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Distribution of common dolphins (*Delphinus* spp.) in the western Atlantic Ocean: a critical re-examination

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Abstract Due to indications that misidentification (largely confusion among dolphins of the genera *Delphinus* and *Stenella*) in the past had led to erroneous assumptions of distribution of the two species of common dolphins (*Delphinus delphis* and *D. capensis*) in the western Atlantic Ocean, we conducted a critical re-examination of records of the genus *Delphinus* from this region. We compiled 460 'plottable' records, required support for confirmation of genus and species identifications, and found many records lacking (and some clearly misidentified). When we plotted only the valid records ($n = 364$), we found evidence of populations in only three areas, and apparent absence throughout much of the tropical/subtropical regions. Off the east coast of the US and Canada, *D. delphis* is found from the Georgia/South Carolina border (32°N) north to about 47–50°N off Newfoundland. Since the 1960s, they have apparently been absent from Florida waters. There is no evidence that dolphins of the genus occur in the Gulf of Mexico. Reports of common dolphins from most of the Caribbean Basin are also rejected, and the only place in that region where they are confirmed to occur is off central-eastern Venezuela (a coastal *D. capensis* population). Off eastern South America, common dolphins appear to be restricted to south of 20°S. There is a coastal long-beaked population found in the South Brazil Bight, and one or more short-beaked populations south and offshore of this (ranging south to at least northern Argentina). The results are very different from commonly-accepted patterns of distribution for the genus in the Atlantic. Most areas of distribution coincide with moderate to strong upwelling and common dolphins appear to avoid warm, tropical waters. This study shows that great care must be taken in identification of similar-appearing long-beaked delphinids, and that uncritical acceptance of records at face value can lead to incorrect assumptions about the ranges of the species involved.

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Introduction

Common dolphins (*Delphinus* spp.) are widespread globally, found in all major ocean basins (with the exception of the high-latitude Arctic and Southern oceans). They extend from the tropics to the cool temperate zones in both hemispheres, and the reported range includes many enclosed and semi-enclosed basins, such as Caribbean Sea, Mediterranean Sea, Black Sea, Persian Gulf, Gulf of Thailand, Sea of Japan, and Gulf of California (see Heyning and Perrin 1994; Perrin 2002; Jefferson et al. 2008). Based on available information (primarily skull morphometric data), Amaha (1994) delineated five putative populations of common dolphins in the Atlantic Ocean: (1) United States/

Canada East coast (2) northwestern Europe (3) West Africa (4) Mediterranean Sea, and (5) Black Sea. However, she did indicate that Atlantic common dolphins can and do occur in other areas outside these regions.

The taxonomy of the genus *Delphinus* has been confused for many decades. Dozens of species have been named, with the main diagnostic differences often being the length of the beak and related tooth counts (see Hershkovitz 1966). Until recently, all common dolphins worldwide had been assumed to represent a single panglobal species, *D. delphis*, but Heyning and Perrin (1994) clearly showed that two different species were represented by long- and short-beaked common dolphins in the eastern North Pacific. These two species, *D. capensis* (long-beaked) and *D. delphis* (short-beaked), were also suggested by Heyning and Perrin (1994) to be present in other ocean basins around the world. It has also become clear that long-beaked and short-beaked common dolphins have different habitat preferences, and the issue of whether all long-beaked common dolphin populations around the world indeed represent *D. capensis* has even come to be questioned in recent years (see Amaha 1994; LeDuc et al. 1999; Esteves and Oviedo 2007). Although most recent authors assume that common dolphins worldwide represent one of these two species, this is an issue that remains unresolved.

Worldwide, common dolphins occupy a wide range of habitats, including oceanic regions, waters over the continental shelf, along the continental shelf break and slope, and over prominent underwater topography (e.g., mid-Atlantic Ridge and seamounts) (e.g., Hui 1979; Au and Perryman 1985; Evans 1994; Ferrero and Walker 1995). Common dolphins of some populations appear to preferentially travel along bottom topographic features, such as escarpments and seamount chains (Evans 1994). In those tropical regions where common dolphins are routinely sighted, they are generally found in upwelling-modified waters (Au and Perryman 1985; Ballance and Pitman 1998; Roden and Mullin 2000). Selzer and Payne (1988) reported that western North Atlantic short-beaked common dolphins were sighted more frequently in areas of high seafloor relief.

Common dolphins are typically characterized as pantropical. Many range maps for the genus *Delphinus* show a more-or-less continuous distribution across the tropical, subtropical, and temperate Atlantic Ocean (e.g., Watson 1981; Jefferson et al. 1993; Amaha 1994; Carwardine 1995; Kinze 2001; Kiefner 2002; Shirihai 2006), or at least widespread occurrence in the Gulf of Mexico and Caribbean Sea (Gaskin 1992). Some have indicated uncertainty in their occurrence in the Gulf of Mexico and Caribbean (Evans 1994). However, in recent years it has become apparent that the species of the genus in fact have much more restricted ranges, with specific habitat preferences in different areas (see Evans 1994; Heyning and Perrin 1994; Jefferson and Schiro 1997; Jefferson and Van Waerebeek 2002). Furthermore, many historical records of common dolphins in the literature have been misidentified (Gaskin 1992; International Whaling Commission (IWC) 2007).

Due to these errors and doubts about the commonly-assumed patterns of distribution for dolphins of this genus, the International Whaling Commission's Small Cetacean Subcommittee (International Whaling Commission (IWC) 2007, p. 306) recently indicated that "a review of records of *Delphinus* from the Caribbean and western tropical Atlantic is badly needed." In this paper, we provide a critical review of records of common dolphins from the western Atlantic Ocean west of 30°W, and attempt to clarify the actual distribution of the two species of common dolphin from this part of the world, based on verified records. A future paper will examine the situation in the eastern Atlantic Ocean.

Materials and methods

Study area

Our study area was the western Atlantic Ocean, west of 30°W longitude (Fig. 1). We divided the study area into four regions for analysis and presentation: (1) *East Coast of the United States and Canada*—from the southern tip of mainland Florida (81°W) to the Arctic (2) *Gulf of Mexico*—the area enclosed by a line connecting the southern tip of Florida to Cuba at 81°W and the shortest line connecting the Yucatan Peninsula to western Cuba (3) *Caribbean Sea*—the area enclosed by a line around the South American mainland, outer margins of the Bahamas, West Indies, and Greater and Lesser Antilles (including Barbados and Trinidad/Tobago), and (4) *East Coast of South America (south of the Caribbean)*—the area south and east of Trinidad and Tobago.

Sources of data and treatment

We searched the published and unpublished literature to extract records reported as common dolphins (any listed as *Delphinus delphis*, *Delphinus capensis*, or *Delphinus* sp.) from the study area. We also contacted colleagues working in the area and made an extensive search for unpublished datasets that might contain records of interest. Records examined included sightings, strandings, fisheries by-catches, and direct captures (for scientific research or live display). A summary of the dataset is shown in Table 1, and a detailed database table is available from the authors. The term 'common dolphin' in the older literature often appears to refer to any dolphin species with a long beak, further complicating the assessment of its occurrence (particularly true for the Caribbean). We did not accept taxonomic

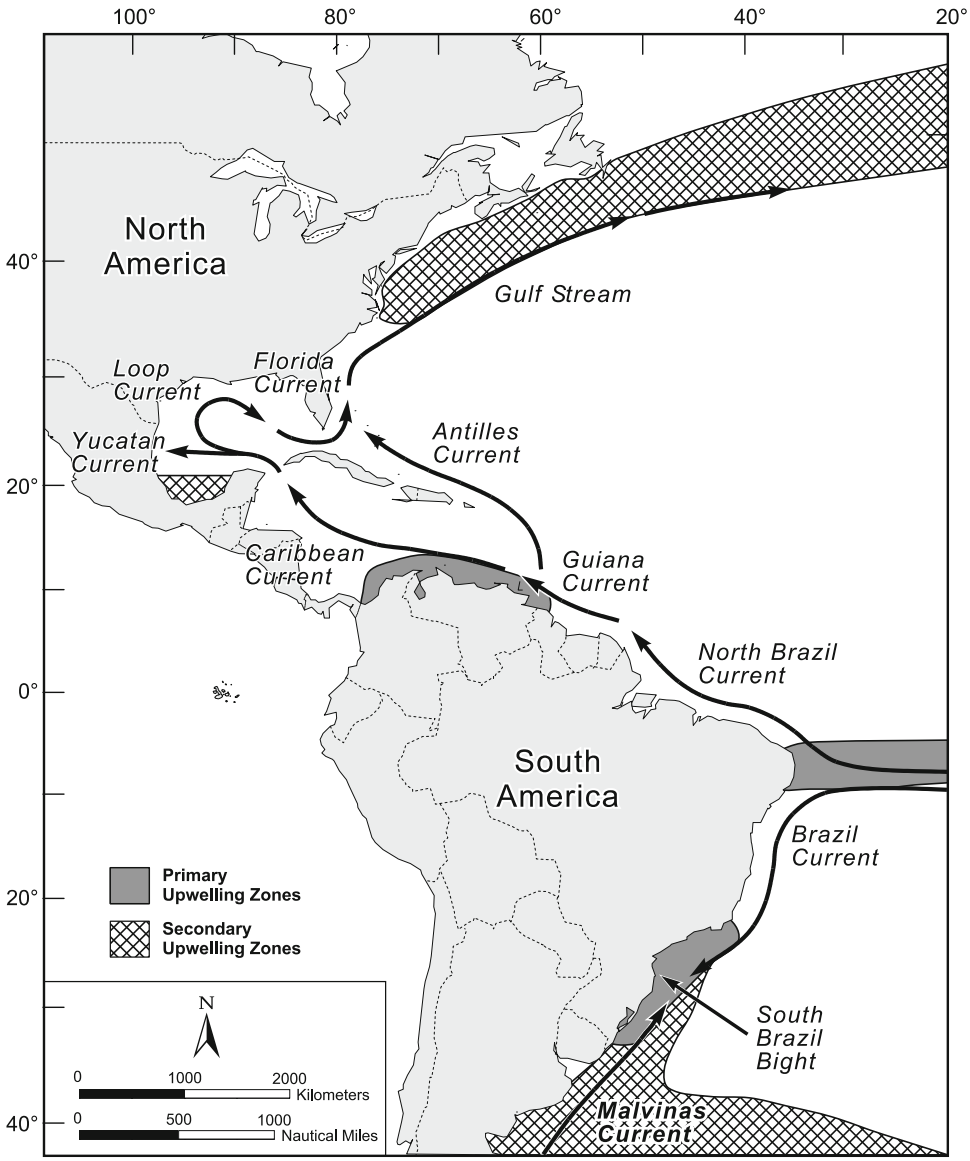

Fig. 1 Map of the study area, showing oceanographic features of relevance (major currents and upwelling zones)

identifications at face value, but each record was scrutinized for information that would lead to confirmation of genus and species identification. This could come from one or more of several sources: (1) photos or video documentation showing diagnostic characters (2) voucher specimens [generally a skull or genetic sample] that confirmed identification (3) sufficiently-detailed drawings of observed animals that showed diagnostic characters, leaving no doubt as to the identification, or (4) observations made by marine mammal scientists known to us to be intimately familiar with the diagnostic characters of common dolphins and those of very similar-appearing species such as *Stenella* spp., especially the Clymene dolphin (*S. clymene*) and spinner dolphin (*S. longirostris*). In particular, before the redescription of *S. clymene* in 1981 (Perrin et al. 1981), there was often confusion of common dolphins with these animals (see Fertl et al. 2003).

All reported records of *Delphinus* spp. with a 'plottable' locality (i.e., those that could be plotted within a few tens of kilometers) were entered into a GIS database, along with information on date, location, source, water depth, school size, etc. The identification of each record was evaluated, and coded with one of four confirmation codes:

(1) *Confirmed* Records that were taken to be virtually certain as *Delphinus*, due to reported diagnostic characters or validation by experienced scientists (see above).
(2) *Accepted* Records that could not be confirmed as *Delphinus*, but were nonetheless accepted as likely accurate, due to their proximity to confirmed records and acceptance by other marine mammal biologists.
(3) *Rejected* Records lacking availability of diagnostic characters and that were of doubtful accuracy, due to

Table 1 Summary of plottable records compiled for this study

Status	Record type	Geographic area			
		SE US Coast	Gulf of Mexico	Caribbean Sea	South America
Confirmed	Sightings	3	–	85	52
	Strandings	22	–	8	81
	Captures	5	–	11	17
	Unknown	5	–	4	1
Accepted	Sightings	50	–	1	1
	Strandings	–	–	–	14
	Captures	–	–	1	3
	Unknown	–	–	–	–
Rejected	Sightings	16	22	17	33
	Strandings	–	–	1	–
	Captures	–	–	1	–
	Unknown	–	–	–	–
Mis-identified	Sightings	–	2	–	–
	Strandings	1	2	–	–
	Captures	–	1	–	–
	Unknown	–	–	–	–
Total		102	27	129	202

conflict with known characteristics of *Delphinus*, or lack of acceptance by experienced scientists.

(4) *Misidentified* Records that were clearly not *Delphinus*, due to the availability of diagnostic characters indicating they were of another species—these were corrected in the database.

We then plotted the records (Fig. 2). Polygons were drawn around the records for each species of *Delphinus* (*D. delphis* and *D. capensis*), based on both the locations of the actual records and known habitat preferences of that species. Although we are aware that long-beaked populations in the Atlantic Ocean may later be assigned to another species, we tentatively refer to them as *D. capensis* in this paper. They were identified as such by the presence of longer beaks, 'flatter' melons, and duller and more-indistinct color patterns than are typical of *D. delphis* (see Jefferson et al. 2008).

The only exception to the above-mentioned approach was for the US and Canadian area north of Cape Hatteras, North Carolina (35°N), where the above approach was deemed infeasible. In this area, there are literally thousands of common dolphin records from many different sources, and the patterns of distribution are relatively clear and well-described. For this area, therefore, we simply reviewed existing literature to identify patterns for the reader. Literature reviewed included published reports (e.g., Sergeant and Fisher 1957; Sergeant 1958; Caldwell and Golley 1965; Caldwell et al. 1971a; Mercer 1973; Selzer and Payne 1988; Gaskin 1992; Gowans and Whitehead 1995; Lucas and Hooker 2000; Waring et al. 2007; Westgate 2007; Westgate and Read 2007), and unpublished gray literature and theses (CeTAP 1982; Waring et al. 1992, 2007; Westgate 2005).

Results

We compiled 460 plottable records reported as common dolphins from the study area, and 364 of these were considered valid (either confirmed or accepted). The records are summarized in Table 1 and mapped in Fig. 2.

East coast of the United States and Canada

There were 102 reported records of common dolphins in the area off the east coast of the United States and Canada south of 35°N (Fig. 2). Of these, 85 were either confirmed or accepted as *Delphinus*. The records were all fairly coastal and they fell into two groups. The vast majority were north of the Georgia/South Carolina border (32°), while there were eight records that were from somewhat further south – off Florida (between the area of St. Augustine and Miami Beach). All of the Atlantic Florida records were from the time period of 1950–1960.

Most of the confirmed records were recorded as *D. delphis* and it is well-documented that common dolphins off the US and Canadian east coasts are short-beaked animals (e.g., Sergeant and Fisher 1957; Sergeant 1958; Mercer 1973; Westgate 2007; Westgate and Read 2007). There is no reliable evidence for the long-beaked common dolphin

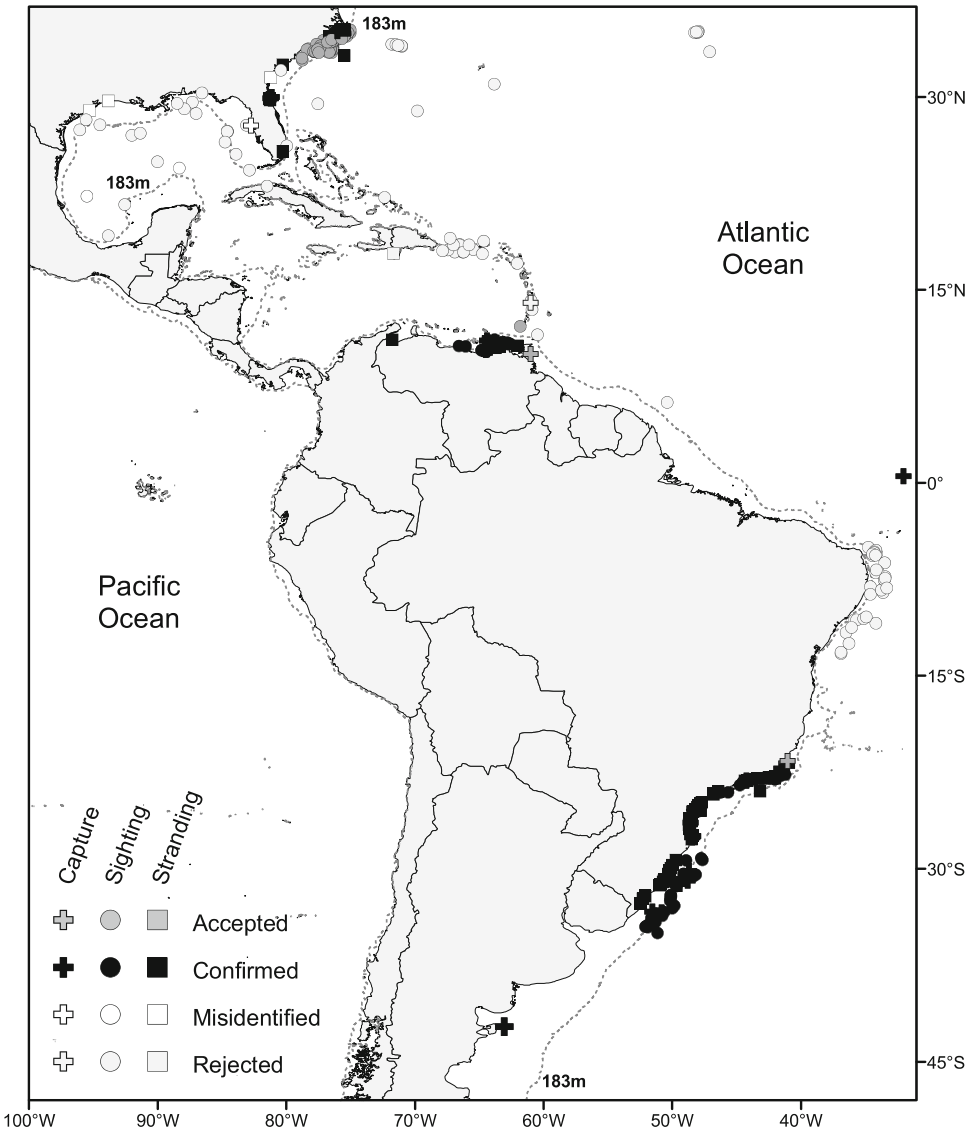

Fig. 2 Map of the study area south of 35°N, showing all *Delphinus* records compiled for this analysis. The valid (confirmed and accepted) records occur mostly in one of several specific areas, rather than throughout the warm waters of the Atlantic Ocean

anywhere in waters of the Atlantic coast of North America, and this species appears to be absent from these waters.

Gulf of Mexico

Of the 27 plottable reports of *Delphinus* from the Gulf of Mexico, five were clearly misidentified (two were known to be and two others suspected to be *S. clymene,* and one was *S. longirostris*). The rest are sightings not supported by reliable details and are rejected. There are no valid records of common dolphins in the Gulf of Mexico.

Caribbean Sea

There were 129 plottable reports of common dolphins from the Caribbean Sea and surrounding islands (Fig. 2). Most (110) were valid, but 19 of these were rejected due to absence of supporting details. Of the valid ones, all except three came from a distinct coastal area off the central/eastern coast of northern Venezuela between 61°50′ and 66°34′W. This is the Cariaco Basin, and it covers the area around Isla de Margarita, the Mochima National Park, Gulf of Cariaco, and Araya and Paria peninsulae. Three valid records were somewhat outside this area and may possibly represent unusual wanderings. These are records from the Gulf of Venezuela in the western part of the country, and from Trinidad.

All of the valid records were from over the continental shelf in relatively shallow water—the average depth was 68.6 m (range = 4–120 m—Fig. 3). The vast majority were documented to be long-beaked animals, and it is probable that the remainder also belong to the long-beaked form. There was no reliable evidence of short-beaked common dolphins in the Caribbean Basin.

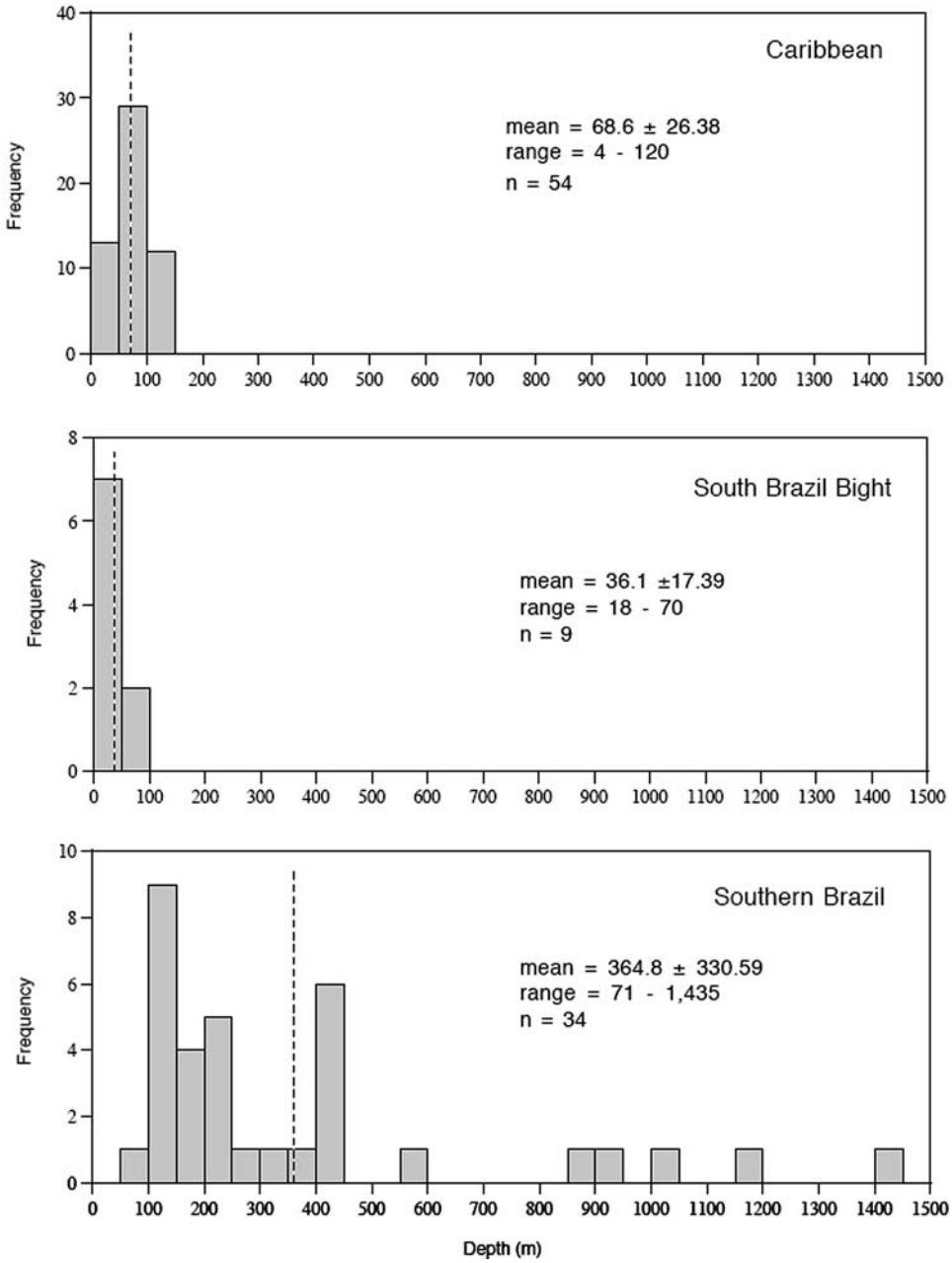

Fig. 3 Histogram of water depths for sightings of common dolphins in different parts of the study area

East coast of South America (south of the Caribbean)

There were 202 plottable reports of common dolphins from the area of South America southeast of the Caribbean Sea, and most were confirmed (151) or accepted (18—Fig. 2). All except one of the valid records were relatively coastal and fell between the latitudes of 21°37′S and 34°31′S, although 'unplottable' records from further south off Argentina are known—see Discussion. A single record from the nineteenth century occurred in offshore waters of the tropical Atlantic (see Discussion).

A wide range of water depths was represented by the records (18–1,435 m—Fig. 3). However, the depths fell into two groups. Records from the South Brazil Bight (north of 26°S) were from shallower waters over the continental shelf (18–70 m), while those south of 26°S were from much deeper waters, mostly beyond the shelf break (71–1,435 m). Both long-beaked and short-beaked records are represented, and the long-beaked records cluster in the area of the South Brazil Bight (mostly between 22° and 26°S). It appears that there is a coastal long-beaked population in the South Brazil Bight, and one or more short-beaked populations that range further south and offshore.

Discussion

East coast of the United States and Canada

The Gulf Stream (the western boundary current of the North Atlantic subtropical gyre) is the dominant oceanographic feature of the western North Atlantic Ocean. It is formed as warm water from the Gulf of Mexico moves northward (as the Florida Current), past Cape Hatteras (35°N) and up along the eastern seaboard of the United States and Canada. It extends offshore further north, although there are seasonal shifts in its location. This is a major northward vector of warm, salty, subtropical waters, and it results in significant warming of the northern portions of the North Atlantic. Once it reaches the Grand Banks, off Newfoundland, the Gulf Stream branches into several fronts as it continues east (its warming influence even extending to Europe). There is a fairly strong and extensive region of upwelling along the US and Canadian east coasts, north of Cape Fear (Xie and Hsieh 1995). This upwelling zone extends offshore further to the north, and it contributes to some of the world's most productive fishing grounds along the banks offshore of the northeastern US and Canada. The continental shelf is relatively broad along much of the eastern seaboard.

We found common dolphins to be present only in the cooler waters off the North American east coast, although past records indicated a slightly more southerly distribution previous to the early 1960s (Fig. 2). Most older (e.g., Watson 1981; Gaskin 1992; Jefferson et al. 1993; Amaha 1994; Carwardine 1995) and some recent (Kinze 2001; Kiefner 2002; Shirihai 2006) overviews of common dolphin distribution showed a much more extensive range in offshore and tropical/subtropical waters than we found to be the case in this paper. Evans (1994), however, appeared to recognize this limited distribution, as did several more recent reviews (e.g., Perrin 2002; Reeves et al. 2002; Jefferson et al. 2008).

Off the east coast of North America, short-beaked common dolphins are known to range between the 200 and 2,000 m depth contours from at least Cape Hatteras north to about 47–50°N off the Canadian coast (Gaskin 1992; Waring et al. 2007; Fig. 4). While the range may have extended further south in the middle of the last century (see discussion below), it appears that common dolphins do not occur with any regularity south of South Carolina at present.

North of Cape Hatteras, *D. delphis* are commonly seen on marine mammal shipboard and aerial surveys (CeTAP 1982; Selzer and Payne 1988; Hain et al. 1985; Kenney and Winn 1986; Waring et al. 1992; Palka 2006), whalewatching trips (Katona et al. 1983), and are also frequently taken in fisheries (Waring et al. 1990). They have not, however, often been seen on surveys that occurred primarily south of Cape Hatteras (see Mullin and Fulling 2003). The sightings that do exist from south of the Cape were made from aircraft, and the difficulty of distinguishing similar species of dolphins is increased when sightings are made from the air.

From January to May, common dolphins regularly range north only to about Georges Bank (ca. 42°N) and are found in Oceanographer, Hydrographer, Block, and Hudson canyons (Waring et al. 1992, 2007). They shift northwards onto the Scotian Shelf and over prominent bottom escarpments (such as the Flemish Cap) from summer to autumn months when water temperatures reach >11°C (CeTAP 1982; Selzer and Payne 1988; Gowans and Whitehead 1995). Common dolphins are occasionally found in the Gulf of Maine during this time of year, but appear to be extremely rare in the Bay of Fundy (Waring et al. 2007). Peak abundance of common dolphins in the southern Gulf of Maine and over Georges Bank appears to coincide, at different times of year, with peak abundances of mackerel (*Scomber scombrus*), butterfish (*Peprilus triacanthus*), and common squids (*Illex illecebrosus* and *Loligo peali*—Selzer and Payne 1988).

Delphinus are common in late summer and autumn months in slope waters of Nova Scotia and southern Newfoundland (Sergeant and Fisher 1957; Sergeant 1958). Common dolphins are frequently seen at this time of year in and near the "Gully", a prominent submarine canyon off Nova Scotia. Gowans and Whitehead (1995) recorded 83 summer sightings there between 1988 and 1994 in water depths from 60 to 2,500 m and water temperatures of 10.5–22.8°C. There have also been several strandings and sightings reported at Sable Island, just to the west of the Gully (Mercer 1973; Lucas and Hooker 2000).

Common dolphins do not normally enter the Gulf of St. Lawrence (Kingsley and Reeves 1998), and are not generally found in waters of Quebec or Labrador (see Alling and Whitehead 1987). Other than the above-described occurrence off Nova Scotia and southern Newfoundland, the species is considered to be an occasional visitor to eastern Canada (Gaskin 1992). In the central Atlantic, there is no evidence that they reach as far north as Greenland (Kapel 1975; Heide-Jørgensen and Leatherwood 1987; Heide-Jørgensen 1990). A reference in Read (1994) as to such apparently refers to bycatches further south off Canada.

The apparent change in distribution of common dolphins in the southeastern United States in the latter half of the 20th century is interesting and deserves some discussion. There are older reports of common dolphins in Florida as far south as Miami (e.g., McBride and Kritzler 1951; Caldwell and Golley 1965; Moore 1953; Layne 1965). Although some of these may have been misidentifications, the photos in Moore (1953) of a captive specimen captured off St. Augustine, leave no doubt as to the identity of that

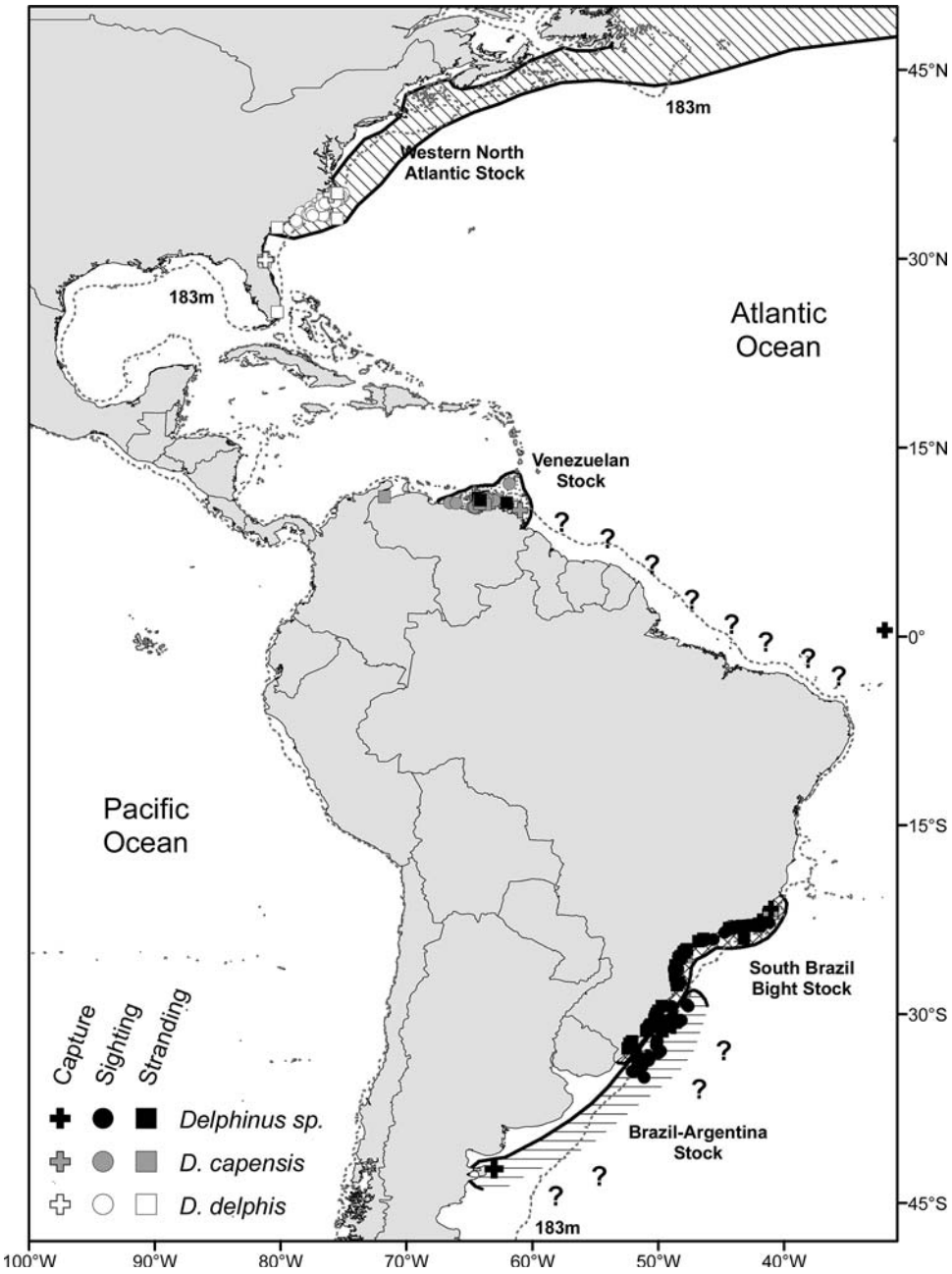

Fig. 4 Map of the entire western Atlantic area, showing all confirmed and accepted *Delphinus* records. Also shown are the boundaries of the four putative stocks of common dolphins. *Question marks* refer to uncertain range limits

specimen as *D. delphis*, as do photos in Essapian (1954, 1962). Common dolphins were regularly observed and captured off the northeastern Florida coast (within 20 km) near St. Augustine during the early 1950s for captive display (Moore 1953; Essapian 1954; Layne 1965). Cumbba (1980) also mentioned *D. delphis* remains in archaeological sites from Dade County (although these cannot be confirmed as *Delphinus*). For unknown reasons, however, *Delphinus* have been conspicuously absent from this region since the early 1960s (Caldwell et al. 1971a; Caldwell and Caldwell 1978; Leatherwood et al. 1976). The last known sightings and strandings were in 1958 and 1960, respectively (Caldwell and Caldwell 1974, 1978). Jefferson and Schiro (1997) speculated that this may have been a result of population or distributional fluctuations, rather than of extirpation by human influences. The specific oceanographic conditions that may have caused this remain unconfirmed, but it is known that SSTs along the east coast of the United States decreased rapidly between 1950 and the mid-1960s, and have slowly increased since then (Friedland and Hare 2007; Hobson et al. 2008). Moore (1953) stated that common dolphins moved out of Florida waters seasonally, once *Stenella* spp. showed up, and it is possible that warmer temperatures in this area have resulted in the long-term displacement of *Delphinus* by *Stenella*. The avoidance of Florida waters during a period of increasing water temperature

is consistent with the apparent preference of these animals for cold-modified waters and their avoidance of truly tropical waters. We expect that it is a prey-availability issue, rather than surface water temperature itself, that is responsible for this. If this explanation is correct, then one might expect common dolphins to return to Florida waters in the future, if surface waters ever cool.

Gulf of Mexico

The Gulf of Mexico is fed from the south by tropical water coming through the Yucatan Channel (Yucatan Current), which then forms a clockwise loop in the central Gulf (although it is highly-variable in position), referred to as the Loop Current. Periodically, rings of warm water pinch-off from the Loop Current and move westwards in the Gulf before dying-out (Biggs and Müller-Karger 1994). The Loop Current moves through the Straits of Florida (as the Florida Current) and becomes the major source of the northward-flowing Gulf Stream. The only significant upwelling in the Gulf of Mexico is in the southern portion, in the Gulf of Campeche, but this is not particularly strong (Xie and Hsieh 1995). It is persistent throughout the year on the Campeche Bank, however (Zavala-Hidalgo et al. 2006)). The Gulf of Mexico is characterized by a broad continental shelf, except for the southwestern portion near Veracruz.

Like many other recent treatments, we found convincing evidence that common dolphins do not occur in the Gulf of Mexico (e.g., Jefferson and Schiro 1997; Perrin 2002; Reeves et al. 2002; Shirihai 2006; Jefferson et al. 2008). While these recent overviews reflected this, most literature published before 1997 showed an extensive distribution throughout the entire Gulf (e.g., Watson 1981; Gaskin 1992; Jefferson et al. 1993; Amaha 1994; Carwardine 1995). This is understandable, but more surprising is that several reviews continued to show common dolphins in the Gulf of Mexico even after Jefferson and Schiro's (1997) findings suggesting that common dolphins do not occur in the Gulf became available (Kinze 2001; Kiefner 2002). Evans (1994) recognized the uncertainty and showed a questionable range in the Gulf of Mexico for this genus.

While there are several specific reports of *Delphinus* spp. in the northern Gulf of Mexico (e.g., Caldwell 1955; Springer 1967; Caldwell and Caldwell 1973; Lowery 1974; Schmidly and Shane 1978; Schmidly 1981; Fritts and Reynolds 1981; Dorf 1982; Esher et al. 1992) and also in the Mexican and Cuban portions of the Gulf (Cuní 1918; Ortega-Ortiz 2002), there is no reliable evidence that common dolphins of either species actually occur there. In fact all reports of *Delphinus* in the Gulf are either clearly misidentifications or are at best highly unreliable (see Evans 1994). Jefferson (1995) and Jefferson and Schiro (1997) thoroughly refuted all specific reports of common dolphins in the northern Gulf of Mexico and most were reassigned as either Clymene or spinner dolphins.

Since the early 1990s, extensive aerial and shipboard surveys have covered nearly all of the waters of the northern Gulf of Mexico with highly-trained and experienced marine mammal observers. No common dolphins have ever been observed on these surveys (Mullin et al. 1991, 1994, 2004; Davis et al. 1998, 2002; Mullin and Hansen 1999; Fulling et al. 2003; Mullin and Fulling 2004). Although the southern Gulf of Mexico (Mexican waters) has been very poorly studied in comparison, no information supporting common dolphins anywhere in the Gulf has come to light since Jefferson and Schiro's (1997) assessment. Ortega-Ortiz (2002) found no confirmed records there, and two previous reports of *D. delphis* were thought to be misidentifications of Clymene dolphins. Therefore, with the exception of a possible straggler from the US east coast, we consider common dolphins to be completely absent from the Gulf of Mexico.

Caribbean Sea

The northwestward-flowing Caribbean Current transports water through the central Caribbean Sea and northward through the Yucatan Channel into the southern Gulf of Mexico. Some of the northward flow from further south diverts around the Caribbean basin and flows north as the Antilles Current, where it forms a source of water for the Gulf Stream. Significant upwelling in the Caribbean is limited to a coastal band along the north coast of South America (from Surinam to Colombia, and centered in the Cariaco Basin of Venezuela—Xie and Hsieh 1995). This upwelling is particularly strong in the months of October through May, and results in high productivity in the Cariaco Basin (Díaz-Ramos et al. 2000; Muller-Karger et al. 2001). Virtually the entire Caribbean basin is surrounded by a relatively narrow continental shelf, and very deep waters lie just offshore of most of the islands of the Greater and Lesser Antilles.

Apparently, common dolphins are absent throughout most of the Caribbean Sea, only occurring in a very limited coastal area off Venezuela, and possibly adjacent waters (Fig. 2). While some recent overviews have correctly shown such a pattern (e.g., Perrin 2002; Reeves et al. 2002; Bastida et al. 2007; Jefferson et al. 2008), most older and some recent literature instead showed an extensive range throughout most or all of the Caribbean basin (e.g., Watson 1981; Gaskin 1992; Jefferson et al. 1993; Amaha 1994; Evans 1994; Carwardine 1995; Kiefner 2002; Shirihai 2006). This misconception is based largely on uncritical acceptance of reported records, many of which were in fact probably *S. clymene* or other species of the genus *Stenella*.

True (1889) reported on two skulls of *Delphinus* from the Bahamas and Jamaica (MCZ 574a, 574b), but these records have been rejected. Several more recent sighting reports of *Delphinus* have been reported throughout the West Indies and the Greater and Lesser Antilles of the eastern and central Caribbean Sea (e.g., Watkins and Moore 1982; Watkins et al. 1985; Mignucci-Giannoni 1989). However, due to the absence of confirmed specimen records for the genus, any *Delphinus* sightings without photographic or other documentation in this region should be considered questionable at best (see Roden and Mullin 2000). Because none of the above records is supported by photos, video, or voucher specimens, and they were either made by non-experts or were made before the widespread recognition of the similar-appearing Clymene dolphin (see Fertl et al. 2003), we have rejected all these records.

Periodic investigations by marine mammal biologists of the small cetacean fisheries of the West Indies (mainly occurring from St. Vincent and St. Lucia) have documented most of the tropical species of long-beaked dolphins known from the Atlantic, but have not reported catches of common dolphins (Caldwell and Caldwell 1971, 1975; Caldwell et al. 1971b; Caldwell 1972; Gaskin and Smith 1977; Reeves 1988).

Since the mid-1990s, there have been several extensive surveys of the Caribbean, with highly-trained and experienced marine mammal observers (Jefferson and Lynn 1994; Swartz and Burks 2000; Swartz et al. 2001, 2002; Roden and Mullin 2000). No common dolphins have been observed on these surveys in the Caribbean, except for those seen in the area around Isla de Margarita off northeastern Venezuela. Vidal et al. (1994) listed the 'common dolphin' as a species 'suspected' to be captured in gillnet fisheries in Honduras, but there is apparently no specific evidence for its occurrence there. Recent surveys throughout the islands of the eastern Caribbean have not reported any sightings of common dolphins (Boisseau et al. 2006; Gero and Whitehead 2006; Jérémie et al. 2006; Rinaldi et al. 2006; Whaley et al. 2006). The same is true for recent detailed work on cetaceans in the Bahamas (Claridge and Balcomb 1993; Herzing et al. 2003; MacLeod et al. 2004; Mobley 2004).

There is a very well-documented population of long-beaked common dolphins off central-eastern Venezuela, inhabiting the waters around Isla de Margarita, the Mochima National Park, Gulf of Cariaco, and the northern coasts of the Araya and Paria peninsulae (Naveira 1996; Romero et al. 2001; Oviedo and Silva 2005; Bolaños-Jiménez et al. 2006—Fig. 2). The westernmost record is from the Gulf of Venezuela (71°47′W), near the border with Colombia (Ramírez Carros and González-Fernández 2004). This may be an extralimital record, however, as extensive work on cetaceans in the Leeward Dutch Antilles has not turned up any evidence of *Delphinus* (Barros and Debrot 2006). Recent surveys in Colombian waters of the Caribbean have not resulted in any sightings of common dolphins in that country (Palacios et al. 1995), and all this suggests that the distribution of the long-beaked common dolphin probably does not extend west of Venezuela. Romero et al. (2002) reported second-hand reports of *D. capensis* in Grenada, but these are rejected due to the lack of supporting details. The only reliable records to the east outside of Venezuela are of a long-beaked common dolphin captured off Trinidad in April 2006 (Boisseau et al. 2006) and a stranding in the Gulf of Paria (Bolanos-Jiménez, unpubl. data), and these may represent the eastern extent of this population's range.

All records of common dolphins in this area are either known or suspected to be of the long-beaked species (*D. capensis*); there is no reliable evidence that the short-beaked common dolphin occurs anywhere in the Caribbean region (see Van Waerebeek in International Whaling Commission (IWC) 2007).

East coast of South America (south of the Caribbean)

The Southwest Atlantic is dominated by the strong, relatively fresh, cold water of the northward-flowing Malvinas Current and the warm water of the weak, southward-flowing Brazil Current (the western boundary current of the South Atlantic subtropical gyre), which mix in a region called the Brazil-Malvinas Confluence (or Subtropical Convergence). There is a moderately-strong region of upwelling in the South Brazil Bight (centered just south of Rio de Janiero—Xie and Hsieh 1995). This is a coastal zone of upwelling, but it does extend some distance offshore and beyond the edge of the continental shelf. It results in cold, nutrient-rich waters that make for very productive fishing grounds (Borzone et al. 1999), and these cold, rich waters are pumped over the continental shelf by cyclonic meanders (Campos et al. 2000). Another current branch, the North Brazil Current, brings warm, relatively-fresh (from the outflow of the Amazon River) water northwards along northern Brazil, French Guiana, and Surinam. The North Brazil Current feeds into the Guiana Current, which is a major source of water for the Caribbean Sea. The continental shelf is relatively narrow along much of the South American coast, only widening in the areas off the mouth of the Amazon River and south of Uruguay.

Common dolphins apparently only occur in the cooler waters of the Southwest Atlantic, south of about 20°S (Fig. 2). While this limited range was recognized by Bastida et al. (2007) and correctly portrayed by Gaskin (1992), most other literature has shown a much more extensive pattern extending far into tropical and subtropical waters (e.g., Watson 1981; Jefferson et al. 1993; Amaha

1994; Evans 1994; Carwardine 1995; Perrin 2002; Kiefner 2002; Reeves et al. 2002; Shirihai 2006; Jefferson et al. 2008). Specific records of common dolphins are largely lacking from these warmer waters, but until Tavares (2006) and International Whaling Commission (IWC) (2007) clarified the situation off Brazil, others apparently perpetuated the misconception based on assumptions that *Delphinus* is a tropical dolphin. As we detail below, we believe this assumption is incorrect or at best, weak.

A single confirmed published record of *Delphinus* (a skull collected from a specimen taken by Lütken 1889) occurs in offshore tropical Atlantic waters. Although the skull (Zoological Museum, University of Copenhagen CN 7x) was confirmed to be *Delphinus* from photos provided by C. Kinze, for several reasons this record may not be an accurate indication of present-day occurrence of common dolphins. The distribution may have changed dramatically in the 120 years since collection. However, recently several unpublished sightings of common dolphins have been reported off northern Brazil, near the equator, and if these sightings are accurate they may indicate a more equatorial population of *Delphinus* off South America (Silva et al. 2008).

Common dolphins have been reported to occur in coastal waters off the east coast of South America, from Brazil to Argentina, including Uruguay (Ximénez et al. 1972; Casinos 1984; Castello and Pinedo 1986; Agudo and Romero 1996). There are a number of definite or probable misidentifications of common dolphins from this area. For instance, Best et al. (1986) reported 30 sightings of common dolphins off northeastern Brazil during a marine mammal survey in the 1980s. However, when the same area was surveyed from 1998 to 2001, no common dolphins were sighted and Clymene dolphins were frequently seen (da Rocha et al. 1999; Moreno 2002). Based on this, Fertl et al. (2003) suggested that the Best et al. sightings were probably Clymene dolphins, and therefore we reject them as common dolphin sightings in this paper.

Existing biological data led Zerbini et al. (2004) to hypothesize that both long-beaked and short-beaked common dolphins occurred off Brazil. Recently, Tavares (2006) reviewed all available records of common dolphins for the Brazilian coast. He found all valid records to be south of 22°S, as we did in this paper. Records from this area indicated the existence of two groups: one inhabiting nearshore, shallow waters associated with the South Brazil Bight and another occurring further south (latitudes higher than 26°S) in offshore and deeper waters (Zerbini et al. 2004, Tavares 2006). Tavares (2006) suggested that the southern group was associated with the Subtropical Convergence, but declined to call these two groups different species. Our data, although including additional records from south of Brazil, shows a nearly identical pattern to that of Zerbini et al. (2004) and Tavares (2006). We concur with their basic findings on distribution, and share the caution about the potential for the presence of two species of common dolphins in these waters. Although we have tentatively placed long-beaked and short-beaked specimens into the *capensis* and *delphis* groups for this analysis, we agree that further work using morphology and genetics will be necessary to determine the relationships of these two groups of animals.

Records are more sparse further south of Brazil. Recently, Goodall et al. (2004) reported on a specimen of *D. capensis* from the "northeast coast of Tierra del Fuego"—this is far south of any other record of the genus, and Goodall et al. considered this specimen to be an extralimital record. The southernmost part of the normal range appears to be Golfo San Matias, Argentina (ca. 42°S) (Capozzo and Junin 1991) and common dolphins are frequently caught in trawls there (Crespo et al. 2000). They have also have been reported to occur off northern Patagonia, Argentina (Berón-Vera et al. 2007; Romero et al. 2008). Although tooth counts and skull measurements presented in Casinos (1984) would seem to align them more closely with *D. capensis* than *D. delphis*, specimens from southern Brazil, Uruguay, and Argentina have yet to be confirmed to species. It is by no means certain that these animals are part of the same population as those in the South Brazil Bight, and only future research will resolve this question.

Overview

Our critical review of common dolphin records and analysis of distribution in the western Atlantic Ocean shows some very distinct patterns. Common dolphins are not widespread tropical/subtropical animals, as so much of the literature indicates, but in fact appear to be found in only a few, restricted regions of this part of the world. These are largely cool temperate regions, and the only 'tropical' areas of known occurrence are two regions of strong coastal upwelling, with correspondingly low surface temperatures off Venezuela and off the South Brazil Bight (see Xie and Hsieh 1995; Díaz-Ramos et al. 2000; Muller-Karger et al. 2001). In fact, common dolphins may be absent from almost all of the tropical and subtropical zones of the western Atlantic. It should be cautioned that there has been relatively little cetacean survey work done in this part of the world, but virtually all 'common dolphin' records from the area so far located have turned out to be misidentifications or were otherwise rejected, due to absence of supporting data for the identifications. The very similar-appearing Clymene dolphin is responsible for much of this confusion (see Fertl et al. 2003). There has been a better effort to collect stranding data along the northern Brazilian coast, but

no common dolphin strandings have been identified there, although there are some indications of possible sightings from this area (Silva et al. 2008).

All of the areas where we found evidence of common dolphin populations are characterized by relatively low surface temperatures and at least seasonal upwelling. The Clymene dolphin, on the other hand, appears to be a truly tropical/subtropical animal, and is frequently found in deepwater areas of warm, low-productivity water, such as the northern Gulf of Mexico (Fertl et al. 2003). While there is a great deal of overlap in overall range, these two species would appear to have somewhat complimentary patterns of habitat preference, much like the case with spotted/spinner and common/striped dolphins in the eastern tropical Pacific (Au and Perryman 1985).

The idea of a single species of common dolphin, found more-or-less continuously throughout all the tropical and temperate waters of the world was clearly an overly-simplistic scenario. With regard to biogeography, our ideas have also evolved in recent years. In the Indian Ocean, the previous view of a widespread distribution in both coastal and offshore waters has been replaced by the knowledge that, while the long-beaked (*tropicalis*-form) common dolphin occurs widely along continental margins, common dolphins appear to be absent from much of the oceanic Indian Ocean and around offshore island groups (see Jefferson and Van Waerebeek 2002).

In the Pacific Ocean, the short-beaked common dolphin appears to have an extensive distribution that includes some oceanic waters of at least the eastern tropical Pacific and much of the central North Pacific (Au and Perryman 1985; Heyning and Perrin 1994; Ferrero and Walker 1995; Jefferson et al. 2008). However, the long-beaked species (*D. capensis*) is apparently limited to a few restricted nearshore continental shelf areas (i.e., around Baja California, Mexico and central/southern California; off Peru; and in Asian waters of southern Japan, Korea, and southern China—Amaha 1994; Heyning and Perrin 1994).

A similar pattern is emerging in the Atlantic Ocean. As this paper has clearly demonstrated, the long-beaked common dolphin (whether eventually shown to be *D. capensis* or another species) has a very restricted range in the western Atlantic (over the continental shelf off Venezuela and in the South Brazil Bight). Interestingly, the occupied area off Venezuela is the one area where coastal upwelling is known to occur in the Caribbean Sea (Longhurst and Pauly 1987), and the species does not occur at all in the North American portion of the North Atlantic. The short-beaked common dolphin has a more wide-ranging occurrence off the east coasts of North America and South America, but apparently is not present in the tropical regions of the Gulf of Mexico and Caribbean Sea (and probably not in equatorial Atlantic waters).

Thus common dolphins may be more accurately characterized as antitropical species (in the sense of Davies 1963). The few places in which common dolphins occur in tropical zones (e.g., off Venezuela and over the Costa Rica Dome in the eastern tropical Pacific) may be anomalies, made possible by unusually cold, productive waters due to strong upwelling cells.

Taking all the information from this review and from the literature into account, it appears that there are at least four separate stocks of common dolphins in the western Atlantic Ocean (Fig. 4):

(1) *Western North Atlantic stock* This is a large population of *D. delphis* that occurs along the east coast of the United States and Canada, numbering approximately 120,743 (CVs = 0.24–0.54) individuals (Waring et al. 2007). Although bycatch in trawls, gillnets, and longlines has been documented, the population trend and status of the stock are unknown (Waring et al. 2007).

(2) *Venezuelan stock* This is an isolated, coastal population of *D. capensis* that occurs over the continental shelf in central/northeastern Venezuela. Its abundance is unknown, but its status is of concern due to past hunting pressure (Romero et al. 1997, 2001), bycatch (Naveira 1996; Bermudez-Villapol and Sayegh 2005), and unregulated dolphinwatching (Bolaños-Jiménez et al. 2007).

(3) *South Brazil Bight stock* This is a population of *D. capensis* that occurs mostly over the continental shelf in the South Brazil Bight and possibly in surrounding waters. The population size is unknown, but based on the size of the habitat it is not expected to be large. This population may be at risk because of bycatch (Siciliano 1994; Di Beneditto et al. 2001).

(4) *Brazil-Argentina stock* This is a population of *D. delphis* that occurs from southern Brazil (probably mostly south of 30°S) to northern Argentina. It is possible that this population ranges far offshore and it may even extend across the South Atlantic to join with animals off West Africa. There are no estimates of abundance for common dolphins in this area, but the status of the stock is also of concern because of bycatch in a variety of fisheries (Bassoi et al. 1996; Zerbini and Kotas 1998; Crespo et al. 2000).

It is still unclear if short-beaked common dolphins in the North and South Atlantic range across the ocean basin to meet-up with populations on the eastern sides off Europe and West Africa, respectively. In fact, their distribution in offshore waters of the Atlantic Ocean, in general, is poorly-known and this is at least partly a result of the sparse marine mammal survey effort conducted in oceanic waters of this ocean basin (at least compared to the Pacific). We plan to conduct a similar review and analysis as the one for

this paper regarding the situation in the eastern Atlantic Ocean. We hope that the uncertainties and unknowns that we describe above will be clarified with further critical examination of common dolphins in the entire Atlantic Ocean.

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