Aquatic Mammals 1997, **23.3,** 135-143

A survey on the behavior of captive odontocetes in Japan

Fumio Nakahara[1] and Akira Takemura

Faculty of Fisheries, Nagasaki University, Bunkyo, Nagasaki 852, Japan

Abstract

The behaviors of the eleven odontocete species in captivity in Japanese aquariums were surveyed by questionnaires. The survey results include the behavior of some little-known species. The behavioral rating differences among species have been correlated with the social structure and taxonomic relation. Species with close taxonomic relation have similar ratings and are clustered in the close distance. Socialized members of the family delphinidae have been rated high in the affiliative/social/contact behavior, the aggression, and the curiosity/manipulation/play. Phocoenidae species have been rated low in most behavior categories, except the sexual behavior, as compared with the delphinidae and the monodontidae species.

Introduction

Numerous studies have been reported on the behavior of odontocetes. Most of studies, however, have been done in the state of captivity, because of the field survey difficulty due to their habitat. The captive state provides the opportunity to gather details of the odontocete behavior that might not be possible to observe in the wild (Nelson & Lien, 1994). As the captive odontocetes are also living in a restricted environment, their behaviors probably differ from the natural behavior. It is important, however, to observe their behaviors in captivity, because the fundamental patterns can be definitely recognized. DeFran & Pryor (1980) found that in many cases the behaviors exhibited by odontocetes can be correlated very well with the behavioral patterns in the wild.

One approach to the study on the cetacean behavior is a questionnaire survey (DeFran & Pryor, 1980; Terry, 1986). DeFran & Pryor (1980) conducted an extensive questionnaire survey of the behaviors exhibited by eleven species including (beluga, *Delphinapterus leucas*; common dolphin, *Delphinus delphis*; pilot whale, *Globicephala* sp.; boto, *Inia geoffrensis*; Pacific white-sided dolphin, *Lagenorhynchus obliquidens*; killer whale, *Orcinus orca*; false killer whale, *Pseudorca crassidens*; spinner dolphin, *Stenella longirostris*; rough-toothed dolphin, *Steno bredanensis*; bottlenose dolphin, *Tursiops gilli* and *T. truncatus*). Terry (1986) did research on tucuxi, *Sotalia fluviatilis*. DeFran & Pryor (1980) suggested that experienced trainers and researchers familiar with cetacean behavior can make up valuable information resources which deserve more serious scientific attention.

The present survey represents the species kept in captivity in Japan, including six species not surveyed in the previous studies (Commerson's dolphin, *Cephalorhynchus commersonii*; Risso's dolphin, *Grampus griseus*; short-finned pilot whale, *Globicephala macrorhynchus*; finless porpoise, *Neophocaena phocaenoides*; harbor porpoise, *Phocoena phocoena*; and Indian Ocean bottlenose dolphin, *Tursiops aduncus*). There are few published reports about the behavior of these species in captivity and in the wild: *C. commersonii* (Cornell *et al*., 1988; Goodall *et al*., 1988; Iochi, 1995), *G. griseus* (Kruse, 1989; Shane, 1995), *G. macrorhynchus* (Brown, 1960; Norris & Prescott, 1961;

Table 1. Normative data on survey respondents

Species	No. of respondents	Mean years observations
Cephalorhynchus commersonii	3	8
Delphinapterus leucas	1	7
Grampus griseus	4	14
Globicephala macrorhynchus	1	7
Lagenorhynchus obliquidens	10	8
Neophocaena phocaenoides	8	9
Orcinus orca	2	11
Pseudorca crassidens	8	9
Phocoena phocoena	1	9
Tursiops aduncus	1	16
Tursiops truncatus	12	12

[1]Present address: Otsuchi Marine Research Center, Ocean Research Institute, University of Tokyo, Akahama, Otsuchi, Iwate 028-11, Japan.

Table 2. Behavioral ratings and profiles for each of the cetacean species

	Species											Total score
	Cc	Dl	Gg	Gm	Lo	Np	Oo	Pc	Pp	Ta	Tt	
Affiliative/Social/Contact behaviors												
Breathing in union	+	0	0	0	+	+	0	+	0	+	+	+6
Leaping in unison	0	0	−	0	+	−	−	0	−	+	+	−1
Swimming in pairs (pectral fin touching)	+	0	0	0	+	+	+	+	+	+	+	+8
Forms male/female pair	+	0	−		0	+	0	+	−	+	+	+3
Strokes other animal	+	+	−	0	0	+	+	0	0	+	0	+4
Solicits stroking from human	−	+	0	−	0	−	+	+	−	+	+	+1
Mean rating (× 10)	34	33	21	26	31	27	31	32	23	40	33	
Aggression												
Threat posture	0	0	−	−	−	−	−	0	−	0	0	−6
Threat sound	−	0	−	−	−	−	−	0	−	−	0	−8
Tooth rakes	−	0	−	−	−	−	0	−	−	−	0	−6
Harasses new/sick tankmates	−	0	−	−	0	−	0	−	−	0	0	−6
Aggressive toward other cetacean species		0	−	0	−	−	0	0	−	+	0	−3
Threatens to attack other cetaceans	0	0	−	−	0	−	0	0	−	0	0	−4
Threatens to attack human	−	0	−	−	−	−	−	−	−	0	−	−9
Threatens to attack apparatus	−	−	−	−	−	−	−	−	−	−	−	−11
Attacks other cetacean	0	0	−	0	0	−	0	0	−	+	0	−2
Attacks human	−	−	−	−	−	−	−	−	−	−	−	−11
Attacks apparatus	−	−	−	−	−	−	−	−	−	0	−	−10
Mean rating (× 10)	17	25	14	15	17	13	20	22	14	27	22	
Care-giving												
Assists/protects new tankmate	−	−	−	−	−	−	−	−	−	−	−	−11
Supports sick/injured tankmate	−	−	−	−	−	−	−	0	−	−	−	−10
Mean rating (× 10)	10	15	13	10	14	10	15	22	10	10	19	
Fear/Stress/Subordination												
Avoids new objects	+	0	0	+	+	+	+	+	0	0	+	+6
High-speed swimming	+	0	0	+	+	+	0	+	0	0	+	+6
Chuffing (Sharp exhalation)		−	−	−	−	−	0	−	−	−	−	−9
Bunching (drawing together when alarmed)	+	+	0	+	+	0	+	+	+	−	+	+7
Gives distress sound	−	−	−	−	−	−	0	−	−	−	−	−10
Shows whites of eyes	−	−	−	−	−	−	−	−	−	−	−	−11
Lies passively on tank bottom	−	−	−	−	−	−	0	−	−	0	0	−8
Subordinates to other cetacean species		−	−	−	−	−	−	−	−	−	−	−10
Prostrates across other's rostrum	−	−	−	−	−	−	−	−	−	0	−	−10
Turns ventral up if threatened	−	−	−	−	−	−	−	−	−	0	−	−10
Other subordinate display	−	−	−	−	−	−	−	−	−	0	−	−10
Tail-slaps	−	0	0	0	0	−	0	0	−	0	0	−3
Mean rating (× 10)	19	18	17	19	17	23	23	22	17	22	21	
Curiosity/Manipulation/Play												
Approaches new objects	+	+	0	0	+	0	0	0	−	+	+	+4
Manipulates new objects	0	+	0	−	0	−	0	0	−	+	+	0
Opens gates, lifts nets etc.		0	−	−	−	−	−	0	−	+	+	−4
Cooperates with other cetaceans	−	0	−	−	−	−	−	−	−	+	0	−7
Removes tag, rope, etc. from other cetacean			−	−	−	−		−	−	−	−	−8
Invents games	−	0	−	−	−	−	+	0	−	0	0	−5
Manipulates noncetacean animals			−		0	0		+	0	−	−	−1
Mimics sounds	−	0	−	−	−	−	−	−	−	−	−	−10
Plays with familiar objects (ball etc.)	+	+	0	0	+	0	+	+	−	+	+	+6
Plays chase with cetacean	0	0	0	0	+	0	0	+	+	+	+	+5
Other games with cetacean (e.g., "keep away")	0	0	−	0	0	−	0	0	−	0	0	−3
Spy-hop	+	+	−	0	0	−	+	+	−	−	0	0
Mean rating (× 10)	26	34	19	19	23	17	27	26	16	30	26	

Table 2. *Continued*

	Species											Total score
	Cc	Dl	Gg	Gm	Lo	Np	Oo	Pc	Pp	Ta	Tt	
Sexual behavior												
Rubs genitals on tank objects	0	−	−	−	−	−	−	−	−	+	0	− 7
Attempts intercourse with conspecific of the other sex	+	0	0	−	0	0	0	−	−	+	0	− 1
Attempts intercourse with conspecific of the same sex	+	0	−	−	0	0	0	−	−	+	0	− 2
Attempts intercourse with other species of the opposite sex		−	−	−	−	−	−	−	−	+	0	− 7
Attempts intercourse with other species of the same sex		0	−	−	−	−	0	−	+	+	−	− 4
Male attempts intercourse with other sex	+	0	0	−	0	0	0	−	−	+	0	− 1
Intercourse with conspecific	+	−	−	−	0	0	−	−	−	+	0	− 4
Intercourse with cetacean of other species		−	−	−	−	−	−	−	−	+	−	− 7
Other sexual behavior	+	0	−	−	−	0	0	−	−	0	−	− 5
Mean rating (× 10)	34	22	18	10	21	21	22	17	13	39	23	
Leaping and Surface Behavior												
Breaches (lands flat on side/back)	0	0	0	0	0	−	−	+	−	0	0	− 2
Porpoises (smooth arching reentry)	+	−	−	−	+	−	−	0	−	+	+	− 2
Other types of leap (e.g., spin)	+	−	−	−	0	−	−	−	−	−	0	− 7
Pectoral slap on water surface	−	−	0	0	−	−	0	−	−	−	−	− 8
Slaps head on water surface	−	−	0	−	−	−	−	0	−	−	0	− 8
Mean rating (× 10)	23	14	23	18	23	11	19	24	10	26	24	

Cc = *Cephalorhynchus commersonii*; Dl = *Delphinapterus leucas*; Gg = *Grampus griseus*; Gm = *Globicephala macrorhynchus*; Lo = *Lagenorhynchus obliquidens*; Np = *Neophocaena phocaenoides*; Oo = *Orcinus orca*; Pc = *Pseudorca crassidens*; Pp = *Phocoena phocoena*; Ta = *Tursiops aduncus*; Tt = *Tursiops truncatus*.
The 'Total score' is the algebraic sum of the row ratings, where minus and plus are understood as − 1 and +1, respectively, and zero as the algebraic zero.
The 'Mean rating' is obtained by summing the raw scores for items and dividing by the number of items rated in that column. Raw scores consist of the average ratings (1–4) given by all respondents for that item.

Brown *et al*., 1966; Shane, 1995), *N. phocaenoides* (Izawa & Kataoka, 1965; Liu *et al*., 1986; Asai, 1992, 1993*a*, 1993*b*), *P. phocoena* (Andersen & Dziedzic, 1964; Andersen, 1969, 1976), and *T. aduncus* (Tayler & Saayman, 1972; Saayman *et al*., 1973).

Methods

The studied odontocete species are Commerson's dolphins (*Cephalorhynchus commersonii*), belugas (*Delphinapterus leucas*), Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), finless porpoises (*Neophocaena phocaenoides*), killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), harbor porpoises (*Phocoena phocoena*) and bottlenose dolphins (*Tursiops aduncus* and *T. truncatus*).

Questionnaires on behavior were sent to participants holding odontocetes at sixteen aquariums in Japan. The name and institutional affiliation of each participant is given in the acknowledgement section.

In this survey, almost the same list of behavioral events used by DeFran & Pryor (1980) was incorporated. The methods for making a list of behavioral events and reasons for grouping the events into seven categories were described by DeFran & Pryor (1980). All of the behaviors were translated into Japanese, as judged to be familiar to the respondents, and in addition two cetacean homosexual behavior events were included, based on the experience of the authors.

Respondents were asked to estimate the frequency of each behavior observed, through use of a scale of (1)–(4); (1) never observed, (2) rarely observed, (3) occasionally (moderately often) observed, and (4) frequently observed.

To clarify a similarity of the behavioral characteristics of each of these species, a cluster analysis was conducted using the mean ratings of species within each of the seven behavioral categories. This

analysis groups together those species within a set that are highly correlated.

Results

The total number of respondents and the observational experiences of respondents are summarized in Table 1. For *D. leucas*, *G. macrorhynchus*, *P. phocoena* and *T. aduncus*, only one respondent returned. Captive environments of each species were different. *T truncatus*, *P. crassidens*, *G. griseus* and *G. macrorhynchus* have maintained together in many aquariums, but most of *N. phocaenoides*, *O. orca* and all *C. commersonii* have maintained only with conspecifics.

The responses to the behavioral questionnaire are summarized in Table 2. The behavioral ratings, shown in Table 2, minus, zero, and plus, indicate the mean rating over the respondents of 1.0 to 2.0, 2.1 to 3.0, and 3.1 to 4.0, respectively. In general terms, minus, zero, and plus, each indicate 'rare occurrences', 'moderate number of occurrences', and 'frequent occurrences' of the behavior, respectively.

The mean ratings within the columns of each behavioral category are based on raw-score ratings and provide the information on the degree, according to which a given category classifies the species.

The comparison of the respondents for *T. truncatus* in the present study with the earlier survey results of DeFran & Pryor (1980) and Terry (1986) show a similarity in the affiliative/social/contact behavior and the care-giving behavior. Other ratings are a little lower in the present study (Fig. 2).

The affiliative/social/contact behaviors are rated relatively high in *C. commersonii*, *D. leucas*, *P. crassidens*, *T. aduncus* and *T. truncatus*, while low for *G. griseus*, *P. phocoena*. Breathing in union and swimming in pairs occurs frequently in most of the species.

Most of the species are rated infrequent on the aggressive behavior. *N. phocaenoides*, *G. griseus* and *P. phocoena* show very low aggressive behavior. Only *T. aduncus* was frequently observed aggressive toward other cetacean species and to attack other cetacean.

The care-giving behavior is rated very low for all species. Especially in *C. commersonii*, *G. macrorhynchus*, *N. phocaenoides*, *P. phocoena* and *T. aduncus*, the care-giving behavior has never been observed.

Fear/stress/subordination are rated relatively low for all species. Avoiding new objects, high-speed swimming and bunching are the most common fear/stress/subordination behaviors in all species.

D. leucas, *T. aduncus*, *O. orca*, *P. crassidens*, *T. truncatus* and *C. commersonii* scored relatively high in the curiosity/manipulation/play. Approaching new objects, playing with familiar objects and playing chase with other cetaceans occur frequently in many species.

Sexual behavior is rated high in *T. aduncus* and *C. commersonii*. On the other hand, *G. macrorhynchus*, *P. phocoena*, *G. griseus* and *P. crassidens* rank relatively low in this category.

The leaping and surface behaviors were scarcely observed in *P. phocoena* and *N. phocaenoides*. Whereas *T. aduncus* have the highest positive rating.

Some other behaviors were observed by respondents. A number of *T. truncatus*, *L. obliquidens*, *D. leucas* and *N. phocaenoides* had been observed to create shimmering, stable rings of the air as part of the play (Asai & Asai; Takayama; Kaneko; Okamura, per. comms.). *D. leucas* at the Kamogawa Sea World expel bubbles from their blowholes and then suck into and spit out from their mouths (Kaneko, per. comms.). Marten *et al.* (1996) described that these bubbles that are clearly not a spontaneous response to the alarm or a standard part of the communication, because of the intricate techniques and practices required to form such rings and helices. *N. phocaenoides* spit quantities of water into the air from their mouths while spy hopping (Hamasaki; Kitamura; Okamura, per. comms.). *C. commersonii* frequently use their flipper serrations for a tactile stimulation, rubbing the front edge of the flipper across the body, the genital slit or flippers of other animals (Wakabayashi, per. comms.). *N. phocaenoides* also use their tubercles on the back for a tactile stimulation (Nakahara, per. observ.).

The results of the cluster analysis (unweighted group average strategy) are shown in Fig. 1. The shortest distance among eleven species is 1.13 for the *P. crassidens* and *T. truncatus* pair. *N. phocaenoides* and *P. phocoena* are clustered next. Clusters are divided mainly into two clusters. One cluster is composed of *P. crassidens*, *T. truncatus*, *O. orca*, *L. obliquidens*, *C. commersonii*, *D. leucas*, and *T. aduncus*. The other cluster includes *N. phocaenoides*, *P. phocoena*, *G. macrochynchus*, and *G. griseus*.

Figure 2 shows the mean ratings of Table 2 for each of species grouped according to the clusterings of Fig. 1. The behavioral ratings of *P. crassidens* resemble the ratings of *T. truncatus* well, except the sexual behavior. *O. orca* is rated lower than *T. truncatus* in the leaping and surface behaviors, and the care-giving behavior. Also ratings of *N. phocaenoides* and *P. phocoena* pair, and of *L. obliquidens* and *C. commersonii* pair are similar, except the sexual behavior.

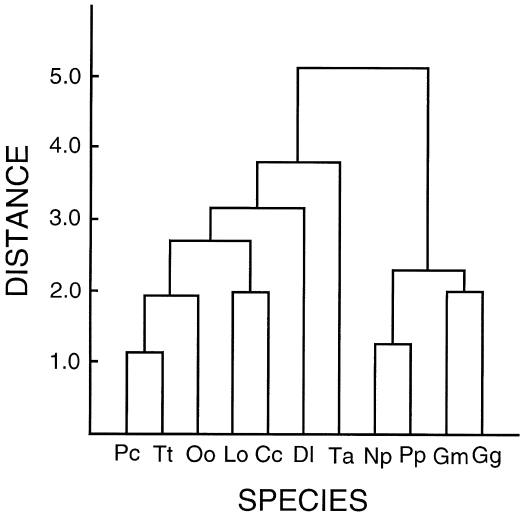

Figure 1. Result of the cluster analysis (unweighted group average strategy). Cc=*Cephalorhynchus commersonii*; Dl=*Delphinapterus leucas*; Gg=*Grampus griseus*; Gm=*Globicephala macrorhynchus*; Lo=*Lagenorhynchus obliquidens*; Np=*Neophocaena phocaenoides*; Oo=*Orcinus orca*; Pc=*Pseudorca crassidens*; Pp=*Phocoena phocoena*; Ta=*Tursiops aduncus*; and Tt=*Tursiops truncatus*.

Discussion

DeFran & Pryor (1980) omitted from the analysis those species of which less than four respondents returned. Though these results are apt to be affected by the respondent's subjectivity, we have included these results for these species for references, because these data are very valuable and only a few aquariums have maintained these animals in Japan.

The results of the present survey, ratings and clusterings, showed the agreement with a previous study (DeFran & Pryor, 1980). The Euclidean distance between *P. crassidens* and *T. truncatus* are very close and *O. orca* is close to these two species in both the previous and present studies. Also clusters are correlated according to the taxonomic classification. *N. phocaenoides* and *P. phocoena*, Euclidean distance being very close, belonging to the same family Phocoenidae.

DeFran & Pryor (1980) suggested that among the social correlates of the behavior, the herd size appears to bear some relationship to the observed species clustering. One cluster (*P. crassidens*, *T. truncatus*, *O. orca*, *L. obliquidens*, *C. commersonii*, *D. leucas*, and *T. aduncus*) is composed of relatively socialized gregarious species, excepting *C. commersonnii* (Table 3). Herd sizes of *P. crassidens*, *T. truncatus* and *O. orca* are typically 10–50, but sometimes several hundred (Martin, 1990; Klinowska, 1991; Jefferson *et al*., 1993). The herds of *P. crassidens* usually contain animals of all ages of both sexes. *T. truncatus* and *T. aduncus* form highly variable herds. Segregation of subadult and adult males probably reflects the dominance in the social structure. *O. orca* is intensely social, living in stable pods. *L. obliquidens* is often in large herds, numbering in the hundreds if not thousands (Martin, 1990). *D. leucas* is very social animal, rarely seen alone and sometimes coming together into groups of many thousands. Small, tight-knit groups of up to 15 animals are usual, typically consisting either of males, or mothers and offsprings (Martin, 1990). Apart from occasional, probably short-term, aggregations of large numbers, sometimes exceeding 100 animals, *C. commersonii* is often seen in small groups of less than 10 animals, and usually of 1–3 (Goodall *et al*., 1988; Martin, 1990; Klinowska, 1991). These socialized species of family delphinidae and monodontidae are characterized by high ratings in inter-individual behaviors, such as the affiliative/social/contact behavior, the aggression, and the curiosity/manipulation/play.

The other cluster includes *N. phocaenoides*, *P. phocoena*, *G. macrorhynchus*, and *G. griseus*. Though adventitious aggregations of 50 or more *N. phocaenoides* and *P. phocoena* are seen occasionally, they are more often encountered singly, in pairs, or in groups of 5–10. The larger concentrations may simply be loose coalitions of these small groups, formed seasonally for migration or for taking advantage of especially rich feeding grounds (Martin, 1990; Jefferson *et al*., 1993). *G. macrorhynchus* is normally seen in groups. The size range is 1–200 and average 40. This species is thought to be multi-male polygynous (Martin, 1990). Most groups of *G. griseus* are quite small, consisting of a dozen or several dozen animals. However, this species does occasionally form large herds, the largest being reportedly containing 4000 individuals. They commonly form mixed aggregations with other dolphin species (Martin, 1990; Klinowska, 1991). Though *G. macrorhynchus* and *G. griseus* are known to form the large herds, socializing behaviors (e.g. frequent body contact and surface displays such as breaching) are rarely observed in the wild (Shane, 1995). The species of this cluster were characterized by low ratings in inter-individual behaviors, as compared with the other cluster.

There were a few disagreements, which may be caused by the effect of captive circumstances, between the present survey and the previous observational studies. *G. macrorhynchus* and *G. griseus* were kept single or in two individuals mixed in many other cetacean species. But they are found in herds as large as 100 or more in nature (Kasamatsu

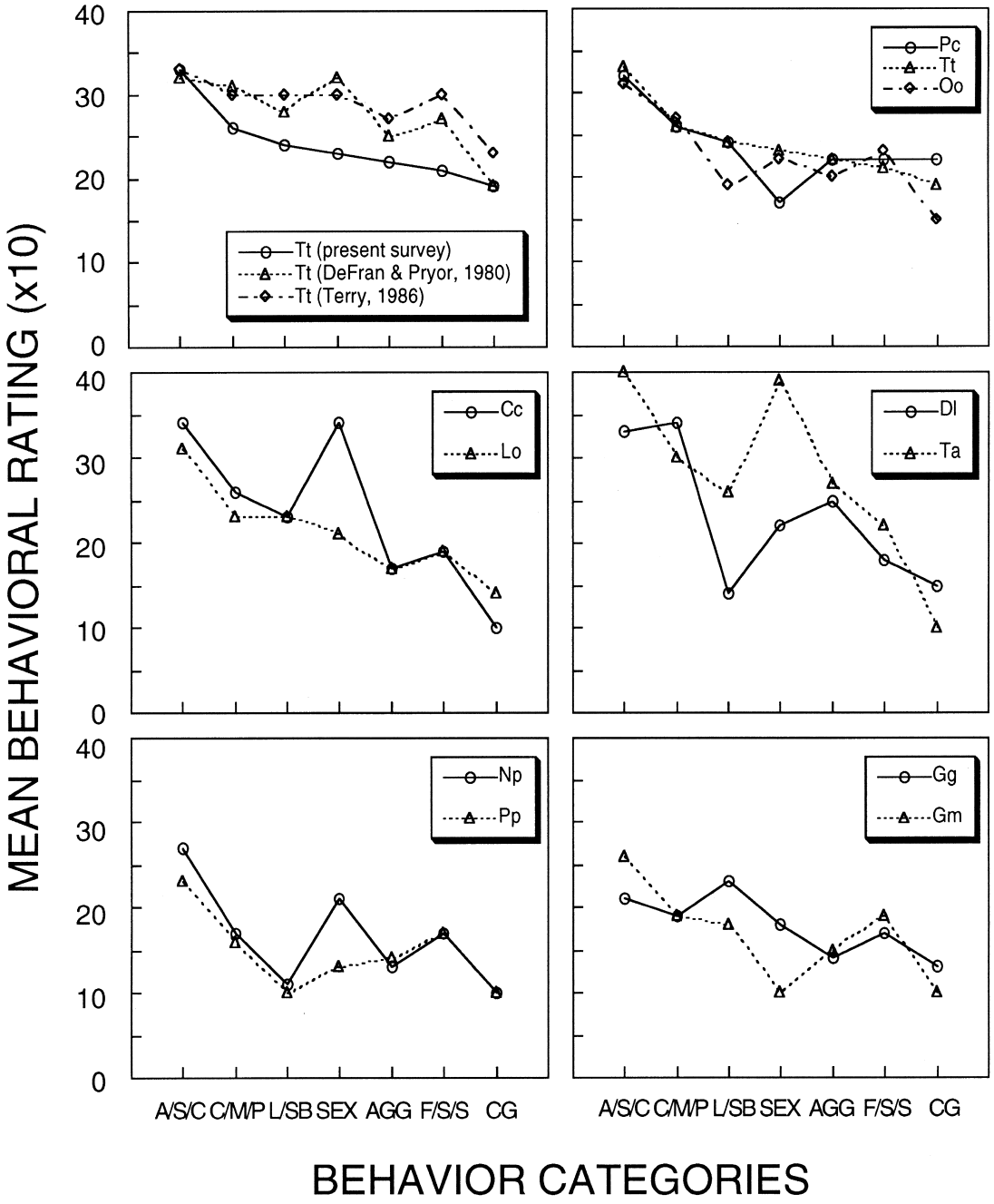

Figure 2. Behavioral profiles for the species, grouped according to the cluster analysis. A/S/C=Affiliative/Social/Contact behaviors; C/M/P=Curiosity/Manipulation/Play; L/SB=Leaping and Surface behavior; SEX=Sexual behavior; AGG=Aggression; F/S/S=Fear/Stress/Subordination; and CG=Care-giving.

& Miyashita, 1991). Though the behavior patterns of *G. macrorhynchus* and *G. griseus* were poorly known, and Shane (1995) reported that socializing behaviors of these species are rarely observed, ratings of the affiliative/social/contact behaviors and the sexual behavior of two species must have

Table 3. Behavioral and ecological characteristics of each of the odontocete species

Species	Habitat	Migration	Group size	Group characteristics	Food and feeding	References
Cc	Coastal, normal offshore limit is about the 100 m deep	Seasonal movements	Often seen in small groups of less than 10, usually 1–3; occasional short-term aggregations over 100		Crustaceans, squids, coastal fishes	Leatherwood & Reeves, 1983; Goodall *et al.*, 1988; Martin, 1990; Klinowska, 1991
Dl	Coastal, estuarine	Seasonal movements	Usually up to 15; sometimes aggregations of thousands	Typically consisting either of males or mothers and offsprings	Benthopelagic fishes, crustaceans, molluscs	Leatherwood & Reeves, 1983; Martin, 1990; Jefferson *et al.*, 1993
Gg	Offshore	Seasonal movements	Dozen or several dozen; occasionally up to 4000	Commonly form mixed aggregations with other dolphin species	Cephalopods, fishes	Leatherwood & Reeves, 1983; Martin, 1990; Klinowska, 1991
Gm	Coastal, pelagic	Seasonal movements	1–200 and average 40	Multi-male polygnous; commonly associated with other species	Cephalopods, fishes	Leatherwood & Reeves, 1983; Martin, 1990
Lo	Continental shelf, continental slope, offshore	Seasonal movements	Often in the hundreds if not thousands	Contain animals of all ages and both sexes; commonly associated with other species	Small schooling fishes, squid	Leatherwood & Reeves, 1983; Martin, 1990; Jefferson *et al.*, 1983
Np	Shallow coastal, estuarine, riverine	Seasonal movements	Singles, pairs, or up to 12; occasional short-term aggregations up to 50	Mother-calf pair is only stable unit of schools	Bottom feeding; small fishes, squids, shrimps	Kasuya & Kureha, 1979; Martin, 1990; Jefferson *et al.*, 1993
Oo	Coastal, pelagic, estuarine, riverine	Resident; Transient=seasonal movements	Stable pods of 3–50, usually 3–25; sometimes aggregations up to hundreds	Stay in their maternal pod throughout life	Medium-sized fishes, pinnipeds, penguins, other seabirds, sea turtles, cetaceans	Leatherwood & Reeves, 1983; Martin, 1990; Klinowska, 1991
Pc	Pelagic	No migrations are known	Typically 10–50; sometimes several hundred	Contain animals of all ages and both sexes	Squids, large fishes, small cetaceans	Martin, 1990; Jefferson *et al.*, 1993
Pp	Coastal, estuarine	Seasonal inshore-offshore migration; year-round resident	Singles, pairs, or 5 to 10; occasionally aggregate into loose groups of 50 to several hundred		Bottom feeding; small schooling fishes, cephalopods	Leatherwood & Reeves, 1983; Martin, 1990; Jefferson *et al.*, 1993
Tt (Ta)	Coastal, pelagic	Distinct inshore & offshore populations; seasonal movements; year-round resident	Highly variable, commonly less than 20, several hundred offshore	Age-sex segregation of subgroups; mother-calf bonds are long-lasting	Individual & cooperative feeding; inshore=fishes, squids, octopi; offshore=bottom-dwelling fishes, squids, schooling fishes	Wells *et al.*, 1980; Shane *et al.*, 1986; Martin, 1990

been low for them. Kasuya & Kureha (1979) suggested that the social structure of *N. phocaenoides* seems to be undeveloped, the mother–calf pair is an only stable unit of schools and about 50% of the encounters are solitary. So affiliative/social/contact behaviors are probably rated too high in the present survey, because the aquariums in this survey have maintained plural adults in a tank. Especially, stroking other animals is rated high, and from our observation, this behavior is frequently seen between the adults in captivity, but it is doubtful whether adults pair-off frequently in the wild.

DeFran & Pryor (1980) also suggested that there appear interesting relationships between the behavioral clusters and the ecological characteristics, specifically feeding ecology. But Gaskin (1982) suggested that it should be obvious that the ecological classification of odontocetes by the diet pattern is impractical, because most odontocetes are opportunistic feeders, and preferences are often dictated by circumstances. It is difficult to consider the behavioral clusters in relation to feeding types.

A difficult aspect of the task requested of the respondents is to generalize behavioral ratings over a period of time (Terry, 1986). Respondents in this survey are also aware of this problem. While the captive environment may have some effects on the behavioral patterns, further studies are needed on wild animals. So we must establish a novel method for the field survey. However, it is important to continue the study of the social behavior of odontocetes in captivity.

Acknowledgements

We wish to express our thanks to the following people for their responses to the behavior survey: K. Kagoshima and T. Kawajiri (Otaru Aquarium); T. Tamura (Asamushi Aquarium); J. Jingu and K. Sawaki (Marinepia Matsushima Aquarium); S. Inoue, S. Kaneko and H. Katsumata (Kamogawa Sea World); T. Mitsuhashi (Sunshine International Aquarium); S. Kitamura (Enoshima Aquarium); S. Hagiware and T. Satomi (Shimoda Floating Aquarium); S. Aihara and Y. Saito (Notojima Aquarium); Y. Asai, C. Asai, F. Sato and H. Sato (Minamichita Beachland Aquarium); H. Taishaku and I. Wakabayasi (Toba Aquarium); T. Ishikawa, Y. Kurihara, K. Taniguchi and M. Yonekura (Adventure World in Shirahama); K. Chimoto and N. Takayama (Osaka Aquarium Ring of Fire); H. Okamura (Miyajima Public Aquarium); M. Nakano, M. Satomura and J. Watanabe (Shimonoseki Municipal Aquarium); H. Hiruda (Marine World Umino-nakamichi); E. Hamasaki (Amakusa Natural Submarine Aquarium); T. Nagasaki (Okinawa Expo Memorial Park Aquarium).

We also thank Masayuki Nakamura, Kaoru Fujimaru and Yoko Saito (Marine World Umino-nakamichi), who gave us the information available. Miki Shirakihara and Hideyoshi Yoshida gave some useful advice. The manuscript has been improved according to the comments provided by Yasuaki Nakahara and reviewers.

References

Andersen, S. (1969) Epimeletic behavior in captive harbor porpoise, *Phocoena phocoena* (L.). In: G. Pilleri (ed.) *Investigations on Cetacea, Vol. I*. pp. 203–205. Institute of Brain Anatomy, University of Bern: Bern.

Andersen, S. (1976) The taming and training of the harbor porpoise, *Phocoena phocoena. Cetology* **24,** 1–9.

Andersen, S. & Dziedzic, A. (1964) Behavior patterns of captive harbor porpoises. *Bull. Inst. Oceanogr. Monaco* **63,** 1 − 20.

Asai, C. (1992) Observation on the behavior of the finless porpoise (1). *Echolocation* **13**(2), 1–3 (in Japanese).

Asai, C. (1993*a*) Observations on the behavior of the finless porpoise (2). *Echolocation* **13**(4), 1–3 (in Japanese).

Asai, C. (1993*b*) Observations on the behavior of the finless porpoise (3). *Echolocation* **14**(1), 1–4 (in Japanese).

Brown, D. H. (1960) Behavior of captive Pacific pilot whale. *J. Mammal.* **41**(3), 342–349.

Brown, D. H. & Norris, K. S. (1956) Observations of captive and wild cetaceans. *J. Mammal.* **37**(3), 311–326.

Brown, D. H., Caldwell, D. K. & Caldwell, M. C. (1966) Observations on the behavior of wild and captive false killer whales, with notes on associated behavior of other genera of captive delphinids. *Los Ang. Cty. Mus. Nat. Histo. Contrib. Sci.* **95,** 1–32.

Cornell, L. H., Antrim, J. E., Asper, E. D. & Pincheira, B. J. (1988) Commerson's dolphins (*Cephalorhynchus commersonii*) live-captured from the Strait of Magellan, Chile. *Rep. Int. Whal. Commn*. (Special Issue 9), 183–194.

DeFran, R. H. & Pryor, K. (1980) The behavior and training of cetaceans in captivity. In: L. M. Herman (ed.) *Cetacean Behavior: Mechanisms and Functions*. pp. 319–362. John Wiley & Sons: New York.

Gaskin, D. E. (1982) *The Ecology of Whales and Dolphins*. Heinemann Educational Books Ltd: London. 459 pp.

Goodall, R. N. P., Galeazzi, A. R., Leatherwood, S., Miller, K. W., Cameron, I. S., Kastelein, R. K. & Sobral, A. P. (1988) Studies of Commerson's dolphins, *Cephalorhynchus commersonii*, off Tierra del Fuego, 1976–1984, with a review of information on the species in the South Atlantic. *Rep. Int. Whal. Commn*. (Special Issue 9), 3–70.

Iochi, A. (1995) Behaviour patterns of two captive Commerson's dolphins, *Cephalorhynchus commersonii*. Graduation Thesis: Tokyo Univ. of Fish., 27 pp (in Japanese).

Izawa, K. & Kataoka, T. (1965) On the rearing and ecological observation of the finless black porpoise (*Neophocaena phocaenoides*). *J. Jap. Ass. Zool. Gardens and Aquariums* **7**(3), 56–62 (in Japanese).

Jefferson, T. A., Leatherwood, S. & Webber, M. A. (1993) *FAO Species Identification Guide. Marine Mammals of the World*. FAO: Rome. 320 pp.

Kasamatsu, F. & Miyashita, T. (1991) *Field Guide of Whales and Dolphins*. University of Tokyo Press: Tokyo. 149 pp. (in Japanese).

Kasuya, T. & Kureha, K. (1979) The population of the finless porpoise in the Inland Sea of Japan. *Sci. Rep. Whale Res. Inst.* **29,** 1–20.

Klinowska, M. (1991) *Dolphins, Porpoises and Whales of the World*. The IUCN red data book. IUCN, Gland. 429 pp.

Kruse, S. L. (1989) Aspects of the biology, ecology, and behavior of Risso's dolphins (*Grampus griseus*) off the California coast. M. S. Thesis, Univ. of California at Santa Cruz, 120 pp.

Leatherwood, S. & Reeves, R. R. (1983) *The Sierra Club Handbook of Whales and Dolphins*. Sierra Club Books: San Francisco. 302 pp.

Liu, R., Klinowska, M. & Harrison, R. J. (1986) The behavior of *Lipotes vexillifer* and *Neophocaena phocaenoides* in the Changjiang river and in captivity in China. In: M. M. Bryden & R. J. Harrison (eds) *Research on Dolphins*. pp. 433–439. Clarendon Press: Oxford.

Marten, K., Shariff, K., Psarakos, S. & White, D. J. (1996) Ring bubbles of dolphins. *Sci. Am*. August, 82–87.

Martin, A. R. (1990) *Whales and Dolphins*. Salamander Books: London. 192 pp.

Nelson, D. L. & Lien, J. (1994) Behaviour patterns of two captive Atlantic white-sided dolphins, *Lagenorhynchus acutus. Aquatic Mammals* **20**(1), 1–10.

Norris, K. S. & Prescott, J. H. (1961) Observation on Pacific cetaceans of California and Mexican waters. *Univ. Calif. Publ. Zool.* **63**(4), 291–402.

Saayman, G. S., Tayler, C. K. & Bower, D. (1973) Diurnal activity cycles in captive and free ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenberg). *Behaviour* **44,** 212–233.

Shane, S. H. (1995) Behavior patterns of pilot and Risso's dolphins off Santa Catalina Island, California. *Aquatic Mammals* **21**(3), 195–197.

Shane, S. H., Wells, R. S. & Würsig, B. (1986) Ecology, behavior and social organization of the bottlenose dolphin: a review. *Mar. Mamm. Sci.* **2**(1), 34–63.

Tayler, C. K. & Saayman, G. S. (1972) The social organization and behavior of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): Some comparisons and assessments. *Ann. Cape Prov. Mus. Nat. Hist.* **9,** 11–49.

Terry, R. P. (1986) The behavior and trainability of *Sotalia fluviatilis guianensis* in captivity: a survey. *Aquatic Mammals* **12**(3), 71–79.

Wells, R. S., Irvine, A. B. & Scott, M. D. (1980) The social ecology of inshore odontocetes. In: L. M. Herman (ed.) *Cetacean Behavior: Mechanisms and Functions*. pp. 263–317. John Wiley & Sons: New York.