Sperm whale habitat use and foraging success off northern Chile: evidence of ecological links between coastal and pelagic systems

Luke Rendell[1,*], Hal Whitehead[2], Ruben Escribano[3]

[1]Sea Mammal Research Unit, Gatty Marine Laboratory, School of Biology, University of St. Andrews, Fife KY16 8LB, UK
[2]Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada
[3]Center for Oceanographic Research in the South-Eastern Pacific (COPAS), Universidad de Concepción,
Casilla 160-C, Concepción, Chile

ABSTRACT: Cold water upwelling along the coast of Chile drives some of the most productive marine ecosystems in the world; one example is the Mejillones upwelling system at 23° S. We studied the distribution, movements and foraging success of the sperm whale *Physeter macrocephalus* off the northern coast of Chile (18° 30′ S to 25° S) over a 9 mo period. We used a small sailing vessel to survey the area using visual and acoustic methods, and followed any sperm whale groups encountered, collecting defecation rate data as an index of foraging success. Both encounter and defecation rates were greater in the southern part of the study area (>22° 30′ S) relative to the north, coinciding with the Mejillones upwelling. Movement patterns were also markedly different, with groups in the southern part of the area having smaller net 12 h displacements, and less directionality, than those in the north, such that they tended to remain in the area associated with high defecation rates. We suggest that the greater foraging success off Mejillones was due to upwelled water being entrained offshore and southward by local physical oceanography, making productivity from coastal upwelling available offshore to pelagic predators.

KEY WORDS: Sperm whale · Distribution · Movements · Foraging · Upwelling

INTRODUCTION

The upwelling of nutrient rich water into the photic zone is crucial to many of the world's most productive marine ecosystems (Barnes & Hughes 1988). One such system is off the Mejillones Peninsula, Chile (~23° S, 71° W). Here, wind-driven upwelling is a major force governing the patterns of coastal circulation. Upwelling plumes develop at all times of the year near the northernmost point of the peninsula, extending up to 50 km offshore (Rodriguez et al. 1991, Marín et al. 2001, Sobarzo & Figueroa 2001). The cold nutrient-rich waters are transported northwest, but then they interact with the poleward Peruvian counter-current (PCC), giving rise to a cyclonic gyre (Marín et al. 2001) which

may act as an efficient retention zone off Mejillones Bay. This retention zone may aggregate and accumulate phytoplankton biomass, as well as dominant zooplankton, near the upwelling focus (Escribano & Hidalgo 2000, Giraldo et al. 2002). Marín et al. (2001) used a combination of *in situ* current measurements, wind data and satellite data, to demonstrate that even though the upwelling plume changes direction and size on a daily basis, it is also a stable feature in the sense that recently upwelled waters can be recirculated and retained nearshore for extended periods (>7 d) and continue to fertilise the photic layer. Furthermore, upwelling in the region as a whole appears to vary very little with season and is a year-round feature (Morales et al. 1996). A conceptual model that

illustrates the circulation resulting from interaction between the upwelling plume and the poleward flow is shown in Fig. 1. This circulation pattern likely fuels primary production in the area, and gross primary production (GPP) can reach up to 9.3 g C m^{-2} d^{-1} (Daneri et al. 2000), making this one of the most productive marine ecosystems in the world (Escribano & McLaren 1999). These processes create a particularly rich habitat where fish spawning takes place, as fish eggs and larvae are abundant and aggregated on the upwelling focus during the winter/spring season (Rojas et al. 2002). In this paper we show that this area of primarily coastal productivity has ecological effects that extend into the pelagic zone and the higher oceanic trophic levels, including a dominant mesopelagic predator, the sperm whale *Physeter macrocephalus*.

Sperm whales are ecologically important oceanic predators, primarily of mesopelagic cephalopods (Clarke et al. 1976, Kawakami 1980, Clarke et al. 1988, Smith & Whitehead 2000), with an estimated worldwide population of about 360 000 (Whitehead 2002), and are thus responsible for a large annual biomass removal. If recent insights into the role of top-down control in marine community structure hold true (Worm et al. 2002, Worm & Myers 2003), then the sperm whale may be a crucial structuring factor in global mesopelagic food webs. Unfortunately, it is extremely difficult to study sperm whale foraging directly, since it mostly occurs at >400 m depth (Rice
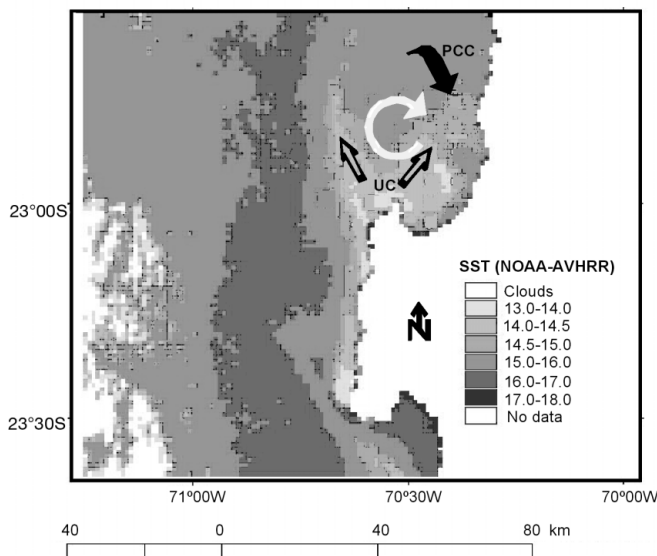

Fig. 1. Conceptual model of coastal circulation during wind-driven upwelling off Mejillones Peninsula (northern Chile). The poleward Peruvian countercurrent (PCC) interacts with the upwelling driven flow (UC) giving rise to a cyclonic gyre. The satellite image of sea surface temperature (SST) was obtained in October 1999

1989). However, defecation rate can be used as an index of foraging success, under the assumption that most defecation occurs at the surface since blood supply to non-essential organs (including the digestive tract) is shut down as an adaptation to deep diving (Kooyman et al. 1981, Whitehead et al. 1989, Smith & Whitehead 1993). The relationship between cold water upwelling and this index of sperm whale foraging has been well studied off the Galápagos Islands (Whitehead et al. 1989, Smith & Whitehead 1993, Whitehead 1996), where there is an evident negative relationship between sea surface temperature (SST) and defecation rate — sperm whales defecate more in cooler upwelling zones, but less in areas and times with warmer surface waters, especially when SST is over 23°C. The short time lag between SST increases and defecation rate decreases led Whitehead et al. (1989) and Smith & Whitehead (1993) to suggest that the mechanism underlying this relationship must be something other than increased primary production working through the trophic levels. They suggested instead that a direct change in the distribution of prey species in response to water temperature is a more likely cause of reduced foraging success at higher SSTs.

Other studies have provided important insight into sperm whale habitat use, associated with both permanent and ephemeral oceanographic features. Jaquet & Whitehead (1996) showed that high secondary productivity as measured by sub-surface biomass is a mesoscale predictor of sperm whale distribution (over scales of about 320 nautical miles); however, they later showed that sub-surface biomass is not a good predictor of foraging success over any scale (Jaquet & Whitehead 1999). Off the US eastern seaboard, Griffin (1999) has shown a clear association between sperm whales and the eastern front of a warm-core ring originating in the Gulf Stream, suggesting that the currents in this spatially mobile oceanographic feature provide ideal habitat for the squid prey of sperm whales; he did not, however, measure foraging success. Waring et al. (2001) used several years of survey data from the same area to show that sperm whales prefer cooler waters than beaked whales, perhaps their principal competitor for mesopelagic squid. On smaller spatial and temporal scales, the movement of sperm whales through their habitat relates closely to foraging success: in areas where foraging is good, sperm whale groups tend to alter course more often, resulting in more convoluted tracklines and lower net displacements (Jaquet & Whitehead 1999). Likewise, low foraging success is associated with more direct courses and larger net displacements (Jaquet & Whitehead 1999). Combined, these studies emphasise the importance of water movement, relatively sharp temperature gradients and relatively low SSTs in producing what

appears to be good habitat for sperm whales because it is suitable for their prey.

Here we relate the distribution, movements and foraging success of sperm whales in the waters off northern Chile to areas of cold water upwelling, and in doing so provide an example of how near-shore oceanographic processes can have ecological effects extending to the deep ocean.

MATERIALS AND METHODS

We collected data from a 13 m auxiliary sailing vessel from April through December 2000 in the waters off northern Chile (18° 30′ S to 25° S). Surveys used both acoustic and, during daylight only, visual searching by a single crew member rotating watch every 3 h. Every 30 min the vessel was slowed and an omni-directional hydrophone (Benthos AQ4 with Ithaco pre-amplifiers) used to listen for the clicks consistently produced by sperm whales. Upon detection, sperm whale groups were tracked using a directional hydrophone. Encounters were defined as continuous periods of visual and/or acoustic contact, and were ended when whales had been neither seen nor heard for more than 1 h. During daylight hours we took photographs of the flukes (tails) of diving whales during foraging periods, and for every fluke-up observed we recorded whether faeces were visible in the water where the whale had just dived, provided the vessel was close enough (generally <15 m) for defecation to be reliably detected. Vessel positions were recorded automatically every 5 min using a Garmin GPS navigator, and environmental data, including SST, were recorded every 3 h.

We analysed the data in Matlab® (using the Mapping Toolbox) and Systat®. We calculated the distance travelled while searching for sperm whales in 1/2° latitude bands as a measure of search effort. Encounter rates were taken as the number of encounters divided by the search distance in each band, giving a measure of relative abundance. We estimated defecation rates in 2 ways. Firstly, we calculated the proportion of the total observed fluke-ups (which precede deep dives) after which feces were detected in each 1/2° latitude band. Secondly, to test for differences between defecation rates in the upwelling and entrainment zone, we calculated the defecation rate for each day spent tracking whales. We assigned each day to one of two broader latitude bands, north and south of 22.5° S (the approximate northern boundary of the strong cold water upwelling off Mejillones), and 1 of 3 time periods — April through June, July through September and October through December. Only days when at least 20 fluke-ups were observed reliably were included, to eliminate extreme proportion values associated with low defeca-

tion observation effort. We analysed these data with a general linear model (GLM) that included categorical independent variables for area (N or S of 22.5° S) and time period (Apr–Jun, Jul–Sep, Oct–Dec), and the daily 06:00 h SST measurements as a continuous independent variable. We used an arcsine-square root transformation to improve normality in the dependent variable, daily defecation rate.

To examine movement patterns, we calculated east–west and north–south displacements of sperm whale groups over 12 h intervals (corresponding to 1 d spent tracking whales). We analysed these data using a GLM that included categorical independent variables for area (N or S of 22.5° S) and movement type (E–W, N–S), the continuous independent variable defecation rate and all interactions.

We estimated model parameters using the backwards stepwise procedure in Systat® with α-to-enter and leave = 0.15. For both this and the ANOVA model, we checked for normal error using the Lilliefors test on the residuals and calculated the first-order autocorrelation of the data to check for possible non-independence between sampling periods.

RESULTS

During 169 d at sea we encountered sperm whales 48 times, and tracked groups for between 1 and 13 d (Fig. 2). Two of these 48 encounters followed visual detection, the remainder followed acoustic detection. Defecation data were collected on 71 d, and more than 20 fluke-ups were observed on 39 of those d; of these, 15 were north and 24 to the south of 22.5° S. Movement data — the displacement between the 06:00 and 18:00 h positions of the group — were available for all 39 d.

Encounter rates were elevated in the southern part of the study area (Fig. 3). Defecation rates were also elevated in this area, with the highest levels corresponding to areas of cold water upwelling and entrainment, south of 22.5° S (Fig. 4). Defecation rates south of this point were higher throughout the study period (Fig. 5), with the exception of a peak around 20° S, where there is another upwelling system off the port of Iquique (Morales et al. 2001). Overall, the range of observed defecation rates were similar to those of previous studies (Smith & Whitehead 1993); while there are a few observations of much higher rates from the Galápagos, the majority of observations there fall within the range we observed.

The GLM of defecation rate showed both latitude and time effects at the 95 % level — defecation rates were higher in the southern portion of the study areas and, across the study area, defecation rates tended to

be higher towards the end of the study (Table 1, Fig. 5). Notably, there was no effect of surface temperature, as 06:00 h SST was not retained in the stepwise fitting (rejected at p = 0.416; Fig. 6). The Lilliefors test on

the residuals did not reject the normality hypothesis (p = 0.066) and autocorrelation was low (0.068).

The GLM of movement indicated that sperm whale groups tended to move further overall in the northern part of the study area, and that groups moved more N–S than E–W throughout the study area (Table 2, Fig. 7), but also that there was a strong interaction between the tendency to move E–W or N–S and the position of the group relative to the Mejillones upwelling. Groups in the north of the study area had substantially greater N–S displacements than E–W, whereas displacements were more evenly distributed in the southern region (Fig. 7). Residuals were not significantly non-normal (Lilliefors test, p = 0.248) and autocorrelation was negative (–0.112).
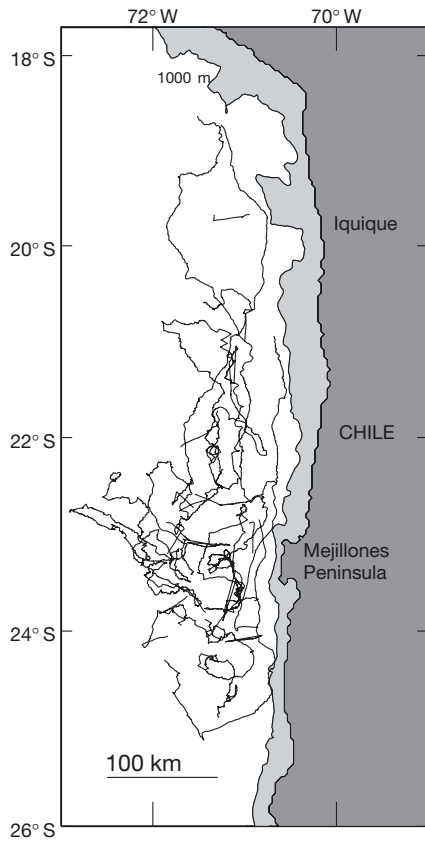
DISCUSSION

Our results show that sperm whale defecation rate and, by inference, foraging success were greater through much of the year, and that overall abundance was also much higher, in the area off and immediately south of the Mejillones upwelling region relative to the area to the north. We do not believe that these differences can be attributed to differences in prey affecting defecation rate and visibility in the 2 areas, since Clarke et al. (1988) report similar stomach contents in all whales caught between northern Peru and central Chile. Our results also show that sperm whales had different movement patterns off and south of Mejillones relative to the northern area; groups displaced less overall and with a much greater E–W component to their movements in the area off the Mejillones upwelling region, whereas in the northern area move-

Fig. 2. Track of research vessel while following sperm whales. Adapted from Whitehead (2003)
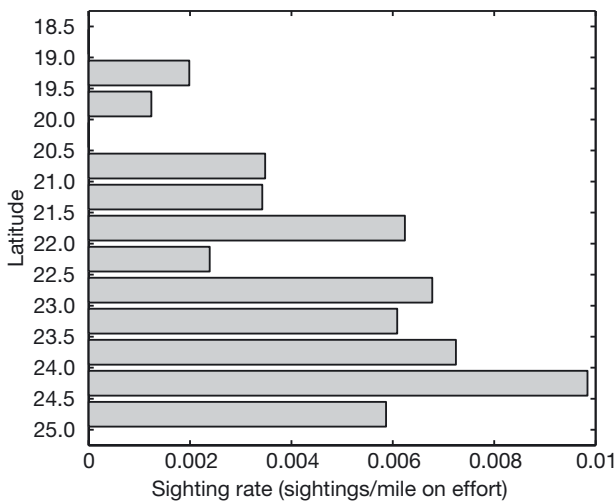

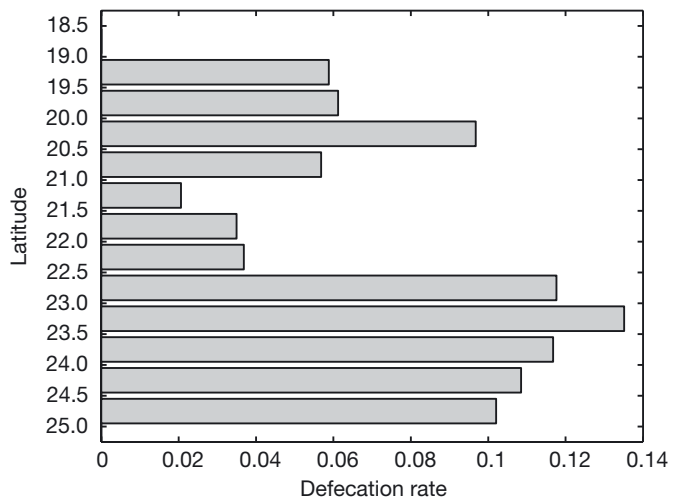
Fig. 3. Sighting rate by latitude band for all months

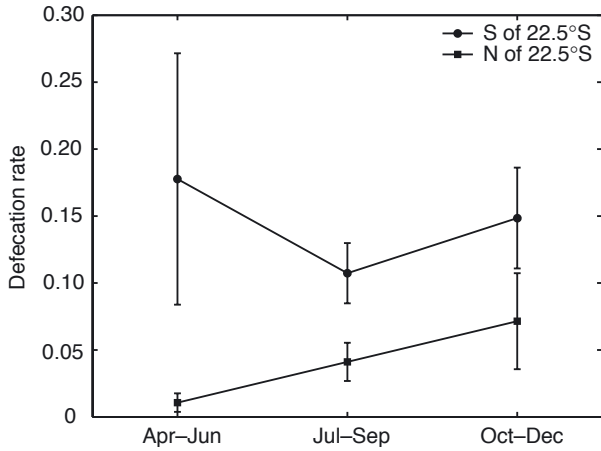Fig. 4. Defecation rate by latitude band for all months

Fig. 5. Defecation rate over time in 2 latitude bands, north and south of the Mejillones upwelling. Points are mean ± SEM
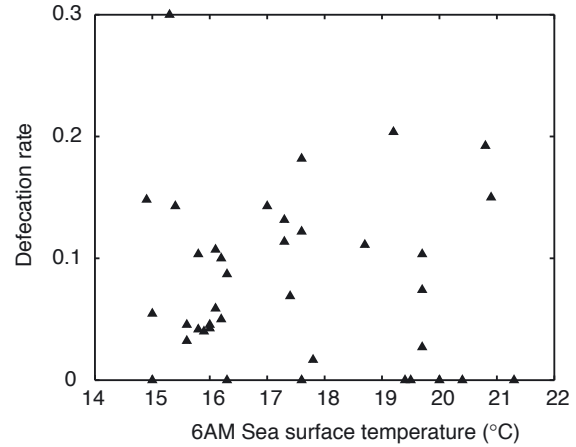

Fig. 6. Defecation rate plotted by day against 06:00 h SST

ments were largely along a N–S axis. Since whale encounters were more common in the southern area, data were available for more days in that area (24 vs 15) but the bias is modest given the size of the observed effect.

These results are undoubtedly related — sperm whales are likely more common in the southern area because it is a rich feeding ground, and when present they tend to stay there by moving little overall and with little directionality. Conversely, in the northern region there seem to be few significant feeding grounds and sperm whale groups move through this area relatively rapidly and directly. One exception to the general pattern is the relatively high defecation rate observed off Iquique, where there is another upwelling. The effects
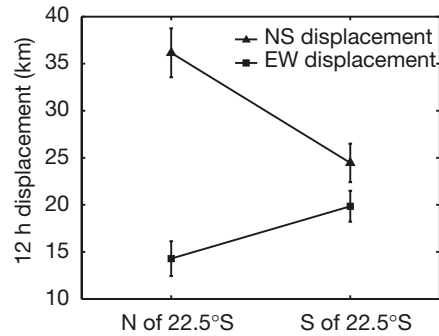

Fig. 7. E–W and N–S displacements over 12 h in 2 latitude bands, north and south of the Mejillones upwelling. Points are mean ± SEM

Table 1. Results of general linear model of daily defecation rate; only terms retained after backwards stepwise procedure (α-to-enter and leave = 0.15) are shown

Source	SS	df	MSS	F	p
Area$_{(N, S)}$	0.152	1	0.152	8.834	0.005
Time period$_{(Apr–Jun, Jul–Sep, Oct–Dec)}$	0.141	2	0.070	4.089	0.025
Error	0.602	35	0.017		

Table 2. Results of general linear model of 12 h movement; only terms retained after backwards stepwise procedure (α-to-enter and leave = 0.15) are shown

Source	SS	df	MSS	F	p
Area $_{(N, S)}$	972	1	972	3.548	0.064
Movement Type$_{(E–W, N–S)}$	3 712	1	3712	13.546	<0.001
Area × Movement Type	2 254	1	2254	8.226	0.005
Error	20 281	74	274		

of this upwelling seem to be relatively minor compared to those of the Mejillones upwelling, which is somewhat puzzling since the upwelling itself might be equivalent to that off Mejillones, at least in terms of chlorophyll levels (Morales et al. 1996, 2001).

We inferred high foraging success from high defecation rates observed both directly off and to the south of Mejillones; this may be due to interactions between upwelling filaments and the PCC respectively. Sobarzo & Figueroa (2001) have shown that relatively narrow (<100 km) filaments of upwelled water from the Mejillones Peninsula may extend hundreds of kilometres offshore. Thus, surface current interactions result in the offshore export of productive, plankton-bearing water from the upwelling focus. This explains

how sperm whales, a pelagic species, can benefit from near-shore upwelling. Once offshore, this productive water would likely be entrained southward by the PCC—although little studied, data so far show that it may influence and exert a southward flow in Peruvian and northern Chilean waters up to 100–300 km from the coast (Strub et al. 1998)—and result in areas offshore and south of the upwelling focus that are relatively productive for oceanic feeders such as mesopelagic squid, the primary prey of sperm whales, as inferred here from elevated defecation rates. This scenario is consistent with Jaquet's (1996) general model of a lag between areas of primary productivity and sperm whale concentrations (see also Jaquet & Whitehead 1996).

We did not observe the direct relationship between SST and defecation rate across days found in previous studies (Whitehead et al. 1989, Smith & Whitehead 1993). The relationship in the present study is trivial, in contrast to similar observations around the Galápagos Islands, even when the Galápagos data are restricted to the upper limit of the Chile SST range (Pearson's correlation with defecation rate, Chile: -0.05, $p = 0.77$; Galápagos: -0.562, $p = 0.029$). N–S, E–W and net displacement similarly had low correlation with 06:00 h SST, with Pearson's correlation coefficients of 0.044 ($p = 0.972$), -0.220 ($p = 0.179$), and -0.006 ($p = 0.789$) respectively. This contrast is interesting, especially since Daneri et al. (2000) report a strong relationship between SST and GPP specifically in these upwelling regions off Chile. One possible explanation for the lack of direct relationship between SST and defecation rate in our analysis could be a delay in material passing up trophic levels. This implies a different relationship between upwelling and defecation rate off the Galápagos than off Chile. In the former, it has been suggested that distributional changes of prey in response to cold water upwelling is responsible for the strong relationship (Whitehead et al. 1989, Smith & Whitehead 1993), whereas the weak relationship we observed off Chile is more consistent with delays in energy flow through trophic levels, as would be expected if sperm whale foraging success off Mejillones had its ultimate root in high primary productivity resulting from strong year-round upwelling.

We have shown that an index of sperm whale foraging success, defecation rate, is strongly related to coastal upwelling of cold, nutrient rich water off Iquique but especially the Mejillones. This provides evidence of an explicit link between near-shore oceanographic processes and the ecology of a wholly pelagic species. It also provides at least partial explanation for sperm whale distribution patterns off northern Chile, and highlights what are likely areas of critical habitat for this species, providing information for focused management efforts. However, our study sampled during 1 yr only, and in an area where productivity can fluctuate dramatically from year to year (Morales et al. 2001). Research over multiple years is therefore needed to establish the magnitude of interannual variation in the patterns we have found.

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