.51 m, $t = -42.7$, d.f. = 1021, $P < 0.0001$). The mean surface current velocity during observations at both sites was almost identical (Llanddulas 0.29 \pm 0.14 m/s, RWB 0.29 \pm 0.15 m/s,

$P = 0.95$). Mean dive duration was slightly higher at RWB than at Llanddulas (Llanddulas 34.75 \pm 8.5 s, RWB 36.96 \pm 7.2 s, $T = -4.25$, d.f. = 1021, $P < 0.0001$). An examination of the relationship between dive depth and dive duration indicated that the slope and intercept were higher at Llanddulas than at RWB (Fig. 2). This suggests that birds spent longer on the seabed at Llanddulas than at RWB for a given depth of water.

Sources of disturbance

Flush distance from the RV Prince Madog varied according to flock size. Larger flocks flushed at distances from 1000 to 2000 m ($n = 26$ observations), while small flocks flushed at distances < 1000 m ($n = 23$ observations). The median flock size of birds that were flushed by the approaching vessel was significantly greater for the 1000–2000 m zone compared with the zone closer to the vessel (Mann–Whitney, $U = 38.5$, $P < 0.001$). There was negligible overlap between areas in which Common Scoter were observed and fishing activity as quantified from Department of Environment, Food and Rural Affairs (DEFRA) overflight data (Fig. 1b). Applying the flush distance zones to the central navigation routes of major shipping activities in Liverpool Bay enabled calculation of the number of Common Scoter that might fall within each of the zones of shipping disturbance. While the majority of birds (97.35%) did not occur within 2000 m of high intensity shipping activity, a greater proportion of Common Scoter fell within 2000 m of less intensively used shipping routes (17.92%) (Fig. 1c,d, Table 3).

Shipping activity in and out of the main eastern Irish Sea ports did not vary significantly through the period of September 2003 to July 2004 (all relationships non-significant with time $P > 0.05$). Thus there were no seasonal patterns in shipping activity that might be relevant with respect to fluctuations of disturbance to Common Scoter throughout the year. However, shipping activity was spatially aggregated at the 3.75 \times 3.25 km grid scale such that *c.* 82% of Common Scoter observed through the period 2002/2004 occurred in cells that had zero shipping activities for ships > 300 t. The number of birds observed declined steeply with increasing levels of shipping activity (Fig. 1d, Table 3). The distribution of Common Scoter differed significantly from an equal distribution of birds among all model cells (Table 3, $\chi^2 = 51\ 173$, d.f. = 6, $P < 0.0001$).

Spatial and temporal variation in prey-types

The median biomasses (AFDW) of bivalves per unit area sampled from the Lancashire and North Wales

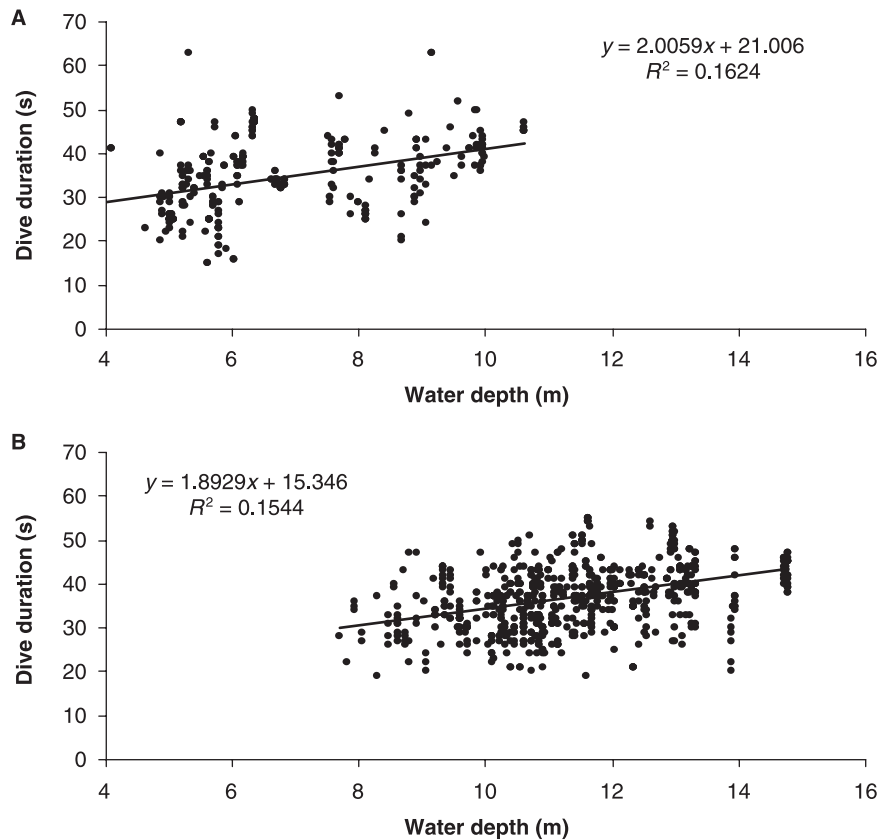


Figure 2. Dive duration (s) of Common Scoters observed primarily from the shore off (A) Llanddulas and (B) Red Wharf Bay.

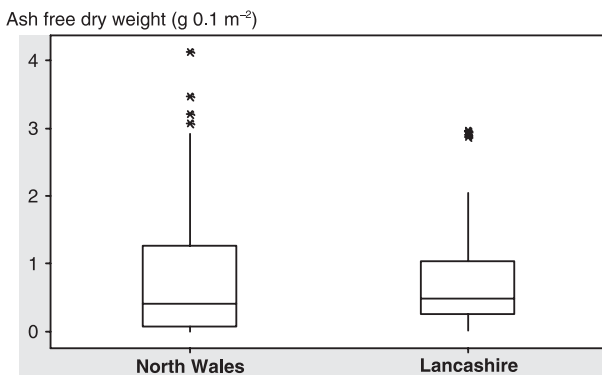


Figure 3. Box and whisker plots of the mean AFDW ($\text{g } 0.1 \text{ m}^{-2}$) for bivalves sampled off the North Wales and Lancashire coast in August 2003 prior to the arrival of over-wintering Common Scoters.

sites were not significantly different (Fig. 3. M.W.U = 7057, d.f. = 167, $P = 0.18$) although there was some evidence to suggest that there was less variability in bivalve biomass at the sites off Lancashire. Mean AFDW of bivalves was higher than that of other

components of the benthos across Liverpool Bay. At the monitoring sites, AFDW of bivalves and other benthic fauna was lower in April 2004 than in August 2003 but this was not a significant decrease for the bivalves (Table 4). However, the coefficient of variation of bivalve AFDW increased significantly from August 2003 to April 2004 which indicated that biomass was more patchily distributed across the seabed by the end of winter (Table 3). At both locations, the biomass of bivalves was significantly related to depth according to a Gaussian relationship. The Gaussian relationship for each site indicated that a peak in bivalve biomass occurred at a depth of 7.88 m and 13.96 m off the North Wales and the Lancashire coasts, respectively (Fig. 4, Table 5). The use of tidal models to hindcast the depth of water beneath Common Scoter observed during overflights indicated that most birds occurred more frequently over water between 7 and 15 m (mean \pm sd 11.12 ± 2.82 m) deep off North Wales and between 13 and 18 m (13.95 ± 2.81 m) deep off Lancashire (Fig. 5). Thus, birds were observed most

Table 3. Total counts of sightings of Common Scoters and the total recorded number of individuals summed over 8 overflight campaigns from autumn 2002 to spring 2004 that fell within three categories: 0–1000 m, 1001–2000 m, and > 2000 m from the centre of shipping lanes with either a high frequency or lower frequency of shipping activity (determined from DTI data). Disturbance was also calculated using the data from the COASTS database expressed as number of ships per 3.7×3.35 km sea area. The number of sea areas (cells) that fell within each disturbance category and the number of Common Scoters observed in those cells is also given (percentage of total in parentheses). See Fig. 1c and d.

	> 2000 m	2000–1001 m	1000–0 m
High frequency shipping			
Count	4116	78	70
Numbers	107 093	838	2077
Percentage	97.35	0.76	1.89
Lower frequency shipping			
Count	3480	362	423
Numbers	90 296	11005	8707
Percentage	82.08	10	7.91
<hr/>			
Ships per year per cell	Number of cells	Number of birds	
0	60 (48)	90 153 (82)	
1–100	23 (19)	7777 (7)	
101–400	23 (19)	6097 (5)	
401–1000	7 (5)	4811 (4)	
1001–3000	4 (3)	933 (1)	
3001–6000	4 (3)	56 (<<1)	
6001–12000	2 (1)	34 (<<1)	

frequently over water that was significantly deeper off Lancashire than off the North Wales coastline (Wilcoxon $Z = -1.94$, $P = 0.025$).

The spatial distribution of different prey types was highly aggregated (Fig. 6). Small oval hard shelled

Table 4. Change in mean (\pm sd) AFDW g 0.1 m^{-2} of bivalves and all other benthic biota for 24 monitoring stations with either low or zero observations of Common Scoters (within 250 m radius of station). The coefficient of variation (C.V.) for bivalves is also given.

	Aug-03	Apr-04	t	d.f.	P
Bivalves	4.31 \pm 6.37	2.85 \pm 4.83	0.89	46	0.19
Bivalves C.V.	0.62 \pm 0.53	0.93 \pm 0.44	-2.16	46	0.017
Other benthos	2.17 \pm 2.06	0.69 \pm 0.54	3.39	46	0.0007

prey (e.g. *Nucula*) were ubiquitous off Lancashire and to a lesser extent off the North Wales coastline but were particularly abundant on the northern shoulder of Shell Flat off Blackpool (Fig. 6a). Very high densities of *Donax* were sampled off the mouth of the River Dee on Chester Flats (Fig. 6a). Oval brittle prey types were relatively ubiquitous but were particularly abundant on Burbo Flats off the mouth of the River Mersey and off the North Wales coast and locally at Shell Flat (Fig. 6b). Elongate prey such as *Pharus* were locally abundant off the River Ribble and off the North Wales coastline and occurred in very high abundance in Red Wharf Bay (Fig. 6c). The distribution of total bivalve biomass (all species amalgamated) indicates that the highest concentrations of bivalve biomass occurred on Shell Flat, off the River Mersey and in Red Wharf Bay (Fig. 7).

DISCUSSION

Overflight observations of birds at sea have the advantage that they enable large-scale surveys of population density to be undertaken within a short

Table 5. Estimates for the Gaussian relationship for biomass with depth giving the mean \pm 95% C.I. for each parameter G is the depth dependent bivalve biomass modifier, G_{\min} is the minimal biomass, G_{\max} is the maximum biomass, S is depth (m), S_m is the depth at which the maximum biomass is attained and V is the variance of the Gaussian curve.

Parameter	Estimate	Upper C.I.	Lower C.I.	F	d.f.	P
North Wales						
G_{\min} (Log 10)	-1.2	-1.63	-0.78	15.53	4,84	0.05
G (Log 10)	0.32	0.02	0.63			
S max.	7.88	6.24	9.52			
V	17.7	-5.21	40.6			
Lancashire						
G_{\min}	0.668	-2.65	3.99	6.59	4,77	0.05
G	3.05	1.41	4.7			
S max.	13.96	12.26	15.66			
V	8.03	-19.93	35.99			

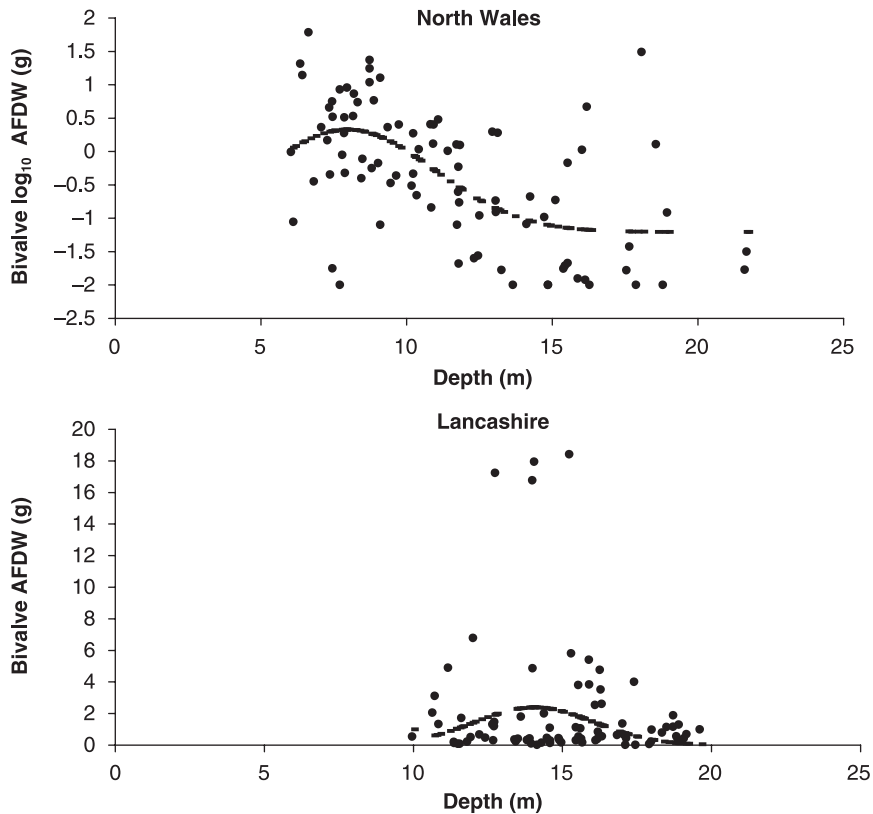


Figure 4. The relationship of bivalve AFDW with depth off North Wales and Lancashire in August 2003. Trend lines are the fit of a Gaussian model (see Table 5).

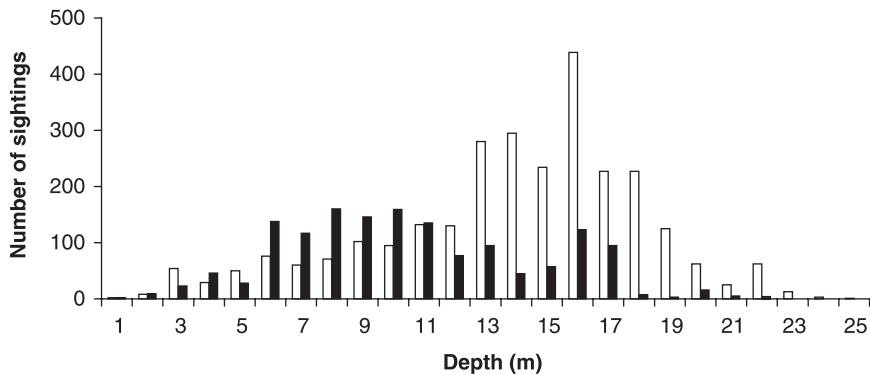


Figure 5. The number of sightings of Common Scoters off North Wales (black bars) and off Lancashire (open bars) in relation to the depth of water over which they were observed. Observations derived from overflights from two over-wintering periods: 2002/2003 and 2003/2004.

time period (Camphuysen *et al.* 2004). Nevertheless, this approach is problematic for a number of reasons, but particularly for diving ducks found in areas of high tidal amplitude. As water depth is a critical parameter for Common Scoters that feed on the seabed, the relative position of an aggregation may shift according to tidal state (low to high water),

which can vary considerably between the start and end of the survey (Table 1). Thus we felt using the sum total of 2 years of overflight observations would eliminate some of the spatial variation of Common Scoter attributed to tidal fluctuations. In addition, we were able to utilize tidal models to hindcast the depth of water beneath each separately

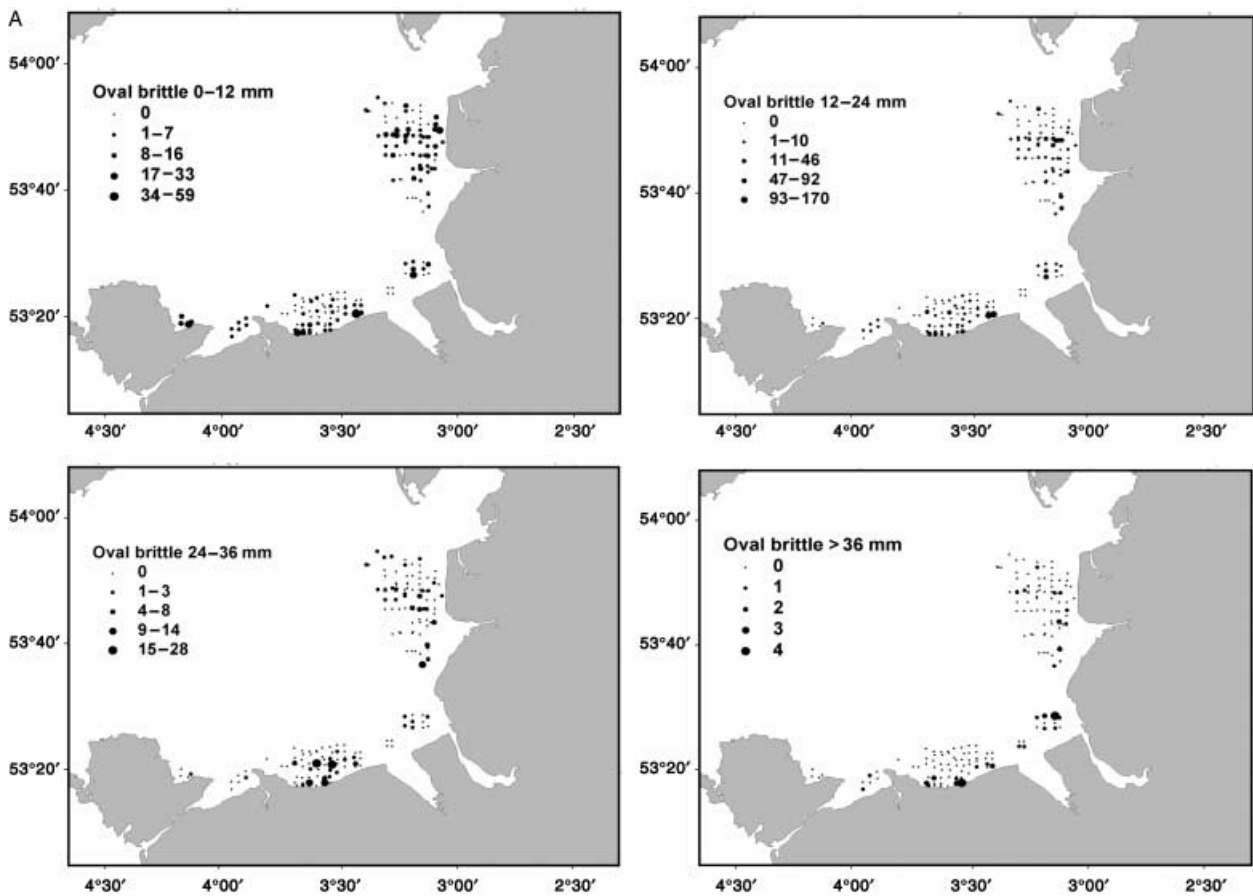


Figure 6. Bubble plots of the abundance of different size-classes of (A) hard ovate bivalve prey (B) brittle ovate bivalve prey and (C) elongate bivalve prey expressed in terms of AFDW ($\text{g } 0.1 \text{ m}^{-2}$). Data were plotted from a total 169 sample sites across the study area.

logged record of Common Scoter/s. Common Scoter located off Lancashire were primarily observed over deeper water than birds observed off the coast of North Wales (Fig. 5). Other shore-based studies have indicated that Common Scoters are found over water depths of between 3 and 20 m, which is similar to our shore based observations for Llanddulas and Red Wharf Bay (Dewar 1924, Madsen 1954, Stott & Olson 1973, Cramp & Simmons 1977, Goudie & Ankeney 1986, Meissner & Bräger 1990, Durinck *et al.* 1993, Bräger *et al.* 1995). However, seaducks can be found in areas where the water is too deep to dive for food (Degraer *et al.* 1999). It is clear from the aerial survey that Common Scoters utilize areas of the sea beyond the range of normal telescopic observations and occur over water up to a maximum depth of 25 m although the majority of birds are found in water shallower than 20 m.

Most authors agree that feeding areas used by Common Scoters are restricted to water of less than

20 m depth due to the constraints imposed by the energetic costs of diving to the seabed to consume benthic prey species. The present study is to our knowledge the first that has quantified the biomass density of prey across the full range of water depths reported by other authors. The depth distribution of Common Scoters off Lancashire and North Wales differed but closely coincided with the depth at which the peak in bivalve biomass occurs in both locations. This depth zone of the biomass peak differed for the two localities and was significantly deeper off Lancashire. Currents and the associated seabed shear stress, can influence food availability for benthic communities (Jenness & Duineveld 1985) and benthic secondary production (Warwick & Uncles 1980, Wildish & Peer 1983). High shear stress results in scouring and high current velocities inhibit feeding activity, while water movement at the sea bed is necessary for the supply of food to the benthos. Below a certain current velocity threshold,

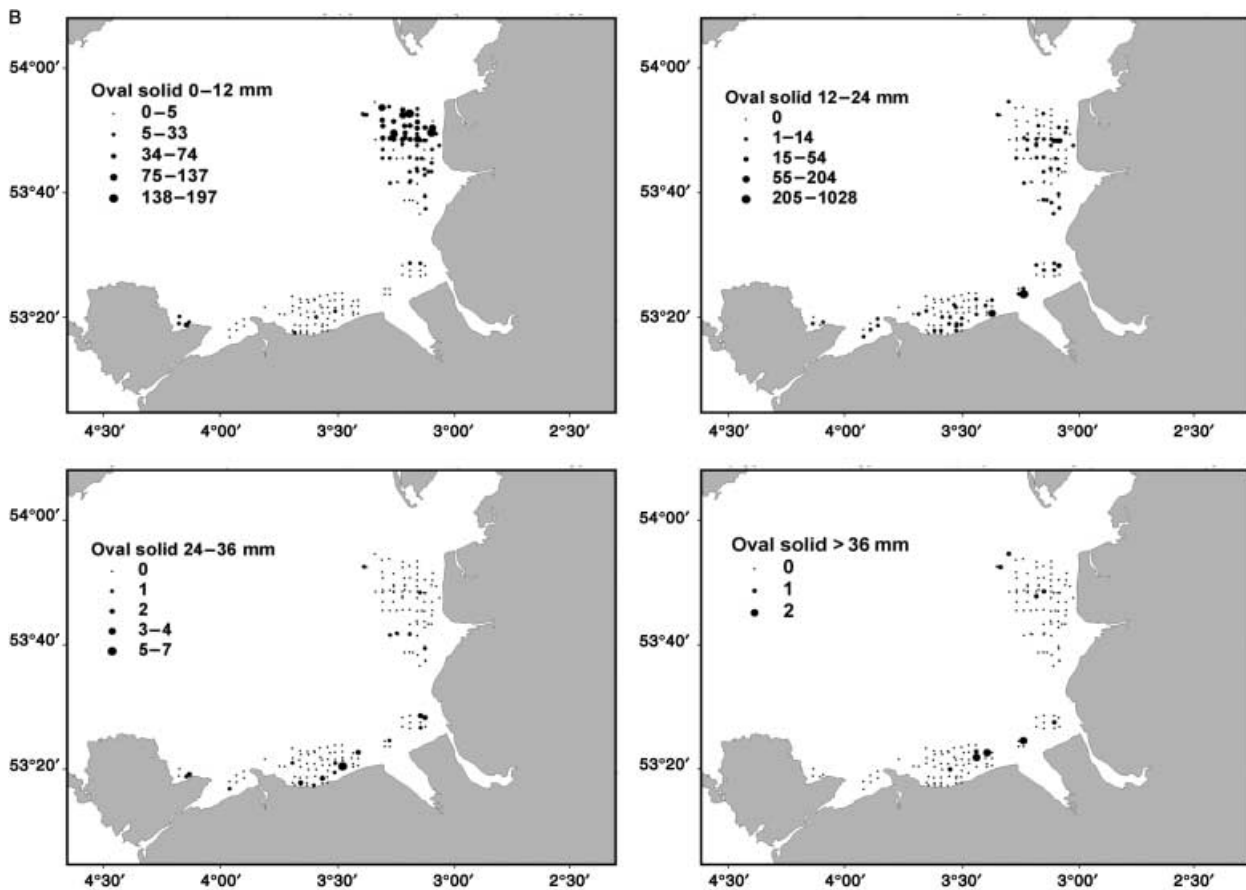


Figure 6. *Continued.*

food particles transported from other areas may begin to sink to the seabed, where they become available as food to the benthos (Creutzberg 1984). In addition to the natural mortality rates, which relate to body-size, sediment movement due to wave action caused by wind and tides, can be a major cause of mortality among benthic animals and has been shown to affect secondary production (Emerson 1989). Both shear and erosion are likely to interact with depth such that at some distance from the shore it is likely that a critical depth occurs where food supply from shear and mortality from erosion coincide to generate optimal conditions for growth. Although the Gaussian model that described the relationship between bivalve biomass and depth was significant for both survey areas there were some sites that had an exceptionally high biomass of bivalve prey, particularly off Lancashire. These exceptional biomass sites occurred in the depth range over which most birds were observed.

Previous studies have attempted to relate the constituents of a benthic community to known large-scale aggregations of Common Scoter. For example, Degraer *et al.* (1999) inferred that the benthos found on offshore subtidal sand banks was indicative of Common Scoter diet given that large aggregations of ducks were observed over these seabed features. Nevertheless, while Degraer *et al.*'s (1999) findings concur with the assertions of other studies (e.g. Stempniewicz 1986, Durinck *et al.* 1993, Leopold *et al.* 1995), their study was not designed to resolve the relationship between the spatial distribution of ducks and the spatial variation in the abundance or biomass of potential prey. Lovvorn & Gillingham (1996) stated that 'detailed mapping of benthic foods on a scale relevant to the foraging energetics of highly mobile birds is currently not feasible, despite the importance of food dispersion to their foraging profitability and sustainable population levels'. The present study is the first in which it has been possible

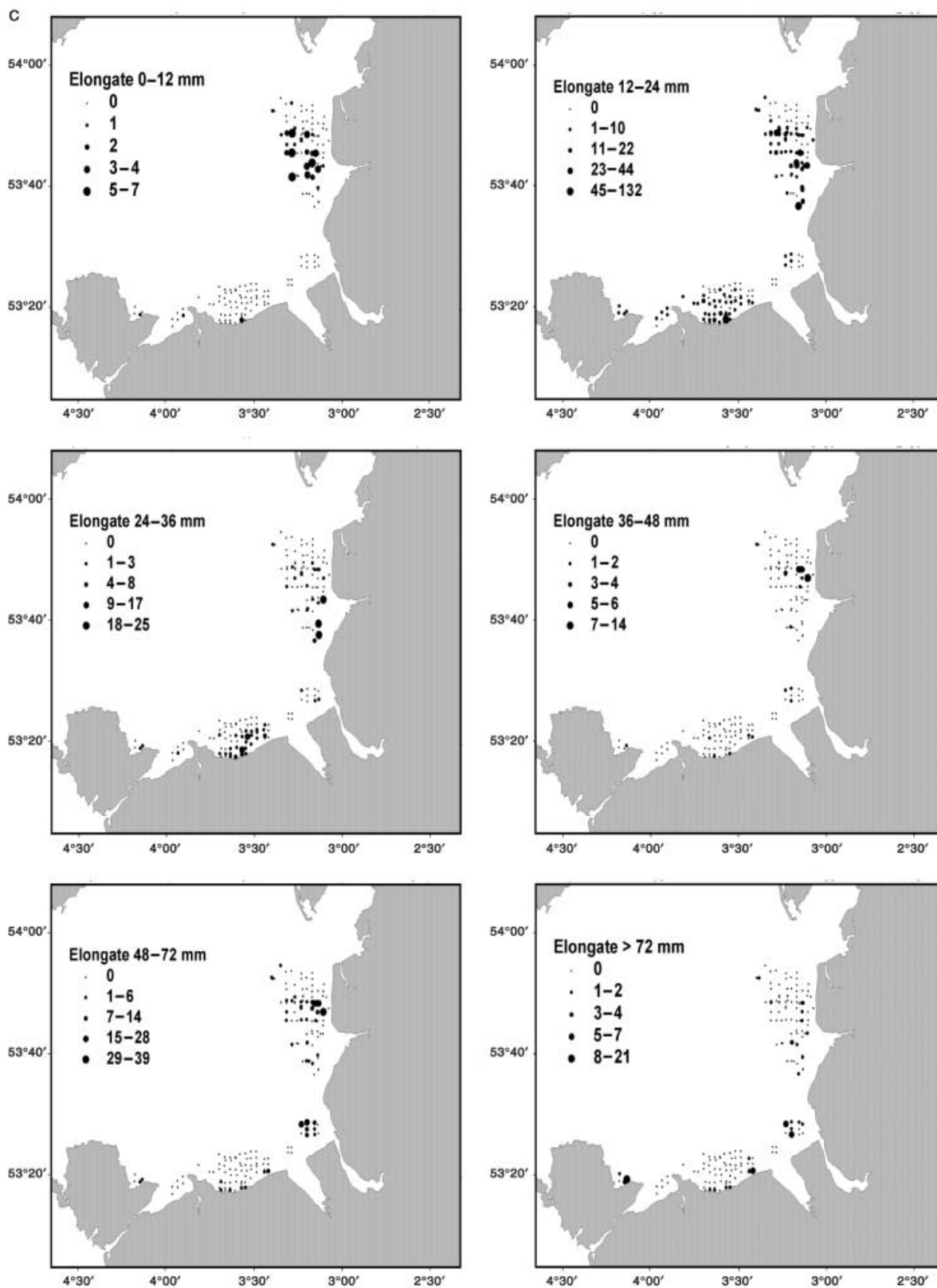


Figure 6. *Continued.*

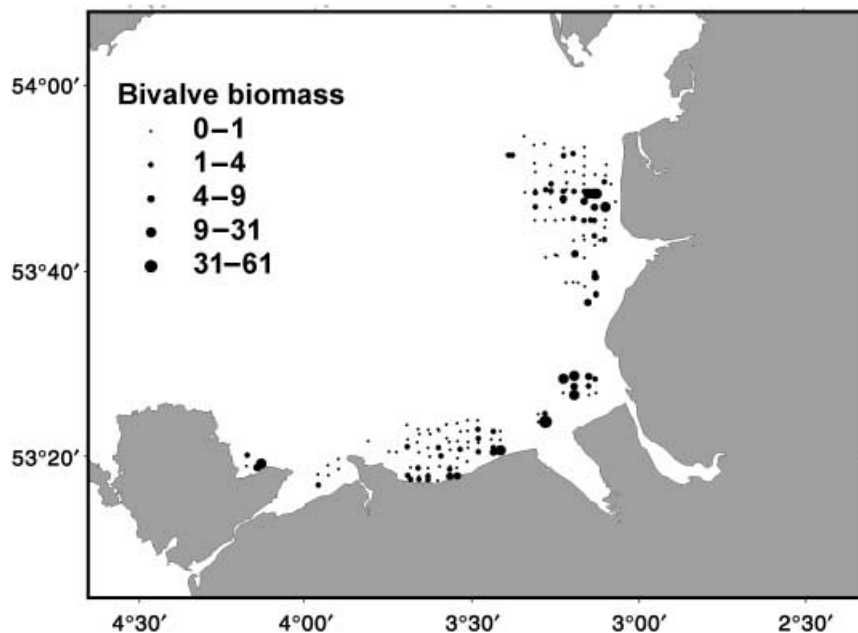


Figure 7. Plotted AFDW ($\text{g } 0.1 \text{ m}^{-2}$) for bivalve molluscs sampled in August 2003.

to discern the relatively fine-scale distribution of Common Scoter over their feeding grounds in relation to potential prey species. All of the prey species in the present study have been reported as prey of Common Scoter in previous studies. It is clear that individual prey species are highly patchy in terms of their distribution, but when the sum biomass of all species was interpolated it was clear that some of the areas with the highest biomass density of potential prey species did not coincide with observations of Common Scoter (e.g. off the River Mersey). It is noteworthy that although there was a very high biomass of bivalves in Red Wharf Bay, Common Scoters were only observed here towards the end of the 2003/2004 winter season. Direct observations of dive times of birds in Red Wharf Bay indicated that dive time was significantly longer than at shallower water sites off Llanddulas North Wales.

The prey-size categories reported in areas utilized by Common Scoters concur with previous studies that have reported that Common Scoters consumed prey of 5–40 mm shell length in size (Kube 1996, Meissner & Bräger 1990, Durinck *et al.* 1993). If length describes the maximum dimension of a prey item this may not be the most relevant parameter with respect to ingestion capability, for example a razor shell (*Ensis* sp.) may be over 50 mm long but only 10 mm wide (MJK pers. obs.), and the elongate

bivalve *Phaus legumen* appeared to be important across Liverpool Bay. Other species such as *Nucula* sp. may be highly abundant but have a small maximum size. They were particularly abundant on the northern shoulder of Shell Flat. Although abundant, consumption of this prey-type may be relatively unprofitable due to the additional energetic costs and dietary constraints associated with processing a high proportion of shell material (Bustnes & Erikstad 1990, Bustnes 1998, Hamilton *et al.* 1999, Lovvorn *et al.* 2003).

Garthe & Hüppop (2004) classified Common and Velvet Scoters as the most sensitive of 26 species of seaducks and seabirds to disturbance by ship and helicopter traffic. In addition to studying the distribution of Common Scoters in relation to environmental parameters and the distribution of their prey, we were able to obtain information regarding the distribution of human disturbance from shipping and fishing disturbance. Using the observations of flush distance from a research vessel we were able to delineate areas of the sea that experienced high incidences of disturbance from shipping. Only a small proportion (2.65%) of Common Scoter observed during overflight observations were located within areas of the sea that experienced major shipping disturbance, whereas c. 18% were located in areas that experienced intermediate

disturbance levels. Fishing activities did not occur in close proximity to areas in which Common Scoters were observed except for the extreme tip of Shell Flat off Lancashire.

Presumably flush distances vary dependent upon factors such as the prevailing weather conditions, the speed of approach of a vessel, the angle of approach, the size (and even colour) of the vessel, human activity visible on the deck, and the fitness of the birds themselves. It may also be that along regularly used shipping lanes birds might become habituated to the presence of boats. However the lack of overlap between intensively utilized shipping lanes and Common Scoter suggests that this does not occur to a significant degree (Table 3).

The effect of human disturbance is often measured in terms of behavioural changes in response to human presence but from a conservation perspective, such disturbance is important only if it affects survival or fecundity and hence leads to a population decline (Cayford 1993, Gill *et al.* 2001, West *et al.* 2002). To demonstrate any such effect on scoter populations through disturbance on their wintering grounds would be virtually impossible. However, Common Scoter as demonstrated, are extremely wary and it has been suggested that species showing the greatest avoidance require the greatest amount of protection (Klein *et al.* 1995). This though may not be true for species where the costs of moving to an alternative site are likely to be small (Gill *et al.* 2001). Wigeon *Anas penelope*, for example show a strong human avoidance (Tuite *et al.* 1984) but for this mainly herbivorous species often grazing on short swards with many nearby alternative feeding sites, costs of moving are probably low. One could argue that this is the case for scoter as upon disturbance there are alternative areas of undisturbed sea to which they could fly and settle. On the other hand fitness costs may be high if there are few or no other nearby suitable feeding areas to which they can go. Furthermore, the additional expenditure of energy associated with each disturbance flight can in some instances lead to a substantial increase in daily energy expenditure and necessitate increased foraging effort in order to compensate (White-Robinson 1982, Riddington *et al.* 1996).

While overflight observations provide useful information on the large-scale distribution of birds at sea, it is infeasible to make detailed observations of birds *in situ* using such techniques. It was clear from our observations that the sex ratio of birds off the North Wales coast changed significantly through

the winter season. Male and subadult birds arrived first, while females and juveniles arrived sometime in December and departed again around about February. Birds aligned themselves into the wind when wind speed was force 4 or higher. At lower wind speeds, the orientation of birds on the water was influenced by sea surface currents. Woakes & Butler (1983) found that the energetic cost incurred by Tufted Ducks *Aythya fuligula* swimming against a current increased rapidly above current speeds of 0.5 m/s. No scoters were observed in areas of the sea with a surface current speed of > 0.6 m/s (from overflight data). Surface current speed is related to seabed shear and while birds may have to reposition more frequently in areas with high surface current speed, these areas may also have lower bivalve biomass. Common scoters were observed infrequently in Conwy Bay, yet this sheltered site might provide shelter during periods of severe weather. However, observations in the present study indicated that Common Scoter remain at the sites of the main Common Scoter aggregations and did not utilize sheltered areas even in conditions of force 7/8 onshore winds.

CONCLUSIONS

The present study indicates that the distribution of Common Scoters is strongly influenced by the distribution and quantity of appropriate prey that are in turn influenced by a combination of physical parameters that include depth, shear stress and wave erosion at the seabed. Peak bivalve biomass occurs further offshore in more wave exposed areas (e.g. off Lancashire) where Common Scoter have to dive to greater depths to access their prey. It is also clear that birds do not utilize other areas where prey are abundant, either because they have insufficient knowledge of these areas (e.g. off the River Dee) or because these areas coincide with areas of high frequencies of shipping disturbance. Of the latter, commercial shipping activities would appear to be the most important, although there exist no data on recreational activities (such as yachting and jet-ski use) that might also have effects. The behavioural data and abundance, seasonal change and quality of prey reported here will be used to inform an individual-based behaviour model (Stillman *et al.* 2000, West & Caldow 2006) to predict the consequence of removing available feeding habitat through the construction of wind farms, however, this will be reported elsewhere.

This study was funded by COWRIE. Full details of the project and the final report are available at www.offshorewind.co.uk. The overflight data used in this study was supported with funding from the Countryside Council for Wales, English Nature, The Crown Estate, BHP, and the developers of the offshore wind farms in Liverpool Bay, and was compiled by Peter Cranswick of the Wildfowl and Wetlands Trust, Slimbridge.

REFERENCES

- Beukema, J.J.** 1995. Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. *Neth. J. Sea Res.* **33**: 219–227.
- Bourne, N.** 1984. Clam predation by scoter ducks in the Strait of Georgia, British Columbia, Canada. *Canadian Technical Report on Fisheries and Aquatic Science* 1331. 17 pp.
- Bräger, S., Meißner, J. & Thiel, M.** 1995. Temporal and spatial abundance of wintering Common Eider *Somateria mollissima*, Long-tailed Duck *Clangula hyemalis*, and Common Scoter *Melanitta nigra* in shallow water areas of the south-western Baltic Sea. *Ornis Fennica* **72** (1): 19–28.
- Bustnes, J.O.** 1998. Selection of blue mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*, by size in relation to shell content. *Can J. Zool.* **76**: 1787–1790.
- Bustnes, J.O. & Erikstad, K.E.** 1990. Size selection of common mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*: energy maximization or shell weight minimization? *Can J. Zool.* **68**: 2280–2283.
- Camphuysen, C.J., Fox, A.D., Leopold, M.F. & Petersen, I.K.** 2004. *Towards Standardized Seabirds at Sea Census Techniques in Connection With Environmental Impact Assessments for Offshore Wind Farms in the U.K.* Royal Netherlands Institute for Sea Research (RNIQZ), Texel, Den Burg, The Netherlands, p. 36. Report to COWRIE (www.thecrown-estate.co.uk).
- Cayford, J.** 1993. Wader disturbance: a theoretical overview. *Wader Study Group Bull.* **68**: 3–5.
- Cramp, S. & Simmons, K.E.L.** 1977. Handbook of the Birds of Europe and the Middle East and North Africa. *The Birds of the Western Palearctic*. Oxford University Press, Oxford.
- Cranswick, P.A., Hall, C. & Smith, L.** 2004. *All Wales Common Scoter Survey. report on 2002/03 work programme*. CCW Contract Science Report no. 615.
- Creutzberg, F.** 1984. A persistent chlorophyll a maximum coinciding with an enriched benthic zone. In *Proceedings of the Nineteenth European Marine Biology Symposium*. pp. 97–108. Cambridge, UK: Cambridge University Press.
- Degraer, S., Vincx, M., Miere, P. & Offringa, H.** 1999. Macrozoobenthos of an important wintering area of the Common Scoter (*Melanitta nigra*). *J. Mar. Biol. Assoc. United Kingdom* **79**: 243–251.
- Dewar, E.** 1924. *The Bird as a Diver*. London, UK: Witherby.
- Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L. & Jennings, S.** 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES. J. Mar. Sci.* **60**: 371–380.
- Durinck, J., Christensen, K.D., Skov, H. & Danielsen, F.** 1993. Diet of the Common Scoter *Melanitta nigra* and velvet scoter *Melanitta fusca* wintering in the North Sea. *Ornis Fennica* **70**: 215–218.
- Emerson, C.W.** 1989. Wind Stress Limitation of Benthic Secondary Production in Shallow, Soft-Sediment Communities. *Mar. Ecol. Prog. Series* **53**: 65–77.
- Ferns, P.N.** 1984. Birds of the British Channel and Severn Estuary. *Mar. Pollution Bull.* **15**: 76–81.
- Fox, A.D., Petersen, A.E. & Fredericksen, M.** 2003. Annual survival and site-fidelity of breeding female Common Scoter *Melanitta nigra* at Myvatn, Iceland 1925–58. *Ibis* **145**: E94–E96.
- Garthe, S. & Hüppop, O.** 2004. Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *J. Appl. Ecol.* **41**: 724–741.
- Gill, J.A., Norris, K. & Sutherland, W.J.** 2001. Why behavioural response may not reflect the population consequences of human disturbance. *Biol. Conservation* **97**: 265–268.
- Goudie, R. & Ankeney, C.** 1986. Body size, activity budgets and diets of seaducks wintering in Newfoundland. *Ecology* **67**: 1475–1482.
- Guillemette, M.** 1998. The effects of time and digestion constraints in Common Eiders while feeding and diving over Blue Mussel beds. *Func Ecol.* **12**: 123–131.
- Guillemette, M., Reed, A. & Himmelman, J.H.** 1996. Availability and consumption of food by common eiders wintering in the Gulf of St. Lawrence: evidence of prey depletion. *Can J. Zool.* **74**: 32–38.
- Hamilton, D.J., Nudds, T.D. & Neate, J.** 1999. Size-selective predation of blue mussels (*Mytilus edulis*) by common eiders (*Somateria mollissima*) under controlled field conditions. *Auk* **116** (2): 403–416.
- Hawkins, P.A.J., Butler, P.J., Woakes, A.J. & Speakman, J.R.** 2000. Estimation of the rate of oxygen consumption of the common eider duck (*Somateria mollissima*) with some measurements of heart rate during voluntary dives. *J. Exp Biol.* **203**: 2819–2832.
- Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E. & Piet, G.J.** 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production and species richness in different habitats. *Can J. Fish Aquat Science* (in press).
- Jenness, M.I. & Duineveld, G.C.A.** 1985. Effects of tidal currents on chlorophyll a content of sandy sediments in the southern North Sea. *Mar. Ecol. Prog. Series* **21**: 283–287.
- Johnston, C.M., Turnbull, C.G. & Tasker, M.L.** 2002. Natura 2000 in UK offshore waters: Advice to support the implementation of the EC Habitats and Birds Directives in UK offshore waters. Peterborough, UK: Joint Nature Conservation Committee.
- Klein, M.L., Humphrey, S.R. & Percival, H.F.** 1995. Effects of ecotourism on distribution of waterbirds in a wildlife refuge. *Cons Biol.* **9**: 1454–1465.
- Kube, J.** 1996. The ecology of macrozoobenthos and seaducks in the Pomeranian Bay. *Marine Science Reports* no. 18. Baltic Sea. Research Institute, Warnemunde, Germany.
- Leopold, M.F., Baptist, H.J.B., Wolf, P.A. & Offringa, H.** 1995. De Zwarte Zeeend *Melanitta nigra*. Nederland. *Limosa* **68**: 49–64.
- Lovvorn, J.R. & Gillingham, M.P.** 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* **77** (2): 435–451.
- Lovvorn, J.R. & Jones, D.R.** 1991. Effects of body size, body fat, and changes in pressure with depth on buoyancy and costs of diving in ducks *Aythya* spp. *Can J. Zool.* **69**: 2879–2887.

- Lovvorn, J.R., Richman, S.E., Grebmeier, M. & Cooper, L.W.** 2003. Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. *Polar Biol.* **26**: 259–267.
- Madsen, F.J.** 1954. On the food habits of diving ducks in Denmark. *Danish Rev. Game Biol.* **2**: 157–266.
- Meissner, J. & Bräger, S.** 1990. The feeding ecology of wintering eiders *Somateria mollissima* and Common Scoters *Melanitta nigra* on the Baltic coast of Schleswig-Holstein, FRG. *Wader Study Group Bull.* **58**: 10–12.
- Nehls, G. & Ketzenberg, C.** 2002. Do common eiders *Somateria mollissima* exhaust their food resources? A study on natural mussel *Mytilus edulis* beds in the Wadden Sea. *Danish Rev. Game Biol.* **16** (1): 47–61.
- Nilsson, L.** 1972. Habitat Selection, Food Choice and Feeding Habits of Diving Ducks in Coastal Waters of South Sweden during the Non-Breeding Season. *Ornis Scand.* **3**: 55–78.
- Oliver, F., Robinson, P. & Harrod, C.** 2001. *Common Scoter Melanitta Nigra in Liverpool Bay*. Countryside Council for Wales, Bangor. Report 470.
- Phillips, V.E.** 1991. Pochard *Aythya ferina* use of chironomid-rich feeding habitat in winter. *Bird Study* **38**: 118–122.
- Rees, E.I.S., Nicholaidou, A. & Laskaridou, P.** 1977. The effects of storms on the dynamics of shallow water benthic associations. In Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., eds. *Biology of Benthic Organisms*. pp. 465–474. Oxford, UK: Pergamon Press.
- Riddington, R., Hassall, M., Lane, S.J., Turner, P.A. & Walters, R.** 1996. The impact of disturbance on the behaviour and energy budgets of Brent Geese *Branta b. bernicla*. *Bird Study* **43**: 269–279.
- Snelgrove, P.V.R. & Butman, C.A.** 1994. Animal Sediment Relationships Revisited – Cause Versus Effect. *Oceanogr. Mar. Biol.: Annu. Rev.* **32**: 111–177.
- Stempniewicz, L.** 1986. The food intake of two scoters *Melanitta fusca* and *M. nigra* wintering in the Gulf of Gdansk, Polish Baltic coast. *Vår Fågelvarldsupplement* **11**: 211–214.
- Stephenson, R., Lovvorn, J.R., Heieis, M.R.A., Jones, D.R. & Blake, R.W.** 1989. A hydromechanical estimate of diving and surface swimming in lesser scaup (*Aythya affinis*). *J. Exp. Biol.* **147**: 507–519.
- Stillman, R.A., Goss-Custard, J.D., West, A.D., le Durell, S.E.A.V., dit, Caldwell, R.W.G., McGroarty, S. & Clarke, R.T.** 2000. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *J. Appl. Ecol.* **37**: 564–588.
- Stott, R.S. & Olson, D.P.** 1973. Food habitat relationship of seaducks on the New Hampshire coastline. *Ecology* **54**: 996–1007.
- Tuite, C.H., Hanson, P.R. & Owen, M.** 1984. Some ecological factors affecting winter wildfowl distribution on inland waters in England and Wales, and the influence of water-based recreation. *J. Appl. Ecol.* **21**: 41–62.
- Underhill, H.C., Gittings, T., Callaghan, D.A., Hughes, B., Kirby, J.S. & Delany, S.** 1998. Status and distribution of breeding of Common Scoters, *Melanitta nigra nigra* in Britain and Ireland in 1995. *Bird Study* **45**: 146–156.
- Vaitkus, G. & Bubinas, A.** 2001. Modelling of seaduck spatial distribution in relation to food resources in Lithuanian offshore waters under the gradient of winter climatic conditions. *Acta Zool. Lithuanica* **11**: 288–303.
- Warwick, R.M. & Uncles, R.J.** 1980. Distribution of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. *Mar. Ecol. Prog. Series* **3**: 97–103.
- West, A.D. & Caldwell, R.W.G.** 2006. The development and use of individuals-based models to predict the effects of habitat loss and disturbance on waders and waterfowl. In *Wind, Fire and Water: Renewable Energy and Birds*. *Ibis* **148** (Suppl. 1): 158–168.
- West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldwell, R.W.G., le Durell, S.E.A.V. & dit, McGroarty, S.** 2002. Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. *Biol. Conservation* **106**: 319–328.
- White-Robinson, R.** 1982. Inland and saltmarsh feeding of wintering Brent Geese in Essex. *Wildfowl* **33**: 113–118.
- Wildish, D.J. & Peer, D.** 1983. Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy. *Can. J. Fish Aquat. Sciences* **40** (Suppl. 1): 309–321.
- Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E. & Christian Nöldeke, E.** 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *Am. Naturalist* **140** (2): 179–200.
- Woakes, A.J. & Butler, P.J.** 1983. Swimming and diving in tufted ducks *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. Exp. Biol.* **107**: 311–329.
- Yates, M.G., Goss-Custard, J.D., McGroarty, S., Lakhani, K.H., Durell, S.E.A., Le, V., dit, Clarke, R.T., Rispin, W.E., Moy, I. & Yates, T.** 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *J. Appl. Ecol.* **30**: 599–614.