

## REVIEW

## Global distribution of Risso's dolphin *Grampus griseus*: a review and critical evaluation

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### Keywords

biogeography, Delphinidae, ecology, habitat preference

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Submitted: 15 December 2012

Returned for revision: 1 March 2013

Revision accepted: 9 April 2013

Editor: KH

doi:10.1111/mam.12008

### ABSTRACT

1. The global range of Risso's dolphin *Grampus griseus* is not well known, and there has been confusion in the literature as to whether the species has a broad, circumglobal range or only occurs along continental margins.
2. To clarify the species' distribution and habitat preferences, we compiled and reviewed all available (published and unpublished) records of sightings and captures of this species for the past 62 years (1950–2012,  $n = 8068$  records). Stranding records were not included.
3. The results showed that the species has a range that extends across ocean basins and spans between at least 64°N and 46°S, and is apparently absent from high-latitude polar waters. Although Risso's dolphins occur in all habitats from coastal to oceanic, they show a strong range-wide preference for mid-temperate waters of the continental shelf and slope between 30° and 45° latitude.
4. Although a number of misconceptions about the distributional ecology of Risso's dolphin have existed, this analysis showed that it is a widespread species. It strongly favours temperate waters and prefers continental shelf and slope waters to oceanic depths. These habitat preferences appear to hold throughout much or all of the species' range.

### INTRODUCTION

Risso's dolphin *Grampus griseus* is a widespread species, and it is relatively conspicuous during marine mammal surveys (compared with some of the smaller delphinids, porpoises, beaked whales, and kogiid whales, which are often difficult to detect). The species is well-known from the major ocean basins (i.e. Atlantic, Pacific and Indian) of the world (Kruse et al. 1999, Baird 2009). Despite this, the details of the global distribution of Risso's dolphins are not well known,

and there appears to be some inconsistency in recent literature on the topic of the species' global range and habitat preferences. In what appears to be the only recent attempt to plot all known records of the species worldwide, Kruse et al. (1999) showed a distribution that was largely restricted to continental margins, with the exception of a small number of records from a few oceanic regions in the Gulf of Alaska, eastern tropical Pacific, Indian Ocean, and between Australia and New Zealand. Their map shows an apparent absence of the species in several coastal regions in

### Glossary of Oceanographic Terms Used

- **Continental shelf:** the extended perimeter of each continent and associated coastal plain, with waters generally less than 180–200 m deep.
- **Continental slope:** the sloping region offshore of the continental shelf, extending out to the beginning of the abyssal plain, with waters generally deeper than 180–200 m.
- **Continental margins:** those waters along the edges of continents, generally including both the continental shelf and slope.
- **Inshore waters:** waters inside enclosed bays, channels or inside of nearshore islands that are protected from oceanic swells and offshore winds. They are often shallow but can in some cases be very deep.
- **Oceanic waters:** waters of the deep, open sea generally beyond the continental margins.
- **Offshore waters:** waters in the open sea or along open coastlines that are exposed to oceanic swells and offshore winds. They are often deep but can be shallow in some regions.
- **Temperate:** waters that lie between the tropics and the polar regions. Seasonal changes in these regions are generally relatively moderate.
- **Tropical:** waters surrounding the Equator that are generally warm and seasonally stable. They are limited by the Tropic of Cancer (23°26'N) in the Northern Hemisphere and the Tropic of Capricorn (23°26'S) in the Southern Hemisphere.

the eastern and western Atlantic Ocean and in nearly all far-offshore, oceanic regions of the Pacific, southern Indian and Atlantic oceans (although they do mention that this may have been effort-related). The map of Kruse et al. (1999) has been cited extensively in the literature to support a range for this species that does not extend to most oceanic regions in the middle of ocean basins. Jefferson et al. (2008) recently followed this basic pattern in their range map but indicated possible occurrence in some additional continental margin areas. Culik (2004) and Taylor et al. (2008) also showed similar patterns of distribution in their range maps for the species.

Several other recent general references have shown a very different pattern, in which Risso's dolphin distribution covered virtually all coastal and oceanic regions of the world, from about 40/50°S to 50/60°N (e.g. Jefferson et al. 1993, Reeves et al. 2002, Shirihai & Jarrett 2006, Bastida et al. 2007, Amano 2009). Although these authors attempted to show the overall species' distribution, the range maps were not based on the plotting of actual records of occurrence, but rather were hypothesized from known patterns of

distribution and interpretations of the species' habitat preferences. Despite this, these maps are also commonly cited and have often been used as indicators of the distribution of the species in the scientific literature.

It remains unclear whether most of the regions of apparent absence in Kruse et al. (1999) are places where the species indeed does not occur, or are simply regions with a lack of appropriate search effort and/or reporting. Are Risso's dolphins really restricted primarily to continental and island archipelago margins? What are their normal northern and southern range limits in each ocean basin? Does the species normally occur in enclosed bodies of water, such as seas, gulfs and bays with narrow openings to the high seas? Is there broad-scale empirical evidence to support the oft-cited (e.g. Kruse et al. 1999, Jefferson et al. 2008, Baird 2009, Bearzi et al. 2011) statement that Risso's dolphins prefer continental slope and shelf edge habitat to other oceanographic regions? These questions remain largely unanswered or unsupported by sufficient evidence.

A considerable amount of information has been obtained on Risso's dolphin distribution as large-scale cetacean surveys began in many areas in the 1970s and appears in scattered literature, some published and some unpublished. There has apparently been no attempt to plot records of occurrence worldwide since Kruse et al. (1999). We aim to clarify the contemporary global distribution of Risso's dolphin, based on verified at-sea sightings and captures (strandings are not used) of the species worldwide. Specifically, we investigate: (i) the global distribution and range limits of normal occurrence; and (ii) distribution related to physiography (shelf, slope and oceanic).

## METHODS

In order to evaluate all contemporary data on the distribution of the species, we searched the published and unpublished literature to extract records reported as Risso's dolphins (or listed as *Grampus* sp.) from throughout the world's oceans and seas for the last 62 years (1950–2012). A total of 467 references (including published literature, as well as unpublished 'grey' reports) were compiled that contained information on Risso's dolphin distribution, and information was extracted from them (the list is available from the senior author). In some cases, authors were contacted for clarification of information. We also contacted colleagues working in areas where published literature is sparse and made an extensive search for unpublished data sets that might contain records of interest. Risso's dolphins are relatively easy to identify (see Jefferson et al. 2008), and thus we did not question taxonomic identifications that were supported by sufficient evidence to rule out other species, or were provided by colleagues known to us to

**Table 1.** Summary of the Risso's dolphin distribution database, including all records of Risso's dolphins from throughout the world's oceans and seas, in published and unpublished literature for the last 62 years (1950–2012)

Ocean basin	Survey effort	Sightings	Captures
Eastern North Pacific	High	1054	14
Western North Pacific	High	363	5
Eastern South Pacific	Moderate	138	0
Western South Pacific	Low	90	4
Eastern North Atlantic	High	3826	1
Western North Atlantic	High	1675	25
Eastern South Atlantic	Low	109	0
Western South Atlantic	Moderate/Low	8	0
Northern Indian Ocean	Moderate	512	9
Southern Indian Ocean	Low	234	1
TOTALS		8009	59

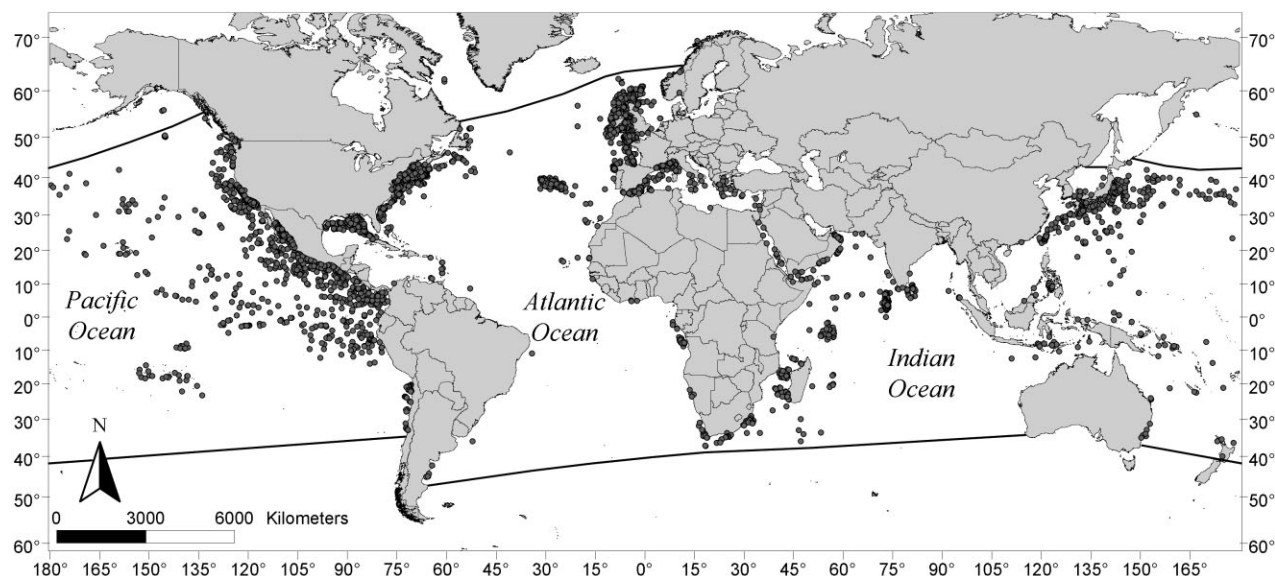
have extensive experience in marine mammal identification. The vast majority of records came from surveys of cetaceans conducted by experienced and/or trained observers. To verify species identifications in older literature, we scrutinized the literature in an attempt to ensure that identification errors were excluded. After verification, records were extracted and entered into a database that included at-sea sightings, fisheries incidental catches and direct captures (most for scientific research or live display). The OBIS/SEAMAP database (<http://seamap.env.duke.edu/species/180457>) was also checked for possible records that may have been missed during the compilation of data.

Strandings were not included because they may give an inaccurate picture of distribution. Although strandings in some cases have been found to be a useful indicator of species' presence and composition (Maldini et al. 2005, Pyenson 2010), they often represent unhealthy animals that may stray far from the actual site where the animal normally lived (see, e.g. Fraser 1949, Worthy et al. 1993, Chit et al. 2011). A summary of the data set ( $n = 8068$  records) is shown in Table 1, and a copy of the detailed database table is available from the authors (although some colleagues provided unpublished data with the agreement that they not be distributed, and thus these records will have to be removed).

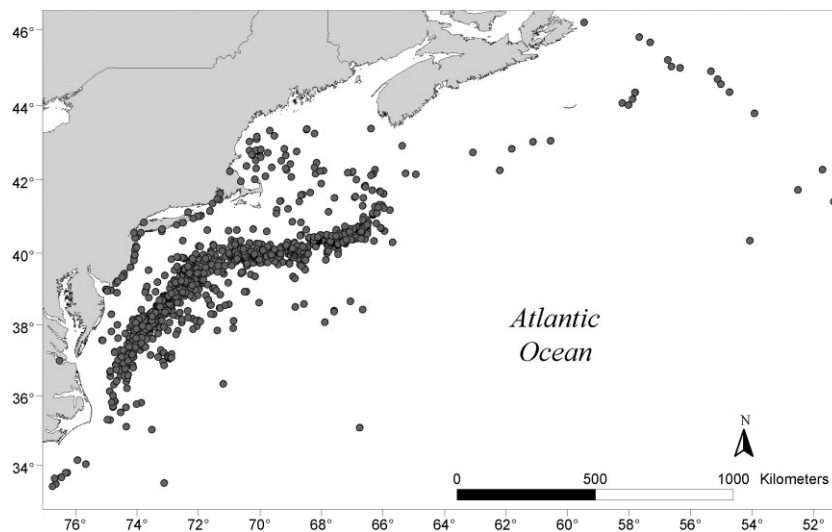
All available records of Risso's dolphin with 'plottable' localities (i.e. those that could be plotted within *c.* 5 km) were entered into a database, along with information on date, ocean basin, record type (sighting or capture), position, group size and reference or source. We then plotted the records since 1950 on maps to evaluate the contemporary distribution of the species. Records that occurred before 1950 were not plotted, as we considered them out-of-date and potentially giving an inaccurate picture of the present-day range of the species (we only considered them in light of potential historical changes in distribution).

## RESULTS

Available Risso's dolphin sighting and capture records, along with proposed range limits, are shown on a map of the world in Fig. 1.



**Fig. 1.** Map of the world, showing sighting and capture records of Risso's dolphins (1950–2012) and proposed range (inside black lines). Proposed range limits were based on the available records of occurrence and known species habitat preferences.



**Fig. 2.** Detail map of the western North Atlantic Ocean, showing sighting and capture records of Risso's dolphins (1950–2012).

### North Atlantic Ocean

In the western North Atlantic Ocean, Risso's dolphins occur from southern Newfoundland and Labrador, Canada ( $\sim 52^\circ$ ), southwards through the Gulf of Mexico and Caribbean Sea to the equator (Figs 1 and 2). There are two records off southern Baffin Island ( $\sim 62^\circ\text{N}$ ; J-F Gosselin, Fisheries and Oceans Canada, pers. comm.), which we consider likely to be extralimital, as they are located several hundred kilometres north of the other Canadian records. There is no evidence that this species penetrates into Hudson Strait or Hudson Bay. The only record indicating distribution in Greenland (Kruse et al. 1999, from Vibe 1950) appears to be in error, and there are no reliable data verifying an occurrence in Greenland waters (F. Ugarte, pers. comm.). The species appears to be uncommon in Venezuelan waters (Bermudez Villapol et al. 2008). Although there are virtually no available records south of Venezuela (for Guyana, Surinam or northern Brazil), we consider this likely to be effort-related, as this region has been very poorly studied in terms of marine mammal distribution (see Anonymous 2007). The absence of records from the southern Gulf of Mexico (Fig. 1) is also largely effort-related, as there has been virtually no marine mammal survey effort in deep waters there.

In the eastern Atlantic, records indicate a range throughout European waters, with current northern distributional limits at the Faroe Islands ( $\sim 62^\circ\text{N}$ ; Bloch et al. 2012) and central Norway ( $\sim 64^\circ\text{N}$ ; N. Øien, pers. comm.), and one verified record from northern Norway at  $\sim 69^\circ\text{N}$  (D. Zanoni, pers. comm.; Fig. 3). This latter record is much further north than the rest and is therefore probably extralimital. Records are numerous in some areas, for example north and west of the British Isles (Evans et al. 2003, Reid et al. 2003),

and around the Azores (Silva et al. 2003, Hartman et al. 2008); these locations correspond with areas of high cetacean survey effort. The records from the British Isles are very extensive, and Risso's dolphins are clearly common around the islands, to around  $60^\circ\text{N}$ , which is likely to be a reflection of the warming influence of the Gulf Stream (Risso's dolphins do not appear to be common in waters of these high latitudes elsewhere – see below). Their range extends southwards to the equator. Records in the southern portion of the eastern North Atlantic, off the west coast of Africa, are comparatively scarce, although sufficient to suggest a continuous occurrence. However, this almost certainly reflects a paucity of reporting (Jefferson et al. 1997, Weir 2010). The range extends into the Mediterranean Sea, especially in the northwestern Mediterranean Sea, off the southeast coast of Spain and off Greece but also to the far eastern Mediterranean (Cañadas et al. 2002, Bearzi et al. 2011). Risso's dolphins have not been documented in the Black Sea or the Baltic Sea. Their distribution also includes shallow waters of the continental shelf, such as the Celtic Sea and the French coastal waters of the western English Channel (Kiszka et al. 2004). There appears to be a large gap in distribution in the deep oceanic waters of the central North Atlantic. This is probably an artefact of the near-absence of marine mammal survey work in the mid-Atlantic and not the result of a true distributional hiatus.

### South Atlantic Ocean

Risso's dolphin probably ranges in the western South Atlantic from the equator to southern Argentina (records at  $\sim 46^\circ\text{S}$ ; Fig. 1), although there are surprisingly few documented records for this ocean basin. We could locate only single sighting or capture records off Brazil (Tormosov et al.



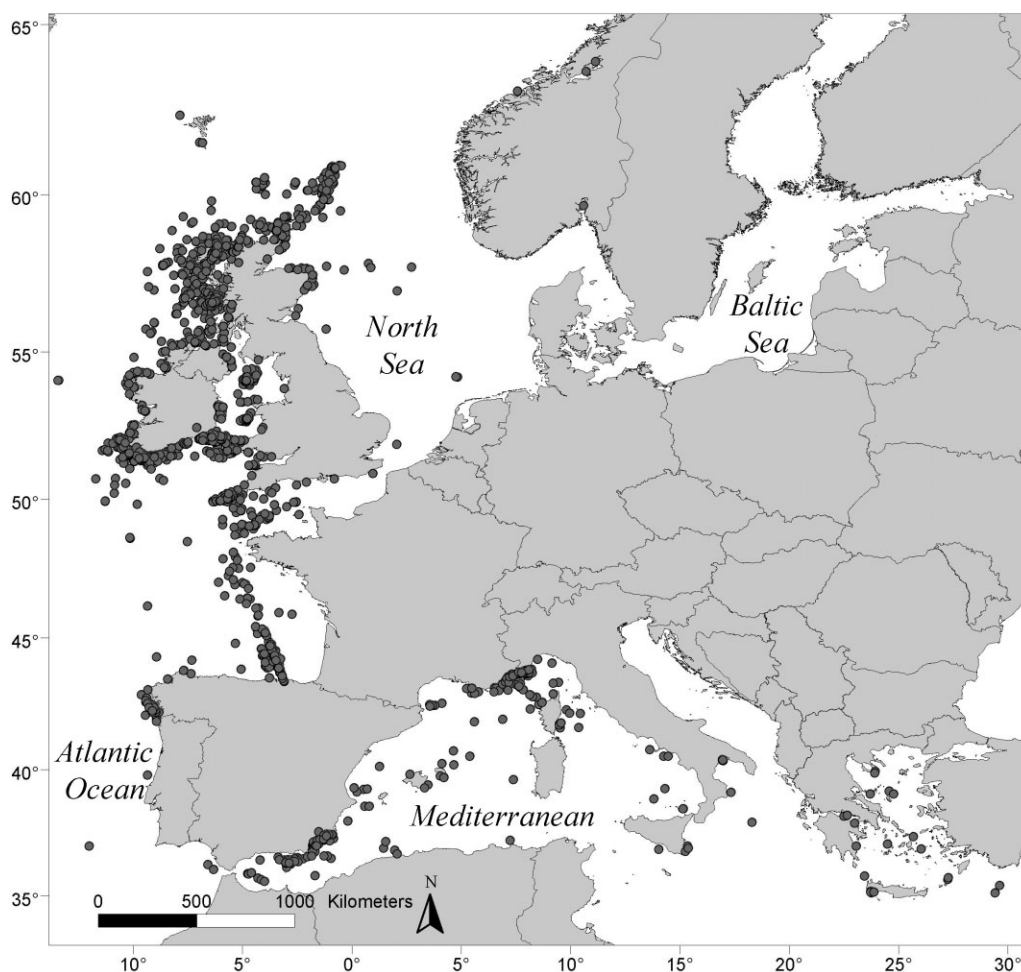


Fig. 3. Detail map of the eastern North Atlantic Ocean, showing sighting and capture records of Risso's dolphins (1950–2012).

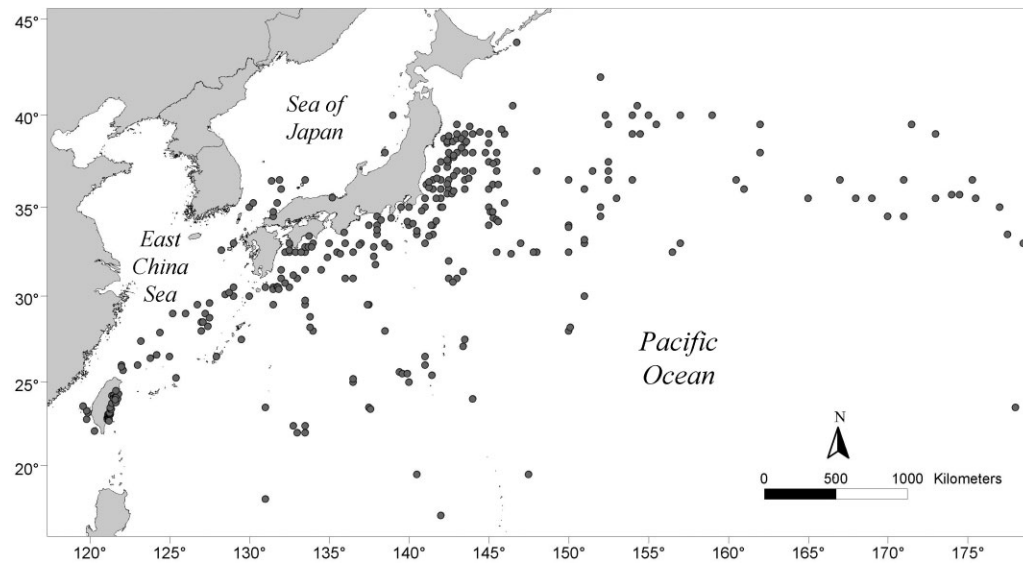
1980) and Uruguay (Passadore et al. 2008) and six records from Argentina (Reyes 2006). Records from Tierra del Fuego are not particularly numerous (mostly strandings, extending south to about 54°S), and these were previously considered to be extralimital, but their increasing frequency in recent years makes this now appear unlikely (Lichter & Goodall 1988, Goodall & Schiavini 1993, Ricciadelli et al. 2012).

In the eastern South Atlantic, Risso's dolphins have been documented from equatorial waters off Gabon southwards to (at least) South African waters (~37°S; Fig. 1). Cetacean survey effort in most countries north of South Africa is relatively scarce; however, the species appears to be reasonably common in areas where survey effort has occurred (e.g. off Angola; Weir 2011). We know of no records of the species from the South Atlantic subantarctic and cold temperate island groups of Tristan da Cunha, Gough Island, South Georgia, Bouvet Island or from the South Orkney Islands. The lack of records in the deep, offshore waters of the

central South Atlantic may not be indicative of a real absence of the species, as this area has received almost no marine mammal survey attention.

### North Pacific Ocean

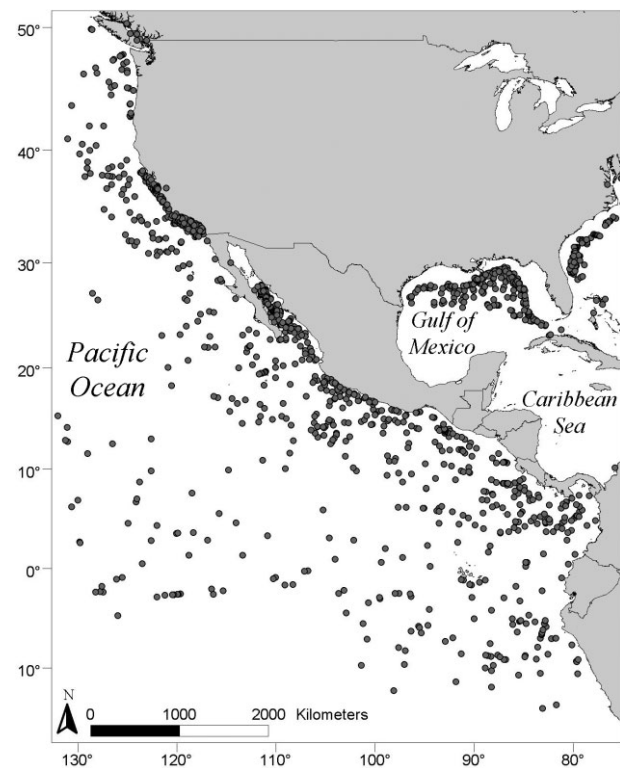
In the western North Pacific Ocean, the documented range of Risso's dolphin extends from central or northern Japan and the southern Kurile Islands southwards to the equator (Fig. 4). The single record from the Commander Islands (Sleptsov 1961) is rather old and is much further north than the rest, and thus we consider that it is not indicative of the current normal range. Although available records are few, the range includes the Sea of Japan and South China Sea, but there is no evidence that it includes either the Sea of Okhotsk (Doroshenko 2002) or the Gulf of Thailand (see Chantrapornsy et al. 1996). The Gulf of Thailand is very shallow, with a mean depth of 45 m, and maximum depth of only 80 m, and thus it may be too shallow to be a pre-



**Fig. 4.** Detail map of the western North Pacific Ocean, showing sighting and capture records of Risso's dolphins (1950–2012).

ferred area of occurrence for the species (see below for a discussion of distribution in relation to depth). However, the Sea of Okhotsk is deeper and appears to contain good habitat for Risso's dolphin. The species is found in similar latitudes and habitat in the eastern North Pacific. It is rather surprising that the species has not been documented in the Sea of Okhotsk, at least in the southern portion, especially when one considers that extensive marine mammal surveys have been conducted there (see Miyashita 1997). There are some records from throughout dispersed locations in Southeast Asia (Fig. 1).

The species' range in the eastern North Pacific has probably been documented better than in any other ocean basin, due to the intensive marine mammal research efforts in very large portions of the region. Risso's dolphins occur from the Queen Charlotte Islands and Gulf of Alaska (~56°N) southwards to the equator (Figs 1 and 5). There are numerous records of the species along the coast of California between 32° and 38°N and from the eastern tropical Pacific coastline from Mexico south to Columbia (Fig. 5). Offshore surveys of the eastern tropical Pacific have also produced numerous oceanic records, including around the island archipelagos of Hawaii and the Galapagos (Fig. 1). Risso's dolphins range well into the Gulf of California in Mexico (Sea of Cortez) and occur throughout this body of water, with the probable exception of the very shallow, northernmost portion. Although there are some records as far north as the Gulf of Alaska, the northernmost records (at 55–56°N – Braham 1983, Kajimura & Loughlin 1988) may be extralimital. Even though suitable habitat might appear to exist, there is little evidence that Risso's dolphins normally inhabit the deep inshore waters of Washington State, British Columbia or



**Fig. 5.** Detail map of the eastern North Pacific Ocean and Gulf of Mexico, showing sighting and capture records of Risso's dolphins (1950–2012).

southern Alaska. Research in this area has been extensive, and only a handful of records have been documented; we consider these probably extralimital. For example, in 21 years of surveys throughout nearly all of the inshore waters of Southeast Alaska, involving well over 10000 marine mammal sightings, Risso's dolphins have never been observed (Dahlheim et al. 2009). There is no evidence that they reach as far north as the Aleutian Islands or extend into the Bering Sea (these areas have been extensively surveyed by the National Oceanic and Atmospheric Administration's National Marine Mammal Laboratory and Southwest Fisheries Science Center). The number of records from the central portion of the North Pacific Ocean makes it reasonably clear that the species is found continuously across the North Pacific Ocean basin; there is no evidence of separate western and eastern Pacific populations.

### South Pacific Ocean

In the western South Pacific, the species is known from the equator to southern Australia and New Zealand (Fig. 1). Based on the small number of records for Australia and New Zealand, it appears that Risso's dolphins are not particularly common in those waters. In extensive cetacean work on the water throughout New Zealand, one researcher has never sighted them (I. Visser, pers. comm., 27 June 2012). There appear to be no records for Tasmania, and it seems doubtful that the species would reach that far south (see Nicol 1987). Our searches for records also produced 64 stranding records from Australia and over 22 from New Zealand (we suspect there are many more that are not published and not available to us), suggesting perhaps that Risso's dolphins are not quite as rare as the sightings and captures suggest, but it does appear that overall Australasia is not a part of the world where the species occurs in its highest densities.

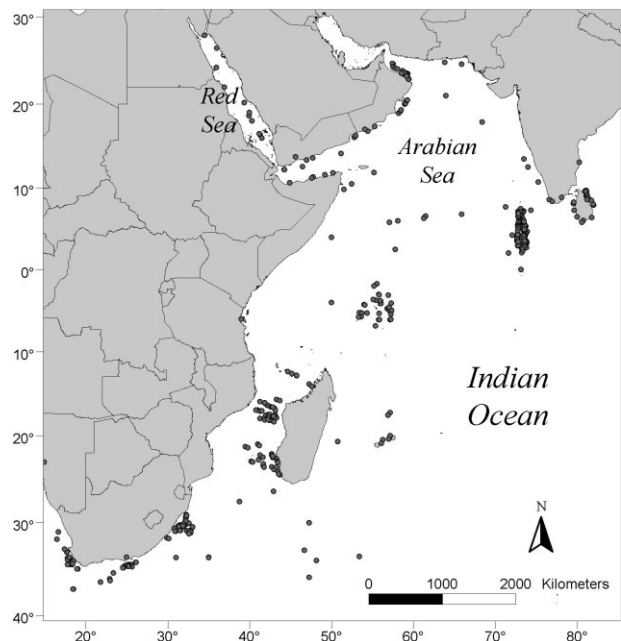
Risso's dolphins apparently occur widely in much of the waters of Southeast Asia, at least in the deeper regions such as throughout the Indo-Malay archipelago, as well as in the Timor and Arafura seas. Although specific records of occurrence are sparse (probably at least partly due to a paucity of marine mammal work in most of the islands), it is widely believed that Risso's dolphins are found throughout virtually the entire Pacific island groups of Micronesia, Melanesia and Polynesia (see Reeves et al. 1999, Miller 2007). For instance, 31 sightings were recorded during aerial surveys in French Polynesia from February to April 2011 (UMS Pelagis, University of La Rochelle, unpublished data). Risso's dolphins were also documented from small boat dedicated surveys in this region, especially from the Marquesas and Society islands (Gannier 2000, 2002).

Risso's dolphins are found from the equator to the central Chilean coast in the eastern South Pacific (Fig. 1). There are a number of records for Chile, and currently dedi-

cated ecological work is being conducted on this species there (Olavarria et al. 2001). No records of occurrence are known for the subantarctic island groups of Macquarie Island, Auckland/Campbell Islands, the Bounty Islands or the Chatham Islands, and these are probably south of the regular range of the species.

### Indian Ocean

Risso's dolphins range throughout the waters of the Indian Ocean, although records are more numerous in the western portion, ranging from India, Sri Lanka and the Arabian Sea south to the east coast of South Africa (Kruse et al. 1991, Ballance & Pitman 1998; Figs 1 and 6). The species appears to be particularly common around some offshore island chains in the region, such as the Maldives and the Seychelles (Keller et al. 1982, Kruse et al. 1991, Anderson 2005; Fig. 6). In the western tropical Indian Ocean, it was the second most common species recorded during surveys conducted between March and July 1995 (Ballance & Pitman 1998). Risso's dolphins were also observed off eastern and southeastern Madagascar (Kruse et al. 1991), and their presence has been suspected off Aldabra, southern Seychelles (Hermans & Pistorius 2008). They have also been recorded along insular slope waters of the island of Mayotte (mean depth of encounter was 1150 m) and in the Comoros Islands (Anderson 2005, Kiszka et al. 2007a, b, 2010a, b). In the southwestern Indian Ocean, dedicated aerial survey data confirm high densities around the northern islands of the



**Fig. 6.** Detail map of the western Indian Ocean, showing sighting and capture records of Risso's dolphins (1950–2012).

Seychelles, as well as in the southern Mozambique Channel (Fig. 6; UMS Pelagis, Université de La Rochelle, unpublished data). Risso's dolphins were also previously common around Sri Lanka, where they were one of the most frequent small cetacean species taken as by-catch and in directed fisheries in the 1980s and early 1990s, and were also frequently seen on surveys (Alling 1988, Leatherwood & Reeves 1989, Kruse et al. 1991). However, they now appear to be rare in Sri Lanka, probably due to the high fisheries mortality (R. C. Anderson, unpublished data). Sightings are more scarce in the eastern portion of the Indian Ocean, including in much of the Bay of Bengal and the southeastern coasts of Indonesia and Australia. Risso's dolphins are found throughout the Gulf of Aden and the Red Sea (Weitkowitz 1992; Fig. 6). They also occur in the Gulf of Oman. Although Kruse et al. (1999) showed three records from the Persian Gulf on their range map, we could find no verifiable sighting or capture records of Risso's dolphin from this region. These three records are therefore considered erroneous, and we concur with Braulik et al. (2010), who suggested that Risso's dolphins are unlikely to occur in the Persian Gulf on a regular basis.

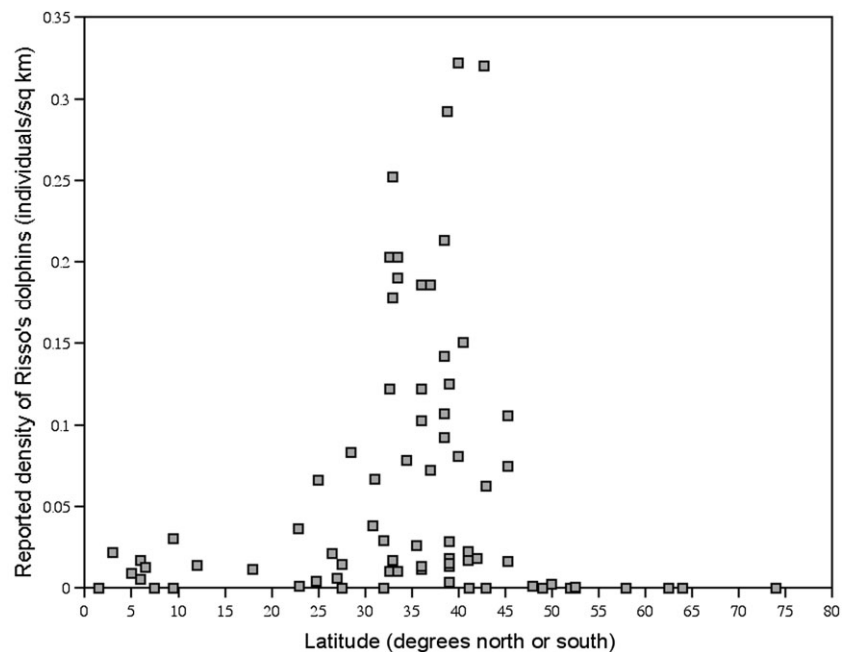
There is no evidence that Risso's dolphins occur around the Indian Ocean subantarctic island groups such as the Prince Edward Islands, Crozet Islands, Kerguelen Islands, Heard Island and St. Paul/Amsterdam Islands. The large apparent gap in distribution in much of the central South Indian Ocean may reflect a lack of survey effort in this region (see Kemper et al. 2005, Best 2007).

## DISCUSSION

### What kind of habitat do Risso's dolphins prefer?

In tropical and subtropical waters, the available data show that, while the species is clearly present (Fig. 1), Risso's dolphin densities (Fig. 7) are uniformly low (with some apparent exceptions, such as the Maldives, where they are abundant, but for which no quantitative density estimates exist; Anderson 2005). In cooler, more temperate waters between about 30° and 45° in both hemispheres, while there are still many low densities reported, there is much more variation and a substantial number of medium and high densities are reported (e.g. Dohl et al. 1983, Miyashita 1986, Barlow 1993, 1995, Forney et al. 1995, Carretta et al. 2000, Palka 2006, Jefferson et al. 2013). These cool-temperate waters appear to be the favoured habitat for Risso's dolphins worldwide and support some exceptionally high densities above 0.25 individuals km<sup>-2</sup> (Fig. 7). In cold temperate to polar waters, higher than latitudes of about 45–50°, Risso's dolphin densities quickly drop off to nearly zero, and they are clearly not present in high latitudes near the poles.

Some of the variation in the mid-latitudes may be explained by habitat preferences, especially as they relate to water depth. Risso's dolphins appear strongly to favour continental shelf and slope waters as opposed to very deep waters of the oceanic zones (see below), although they do occur in the latter areas, just at lower densities. The presence



**Fig. 7.** Reported densities of Risso's dolphins from the literature, by latitude.



of Risso's dolphins in a wide range of habitats from coastal, shallow waters to deep, oceanic waters suggests that there may be population-specific and/or ecotype-specific habitat specialization in this species. These issues deserve further study.

### Are Risso's dolphins restricted to continental margins?

It has been known for several decades that the distribution of Risso's dolphin is affected by water depth (e.g. Kruse 1989, Fabbri et al. 1992, Baumgartner 1997). Furthermore, nearly every study of the habitat preferences of this species provides evidence that it preferentially occurs over topography with steep-sloped bottoms near the outer edge of the continental shelf or upper slope (Kruse 1989, Baumgartner 1997, Cañadas et al. 2002, Azzellino et al. 2008, Praca & Gannier 2008). A rehabilitated Risso's dolphin that was released in the Gulf of Mexico and tracked for 23 days followed this pattern as well. This animal moved in waters with an average depth of 548 m and performed dives of up to 400–500 m (Wells et al. 2009). Three Risso's dolphins tracked in southern California moved in waters with an average depth of 900–974 m (Falcone & Schorr 2011). This does not mean the animals do not occur elsewhere, and certainly there are records of the species in deep oceanic waters and in shallow waters a great distance from the shelf edge. Risso's dolphins are routinely recorded in shelf and coastal waters around the British Isles (Evans et al. 2003, Reid et al. 2003) and in the shallow waters of the north coast of Brittany (France) during summer, where they apparently feed on cuttlefish *Sepia officinalis* (Kiszka et al. 2004). As an extreme example, in 2009, the first author observed a large group of Risso's dolphins mixed with California coastal bottlenose dolphins *Tursiops truncatus* in southern Monterey Bay, in waters of about 2–5 m depth, just outside the surf zone and at least 8–10 km from the nearest deep water (>180 m deep). However, presence in water this shallow and close to shore is undoubtedly unusual.

Clearly, Risso's dolphins are not restricted to continental margins. Past assessments of Risso's dolphin distribution may have been biased by the much greater tendency for sightings to be recorded in waters close to continental or island archipelago margins. While Risso's dolphins do occur in higher densities along the continental slope and outer continental shelf waters (see above), there is now abundant evidence that the species also inhabits oceanic waters far from shore. The large number of distribution records for offshore waters of the eastern tropical Pacific, as well as other such records from places such as the western Pacific, eastern Indian Ocean and the North Atlantic and Gulf of Mexico provide ample evidence that Risso's dolphin is a species that extends from nearshore waters out to oceanic

water depths. While our maps show a paucity of records in the middle of ocean basins (especially in the Atlantic), we believe that Risso's dolphin extends across all these basins, and the absence of records may simply be an artefact of low search effort there.

### Do Risso's dolphins occur in enclosed bodies of water?

The presence of verified distribution records makes it clear that Risso's dolphins do occur in many enclosed bodies of water, such as the Gulf of California, Sea of Japan, Red Sea, Mediterranean Sea (where they are quite common) and the Gulf of Mexico. All of these areas have sections of deep water (>100–200 m depth).

Some other such bodies of water appear to be outside the normal range of Risso's dolphin. Puget Sound, the inshore waters of British Columbia, and southeast Alaska are not considered a normal part of the range of Risso's dolphin. Although there have been several stranding records of the species in inshore waters of Washington (Everitt et al. 1979, Osborne et al. 1988) and southern British Columbia (Baird & Stacey 1991), these are considered anomalous. Recent sightings of the species in Puget Sound are rare and of just a few individuals, and also appear to be anomalous (C. Emmons, pers. comm., 14 July 2012). There are no records for the Black Sea, which is documented to be inhabited by only three species of cetaceans (*Delphinus delphis*, *T. truncatus* and *Phocoena phocoena*). The Baltic Sea is similarly thought to be inhabited by only three or four small cetacean species, and although there are several stranding records of Risso's dolphin for the Baltic, the species is considered extralimital there (Aguayo 1978).

The apparent absence of Risso's dolphins from the Persian (Arabian) Gulf is interesting, especially because this is a region that has commonly been included as part of their range in the past, generally with no supporting evidence cited, or based on apparently erroneous information (see, e.g. Kruse et al. 1999). The waters of this basin are probably too shallow (with an average depth of 50 m and a maximum of just 90 m) and warm to be favoured habitat for the species. The same may also be true of the Gulf of Thailand. Potential distribution in these areas deserves further study.

There is still some doubt about some other similar bodies of water: the Sea of Okhotsk and the inner Gulf of Maine/Bay of Fundy. Based on known habitat preferences, these are areas in which the species might be expected to be present, but there are no specific locality records. While the species is mentioned by some Russian scientists for the Sea of Okhotsk (e.g. Doroshenko 2002), there appear to be no specific, verifiable locality records there to confirm this.

## Do Risso's dolphins prefer tropical or temperate waters?

There has been some controversy as to whether Risso's dolphins are primarily a tropical or a temperate species. Leatherwood et al. (1980) argued, following Davies (1963), that they were inhabitants primarily of tropical waters and reached their range limits in temperate zones, whereas Kruse (1989) seemed to favour the idea that Risso's dolphins are more properly characterized as a cool-water species. While most small cetaceans exhibit clear preferences for either warm or cold waters, with their ranges centering either on tropical and subtropical regions or temperate zones, Risso's dolphins have not been previously shown to have a strong preference for either warm or cold waters.

Risso's dolphins are reportedly common in some areas with very warm waters [such as the Maldives, around Sri Lanka (at least in the past), and the east coast of Taiwan]. Yet they are also very common in temperate regions that are characterized by much cooler temperatures (such as Monterey Bay, California; the Azores; and around the British Isles). Unfortunately, reliable estimates of density are not available for all of these areas. A detailed examination of Risso's dolphin density by latitude reveals that these animals occur at medium and high densities almost exclusively in temperate waters between about 30° and 45° latitude in both hemispheres (e.g. Dohl et al. 1983, Miyashita 1986, Barlow 1993, 1995, Forney et al. 1995, Carretta et al. 2000, Palka 2006, Jefferson et al. 2013). While they are widely distributed throughout the tropical oceans of the world, and may be reasonably common in a few, localized spots with warm waters (such as the Maldives and possibly the Seychelles), overall densities of the species in tropical waters appear to be comparatively low. In fact, all available density estimates for regions within 20° of the equator are less than 0.04 individuals km<sup>-2</sup> (Best et al. 1986, Wade & Gerrodette 1993, Gerrodette & Palacios 1996, Dolar et al. 2006, Gerrodette et al. 2008; Fig. 7). Although we do not currently have density estimates for many parts of the range, available data suggest that this is a pattern that may span the entire global range of the species.

## CONCLUSIONS

Some erroneous conclusions have been made in the past regarding Risso's dolphin distribution and habitat preferences, based on incomplete information and absence of survey data from large portions of the world's oceans (in particular, most oceanic regions). In this review, *Grampus griseus* is clearly shown to be a species with a circum-global range extending from at least 64°N to 46°S latitude. The species occupies both continental shelf/slope and oceanic waters throughout its range, but shows a clear preference for

outer continental shelf and slope water depths. It also appears to favour mid-latitudes ranging from 30° to 45°, and this is where the species' highest densities are consistently found in most ocean basins. It is hoped that surveys in relatively unstudied areas (especially in the Atlantic and Indian oceans) will allow for a more complete examination of the global range of Risso's dolphin in the near future.

## ACKNOWLEDGEMENTS

Many people and organizations provided information and/or data to this project. For access to unpublished data, we thank MCR Ltd, International Fund for Animal Welfare (IFAW), Kees Camphuysen and the NZG/Marine Mammal Database, UMS Pelagis/Marine Mammal Research Center (University of La Rochelle, France), Shetland Biological Records Centre, European Seabirds at Sea Database, Peter Evans/Sea Watch Foundation, Marijke de Boer, NORCET (Northern North Sea Cetacean Ferry Surveys), Hebridean Whale and Dolphin Trust, Sea Life Surveys, Ruth H. Leeney, Institute of Marine Research, Norway, Organisation Cetacea, Irish Whale and Dolphin Group, MARINELife, WDC (Whale and Dolphin Conservation), University of Valencia, M.E.E.R., POPA (Azores Fisheries Observer Program), Fisheries and Oceans Canada, Groupe de Recherche sur les Cétacés, Tethys Research Institute, CEMMA (Coordinadora para o Estudo dos Mamíferos Mariños), North Atlantic Right Whale Consortium, Cetacean Conservation Pakistan, Brian D. Smith, Keith D. Mullin, Karen Stockin and the Southwest Fisheries Science Center (special thanks to Jay Barlow and Tim Gerrodette). Funding for survey data provided by JJK was from the Agence des Aires Marines Protégées and Indian Ocean Commission. Phil Hammond of the SMRU graciously agreed to calculate unpublished estimates of density and abundance for the SCANS-II and CODA surveys. Bob Brownell and Yulia Ivaschenko helped in tracking down some of the Russian records. Vanessa James assisted in extracting records from maps and tables in the literature and Hiedi Chan assisted with translation of some Chinese literature. This manuscript was critically reviewed by R. L. Brownell, Jr., G. Bearzi and two anonymous referees from *Mammal Review*. To all of these individuals and organizations, we express our heartfelt gratitude.

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