



REVIEW

Dolphin sympatric ecology

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Abstract

Interspecific associations between two or more species of the family *Delphinidae* have been reported by many scientists, but the sympatric ecology of such dolphin associations has not been studied in great detail. A few field investigations have been conducted on this subject in different parts of the world on species such as bottlenose dolphins (*Tursiops* spp.), short-beaked common dolphins (*Delphinus delphis*), and killer whales (*Orcinus orca*). Sympatric dolphins seem to use different strategies to co-exist when resources appear to be limited, including dietary divergence (different prey preference, slightly diverse diet, different feeding time) and/or different habitat use (shallow versus deep waters, flat areas versus submarine canyons and escarpments, different travel routes). This paper presents a review of some well-studied dolphin species found in sympatry and discusses the nature of habitat and resource partitioning as well as studies on aggressive behaviour displayed by species living in the same habitat.

Key words: *Dolphins, habitat partitioning, resource partitioning, sympatry*

Introduction

The literature contains numerous accounts of associations and interactions between different species of the family *Delphinidae* world-wide (Table I). Only a few sympatric populations of small odontocetes, however, have been well investigated in the field (common bottlenose dolphins, *Tursiops truncatus* – hereinafter bottlenose dolphin – and Indo-Pacific bottlenose dolphins, *Tursiops aduncus*: Hale et al. 2000; Wang et al. 2000; short-beaked common dolphins, *Delphinus delphis*, and bottlenose dolphins: Politi et al. 1998; Bearzi et al. 2005; short-beaked common dolphins, long-beaked common dolphins, *Delphinus capensis*, and bottlenose dolphins: Bearzi 2003; short-beaked common dolphins and striped dolphins, *Stenella coeruleoalba*: Frantzis & Herzing 2002; transient and resident killer whales, *Orcinus orca*: Bigg et al. 1987, 1990; Baird et al. 1992; Baird 1994; Ford et al. 1998; Saulitis et al. 2000). In this paper, *sympatry* is defined as the co-occurrence of two or more dolphin species in the same immediate habitat, which might be called *direct sympatry*, where *broad sympatry* simply means two or more species occurring over the same wider geographical area.

Interspecific associations between dolphins may be beneficial for at least one species for several reasons, particularly in offshore waters (e.g. increased feeding, decreased predation rates; Norris & Dohl 1980; Baraff & Asmutis-Silvia 1998; Scott & Cattanach 1998; Wilson 2000; Gyax 2001). The goal of this paper is to review the present literature on the sympatric ecology of some well-studied dolphin species and discuss the different strategies employed by these species to co-exist, reducing the possible occurrence of direct competition for food resources (Roughgarden 1976).

Sympatric ecology of some well-studied species of *Delphinidae*

Field studies on dolphin sympatric associations have been mentioned in the literature (Table II). This paper presents a review of well-studied species found in sympatry.

Bottlenose dolphins and Indo-Pacific bottlenose dolphins

Populations of bottlenose dolphins are known to inhabit pelagic waters as well as coastal areas (Leatherwood et al. 1983), showing morphological,

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Table I. Accounts of associations and interactions between different species of the family Delphinidae observed in the field. For extensive lists of cetaceans found in associations in the eastern Pacific Ocean and the Gulf of California, also see Hill & Barlow (1992), Carretta & Forney (1993), Mangels & Gerrodette (1994), Carretta et al. (1995), Frantzis & Herzing (2002).

Species	Reference
<i>Globicephala macrorhynchus</i> , <i>Tursiops truncatus</i> , <i>Lagenorhynchus obscurus</i> , <i>Orcinus orcas</i> <i>Stenella attenuata</i> , <i>Stenella longirostris</i>	Norris & Prescott 1961 Perrin et al. 1973 Norris & Dohl 1980 Norris et al. 1994 Ballance & Pitman 1998 Saayman & Tayler 1973
<i>Tursiops aduncus</i> , <i>Sousa chinensis</i> <i>Stenella coeruleoalba</i> , <i>Delphinus delphis</i>	Au et al. 1979 Au & Perryman 1985 Polacheck 1987 Forcada et al. 1994 Das et al. 2000 García et al. 2000
<i>L. obscurus</i> , <i>Grampus griseus</i> <i>Globicephala melas</i> , <i>O. orcas</i> <i>D. delphis</i> , <i>Delphinus capensis</i>	Würsig & Würsig 1980 Bloch & Lockyer 1988 Leatherwood et al. 1988 Hill & Barlow 1992 Bearzi 2003
<i>Lagenorhynchus acutus</i> , <i>D. delphis</i> , <i>G. melas</i>	Selzer & Payne 1988 Gowans & Whitehead 1995
<i>T. truncatus</i> , <i>S. chinensis</i> <i>O. orcas</i> , other <i>Delphinidae</i> <i>Globicephala</i> sp., <i>D. delphis</i> <i>D. delphis</i> , <i>T. truncatus</i>	Corkeron 1990 Jefferson et al. 1991 Overholtz & Waring 1991 Bearzi 1997 Bruno et al. 2004 Shane 1995
<i>G. macrorhynchus</i> , <i>G. griseus</i> <i>G. griseus</i> , <i>Lagenorhynchus obliquidens</i> , <i>Lagenorhynchus hosei</i> , <i>Lagenorhynchus borealis</i> , <i>Phocoenoides dalli</i> <i>T. truncatus</i> , <i>Phocoena phocoena</i> <i>G. macrorhynchus</i> , <i>D. capensis</i> <i>G. macrorhynchus</i> , <i>Peponocephala electra</i> <i>Stenella frontalis</i> , <i>T. truncatus</i> <i>G. melas</i> , <i>L. acutus</i> <i>S. coeruleoalba</i> , <i>D. delphis</i> , <i>G. griseus</i>	Shelden et al. 1995 Ross & Wilson 1996 Weller et al. 1996 Migura & Meadows 2002 Herzing & Johnson 1997 Baraff & Asmutis-Silvia 1998 Frantzis & Herzing 2002

osteological, and molecular differentiations (Walker 1981; LeDuc & Curry 1998; Rossbach & Herzing 1999). The frequent presence of bottlenose dolphins along the coastline has made this dolphin one of the best-known cetaceans (e.g. Shark Bay, western Australia: Connor & Smolker 1985; Connor et al. 1998; the Firth of Tay, Scotland: Wilson et al. 1993; Wilson 1995; Sarasota Bay, Florida: Scott et al. 1990; Wells 1991; Argentine Bay: Würsig 1978; Croatia, Mediterranean Sea: Bearzi et al. 1997, 1999; and in southern California: Weaver 1987; Hansen 1990; Weller 1991; Defran et al. 1999). Coastal populations usually live in small groups (five to 25 individuals) within 1 km of the shore and often reside in a specific area, whereas pelagic populations are found in larger schools (25–150 individuals) in the open ocean (Bearzi et al. 1999; Defran & Weller 1999).

Sympatric species of the genus *Tursiops* have been described by a few investigators. For instance, bottlenose dolphins and Indo-Pacific bottlenose dolphins appeared to be in direct sympatry around the Chinese waters of the Penghu archipelago and were

observed in mixed schools that frequently included other dolphin species as well (Yang 1976; Zhou & Qian 1985). These two species, however, differed ecologically: bottlenose dolphins preferred the coastal and shallow waters of the continental shelf, feeding upon benthic or reef-dwelling fish and cephalopods, whereas Indo-Pacific bottlenose dolphins favoured offshore waters, feeding mostly on schooling epipelagic and mesopelagic species (Wang et al. 2000).

In the Indian and western Pacific Oceans, Hale et al. (2000) recorded different preferences in habitat choice for the same species, with bottlenose dolphins frequenting both shallow waters and offshore reefs and Indo-Pacific bottlenose dolphins inhabiting estuaries and coastal waters. This study showed that some areas were occupied exclusively by one species, with coastal regions of sympatry in their distribution.

Sympatric bottlenose dolphins and Indo-Pacific bottlenose dolphins also seemed to exist in south African waters (Wang et al. 2000), although Ross (1977) described these species as being typically

Table II. Field studies of sympatric associations of the family Delphinidae.

Species	Site	Reference	
<i>O. orca</i> (transient and resident)	Eastern North Pacific	Baird 1994	
	British Columbia	Baird et al. 1992	
		Baird & Dill 1995, 1996	
	Vancouver Island	Bigg 1982	
	British Columbia and Alaska	Baird & Whitehead 2000	
		Barrett-Lennard et al. 1996	
	British Columbia and Washington State	Bigg et al. 1987, 1990	
	Coastal British Columbia and adjacent waters	Ford et al. 1998	
	British Columbia	Guinet 1990	
		Morton 1990	
<i>T. truncatus</i> and <i>T. aduncus</i>	Prince William Sound (Alaska)	Saulitis et al. 2000	
	Indian and western Pacific oceans	Hale et al. 2000	
<i>D. delphis</i> and <i>D. capensis</i>	Taiwan and south-central China (Chinese waters)	Wang et al. 2000	
	Santa Monica Bay (California)	Bearzi 2003	
<i>L. acutus</i> and <i>D. delphis</i>	Southern California Bight (eastern north Pacific)	Banks & Brownell 1969	
	California coast	Evans 1975	
		Heyning & Perrin 1994	
	Eastern north Pacific and adjacent waters	Rosel et al. 1994	
	Eastern Pacific	Hill & Barlow 1992	
	Scotian shelf (Nova Scotia)	Leatherwood et al. 1988	
	Northeastern USA	Perrin et al. 1985	
	Eastern tropical Pacific	Gowans & Whitehead 1995	
		Selzer & Payne 1988	
	<i>L. acutus</i> , <i>D. delphis</i> , and <i>G. melas</i>	Biscay Bay (northeast Atlantic)	Au et al. 1979
Au & Perryman 1985			
Southeastern coast of Spain		Polacheck 1987	
Gulf of Corinth (Greece, Mediterranean Sea)		Das et al. 2000	
Hawaii (eastern tropical Pacific)		Sagarminaga & Cañadas 1995, 1998	
		Frantzis & Herzing 2002	
<i>S. coeruleoalba</i> and <i>D. delphis</i>		Western tropical Indian Ocean	Norris & Dohl 1980
			Norris et al. 1994
		Hawaii	Perrin et al. 1973
			Psarakos et al. 2003
	Central Philippines	Ballance & Pitman 1998	
	Bahamas waters	Baird et al. 2001	
	Eastern tropical Pacific	Dolar 1999	
	Northeastern Pacific	Herzing & Johnson 1997	
	Santa Catalina Island (California)	Polacheck 1987	
	Kalamos Island (Greece)	Norris & Prescott 1961	
Shane 1995			
<i>T. truncatus</i> and <i>D. delphis</i>	Kalamos Island (Greece)	Ferretti et al. 1998	
		Politi 1998	
		Politi et al. 1998	
<i>T. truncatus</i> , <i>D. delphis</i> , <i>S. coeruleoalba</i> and <i>Sousa</i> sp.	Cape coast of south Africa	Bruno et al. 2004	
		Saayman et al. 1972	

allopatric. Ross (1977) noted different prey in the stomachs of bottlenose dolphins and Indo-Pacific bottlenose dolphins, with the former species exploiting deep reefs located offshore and the latter preferring shallow inshore waters.

Short-beaked common dolphins in associations with long-beaked common dolphins, bottlenose dolphins, and striped dolphins

Inshore populations of the genus *Delphinus* have been described for different areas world-wide, including the Southern California Bight, California

(Evans 1975; Bearzi 2003), South Africa (Young & Cockroft 1994), Bay of Plenty, New Zealand (Neumann 2001a,b) and the Mediterranean Sea (Bruno et al. 2004; Bearzi et al. 2005), whereas the ecology of offshore communities remains largely unknown (Evans 1994). Several populations of common dolphins stay in large schools that can reach thousands of individuals, but often separate into smaller basic social units of about 30 individuals (Evans 1994; Bearzi et al. 2003).

There is no known gene flow between short-beaked common dolphins and long-beaked common dolphins, and they occur sympatrically in tropical

and temperate waters (Heyning & Perrin 1994; Rice 1998).

In Santa Monica Bay, California, the direct sympatric ecology of short-beaked common dolphins and long-beaked common dolphins was investigated (Bearzi 2003). The two species were both observed year-round mostly offshore (>500 m from shore), generally near submarine escarpments and canyons. Short-beaked common dolphins and long-beaked common dolphins were sympatric in the bay, but they were never seen in mixed schools (Bearzi 2003). The co-existence of these species is probably explained by an abundance of anchovies (*Engraulis mordax*), among their favourite food, and other prey in areas of local upwelling such as submarine canyons and escarpments, as also reported by other authors (Mais 1974; Evans 1975; Hui 1979). These sympatric species had a similar diet (Fitch & Brownell 1968). However, slight differences in their prey were observed (Schwartz et al. 1992). This difference in diet might indicate how partitioning of ecological niches may have reduced the occurrence of competition for food resources when the dolphins were in direct sympatry (Bearzi 2003).

In the same bay, the broad sympatric ecology of bottlenose dolphins, short-beaked common dolphins and long-beaked common dolphins was also investigated (Bearzi 2003). High abundance and year-round occurrence of the three species appeared to be correlated to prey abundance and, consequently, to the oceanography of this region (Bearzi 2003), as also reported for other small odontocetes in different locations (Cockcroft & Peddemors 1990; Gowans & Whitehead 1995; Defran et al. 1999). Eighty per cent of the sightings of bottlenose dolphins (n = 157) were found in shallow waters (<500 m from shore), and they were generally separated from the distribution of the two species of common dolphins showing spatial habitat partitioning (Bearzi 2003). A few sightings of feeding bottlenose dolphins, however, were recorded near the deepest submarine canyons, in similar feeding locations of the two species of common dolphins. Considering that bottlenose dolphins and the two species of common dolphins generally fed on different prey (for a review of preys consumed by the three *Delphinidae*: Bearzi 2003), these species were likely to have co-occurred at these locations without competition for resources (Bearzi 2003).

Das et al. (2000) also reported slightly different dietary preferences for sympatric striped dolphins and short-beaked common dolphins in the northeast Atlantic (Bay of Biscay). In this area, both species were quite opportunistic feeders, taking advantage of seasonally or locally abundant preys. However, striped dolphins were observed displaying more

opportunistic trophic habits compared with common dolphins.

Habitat partitioning and direct sympatry have been observed for short-beaked common dolphins and other delphinids by Gowans & Whitehead (1995). These authors examined the summer distribution of short-beaked common dolphins, Atlantic white-sided dolphins (*Lagenorhynchus acutus*), and long-finned pilot whales (*Globicephala melas*) in the highly productive waters in and near a submarine canyon of the Scotian Shelf called the Gully. Their results demonstrated that: (1) these species were much more abundant inside the Gully than outside, and (2) they used some areas of the Gully slightly differently, showing spatial partitioning of habitat. Atlantic white-sided dolphins and short-beaked common dolphins divided the Gully temporally but not geographically, whereas pilot whales ranged widely over the entire study site, preferring locations with flat relief.

Habitat partitioning and direct sympatry were also observed for short-beaked common dolphins and bottlenose dolphins in the eastern Ionian Sea near the island of Kalamos, where a small group of bottlenose dolphins shared the same inshore waters of the archipelago with about 100 short-beaked common dolphins (Politi et al. 1998; Bruno et al. 2004). These two sympatric species had adopted different foraging strategies, with common dolphins feeding in the water column or near the surface and bottlenose dolphins focusing on bottom prey (Ferretti et al. 1998). In spite of such sympatry, the two species rarely mixed and showed no direct interactions (Bearzi et al. 2005). These results suggested a separation of niches that may have reduced direct competition for food resources (Bruno et al. 2004).

Sympatric short-beaked common dolphins and striped dolphins have been observed in three different areas of the Mediterranean: Alboran Sea (Garcia et al. 2000), south Tyrrhenian Sea (Mussi et al. in press) and Gulf of Corinth (Frantzis & Herzing 2002). Frantzis & Herzing (2002) also observed striped dolphins and short-beaked common dolphins in mixed-species associations with Risso's dolphins (*Grampus griseus*). In all mixed-species sightings, Risso's dolphins and common dolphins were always the minority species present and interspecific rake marks on Risso's dolphins indicated potentially complex and regular interspecific interactions among these species. Among the accountable factors for mixed-species associations in the Mediterranean Sea there were: (1) the relative abundance of each species, and (2) the potential dependence of common dolphins on striped dolphins when the former could not form single-species groups (Frantzis & Herzing 2002).

Transient and resident killer whales

In the eastern north Pacific, two forms of killer whales, *resident* and *transient*, are distinguished (Bigg 1982; Baird & Dill 1995). These whales concentrate in cold regions of high productivity in which pods occupy very large ranges (Baird 2000). Groups of this species generally occur in small pods, usually with less than 40 individuals (Dahlheim & Heyning 1999), and resident pods are typically larger than transient pods (Bigg et al. 1987; Morton 1990; Baird 1994). Residents and transients show differences in acoustics, morphology, pigmentation patterns, and genetics (Barrett-Lennard et al. 1996; Ford et al. 1998; Baird 2000). Besides significant differences, these populations are well known to live sympatrically (Table II).

In British Columbian and Washington waters, two communities of northern and southern resident killer whales live in broad sympatry with transient killer whales while displaying remarkable differences in feeding behaviour (Baird 2000; Saulitis et al. 2000). Resident populations feed primarily on fish, while transient whales prey on marine mammals, mainly pinnipeds (Bigg et al. 1990; Ford et al. 1998; Saulitis et al. 2000). Bigg et al. (1990) and Ford et al. (1998) observed that resident killer whales of British Columbia, Washington and Alaska, eat mostly salmonids, of which 50% were chinook (*Oncorhynchus tshawytscha*), the largest and most energy-rich species present year-round in these areas. Similarly, resident killer whales in Prince William Sound, Alaska, fed primarily on coho salmon (*Oncorhynchus kisutch*), while transient killer whales fed on harbour seals (*Phoca vitulina*) and Dall's porpoises (*Phocoenoides dalli*; Saulitis et al. 2000).

In the various study areas, transients travel and forage more than residents (88.5–94.5 versus 58–72% of the time), whereas residents socialize and rest more than transients (Morton 1990; Felleman et al. 1991; Baird 1994; Saulitis et al. 2000). Saulitis et al. (2000) also reported that different prey choices among populations of killer whales were accompanied by different foraging strategies. Residents, for instance, foraged in co-ordinated pods swimming at high speed, lunging, encircling and chasing fish at the surface (Similä & Ugarte 1993; Barrett-Lennard et al. 1996); mammal-eating transients either swam along shorelines or in dispersed formation across open areas (Barrett-Lennard et al. 1996; Saulitis et al. 2000).

Baird & Dill (1995) found high variability in habitat use between resident and transient whales, with transient animals spending far more time in shallow waters. Dissimilarities also existed in diving patterns of these populations, with resident animals spending most of their time in the top 20 m of the

water column and feeding on salmonids, with transient animals displaying longer mean dive durations between 20 and 60 m (Bigg et al. 1990; Baird 1994, 2000).

Associations between transient and resident killer whales have rarely been seen (Morton 1990; Baird & Dill 1995; Barrett-Lennard et al. 1996). Observations in Prince William Sound and coastal British Columbia show that these populations do not associate, probably because of their strikingly different diet (Ford et al. 1998; Saulitis et al. 2000).

Ecological separation within sympatric dolphin communities

When species that require similar resources occur in the same habitat they tend to partition the available resources, thus reducing competition (Roughgarden 1976). Two or more competing species usually divide the resources by occupying different physical locations or by feeding on different prey (Roughgarden 1976; Pianka 1978). These strategies have been observed for a large number of taxa, including primates (Jones & Sabater-Pi 1971; Tutin & Fernandez 1984; Kuroda et al. 1996; Yamagiwa et al. 1996; Stanford & Nkurunungi 2003) and carnivores (Wu 1999; Fedriani et al. 2000; Wang & Fuller 2001). In-depth field investigations of habitat partitioning and resource use for small odontocetes are complicated due to the difficulties of observing these animals in the open ocean, but comparative inferences can be formulated based on existing studies.

Strategies adopted by sympatric species to co-exist

Investigations on a few sympatric species of the family *Delphinidae* conducted world-wide illustrate how these animals seem to adopt similar strategies to co-exist (Table III) and show that ecological separation between sympatric species is based primarily on diet and habitat use.

Dietary divergence within habitat. When food is abundant, different dolphin species with overlapping diets may be found together in the same habitat (Selzer & Payne 1988; Gowans & Whitehead 1995). The prey may come in schools large enough to accommodate mixed-species aggregations of predators and complete dietary overlap at certain times, but such large prey patches are not consistent enough to support these overlaps all the time (Tarasevich 1957; Bearzi 2003). In situations where diets frequently overlap but food cannot support competing predators, it appears that sympatric species tend to exhibit different prey preferences (Gowans & Whitehead 1995). Many species of small

Table III. Ecological separation within sympatric dolphin communities.

Trait	Species and location	Reference
Dietary divergence within habitat		
Different prey preference	<i>O. orca</i> (transients and residents), British Columbia, Alaska, and Washington State	Bigg et al. 1990 Felleman et al. 1991 Baird 2000 Saulitis et al. 2000
	<i>D. delphis</i> , <i>T. truncatus</i> , Kalamos Island (Greece)	Ferretti et al. 1998 Politi et al. 1998
	<i>Tursiops</i> sp., various areas around the world	Hale et al. 2000
	<i>D. delphis</i> , <i>S. coeruleoalba</i> , Northeast Atlantic	Das et al. 2000
Diet overlap/slightly different diet	<i>D. delphis</i> , <i>D. capensis</i> , Santa Monica Bay (California)	Bearzi 2003
	<i>L. acutus</i> , <i>D. delphis</i> , <i>Globicephala melas</i> , Scotian shelf (Nova Scotia)	Gowans & Whitehead 1995
	<i>L. acutus</i> , <i>D. delphis</i> , Continental shelf of the northeastern USA	Selzer & Payne 1988
Diet overlap/different seasons or time	<i>L. acutus</i> , <i>D. delphis</i> , <i>G. melas</i> , Scotian shelf (Nova Scotia)	Gowans & Whitehead 1995
	<i>S. longirostris</i> , <i>S. attenuata</i> , Hawaii (eastern tropical Pacific)	Norris & Dohl 1980 Norris et al. 1994
	<i>S. longirostris</i> , <i>S. attenuata</i> , Eastern tropical Pacific	Perrin et al. 1973
Different habitat use		
Shallow versus deep waters, and/or inshore versus offshore populations	<i>O. orca</i> (transients and residents), British Columbia and Washington State	Baird & Dill 1995 Baird 1994, 2000
	<i>D. delphis</i> , <i>D. capensis</i> and <i>T. truncatus</i> , Santa Monica Bay (California)	Bearzi 2003
	<i>D. delphis</i> , <i>T. truncatus</i> , Kalamos Island (Greece)	Ferretti et al. 1998 Politi et al. 1998 Bruno et al. 2004
	<i>T. truncatus</i> and <i>T. aduncus</i> , Chinese waters	Wang et al. 2000
	<i>T. truncatus</i> , <i>Sousa</i> sp., and <i>S. coeruleoalba</i> , southeastern Cape coast of South Africa	Saayman et al. 1972
	<i>S. longirostris</i> , <i>S. attenuata</i> , Hawaii (eastern tropical Pacific)	Perrin et al. 1973 Norris & Dohl 1980 Norris et al. 1994
	<i>S. longirostris</i> , <i>S. attenuata</i> , <i>T. truncatus</i> , Hawaii	Baird et al. 2001
	<i>S. longirostris</i> , <i>Lagenodelphis hosei</i> , Central Philippines	Dolar 1999 Dolar et al. 2003
	<i>S. coeruleoalba</i> , <i>D. delphis</i> , southeastern coast of Spain	Sagarminaga & Cañadas 1995
Flat areas versus steeper areas	<i>L. acutus</i> , <i>D. delphis</i> , <i>G. melas</i> , Scotian shelf (Nova Scotia)	Gowans & Whitehead 1995
Different travel routes related to bottom topography	<i>O. orca</i> (transients and residents), British Columbia and Washington State	Morton 1990 Felleman et al. 1991 Baird 2000

odontocetes, such as short-beaked common dolphins and bottlenose dolphins, are well known to be opportunistic feeders that can vary their diet according to the availability of the most abundant and catchable prey (Evans 1975, 1994; Klinowska 1991). A small difference in prey preference may be enough to support the feeding requirements of more than one species, allowing sympatric dolphins to co-exist (Hoelzel 1998).

Slightly different diets for sympatric striped dolphins and short-beaked common dolphins were observed by Das et al. (2000) in the northeast Atlantic (Bay of Biscay). Ross (1977) reported more striking differences in prey preferences for sympatric bottlenose dolphins for the Indian and western Pacific Ocean. However, sympatric species of the family *Delphinidae* can also show a completely different diet, as illustrated for resident and transient killer whales (Bigg et al. 1990; Baird 2000).

In addition to differences in prey preferences, sympatric dolphin species can show dietary separation in times of day and/or during different times of year (Table III). This behaviour was observed for Atlantic white-sided dolphins and short-beaked common dolphins in the Gully (differences in times of year as well as prey depth and species: Gowans & Whitehead 1995) and for spotted dolphins (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific (differences in times of day as well as prey depth, size and species: Perrin et al. 1973).

Different habitat use. Sympatric dolphins may also use the same microhabitat in a different way, such as exploiting resources found at different depths (Table III). A separation of niches based on depth was proposed in the eastern Ionian Sea for bottlenose and short-beaked common dolphins (Ferretti et al. 1998; Politi et al. 1998).

Sympatric species can also display ecological separation utilizing inshore and offshore waters, as observed by Wang et al. (2000) for bottlenose

dolphins living in Chinese waters, Dolar (1999) for spinner dolphins and Fraser's dolphin (*Lagenodelphis hosei*) in the Sulu Sea, Bearzi (2003) for bottlenose dolphins in sympatry with short-beaked common dolphins in Californian waters, and Baird & Dill (1995) for transient and resident killer whales in British Columbia and Washington State. Resident and transient killer whales also used the same habitat but with different travel routes, sometimes related to the bottom topography (Morton 1990; Felleman et al. 1991; Baird 2000).

Aggressive behaviour and competition between sympatric species

Direct competition and aggressive behaviour between sympatric species of the family *Delphinidae* have only occasionally been observed (Table IV). Ross & Wilson (1996) witnessed four violent dolphin–porpoise interactions in the Moray Firth, Scotland, but these authors did not discuss possible reasons for these interactions. In the same study area, Patterson et al. (1998) recorded aggressive behaviour by sympatric bottlenose dolphins towards harbour porpoises, suggesting that infanticide may be a factor responsible for this type of behaviour. Baird (1998) also reported aggressive behaviour by a Pacific white-sided dolphin on a neonatal harbour porpoise in Washington State. His study showed that aggression was more the result of an object-oriented play than aggressive behaviour displayed by one species competing for food, mate, or space. In the western edge of Great Bahama Bank, Herzing et al. (2003) observed interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins, with male spotted dolphins displaying dominant mounting behaviour towards bottlenose dolphin males. In Hawaiian waters, Psarakos et al. (2003) also observed aggressive behaviour between sympatric spinner and spotted dolphins. This type of interaction was accompanied by interspecific copulation.

Table IV. Aggressive behaviour between sympatric dolphins.

Aggressive behaviour ^a		Location	References
Aggressors	Victims		
<i>T. truncatus</i>	<i>P. phocoena</i>	Moray Firth (Scotland)	Ross & Wilson 1996 Patterson et al. 1998
<i>L. obliquidens</i>	<i>P. phocoena</i>	San Juan Island (Washington State)	Baird 1998
<i>S. frontalis</i>	<i>T. truncatus</i>	Great Bahama Bank, Bahamas	Herzing et al. 2003
<i>S. longirostris</i>	<i>S. attenuata</i>	Hawaii (eastern tropical Pacific)	Psarakos et al. 2003
<i>G. griseus</i>	<i>S. coeruleoalba</i>	Gulf of Corinth, Greece	Frantzis & Herzing 2002
	<i>D. delphis</i>		
<i>G. griseus</i>	<i>G. melana</i>	Santa Catalina Island, California	Shane 1995

^aThis list does not include predatory–prey mixed-species interactions observed for transient killer whales feeding on small cetaceans.

It is clear that by contrasting these infrequent examples of interactions, the majority of the investigations conducted world-wide to date show that dolphins tend, whenever possible, to avoid direct competition by using behavioural, dietary and physiological habitat specializations (Table II).

Future research: do sympatric associations among dolphins reflect social complexity?

Species such as bottlenose dolphins and short-beaked common dolphins exhibit a fission–fusion grouping pattern (Connor et al. 2000; Bruno et al. 2004) in which proximate changes in group size and composition appear to reflect proximate availability and distribution of food resources. The key factor that may account for this grouping in dolphins is usually prey, the occurrence of which is ephemeral and patchy, particularly in offshore waters (Clapham 1993).

Dolphins also exhibit high levels of encephalization, having the largest brain-to-body size ratio among the cetaceans (Reiss et al. 1997; Marino 1998; Marino et al. 2000). Such encephalization may enable these animals to forage for widely dispersed, frequently changing food sources, and to cope with the complexities of group life that follow from such a fluid foraging pattern (Würsig 1978; Würsig & Würsig 1980). If fission–fusion grouping is a response to a complex foraging environment and has placed intelligence and social complexity at a premium in these animals, how may it have affected sympatric associations? Ecological information about sympatric dolphins is scarce in comparison with other large brained species such as great apes (Bearzi 2003). Because dolphins' ecological problem-solving needs and abilities parallel those of great apes (Marino 1996, 1998; Reiss et al. 1997) it is possible that similar strategies that rely on cognition and memory have facilitated divergence of foraging strategies when in sympatry with other cetacean species.

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