Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf

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Abstract: In this paper we examine the summer distribution of three species of small odontocetes in the highly productive waters in and near the Gully, a submarine canyon on the edge of the Scotian Shelf. Atlantic white-sided dolphins (Lagenorhynchus acutus) and common dolphins (Delphinus delphis) were not randomly distributed with respect to depth, sea-floor relief, month of sighting, or sea-surface temperature. Long-finned pilot whales (Globicephala melas) were not randomly distributed with respect to month or sea-surface temperature. These species used the Gully slightly differently, although there was overlap. White-sided dolphins were seen only in the core of the canyon, but were sighted at all temperatures, depths, and sea-floor reliefs and throughout the summer field season. Common dolphins had a modest range throughout the deeper waters and were not seen in the summer before July, when the water warms. Pilot whales ranged widely over the study area, preferring areas with fairly flat relief and common dolphins partition the Gully temporally but not geographically.

Résumé : Nous avons étudié la répartition estivale de trois espèces de petits odontocètes dans les eaux très productives de la région de la « Gully », un canyon sous-marin à la limite du plateau continental néo-écossais. La répartition des Dauphins à flancs blancs (Lagenorhynchus acutus) et des Dauphins communs (Delphinus delphis) était dépendante de la profondeur, du relief sous-marin, de la température de surface de l’eau et du mois durant lequel ils étaient observés. La répartition des Globicéphales noirs (Globicephala melas) dépendait uniquement de la température de surface de l’eau et du mois durant lequel ils étaient observés. Ces espèces utilisent les eaux de la « Gully » de façons différentes, mais il y a parfois chevauchement. Les Dauphins à flancs blancs n’occupent que le centre du canyon, mais ils ont été observés à toutes températures de surface, à toutes profondeurs et durant toute la saison d’observation. Les Dauphins communs occupent une zone limitée dans les eaux plus profondes, et ils n’ont jamais été observés avant juillet, au moment du réchauffement des eaux. Bien que répartis dans toute la région étudiée, les globicéphales préfèrent les zones de faible relief et n’apparaissent que tard dans la saison alors que les eaux sont chaudes. Il semble donc que les Dauphins à flancs blancs et les Dauphins communs se partagent les eaux de la « Gully » selon un axe temporel plutôt que géographique.

Introduction

Little research has been conducted on the distribution of small toothed cetaceans on the edge of the Scotian Shelf. The Gully, a prominent submarine canyon near Sable Island (Fig. 1), is inhabited by sperm whales (Physeter macrocephalus), northern bottlenose whales (Hyperoodon ampullatus), long-finned pilot whales (Globicephala melas), common dolphins (Delphinus delphis), and white-sided dolphins (Lagenorhynchus acutus) (Faucher and Whitehead 1991). Other species of toothed and baleen cetaceans are occasional visitors (Faucher and Whitehead 1991). Previous studies examining the distribution of sperm whales and northern bottlenose whales indicated that these two species, which have similar diets, partition the Gully into largely separate habitats (Whitehead et al. 1992). This project examines the distributions of the pilot whales, common dolphins, and white-sided dolphins in June, July, and August.

When species that require similar resources occur in the same habitat they tend to partition the available resources, reducing competition (Roughgarden 1976). Two or more competing species can divide the resources by occupying different physical locations or by feeding on different prey (Roughgarden 1976). Pilot whales and common and white-sided dolphins feed on squid and fish (Evans 1982; Overholtz and Waring 1991; Waring et al. 1990) and therefore may be competing with each other for the same prey. However as they are all sighted in the Gully we might expect them somehow to be partitioning the resources by inhabiting a different geographic range by feeding on different prey species.

In general, the distribution of cetaceans is strongly influenced by the distribution of their prey (Acevedo and Würsig 1991; Cockcroft and Peddemors 1990; Smith and Whitehead 1991; Cockcroft and Peddemors 1990; Smith and Whitehead 1991).
Fig. 1. Location of the Gully with reference to mainland Nova Scotia and Sable Island. The broken line encloses the study area.

Table 1. Records of all small odontocetes sighted in or near the Gully.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of sightings</th>
<th>Sighting rate (no./h)</th>
<th>Mean group size</th>
<th>Mean Temperature range (°C)</th>
<th>Depth range (m)</th>
<th>Mean sighting duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-sided dolphins</td>
<td>100</td>
<td>0.07</td>
<td>8 ± 8</td>
<td>7.9 - 22.3</td>
<td>100 - 2200</td>
<td>43 ± 123</td>
</tr>
<tr>
<td>Common dolphins</td>
<td>83</td>
<td>0.06</td>
<td>14 ± 27</td>
<td>10.5 - 22.8</td>
<td>60 - 2500</td>
<td>38 ± 51</td>
</tr>
<tr>
<td>Pilot whales</td>
<td>32</td>
<td>0.02</td>
<td>10 ± 8</td>
<td>8.5 - 22.5</td>
<td>23 - 2100</td>
<td>24 ± 31</td>
</tr>
<tr>
<td>Striped dolphins</td>
<td>26</td>
<td>0.02</td>
<td>10 ± 8</td>
<td>13.0 - 22.3</td>
<td>800 - 2500</td>
<td>20 ± 17</td>
</tr>
<tr>
<td>Bottlenose dolphins</td>
<td>3</td>
<td>0.002</td>
<td>17 ± 16</td>
<td>13.9 - 15.3</td>
<td>230 - 1700</td>
<td>10 ± 7</td>
</tr>
</tbody>
</table>

*Values are given as means ± 1 SD.

1993). Correlations between cetacean distribution and environmental variables such as sea-floor relief (the change in depth over a given range), depth, and sea surface temperature are unlikely to be direct causal relationships. Instead these relationships are created by the effects of oceanographic features on prey densities (Gaskin 1968; Reilly 1990; Selzer and Payne 1988).

Studying the diet of these species directly is difficult and was beyond the scope of our research. In this study we correlate incidental sightings of small odontocetes with environmental and temporal variables and investigate habitat partitioning with respect to these variables.

The species

Atlantic white-sided dolphins (2.5 m long) are only found in the North Atlantic. They range from West Greenland to Cape Cod in the west and from Norway to England in the east (Mercer 1973).

Common dolphins, also known as saddleback, white-bellied, or hourglass dolphins (1.8 - 2.3 m long), tend to be found in pods of about 8 members, but are commonly seen in aggregations of 200 or more (Gaskin 1992a). They are widely distributed in warm waters of the Atlantic, Pacific, and Indian oceans but rarely close to shore. In the North Atlantic, they are not found north of Newfoundland (Mercer 1973).

Long-finned pilot whales are large odontocetes, males being 6.2 m long and females 5.5 m. In the field, they are almost impossible to distinguish from short-finned pilot whales (Globicephala macrorhynchus). However, the distribution of long-finned pilot whales stretches from Iceland to New England, while short-finned pilot whales are found only from New Jersey to the West Indies (Mercer 1973). Thus, we assumed that all pilot whales sighted in the Gully were long-finned.

Striped dolphins (Stenella coeruleoalba) and bottlenose dolphins (Tursiops truncatus) were also occasionally sighted in the Gully (Table 1).

Methods

Field research

Data were collected in 1988 (8-21 July, 25 July - 6 August), 1989 (16-30 July, 1-14 August), 1990 (14-28 June, 2-18 July, 25 July - 11 August), 1993 (10-24 July), and 1994 (1-17 August) during research on northern bottlenose whales and sperm whales. From 1988 to 1990, studies were carried out from Elendil, a 10-m sloop with crews of four to six, and in 1993 and 1994 from Balaena, a 13-m cutter with crews of five or six.

Visibility, sea-surface temperature and other environmental measures were recorded at stations carried out every 3 h. The position of the boat was obtained using a Seaport Loran-C
in 1988–1990 and a Trimble Transpak Global Positioning System (GPS) in 1993 and 1994. At depths of less than 1000 m we used a Simrad Skipper 603 vertically mounted depth sounder to determine depth, and for depths over 1000 m readings were taken from bathymetric charts. Sea-floor relief was calculated from these charts as the maximum change in depth within radii of \( \frac{1}{2}, 1, \) and 2 naut. mi. (1 naut. mi. = 1.85 km) of the position of the boat.

The primary focus of the field research was to collect data on sperm and bottlenose whales. Incidental sightings of small odontocetes occurred during surveying for bottlenose or sperm whales, while bottlenose or sperm whales were being followed, in transit to and from port, and while the boat was have-to in the study area. Whenever cetaceans were sighted, we recorded the species (if possible), the time first sighted, the time last sighted, the group size, the location of the boat, and ocean depth. Analysis was only carried out on sightings in which species identification was certain. As the animals had to come to within 300 m of the boat for the species to be ascertained, the location of the boat closely approximates the position of the animals. Depths and sea-floor reliefs were calculated from the locations. As the sea-surface temperature was not recorded at each sighting, we used the sea temperature for the closest 3-h station. During the different study years, sighting rates varied in a similar manner with respect to location and oceanographic and environmental measures, therefore data from all of the years were grouped.

**Analysis**

As data were opportunistically collected, effort was not equal throughout the Gully. To control for this variability, sightings were converted to indices of abundance, calculated by dividing the number of sightings of a species within areas and categories of depth, sea-floor relief, sea-surface temperature, or month by the number of 3-h stations for that area or category.

Statistical analysis of the distribution of each species allowed the following hypotheses to be compared using a G test:

- \( H_0 \): the distribution of sightings with respect to an environmental variable was random, therefore the expected number of sightings in each category of the variable (depth, sea-floor relief, sea-surface temperature, or month of sighting) was proportional to the number of 3-h stations in that category.
- \( H_A \): the distribution of sightings was not random, therefore the expected number of sightings in each category of a variable was not proportional to the number of 3-h stations in that category.

Similarly, resource partitioning tests were used to compare habitat use by white-sided and common dolphins, using a G test, on the following hypotheses:

- \( H_0 \): the expected number of sightings of white-sided dolphins in a particular category of a variable was proportional to the expected number of sightings of common dolphins in the same category.
- \( H_A \): the expected number of sightings of white-sided dolphins in a particular category of a variable was not proportional to the expected number of sightings of common dolphins in the same category.

Habitat partitioning could not be studied for pilot whales, as the number of observed sightings was too low to give statistically reliable results (Table 1).

During a sighting, two species were arbitrarily defined as being associated if they were sighted within 15 min of each other.

**Results**

**Distribution**

Table 1 summarizes the sightings of all small toothed cetaceans in the Gully. White-sided dolphins, common dolphins, and pilot whales were sighted many times within a broad range of sea-surface temperatures and depths. On average, a pod of white-sided dolphins was sighted once every 14 h of effort and the mean length of the sighting was 43 min. Some sightings of white-sided dolphins were very brief, while one sighting lasted over 17 h. Common dolphins were sighted once for every 17 h of effort, the mean length of sightings being 38 min. Pilot whales were sighted once for every 50 h of effort, and the mean length of sightings was 24 min. Striped dolphins were sighted only in relatively warm, deep waters, and bottlenose dolphins were sighted only 3 times.

Figure 2A shows variation in the indices of abundance of white-sided dolphins in and near the Gully, within a 15' latitude and longitude grid, wherever more than four 3-h stations were recorded. White-sided dolphins were found almost exclusively in the canyon itself and have the most restricted range of the three species. No white-sided dolphins were observed on the shelf near the canyon, although the boat passed through these areas traveling to and from Halifax and Sable Island.

Figure 2B similarly indicates the distribution of common dolphins throughout the Gully. They were found in the main part of the canyon but especially in the deep waters to the south of it.

Pilot whales (Fig. 2C) were found in the shallower portions of the Gully, but not on the shelf, nor in very deep water. Both pilot whales and white-sided dolphins were sighted on the shelf near mainland Nova Scotia, far from the Gully.

The distribution of common and white-sided dolphins was not random according to depth, sea-floor relief, sea-surface temperature, and the month in which they were sighted (Table 2). The sea-floor relief was initially calculated over three different radii \( (\frac{1}{2}, 1, \) and 2 naut. mi.). As the distribution of each species showed a similar pattern for all three measures of sea-floor relief, only the results for the 2 naut. mi. radius are shown. Pilot whale distribution was significantly different from random with respect to sea-surface temperature and month of sighting, but not significantly different for depth or sea-floor relief. For pilot whales a small sample size often results in the predicted number of sightings falling below the critical value of 3 sightings per category, making these tests theoretically invalid.

The index of abundance with respect to depth is shown in Fig. 3A. White-sided and common dolphins were most abundant over depths of 1000–2500 m, common dolphins being
Fig. 2. Distribution of white-sided dolphins (A), common dolphins (B), and pilot whales (C) in the Gully as indicated by the index of abundance (shown by proportional size of the circle) in each 15' × 15' rectangle. Crosses indicate rectangles in which at least four 3-h stations occurred but no white-sided dolphins were sighted. The number below the cross or circle represents the number of 3-h stations in that rectangle.
Table 2. Measures of the distribution of commonly sighted small odontocetes within the Gully.

<table>
<thead>
<tr>
<th></th>
<th>Depth (m)</th>
<th>2 naut. mi. sea-floor relief (m)</th>
<th>Sea-surface temp. (°C)</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>White-sided dolphins</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1239</td>
<td>668</td>
<td>14.2</td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>100</td>
<td>100</td>
<td>7.9</td>
<td>16 June</td>
</tr>
<tr>
<td>Maximum</td>
<td>2200</td>
<td>1100</td>
<td>22.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Common dolphins</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1170</td>
<td>618</td>
<td>16.9</td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>60</td>
<td>2.5</td>
<td>10.5</td>
<td>12 July</td>
</tr>
<tr>
<td>Maximum</td>
<td>2500</td>
<td>1100</td>
<td>22.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pilot whales</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>775</td>
<td>487</td>
<td>17.3</td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>23</td>
<td>0</td>
<td>8.5</td>
<td>16 June</td>
</tr>
<tr>
<td>Maximum</td>
<td>2100</td>
<td>1000</td>
<td>22.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Three-hour environment</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>965</td>
<td>538</td>
<td>15.5</td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>12</td>
<td>0</td>
<td>7.9</td>
<td>16 June</td>
</tr>
<tr>
<td>Maximum</td>
<td>2200</td>
<td>1100</td>
<td>23.0</td>
<td></td>
</tr>
</tbody>
</table>

Note: Statistical tests refer to random versus nonrandom distribution hypotheses.
especially prevalent over deeper waters. Pilot whales were most abundant over the shallowest and deepest waters, although this variation is not significant.

Sea-floor relief measures the gradient of the ocean bottom. Figure 3B shows the index of abundance of each species for reliefs over a 2 naut. mi. radius. White-sided and common dolphins were generally more abundant than expected over steep gradients, while pilot whales were slightly more abundant over flatter reliefs.

Sea-floor relief and depth are related variables \((r = 0.68)\), as shallow water tends to have relatively flat relief. However, each measure may represent a different determinant of cetacean distribution.

Relationships between dolphin abundance and sea-surface temperature are shown in Fig. 3C. White-sided dolphins were abundant in cooler water, while common dolphins were more abundant in warmer water. The abundance of pilot whales also increased with increasing temperature.

The sighting rates of the species in the Gully varied by month, as shown in Fig. 3D. Sea-surface temperatures rose with calendar date \((r = 0.78)\) and showed a consistent pattern over all 4 study years. White-sided dolphins were most abundant in June. Common dolphins were not sighted in June, when the lower temperatures were recorded. Pilot whales were seen in all 3 months; however, their abundance increased later in the summer. During two additional cruises to the Gully during the fall (30 September – 8 October 1989) and winter (7–13 February 1990), pilot whales and common dolphins were not sighted. White-sided dolphins were sighted only in October.

Fog was very common in the Gully, especially early in the summer. This could bias the distribution of cetacean sightings toward fog-free conditions, as dolphins and whales were more difficult to spot and identify in fog. However, when all sightings and 3-h stations with visibility of less than 1 km were eliminated from the data set, geographical distribution patterns and variation in abundance with environmental variables were not affected, nor did the sighting rates dramatically increase.

**Habitat partitioning**

White-sided and common dolphins appear to partition the Gully on the basis of sea-surface temperature and season rather than geography. These species exhibited similar distributions with respect to depth \((G = 9.135, 0.5 > p > 0.1)\) and sea-floor relief (2 naut. mi. radius, \(G = 0.861, 0.975 > p > 0.9\)). Common dolphins were sighted more often in warmer waters than were white-sided dolphins \((G = 33.619, p < 0.001)\). Similarly, common dolphins were relatively more abundant later in the summer than were white-sided dolphins \((G = 39.575, p < 0.001)\).

**Species associations**

White-sided dolphins were often associated with other species (Table 3). Half of the sightings of these dolphins occurred within 15 min of a sighting of another species. The frequent association between white-sided dolphins and bottlenose whales probably occurs because the distributions of these two species are very similar. White-sided dolphins also associate with other odontocetes and baleen whales. Common dolphins were sighted with other species 41% of the time. They were most often associated with bottlenose whales, although they were also seen with other odontocetes, especially striped dolphins, another warmer water species, as well as humpback whales (Megaptera novaeangliae) and fin whales (Balaenoptera physalus). Pilot whales were frequently associated with other species. More than 66% of pilot whale sightings were of pilot whales by themselves. They were sighted with several different species of toothed and baleen whales, although they were never associated with sperm whales.

**Discussion**

**Distribution**

Small odontocetes are very common in the Gully during the summer. For common and white-sided dolphins, sighting rates were much higher near the Gully than in areas they passed through when traveling to and from the Gully. This high cetacean abundance is presumably related to the biological and physical oceanography of the Gully, which is, unfortunately, largely unknown at present.

Cetacean distribution is often correlated with prey distribution (Acevedo and Würsig 1991; Cockcroft and Peddemors 1990; Smith and Whitehead 1993). It is hard to assess this relationship in the Gully, as relatively little is known about the prey preferences of pilot whales and common and white-sided dolphins in this area, or the distribution of potential prey species. However, some inferences can be drawn from studies in other areas.

The diet of pilot whales in the Atlantic Ocean is mainly composed of long-finned squid (Loligo pealei), short-finned squid (Illex illecebrosus), and mackerel (Scomber scombrus), although they also eat cod (Gadus morhua), haddock (Melanogrammus aeglefinus), Atlantic herring (Clupea harengus), butterfish (Peprilus triacanthus), hake (Merluccius sp.), and Greenland turbot (Reinhardtius hippoglossoides) (Evans 1982; Mercer 1975; Overholtz and Waring 1991; Waring et al. 1990). Common dolphins in the North Atlantic feed mainly on mackerel and long-finned squid, although they also eat herring, whiting (Merlangius merlangus), pilchard (Sardina pilchardus), and anchovy (Engraulis encrasicolus) (Evans 1982; Overholtz and Waring 1991; Waring et al. 1990). Fewer data are available on the diet of white-sided dolphins,
Fig. 3. Distribution of each of the commonly sighted species of small odontocetes in the Gulf with respect to depth (A), sea-floor relief within a 2 naut. mi. radius (B), sea-surface temperature (C), and month (D) as indicated by the index of abundance.
as they are rarely incidentally caught by the fishing industry. They primarily consume fish, such as herring, whiting, cod, and mackerel, as well as cephalopods, such as squid (Evans 1982; Overholtz and Waring 1991; Waring et al. 1990).

Thus, there is the potential for competition for food among these three species in the Gully. However, there do seem to be some diet differences. For instance, short-finned squid are an important food for pilot whales off Newfoundland (Mercer 1975), but neither white-sided nor common dolphins have been reported as by-catch of the short-finned squid fleet off the eastern United States (Waring et al. 1990). Commercial fisheries have exploited the Gully area for hake, short-finned squid, haddock, and cod, known prey species of pilot whales and common and white-sided dolphins. Many other prey species have also been reported as by-catch of these directed fisheries; these include herring, Greenland turbot, mackerel, and butterfish. However, most fishing occurs on the edge of the canyon rather than in the centre (Fisheries and Oceans Canada, unpublished data). There is, therefore, no clear picture of prey distribution or densities in the Gully.

The cetacean distribution in and near the Gully corresponds well to that found in most other studies in the western North Atlantic. Sergeant et al. (1970) reviewed stranding data in Nova Scotia and Newfoundland from 1948 to 1968. Both long-finned pilot whales and white-sided dolphins stranded on Sable Island during this period, indicating their presence in the general area of the Gully. White-sided dolphins were classified as an offshore species, as they stranded more commonly on Sable Island than inshore. The study did not note any strandings of common dolphins throughout this period. However, they were frequently observed at sea off Nova Scotia and in southern Newfoundland waters.

Selzer and Payne (1988) studied the spring and fall distribution of common and white-sided dolphins in the Gulf of Maine, approximately 750 km to the west of the Gully. Common dolphins were most abundant in a broad band parallelizing the continental slope between the 100 and 200 m depth contours and were found farther north in the spring than in the fall, coinciding with the distribution of mackerel, butterfish, and squid, known prey species. White-sided dolphins were distributed throughout the Gulf of Maine in the fall. In the spring they concentrated in the Great South Channel, another submarine canyon on the shelf edge. This distribution correlates with the distribution of the sand lance (Ammodites americanus), which is a possible prey species. White-sided dolphins were found at lower sea-surface temperatures than were common dolphins. Selzer and Payne (1988) noted that the majority of their sightings of both species were in areas of greatest sea-floor relief.

The Cetacean and Turtle Assessment Program (CETAP) (1982) investigated the distribution of whales and dolphins on the continental shelf within the United States’ exclusive economic zone. Pilot whales in that study were generally distributed along the shelf edge in relatively warm water. However, the study lumped long- and short-finned pilot whales together, making comparisons with this study difficult. CETAP also concluded that common dolphins inhabit a broad band along the shelf edge and are found in warmer waters than are white-sided dolphins.

In the CETAP (1982) study, white-sided dolphins were most abundant in cooler, northern waters, and were rarely found south of 40° N. However, they described white-sided dolphins as inhabiting the continental shelf shoreward of the 100 m contour line rather than the shelf edge. The mean depth of white-sided dolphin sightings in the CETAP study was 165 m, and 90% of their sightings were in water less than 300 m deep. There are several potential explanations for the difference between the distributions of white-sided dolphins described in this paper and by CETAP. One possibility is that the white-sided dolphins sighted in the CETAP study were feeding on different prey than those in the Gully, which created this differing distribution. It is impossible to test this prediction without knowing the diets in both areas. The dolphins in the CETAP study were found close to the southern limit of their range, which may have created an unusual distribution. Like bottlenose dolphins in the Pacific and in the Atlantic south of the Gully, white-sided dolphins may exist as two different populations, coastal and offshore (Blaylock 1988; Duffield et al. 1983). White-sided dolphins are present in inshore Canadian coastal waters, especially in the Bay of Fundy (Gaskin 1992b), as well as offshore, as this study indicates.

Migration can play an important role in cetacean distribution. While very little is known about migration in these species, some preliminary analysis has been done. Common dolphins and long-finned pilot whales may move north from George’s Bank onto the Scotian Shelf in the summer, then south in the early fall (Waring et al. 1990), which is consistent with the monthly distributions we found in the Gully. Data from fall and winter trips to the Gully indicate that white-sided dolphins are present in the fall, while common dolphins and pilot whales may or may not be present. In the southern hemisphere, common dolphins migrate closer to the pole in the summer and farther away in the winter, this is correlated with the movements of pilchard (Sardinops ocellatus) (Cockcroft and Peddemors 1990). In contrast, common dolphins in the eastern tropical Pacific do not show migratory patterns (Reilly 1990). This suggests that common dolphin migration may be closely tied to remaining in waters above a critical temperature.

Habitat partitioning

Similar species may partition a habitat to avoid competition (Roughgarden 1976). This appears to apply to sperm and bottlenose whales in the Gully. Sperm whales tended to be located about 10 km north of the core concentrations of bottlenose whales. As there was very little overlap between the distributions of these two species, one species may have competitively excluded the other from its area (Whitehead et al. 1992). Exclusion through competition does not appear to be occurring in the case of white-sided and common dolphins, as they were found over the same geographic areas, and were seen within 15 min of each other several times, sometimes with individuals of the two species intermingled. This lack of geographic separation may be due to a superabundance of food, that can cause species that are normally separate to be found in the same area (Selzer and Payne 1988). However, it is difficult to tell whether the Gully is a region of superabundant food without more information on prey densities in the area. Another potential reason
why the distributions of common and white-sided dolphins overlap in the Gully may be that each species is feeding on different prey types and is therefore not exerting a strong competitive pressure on the other. Alternatively, a shared distribution may have nothing to do with food sources. Each species may be using the Gully for different purposes; one might be feeding while the other is simply migrating through the area. Given the current information available it is difficult to determine why these two species do not appear to partition the Gully geographically.

It is also difficult to determine why the two species are partitioning the Gully temporarily and (or) with respect to seawater temperature. As white-sided dolphins are, in general, a more northerly species than common dolphins (Evans 1982), they may be able to live year-round in the Gully, withstanding the cold winters, while common dolphins, which require more temperate conditions, must migrate farther south.

Species associations
The CETAP study also looked at associations between different species. All of the species they studied were sighted with other cetaceans much less frequently than in our study. As our study focused on a single canyon with a very high density of cetaceans, while CETAP looked at the cetacean distribution over the entire shelf, this discrepancy is not surprising. CETAP found that while white-sided dolphins often associate with other species, they were only rarely associated with other odontocetes (CETAP 1982). Our study indicates a high association with odontocetes, especially the northern bottlenose whale, which does not usually inhabit the CETAP study area.

In the CETAP study, common dolphins were infrequently sighted with other cetaceans. The few associations observed were between common dolphins and striped dolphins, fin whales, or pilot whales (CETAP 1982). In the Gully, common dolphins associated with all of these species, in addition to white-sided dolphins and sperm, northern bottlenose, and humpback whales.

In the CETAP study, pilot whales were often observed with other cetaceans, most commonly bottlenose dolphins (CETAP 1982). In the Gully, pilot whales were the only species associated with bottlenose dolphins. However, as bottlenose dolphins were only sighted in the Gully 3 times, the lack of associations with common and white-sided dolphins is not surprising.

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