Marine top predator foraging habitat predicted from a detailed understanding of temporal and spatial oceanographic processes

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Abstract

Any fisherman can tell you there are 'hotspots' or areas where high densities of fish are likely to be found again and again. What makes these regions so predictive and interesting to fish and higher order predators? In a multi-disciplined EU study (Interactions between the Marine Environment, Predators and prey: implications for Sustainable Sandeel fisheries. QRRS 2000-30864; IMPRESS) investigating the foraging habitat of seabirds with both field investigations and a use of long-term date, we found that seabird foraging patterns provided vital clues as to what particular physical aspects of the marine ecosystem are critical to defining 'hotspots' (regions where there are critical ecosystem linkages between the trophic layers).   With spatially targeted at-sea observations of fish-eating seabirds we were able to identify causal links with daily bird foraging behaviour and regionally and temporally specific physical characteristics.   Using a 1-D bio-physical model parameterised with site-specific data, we produced a 30-year time series to characterised several temporal and spatial components of the annual primary production within the study area. The combination of our short and long term temporal investigations and our detailed spatial investigations provides insights into physical and biological reasons for the spatial connectivity of ecosystems.

Introduction

The oceans are the medium in which predator – prey interactions occur. The objective of this study was to determine how oceanographic features could be used to define seabird foraging habitats, and whether variability in any of these features could be causative in controlling variability in prey availability. We approached this objective using two very different temporal and spatial scales as the variability of the 3-dimensional structure of the study area is driven by the variability of tidal currents, wind stress, solar heating and freshwater input on time scales ranging from minutes to years. The competition between the mixing and buoyancy inputs is particularly important in determining the strength of vertical stratification, and the depth of the surface mixed layer. The extent to which a water column is mixed or stratified is pivotal in setting the environmental conditions for primary production (Miller 2004). There are correlative links between inter-annual changes in the success of higher predators and their prey and the basic physical oceanography as it forces the primary production of the region (Yen et al. 2004 , Steinngrund and Gaard 2005). Understanding the causes of inter-annual variability in the timing of the onset of stratification and the spring bloom is thus a key requirement in developing a broader understanding of annual predator-prey interactions. However, the combination of currents, stratification and primary production can also play an immediate role in the horizontal and vertical aggregation of planktonic organisms, which, in turn, attract larger predators such as fish, birds and cetaceans to a particular foraging location where physical predator-prey interactions occur on an hourly / daily bases. Thus the collation of old and collection of new meteorological and oceanographic information gathered in this study was structured to better our understanding of both the annual/seasonal cycle of primary production and the location specific, hourly/daily variation in vertical characteristics of the water column.

Methods

Summary and collation of available (pre 2001) oceanographic / meteorological data
At the start of the project a review was made of all relevant data sources which could provide the oceanographic and meteorological data for the long-term analyses of the study area (Fig 1). The most consistent collection of oceanographic data began with the survey of the area by FRS in 1997 taking up to 20 CTD cast within the study area 3 times a year (generally in March, June and October – see Camphuysen 2005 for details). Meteorological observations were available as daily means from two weather stations: Leuchars (56.377°N, 2.861°W) and Mylnefield (56.458°N, 3.072°W). These sites were chosen because of their close proximity

to the study area, and also as both are surrounded by low-lying land. The relevant data was available back to 1974.

A summary of the data up to and including 2000 provided a basic understanding of the seasonal dynamics of the study area. Typical of a shallow sea, the water column for the entire study area is well mixed for most of the year (especially during the winter months of October to March). The onset of stratification is usually observed in April and reaches a maximum in late July/ early August. Summer data showed a variable picture in terms of how strongly or weakly stratified the water column could be and also indicated that there is great spatial variability in the stratification of the water column. The western and/or eastern extremes of the study area generally being the more strongly stratified regions. The western region, close to the coast, is influenced by fresh water while the eastern region away from the coast is deep enough for the thermal surface stratification not to be eroded by tidal mixing.

Moorings
In 2001 and 2002 three moorings were deployed in the study area from March to October in what were assumed to be 3 contrasting water column characteristics: a *bank region*, a shallow sea region and a well mixed region. The moorings were designed to provide very detailed temporal information within each region with recordings every 10 minutes on a series of temperature loggers placed vertically at 5 to 10 meter intervals (Fig 2). Recordings of current speeds where measured every 20 minutes and fluorometers (giving an indication of the ambient chlorophyll concentration) took readings once every hour. The moorings provided information on the changes in the vertical structure, including the depth of the surface mixed layer, the strength of the thermocline (Fig 2) and the abundance of chlorophyll (Fig 3)**.** The moorings provided detailed evidence of the annual timing of the stratification of the water and the initiation of the spring bloom and were used to parameterise site-specific 1-dimensional coupled bio-physical models (see details below under the heading 1-D modelling).

Pelagia cruise June 6-19 2003: Transects
During the IMPRESS project two weeks of dedicated surveys were scheduled to be performed in the third field season in a period chosen in response to research needs developed during the project. During the surveys, hydrographical observations would be combined with detailed behavioural and distributional studies of foraging seabirds and prey availability (acoustic signal). The surveys were to be designed to test predictions of foraging seabird behaviour, oceanographic characteristics and prey distribution that arouse from the previous 2 years of field work (both at colonies and at sea). Therefore, it was felt that it would be a top priority to simultaneously collect the physical properties and bird abundance and behaviour

information over the entire region at as fine a horizontal scale as possible. The accomplishment of this task would greatly increase the ability to define species specific foraging habitat and to produce a predictive map of potential bird foraging habitats within the study area.

Covering the *study area* (Fig 1) the *Pelagia* cruise completed 8 transects, with 2 of them repeated. The sampling was done with the use of a Scanfish (undulating CTD) such that continuous vertical and horizontal information on temperature, salinity, density and abundance of chlorophyll was collected at 1.0 second intervals and approximately 0.5 to 1.0 meters vertical resolution. Rich spatial detail is obvious (Fig 4 and 5) with multiple locations displaying different degrees of mixing and was therefore used in subsequent analysis of characterising predatory foraging habitat.

The field methods for ornithological observations have been refined and tested in the past 3-5 years during surveys in late June and July off the Scottish east coast. Novel in these census techniques is the careful description and coding of all foraging behaviour types and the tendency to aggregate and form mixed flocks in some areas, whereas mono-specific foraging is more typical in other areas. The data collected during these surveys will provide exact locations and behaviour types of foraging behaviour. These ship-based surveys were conducted using strip-transect counts, which were developed as a standard for surveying the North Sea (Tasker et al. 1984). Counts were conducted from the top-deck of the ship during steaming, by two observers operating a 300-m-wide transect on one side and ahead of the ship. Birds were typically first sighted with the naked eye and identified using binoculars. Standard counting units were five minute time periods (see Tasker et al. 1984 for details). It was important that feeding or foraging seabirds could be readily separated from non-feeding individuals. Standard recording methods (Tasker et al. 1984) were therefore slightly modified, so that the behaviour of seabirds observed was recorded, coded and stored on a database (Camphuysen & Garthe 2004). Broadly following the descriptions of Ashmole (1971), several types of feeding behaviour were recog-nised, including: aerial pursuit; dipping surface seizing or pecking at the surface; scooping; pursuit plunging; surface plunging; deep plunging; pursuit diving; scavenging at fishing vessels; and actively searching for prey.

However, in order to compare the continuous physical water column characteristics measure by the Scanfish to the at-sea 5 minute bin observations of top-predators, summaries of important physical and biological characteristics of the water column such as mean stratification of water column, depth and gradient of pcyncoline, depth of maximum

chlorophyll abundance, sum of water column chlorophyll and bottom depth (etc.) were created for each 5 minute bin.

The detailed oceanographic information allowed the spatial definition of separate regions with different mixing and/or productivity characteristics. The detail available suggested that what we considered as the former Banks region with only the sparser physical historical data should be more accurately viewed as 2 types of regions (Inner and Outer Banks) due to proximity and interaction with the Shallow sea front region and what we now call the Outer Bank region (see the regions defined in Fig 7).

1-D bio-physical modelling 1974- 2003

At the start of the project we had a prototype 1-D coupled model available (Sharples, 1999). Over the course of the project several modifications have been made aimed at improving the user interface, keeping the model up to date (specifically in its calculation of turbulent mixing), configuring the model to the IMPRESS study region, and providing appropriate model output. In the first two years of the project the user-interface of the model was completely re-designed, and the model was set-up to accept meteorological data for the study region (acquired from the British Atmospheric Data Centre). The first mooring deployment was used to calibrate the model to the local oceanographic (i.e. the depths and tidal constituent current amplitudes and phases). An updated turbulence scheme was also incorporated. In 2004 the only additional changes made were incorporation of the latest meteorological information, and a re-write of the integration scheme used by the Coriolis term of the model (to a scheme that has been shown to conserve the energy of inertial oscillations correctly). Data from the second mooring deployment was used to validate the model (primarily in terms of the model prediction of the onset of spring stratification). Long term sea temperature data held by ICES was used to provide a means of assessing the model's capability of the full 30 years of available meteorological data.

Several experiments were then conducted with the model, over the entire 1974-2003 meteorological series available, towards understanding the controls of the timing of spring stratification and the spring bloom. The main model findings were that over the 30 years meteorological variability drives most of the inter-annual variability of both the onset of stratification (86% of the variance) and the spring bloom (70% of the variance), with variability in the spring solar irradiance being more important than variability in wind stress. Tidal variability, acting through the spring-neap cycle, can have a marked effect by causing a double spring bloom. Correlation of the meteorological data with the North Atlantic Oscillation (NAO) suggests that the NAO plays a significant, but not dominant, role in

generating inter-annual variability in the timing of spring stratification and the spring bloom (Sharples et al. Submitted).

The output of the 1-D model provides the most accurate and long term predictions on the annual timing of the most important seasonal events in the marine ecosystem. The modelling work provides an estimate of the annual timing of the spring bloom, the onset of stratification and the end of the surface bloom. The daily output of model allows relative annual estimates of the sum of primary production before the spring bloom, during the surface bloom and for the subsurface production after the spring bloom. All of these annual variables can be compared to both predator and prey population variables such as breeding success and growth.

Results

Seabird foraging habitat

The continuous oceanographic data (from the *Pelagia* 2003 cruise, Fig 4 and 5) produced a very detailed 'snapshot' of the water column characteristics underneath foraging birds. Therefore we investigated the differences in water column characteristics that the three species of seabirds (Guillemots, Kittiwakes and Gannets) selected to forage in. The mean and standard error of a range of physical and biological characteristics are calculated from the locations of all foraging birds of each species observed during the transect surveys on the Pelagia 2003 cruise (Table 1). The results of this analysis show that indeed the mixing properties (as indicated by stratification (Fig 5), i.e. the differences between the top and bottom of the water column, using either temperature or density differences) of the water column in which different species feed were significantly different. Gannets were found foraging in the most stratified water, while Kittiwakes used water that was less stratified than that of the Gannets, but more so than the water columns over which Guillemots mainly foraged.

Table 1.The means (± SE) for water column attributes of locations where seabirds were found foraging across the study area during the June 2003 RV Pelagia survey. The physical and biological data is derived from scanfish data in 5-min bins, corresponding with the 5-min binned bird observations. Means which are significantly different between all three species (one-way ANOVA, S-Plus) are marked with an asterisk (*).

Physical parameter	Guillemot (n=351)	Kittiwake (n=142)	Gannet (n=49)
SST	11.7 ± 0.03*	11.9 ± 0.05*	12.4 ± 0.09*
BT	8.7 ± 0.01*	8.6 ± 0.02*	8.4 ± 0.03*
Difference in temperature	3.0 ± 0.04*	3.3 ± 0.06*	3.9 ± 0.11*
SSS	34.47 ± 0.011	34.55 ± 0.015	34.62 ± 0.025
BS	34.71 ± 0.006	34.77 ± 0.010	34.85 ± 0.018
Stratification ± difference in density	0.71 ± 0.011*	0.75 ± 0.015*	0.88 ± 0.024*
CHL max	0.282 ± 0.015	0.255 ± 0.007	0.243 ± 0.013
Depth of food max	14.2 ± 0.22*	14.8 ± 0.32*	17.6 ± 0.76*
Top of pycnocline	5.7 ± 0.15	6.0 ± 0.23	7.8 ± 0.51
Bottom of pycnocline	22.8 ± 0.40	22.9 ± 0.54	25.9 ± 0.77
Gradient of pycnocline	0.056 ± 0.004	0.055 ± 0.002	0.056 ± 0.003
Maximum Depth	47.9 ± 0.44*	50.8 ± 0.63*	54.7 ± 1.15*

Using this information on what numerical value of stratification (note that this will be particular to the 2003 data as the level of stratification at any given time is weather dependent) is important to the individual bird species. We can now proceed to define the regions of study area in terms of the water column characteristics that the study species appear to use. The following definitions of the regions are used in the following analysis (rather than conforming strictly to the physical boundaries shown in Fig 6).

Offshore Stratified: Difference in top – bottom temperatures is $\geq 3.8°C$ (this definition includes the Offshore bank shown in Fig 6)

Well mixed (both shallow and deep regions): Difference in top – bottom temperatures is $\leq 2.0°C$ (note that this region is called well mixed in a relative sense as compared to the remainder of the study area)

Inner Bank: Difference in top – bottom temperatures is ≥ 2 & $< 3.1°C$, with SSS (sea surface salinity) > 34.40 PSS -78

Outer Bank: Difference in top – bottom temperatures is $\geq 3.1 < 3.8°C$, with SSS (sea surface salinity) > 34.40 PSS -78

Freshwater influenced: SSS (sea surface salinity) < 34.40 PSS –78

Guillemots were relatively evenly distributed across the regions, but were most abundant in the Inner Bank region (Table 2, Fig 7). Nearly half of all Kittiwakes seen foraging were observed within the Outer Bank region and two thirds of all Gannets were found in the Offshore stratified region (Table 2, Fig 7). This separation of bird species determined mainly by the difference in stratification (using top and bottom temperature differences) indicates that their foraging habitat can be defined using rather straightforward and predictable physical characteristic of the water column. Within the Freshwater influenced region, even with the additional stratification differences driven by the presence of fresh water, the same difference in top and bottom temperatures still separates species with 77% and 95% of Kittiwakes and Gannets (respectively) being found in locations with a temperature difference of greater than 3.1°C. In those same locations only 32% of the total number of Guillemots within the Freshwater influenced region are present.

Table 2. The total abundance and percentage of foraging birds found within the different regions of the study area.

	Guillemot (n=3423)	Kittiwake (n=921)	Gannet (n=344)
Well mixed	627 (18.3%)	31 (3.4 %)	0 (0.0%)
Inner Bank	1241 (36.3%)	172 (18.7%)	14 (4.1%)
Outer Bank	553 (16.2%)	402 (43.6%)	57 (16.6%)
Offshore stratified	357 (10.4%)	202 (21.9%)	231 (67.2%)
Freshwater influenced	645 (18.8%)	114 (12.4%)	42 (12.2%)

It is also very important to report that 82% of the foraging animals were seen in only 24% of the total study area and that 60% were found in only 11% of the sampled study area. These result indicates that within each type of foraging habitat only a small percentage of the area is used for foraging.

Moorings and 1-D bio-physical modelling: Timing of the bloom and seabird breeding success

We compared the breeding success of kittiwakes and guillemots on the Isle of May to the timing of the spring bloom and stratification in the Bank and the Shallow Sea Front regions. For both species results were similar for the two oceanographic regions and for both indices of timing. Kittiwakes bred more successfully in the years when the spring bloom and stratification in either region occurred later. Breeding success increased by 0.13 chicks/pair for every five days delay in timing of the spring bloom (Fig 8). There was no evidence that the effect of date of the spring bloom on breeding success was different in fishing and non fishing years (interaction: $F_{1,16} = 2.40$, $p = 0.14$), but breeding success was 0.66 + 0.098 (se) chicks higher in years without fishing than in years with fishing ($F_{1,16} = 44.92$, $p < 0.001$). The final model containing both the effects of spring bloom date and the sandeel fishery explained 74% ($p < 0.001$) of the variance in breeding success. Separating years with or without a fishery, the effect of climate alone explained 56% of the variance in breeding success in years without a fishery and 10% of the variance in years with a fishery. This suggests that important climatic variables are more easily identified in the absence of the confounding effects of a fishery. A similar analysis carried out for guillemots, revealed that although there same trends in an increase in breeding success with a delaying in spring bloom were observed, neither the timing of the spring bloom, nor stratification in either oceanographic region, had a significant effect on breeding success. (For further details of this analyses see Scott et al. 2006)

Discussion

Spring bloom and seabird breeding success

Kittiwakes are surface feeders and as such are more dependent on prey being present in the upper water column. Our finding therefore lead us to speculate that a later spring bloom increases the availability of prey in the upper water column during the breeding season. We suggest that the mechanism by which this is achieved is through a slowing down in the growth of juvenile sandeels, possibly coupled with a delay in the emergence of adult sandeels. With elevated levels of food occurring relatively late in the season, the trade off between predation and feeding may force fish to take longer to acquire adequate levels of food needed to survive the next winter. Either the slowing of fish growth or the extension of the time window during which sandeels are feeding actively in the water column, could potentially provide an increase in prey availability, especially to surface feeders.

These results accord well with those of Rindorf et al. (2000) who found that breeding success of Isle of May seabirds was higher when sandeel abundance peaked later in the season. Although spring bloom timing here is modelled rather than measured, it is a more proximate and thus a much more interpretable correlate of breeding success than a single weather variable such as sea temperature. Using this biologically meaningful and locally specific index we have concluded that, under similar climatic conditions, kittiwakes suffer an additional reduction in breeding success in years when a commercial sandeel fishery is operating. Our approach allows us to separately quantify fishing and climate effects and indicates that the presence of a local sandeel fishery decreases breeding success of Isle of May kittiwakes by 0.66 chicks/pair whereas every 5 day delay in the date of the spring bloom increases breeding success by 0.13 chicks/pair.

Seabird foraging habitat

The description of different regions in the study area (Fig 6) was based on physical attributes, mainly the mixing properties of the water column which are determined by the strength of tidal currents and the water depth. This is a static description of the regions, one that will remain constant between years as tidal strengths and depths do not vary annually. Due to the different mixing properties of these regions, different levels of primary production would be expected, and possibly different trophic chains with different species of phyto- and zooplankton. These differences in mixing properties will also affect the aggregation level of primary and secondary production and therefore may influence the aggregation level of foraging fish species. The difference in aggregation of the seabird's prey may play an important role in determining the availability of fish to bird species with a range of foraging techniques.

It is clear that on both large (10s of km) and small (<10km) spatial scales, Kittiwakes were foraging in more stratified water than Guillemots. The need for more stratified water implies that Kittiwakes are more limited in the locations in which they can forage than Guillemots and at times of greater mixing (i.e. very windy weather, spring tides) they may have to fly greater distances to deeper water where stratification is more likely to be present. Guillemots were found to be able to exploit a greater range of water mass characteristics but do not select to forage in water that is strongly stratified. In this study area their preferred water column characteristics are found closer to the Isle of May colony than the strongly stratified water

masses which occur seaward of the Shallow sea front. Gannets preferentially foraged in the strongly stratified waters seaward of the Shallow sea front.

Conclusions

The combined use of biologically meaningful measures derived from the 1D physical-biological model, detailed simultaneous oceanographic characteristics and seabird foraging behaviour are providing important new insights into the mechanisms that link meteorological conditions and spatial oceanographic characteristics with top predator breeding and foraging success. Both the long term and spatially localized aspects of this study point to primary production being a key player in the lives of 4th trophic order predators. These results add weight to the bottom-up approach for the functioning of marine ecosystems that have been found in other studies (Genin 2004, Yen et al. 2004 , Steinngrund and Gaard 2005). These results also suggest that profitable areas of study (in terms of understanding marine ecosystems) would be to but more emphasis on collecting the oceanographic characteristics of the spatial locations of large visible foraging predators and to understand more fully why within the regions of foraging habitat there is only a small percentage of the area used. These studies should focus on the differences in primary production of these regions as possible mechanism for the occurrence of hotspots for foraging.

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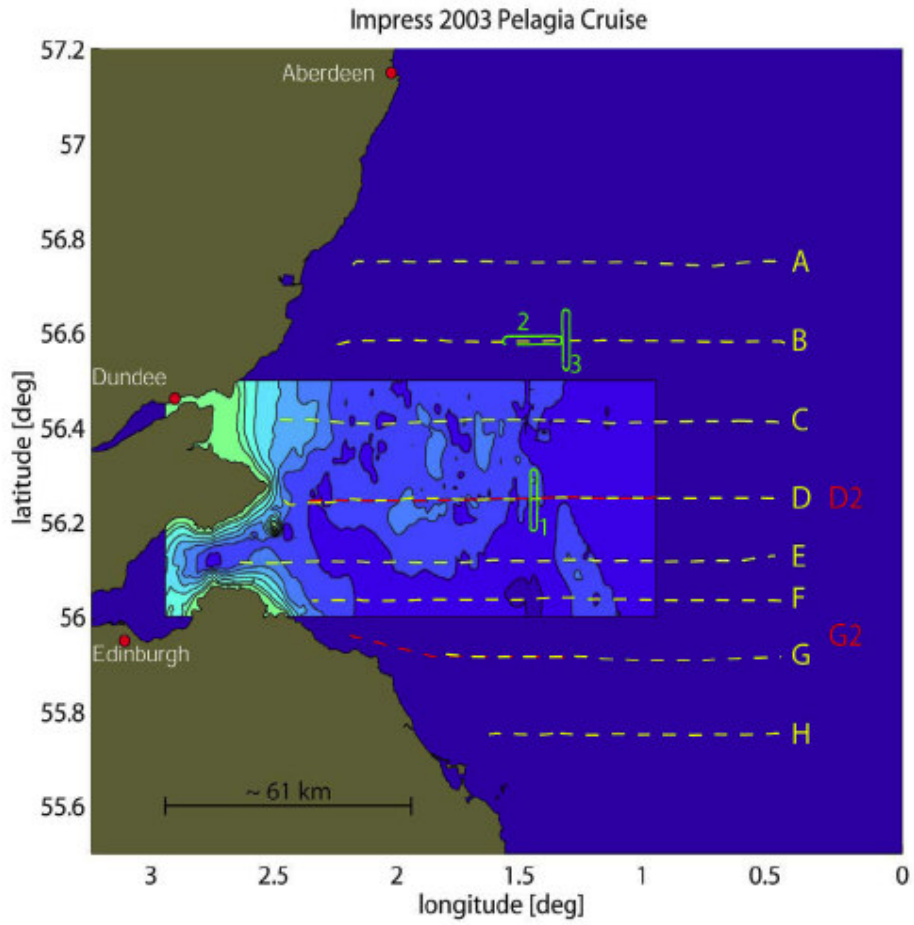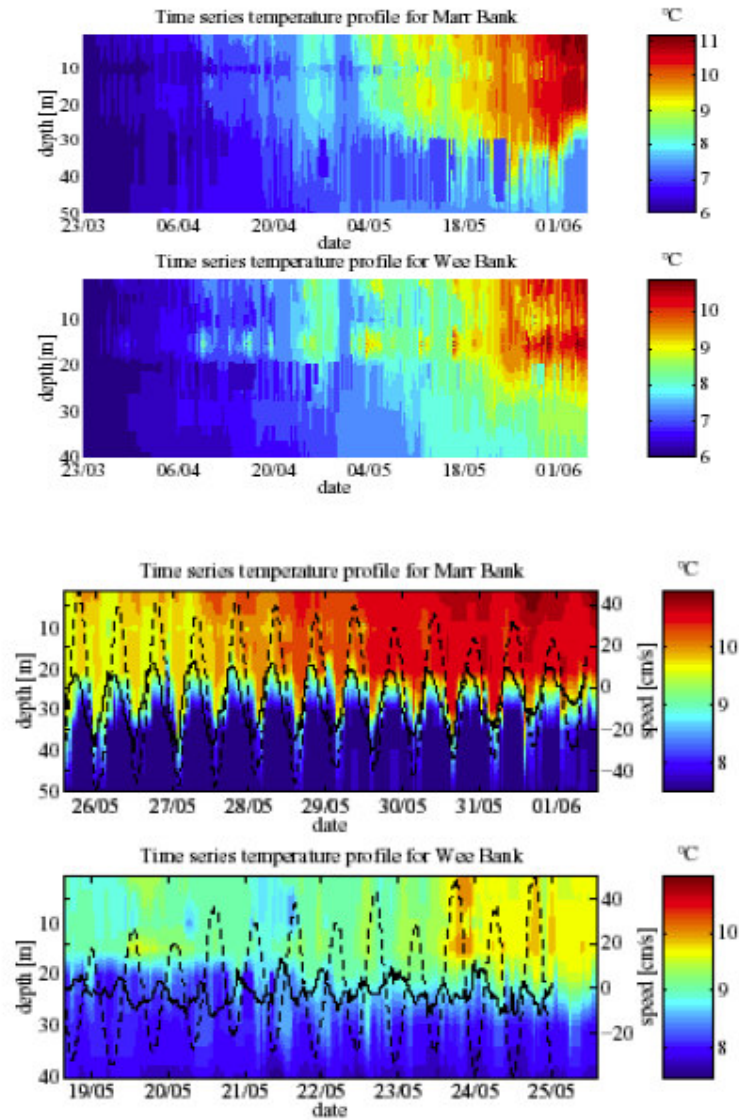
Fig 1 Locations of transect tracks and mini-surveys (green ovals) for *Pelagia* Cruise June 6-19 2003. Bathymetry map covers the area of the previous FRS coverage of area in 2001 and 2002

Fig 2. (top panel) The temperature data (every 10 minutes) over a 2 month period from the miniloggers on the Marr and Wee Bank mooring at set depths (1, 5, 10, 15, 20, 30, 35 and 50m). (bottom panel) The temperature data (every 10 minutes) over a 1-week period from the miniloggers on the Marr and Wee Bank mooring at set depths (1, 5, 10, 15, 20, 30, 35 and 50m). The N-S currents are plotted as a dashed line (positive is to the North), the E-W currents as a solid line (positive to the East
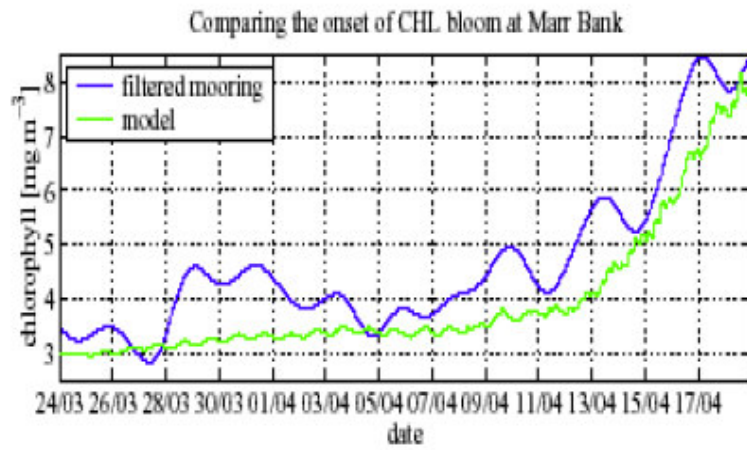
Fig 3 A comparison between the 1-D model output of hourly chlorophyll abundance and the empirical hourly data collected on chlorophyll abundance from the moorings at the Marr Bank site.
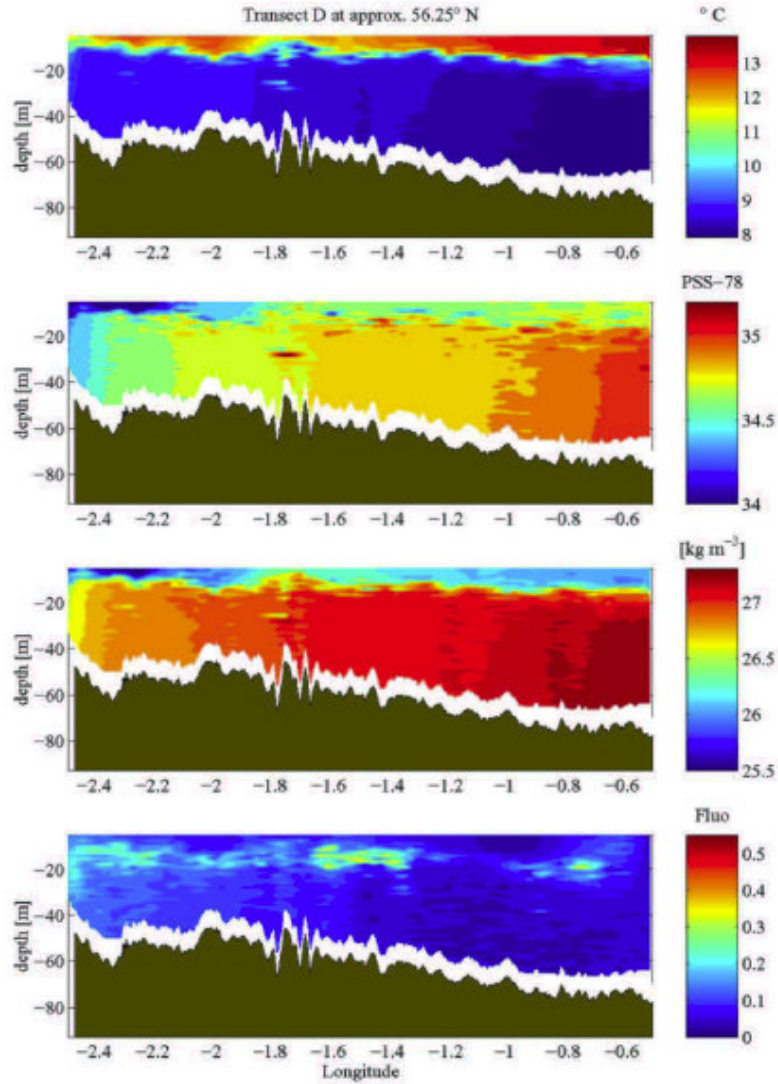
Fig 4. An example from Transect D of the Scanfish output temperature (top panel), salinity (second panel from top), density (second panel from bottom), and flouresence (bottom panel). The vertical data are continuously collected, with the 300 m being the farthest distance between down and up profiles.
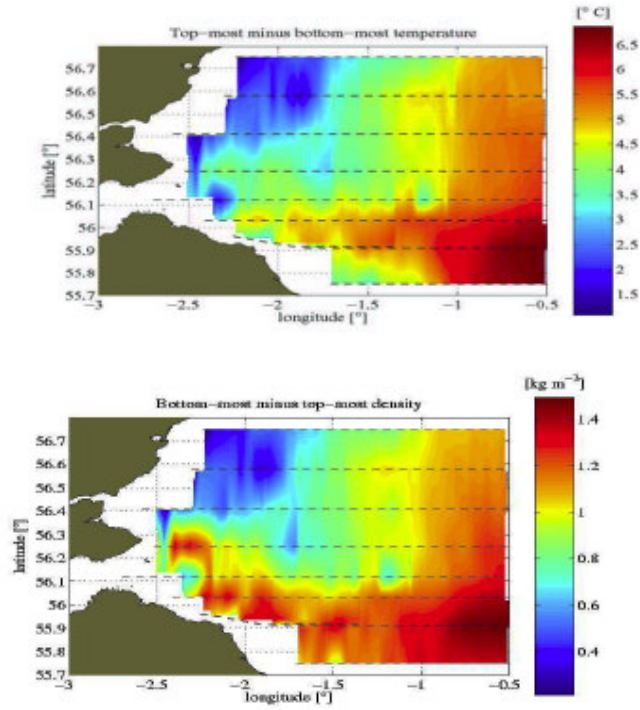
Fig. 5 The degree of thermal (top panel) and density (bottom panel) stratification across the June 6-19 *Pelagia* Cruise produced with data collected by the Scanfish.
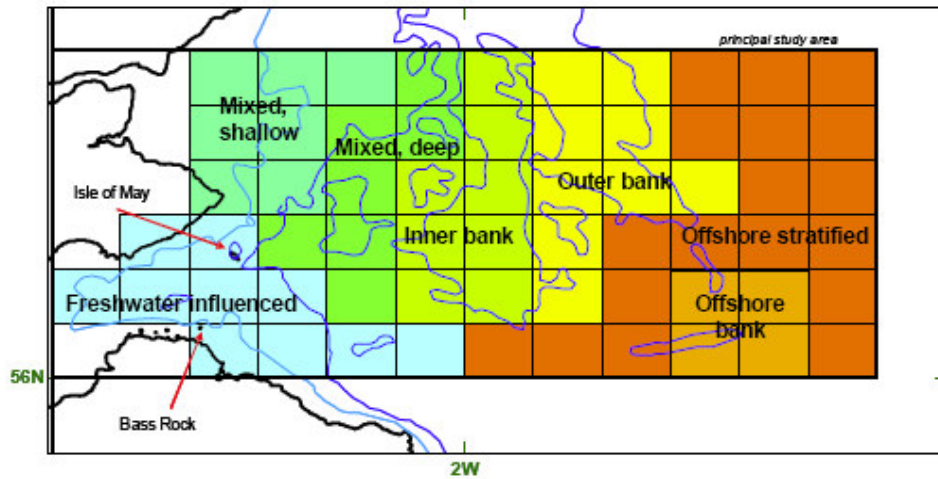

Fig 6. Partitioning of the study area into seven broad regions based on the topographic features, the degree of stratification and the influence of freshwater .
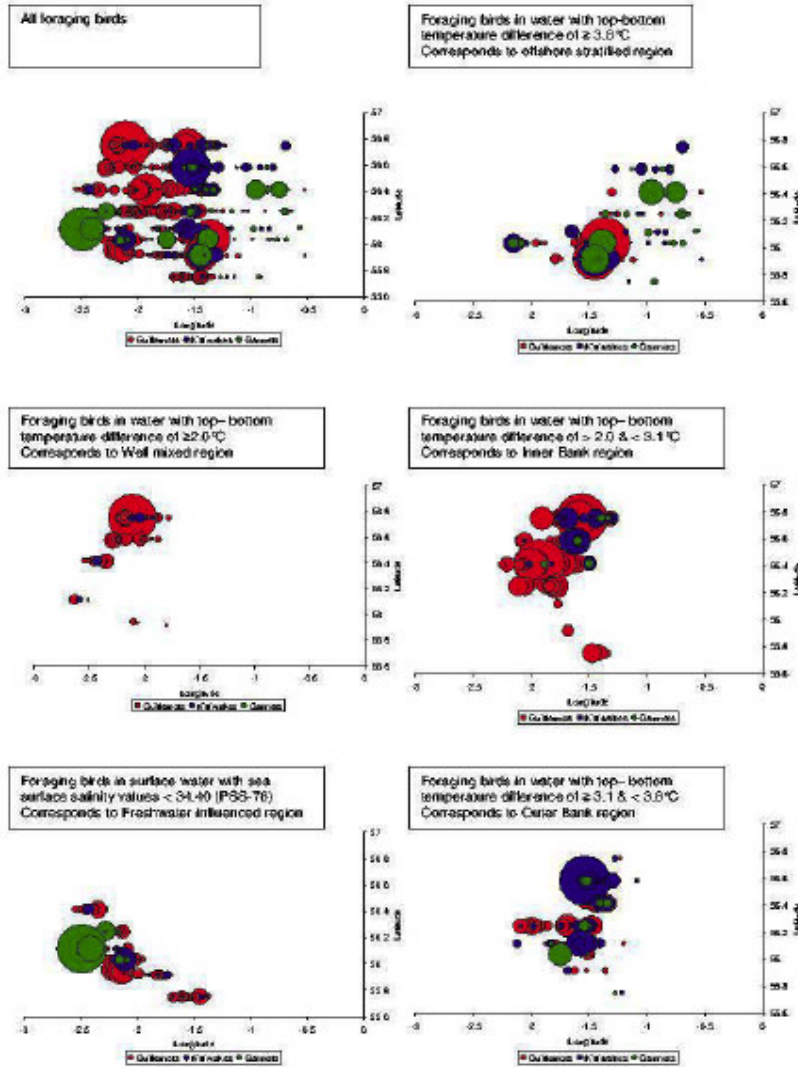
Fig 7. Spatial results in terms of numbers of birds (Guillemots in red, Kittiwakes in blue and Gannets in green) found foraging within regions defined by physical characteristics. The spatial separation of bird species correspond very well to the static regions defined in Fig. 6.
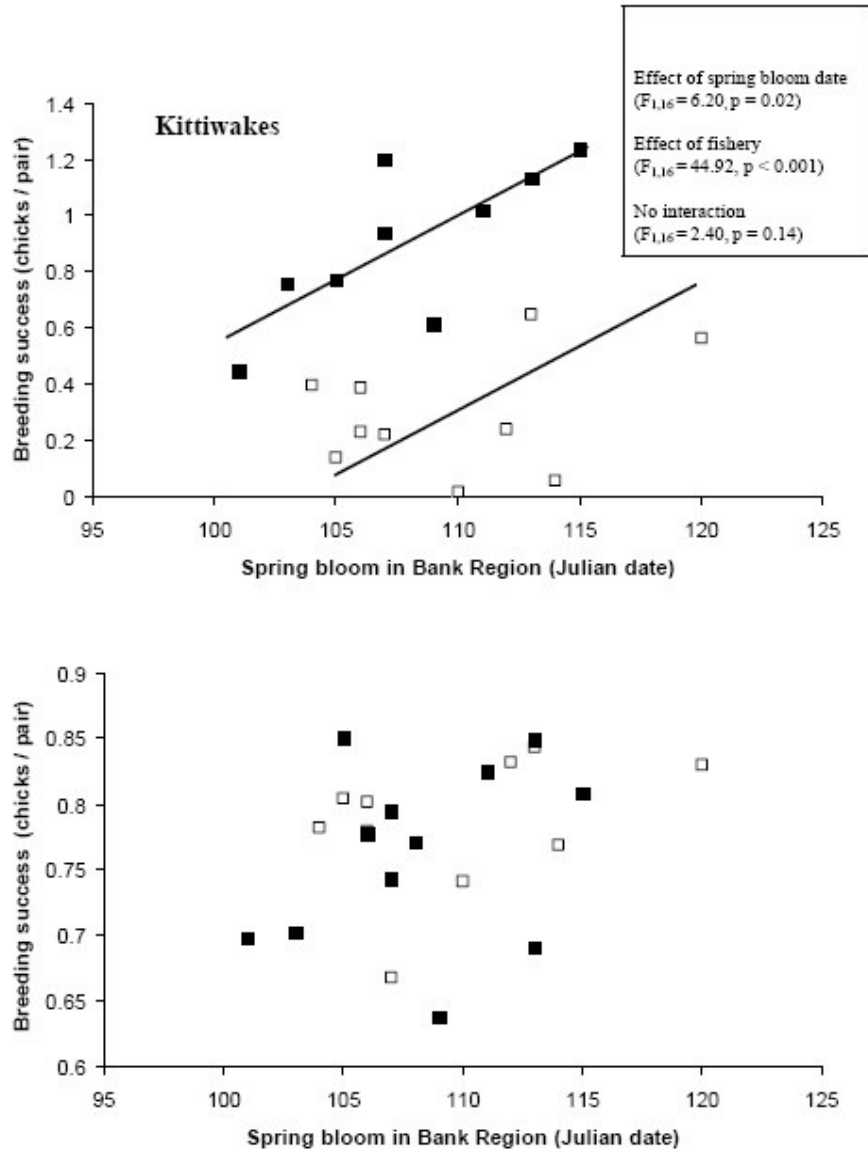
Fig 8: Breeding success of black-legged kittiwakes (1985-2003; top panel) and common guillemots (1982-2003; bottom panel) on the Isle of May in relation to the start date of the spring bloom in the Bank region as estimated by the 1-D physical-biological model. Years with no commercial fishery for sandeels are represented by filled squares and years with a fishery with open squares