Niche Separation and Niche Overlap in the Delphinoidea (Delphinidae, Phocoenidae and Monodontidae)

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Gygax, L. (2002) Niche Separation and Niche Overlap in the Delphinoidea (Delphinidae, Phocoenidae and Monodontidae). Available on http://www.proximate-biology.ch/lgygax/phd/info.html: The Delphinoidea species can be successfully classified by ecological variables using discriminant analysis in a step-wise procedure and thus the species seem to have non-identical niches. In a first step, the Delphinoidea species can be split in three groups according to body length: 17 species of small Delphinoidea, 6 species of large Delphinoidea and the killer whales (*Orcinus orca*). The large Delphinoidea can then be categorised on their own with a remaining classification error of about 10 %. To achieve a similar result for the small Delphinoidea they have to be split according to region. Data for the North Atlantic and the North Pacific are evaluated. Though all the species of the North Atlantic also occur in the North Pacific these categorisations have much lower misclassification rates. This indicates that niches are more strictly separated within a region than between regions and thus some species in the North Atlantic may occupy similar niches to those of other species in the North Pacific. Body length was again the most important variable in the discriminant analyses on the three species subsets. This is surprising in that one would assume that species of similar body length tend to occupy similar niches and would thus displace each other by competition into ecological niches that differ *e.g.*, in their physical characteristics and/or their prey spectrum.

Every species is assumed to have found its own niche over the course of its evolutionary development. A niche can be seen as the specialisation of a species and it is thought that no two sympatric species may occupy the same niche. Competition would be high and such that species would specialise into different niches (Pianka, 1976).

This is not different for the Delphinoidea. But, though data on these species has rapidly accumulated over the recent years, no attempt has been made so far to investigate niche separation and niche overlap in the Delphinoidea quantitatively and comprehensively. Most studies have compared only few species in a restricted geographical area (*e.g.*, Perrin *et al.*, 1973; Perrin, 1975; Scott and Cattanach, 1998) or closely related sympatric subspecies differing in their ecology such as bottlenose dolphins (Hersh, 1990; Hoelzel *et al.*, 1998) common dolphins (Rosel *et al.*, 1994), and killer whales (*e.g.*, Morton, 1990; Ford *et al.*, 1994).

In a recent interspecific comparison Gygax (2000) showed that species is the one most important predictor of group size in Delphinoidea, *i.e.*, group size of Delphinoidea species could be predicted well by the species but ecological variables had only little predictive power. Though many species show highly variable group sizes, group size does on average show some species specificity. Of course, there are several species with similar group sizes and thus not all the species are different.

Still, the group sizes could represent a part of the specific niche of a species. It is then tempting to see whether and how group size and variables on the physical environment, the diet and the life-history might be used to differentiate between these species.

In addition to a better understanding of the ecology of the different species this approach potentially gives new insights into their still unresolved phylogeny complementing evolutionary information based on DNA and morphology (*e.g.*, LeDuc *et al.*, 1999). One would expect the highest niche segregation between the families Delphinidae, Phocoenidae and Monodontidae which seem to have split early at almost the same time (Milinkovitch *et al.*, 1993, 1994; Árnason and Gullberg, 1996). The same is true within the subfamilies as a contemporaneous radiation is suggested at least for some subfamilies of the Delphinidae (Delphininae, Globicephalinae and Cephalorhynchinae, Ohland *et al.*, 1995) and the species of the Phocoenidae (Rosel *et al.*, 1995a).

The segregation into different niches is investigated in the present study using discriminant analyses. This will show whether and how the Delphinoidea species can be differentiated by their ecology, sociobiology and life history. The variables used to reflect these concepts were physical parameters of the habitat, group size, diet composition, body length and body length dimorphism.

Methods

Data base — The data used for the present study is part of a larger data set put together from published and unpublished literature available up to November 1998 (the data base and a more detailed description including all references are available on http://proximate-biology.ch/lgygax/phd/info.html). The aim of the principal database was to collect data on group size in Delphinoidea and to complement this data with information on life-history, physical environment and diet. An attempt was made to estimate all this information as exactly as possible. Single studies reporting group size were chosen as the replicates to catch as much variability in group sizes as possible but to ensure that only data from one location ("population") contributed to the reported numbers.

A case in the data base was defined by each (independent) study that reported some measure of group size (Table 1). This information was then complemented. In most cases environmental variables were complemented with the aid of depth and surface temperature maps. Information on the life-history variables came from one or several other publications (per region) as did information on prey (Table 1). All values are local means (*e.g.*, body length is the average length achieved by animals of a certain species in a certain geographical region). If several sets of information for one species and region were available for group size and diet and/or life-history data, the different kind of information was randomly combined. If no information was available for a given species in a specific region the information from the geographically closest location was chosen as the best estimate. This is based on the assumption that animals in geographically close regions are similar and that, in principal, they would have values in these variables that are similar to those of near regions.

Variables — The response variable for the discriminant analysis is **species**. This was used as indicated in the papers (an overview can be found in Rice, 1998). As explanatory variables the following were included in the discriminant analysis:

The **average group size** was defined as the average of all observed groups in a given study. A group was usually defined as all animals that were spatially close together and were engaged in the same behaviour.

The **physical environment** was characterised using type of habitat, a measure of habitat

Table 1: Number of studies from which information on the explanatory variables have been gathered. There are at least as many for the physical environment as for group size because these variables have been inferred from the location of the sightings where no specific information could be found. The number of studies including information on diet and body length measurements (and not only estimates) are also given.

	group size physical env.	diet	body length
Cephalorhynchus commersonii	7	7	4
Sotalia spp.	7	4	1
Phocoena phocoena	24	24	5
Phocoena spinipinnis	5	4	2
Stenella longirostris	6	8	5
Lagenorhynchus obscurus	9	6	4
Lagenorhynchus obliquidens	12	8	4
Phocoenoides dalli	31	14	4
Delphinus delphis	28	21	6
Stenella frontalis	6	4	1
Stenella attenuata	12	15	2
Stenella coeruleoalba	24	16	6
Sousa plumbea	7	9	1
Lissodelphis borealis	9	5	1
Lagenodelphis hosei	6	8	2
Tursiops truncatus	81	40	4
Lissodelphis peronii	7	4	1
Grampus griseus	29	13	2
Delphinapterus leucas	5	12	5
Pseudorca crassidens	10	8	1
Monodon monoceros	6	8	2
Globicephala melas	16	19	5
Globicephala macrorhynchus	10	6	2
Orcinus orca	82	111	4

structure, the latitude, the typical temperature, the temperature range, the relative temperature range per typical temperature, the typical depth, the depth range and the relative depth range per typical depth at the locations where animals were observed. Some of these variables are highly correlated. Principal component analysis (PCA) identified four principal components (PC) that accounted for 92 % of the variability in the original data. These four PCs were included in the discriminant analysis as explanatory variables. Ocean "**openness**" increases with distance from shore (less structured, more open and deeper water). "**Warmth**" increases with temperature and decreases with latitude and is thus a reflection of the water temperature. "**Specificity**" is negatively correlated with range of temperature and thus with variability of temperature, and "**smoothness**" shows high values for little structured but shallow areas.

For the description of the **diet** data, four food categories were available but only three of them are included in the present analysis (cephalopods, fishes and mammals/birds). Information on the small invertebrates (mainly crustacea) was discarded because it was often not known whether they were prey of the dolphins themselves or represented secondary feeding. For each of the three main food categories information was available on the occurrence, the frequency and the proportion (resulting in a total of 9 variables). The occurrence just indicated whether the food category had occurred in a sample or not, the frequency is the proportion of individuals in which the food category occurred (*e.g.*, number of stomachs with category by total number of stomachs in sample) and the proportion is the relative amount of a food category in the total sample (*e.g.*, number of items of category by total number of items in sample). The three main categories of cephalopods, fishes and mammals/birds were further classified as benthic, mesopelagic or pelagic (resulting in a total of 27 categories) and as social, solitary or both (resulting in a total of 81 categories).

Due to the correlations among these variables they were also subjected to a PCA prior to inclusion into the discriminant analyses. This resulted in three sets of diet PCs (of which each explained over 90 % of the variability of the original variables): set 1 consisted of six PCs if the PCA was done with all 81 food categories, set 2 consisted of six PCs if the PCA was conducted using the 27 occurrence variables, and set 3 consisted of five PCs if the PCA was based on the 9 main food categories (occurrence, frequency and proportion).

Only one of these three sets was included in any given analysis. More cases were available for set 2 than for set 1 and 3. As these variables are not of great importance in the discriminant analyses no attempt at an interpretation of the PCs is made.

Life-history parameters can be represented by measures of length, mass, dimorphism, maturation and reproduction. The data on these parameters is still sketchy at the population level and often there is only one reported measure for each species. Thus, only the asymptotic length of females and length dimorphism (length of females / length of males) were used in this study. Both these measures were log-transformed.

Statistical methods — Discriminant analysis was used to classify the different species and the models were conducted using a 10-fold cross-validation scheme (Venables and Ripley, 1997, p. 493) thus avoiding overfitting to the available data. Figures and calculations were done with R Version 0.63.1 and 0.64.1 (http://www.r-project.org/R). The discriminant analyses were calculated using the procedure lda from the package "MASS" V 6.1-2 originally coded by W. N. Venables & B. D. Ripley ported to R by B. Ripley (Venables and Ripley, 1997, chapt. 13.3). Models were restricted to the cases for which all variables included in a given model were available and to those species with at least five cases.

Results

"Naive" classification — In a first analysis, all explanatory variables were used to classify Delphinoidea species. These models included 13, 23 and 13 species and 169, 406 and 169 cases for the three sets of diet variables, respectively. Misclassification errors amounted to 25, 32 and 22 % even though the two species with the biggest number of cases (bottlenose dolphins and killer whales) were correctly classified amounting to over 30 % correct classifi-

Table 2: Categorisation of the Delphinoidea species using only body length as an explanatory variable. Rows are known species, columns predicted species (species are ordered with increasing average body length). Numbers give the number of cases. All values off the diagonal are misclassifications. Correct classifications in bold.

	Cc	Ss	Pp	Pi	Sl	Lo	Lq	Pd	Dd	Sf	Sa	Sc	Sp	Ll	Lh	Tt	Lp	Gg	Dl	Pc	Mm	Gs	Gm	Oo
Cc	**2**	2	3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ss	·	·	7	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pp	·	·	**24**	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pi	·	·	5	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sl	·	·	3	·	·	·	·	1	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lo	·	·	3	·	·	·	·	6	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lq	·	·	·	·	·	·	·	12	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pd	·	·	·	·	·	·	·	**25**	6	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dd	·	·	·	·	·	·	·	19	**9**	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sf	·	·	·	·	·	·	·	·	3	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·
Sa	·	·	·	·	·	·	·	3	2	·	·	7	·	·	·	·	·	·	·	·	·	·	·	·
Sc	·	·	·	·	·	·	·	3	7	·	·	**3**	·	·	·	11	·	·	·	·	·	·	·	·
Sp	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	6	·	·	·	·	·	·	·	·
Ll	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	9	·	·	·	·	·	·	·	·
Lh	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	6	·	·	·	·	·	·	·	·
Tt	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	**81**	·	·	·	·	·	·	·	·
Lp	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	7	·	·	·	·	·	·	·	·
Gg	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	**29**	·	·	·	·	·	·
Dl	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	3	·	·	·	·
Pc	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	**10**	·	·	·	·
Mm	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	6	·	·	·	·
Gs	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	6	·	**4**	6	·
Gm	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	6	**4**	·
Oo	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	**82**

Cc: Cephalorhynchus commersonii, Ss: Sotalia spp., Pp: Phocoena phocoena, Pi: Phocoena spinipinnis, Sl: Stenella longirostris, Lo: Lagenorhynchus obscurus, Lq: Lagenorhynchus obliquidens, Pd: Phocoenoides dalli, Dd: Delphinus delphis, Sf: Stenella frontalis, Sa: Stenella attenuata, Sc: Stenella coeruleoalba, Sp: Sousa plumbea, Ll: Lissodelphis borealis, Lh: Lagenodelphis hosei, Tt: Tursiops truncatus, Lp: Lissodelphis peronii, Gg: Grampus griseus, Dl: Delphinapterus leucas, Pc: Pseudorca crassidens, Mm: Monodon monoceros, Gs: Globicephala melas, Gm: Globicephala macrorhynchus, Oo: Orcinus orca

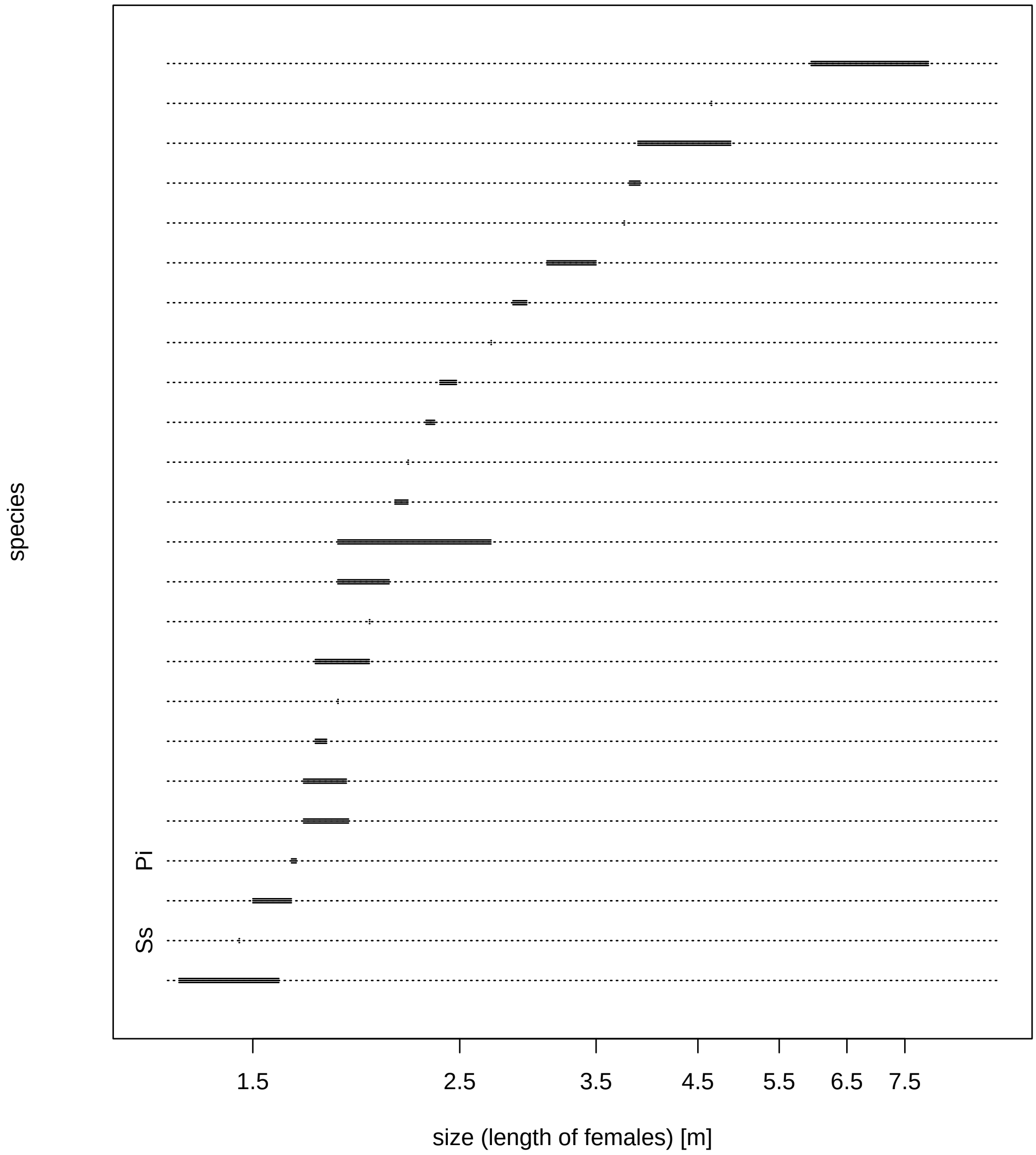
species
Pi
Ss
1.5
2.5
3.5
4.5
5.5
6.5
7.5
size (length of females) [m]

Table 3: Categorisation of the large Delphinoidea species using all available variables. Rows are known, columns predicted species (species are ordered with increasing average body length). Correct classifications in bold.

	Gg	Pc	Mm	Gs	Gm
Grampus griseus (Gg)	**28**	·	·	·	·
Pseudorca crassidens (Pc)	·	**10**	·	·	·
Monodon monoceros (Mm)	·	·	**5**	1	·
Globicephala melas (Gs)	·	·	6	**5**	5
Globicephala macrorhynchus (Gm)	·	·	·	·	**9**

cations in each analysis by themselves.

If the different variables were used singly for a discriminant analysis it could be seen that the most important variable was body length. The misclassification error of 38 % in the discrimination using body length only is almost as low as in the full models above (cases: 439, species: 24). The other 23 available variables result in misclassification errors of 55 to 86 % (median 72 %; cases: 178 to 439, species: 13 to 24) when used singly.

Similarly sized species: killer whales, large and small Delphinoidea — Using only body length for discrimination, the Delphinoidea can be split into three groups that are correctly predicted (Table 2, Fig. 1) by the model. With increasing average body length these groups contain the seventeen "small" Delphinoidea *Cephalorhynchus commersonii*, *Sotalia* spp., *Phocoena phocoena*, *P. spinipinnis*, *Stenella longirostris*, *Lagenorhynchus obscurus*, *L. obliquidens*, *Phocoenoides dalli*, *Delphinus delphis*, *Stenella frontalis*, *S. attenuata*, *S. coeruleoalba*, *Sousa plumbea*, *Lissodelphis borealis*, *Lagenodelphis hosei*, *Tursiops truncatus*, *Lissodelphis peronii*, the six "large" Delphinoidea *Grampus griseus*, *Delphinapterus leucas*, *Pseudorca crassidens*, *Monodon monoceros*, *Globicephala melas*, *G. macrorhynchus* and the even larger killer whales, *Orcinus orca*. Note that the families of Monodontidae (*Delphinapterus leucas*, *Monodon monoceros*), Phocoenidae (*Phocoena phocoena*, *P. spinipinnis*, *Phocoenoides dalli*) and Delphinidae are not separated in this classification nor are they responsible for a majority of the misclassifications.

In the following subsections the categorisation within the large and small Delphinoidea is further investigated.

Large Delphinoidea — Only set 2 of the diet PCs, the set based on the prey occurrence variables, can be included in the classification of the large Delphinoidea as there were too few cases with information on frequency and proportion of prey categories.

The classification of these large Delphinoidea species is quite successful with a misclassification rate of 17 % which is reduced to 10 % if the five misclassifications between the largely allopatric Globicephala species are not counted as such (total number of cases: 69, number of species: 5, Table 3).

For this and other successful classifications below I investigated which of all the available variables are important for the discrimination

Table 4: Categorisation of the small Delphinoidea species of the North Atlantic using all available variables. Rows are known, columns predicted species (species are ordered with increasing average body length). Correct classifications in bold.

sets of diet PCs	1				2				3			
misclassification	8 %				12 %				8 %			
	Pp	Dd	Sc	Tt	Pp	Dd	Sc	Tt	Pp	Dd	Sc	Tt
Phocoena phocoena (Pp)	**11**	·	·	·	**16**	·	·	·	**11**	·	·	·
Delphinus delphis (Dd)	·	**6**	2	·	·	**3**	7	·	·	**4**	4	·
Stenella coeruleoalba (Sc)	1	3	**10**	·	·	3	**11**	·	·	2	**12**	·
Tursiops truncatus (Tt)	·	·	·	**39**	·	·	·	**46**	·	·	·	**39**

of these species. To achieve this, an allsubset analysis was conducted for one to six explanatory variables, *i.e.*, all models with one variable were calculated, then all combinations of two variables and so on. Misclassification errors were then plotted against the number of included variables and either a minimum or a change in slope from a steep loss to a flatter loss in misclassification rate was identified to choose an 'ideal model'. Typically, a minimum was reached in the models including 3 to 5 variables and misclassification errors dropped by 10 to 15 % compared to the best single variable model.

Additionally, the ten models with the lowest misclassification rate for a given number of variables were inspected in detail for consistency in the variables.

The 'ideal' model for the large Delphinoidea includes the variables openness, body length, body length dimorphism, and two of the diet PCs. The most crucial variable for this categorisation also seems to be the body length and dimorphism. Dimorphism and body length alone reach a misclassification error of 23 % and 34 %, respectively, and these two variables together reach a misclassification error of 14 %. Other models that manage to categorise the species well all include the variable body length, too. An additional indication of the importance of body length is the fact, that only species adjacent in body length are misclassified (Table 3). Length dimorphism also helps to distinguish the species. With increasing dimorphism and some overlap we find the long-finned pilot whale, the melon-headed whale, the short-finned pilot whale, the narwhal and Risso's dolphin. It is not obvious from two-variate plots what additional information is provided by the variables other than body length.

Small Delphinoidea — The classification of the small Delphinoidea was not as successful. The discriminant analysis resulted in misclassification errors of 29, 41, 27 % (number of cases: 148, 256, 148; number of species: 10, 16, 10) for the three sets of diet variables, respectively.

One reason for the high misclassification rate might be that different species occupy the same niche in different regions and thus the same type of evaluation was conducted for the two

Table 5: Categorisation of the small Delphinoidea species of the North Pacific using all available variables. Rows are known, columns predicted species (species are ordered with increasing average body length). Correct classifications in bold.

sets of diet PCs	1					2								3				
misclassification	14 %					14 %								16 %				
	Dd	Lq	Pd	Sa	Ll	Pp	Dd	Lq	Pd	Sa	Ll	Sc	Tt	Dd	Lq	Pd	Sa	Ll
P. phocoena (Pp)						**6**	·	·	·	·	·	·	·					
D. delphis (Dd)	**6**	·	·	·	·	·	**7**	2	·	1	·	·	·	**6**	·	·	·	·
L. obliquidens (Lq)	1	**4**	·	1	·	·	3	**8**	1	·	·	·	·	2	**3**	·	·	1
P. dalli (Pd)	2	·	**23**	·	·	·	·	·	**31**	·	·	·	·	4	·	**21**	·	·
S. attenuata (Sa)	2	·	·	**3**	·	·	2	·	·	**3**	·	·	·	1	·	·	**4**	·
L. borealis (Ll)	1	·	·	·	**6**	·	·	·	·	·	**4**	3	·	·	·	·	·	**7**
S. coeruleoalba (Sc)						·	·	·	·	·	1	**6**	·					
T. truncatus (Tt)						·	·	·	·	·	·	·	**17**					

oceanic regions for which enough data was available: the North Atlantic and the North Pacific.

Small Delphinoidea by ocean — North Atlantic and Mediterranean. The four small Delphinoidea in the North Atlantic for which enough cases were available are classified with an error rate of 8, 12, 8 % (number of cases: 72, 86, 72) for the three sets of diet variables, respectively (Table 4).

The 'best' models for the small Delphinoidea of the North Atlantic included the variables specificity, body length, body length dimorphism, diet PC 2 and diet PC 5 for diet set 1, the variables body length, diet PC 3, diet PC 5 and diet PC 6 for diet set 2 and the variables openness, body length, length dimorphism and diet PC 1 for diet set 3.

In all three classifications using either of the three sets of diet variables, body length was again the most important variable (reaching misclassification errors of 19, 20 and 17 % on its own, respectively) besides some variables of the physical environment and some of the diet variables. Again it is not obvious from bivariate plots how these additional variables contribute to the success of the classification. Thus, it is not surprising that the misclassifications that still occurred are mainly between species of adjacent body length (Table 4).

North Pacific. The discriminant analysis of the small Delphinoidea of the North Pacific resulted in misclassification errors of 14, 14, 16 % (number of cases: 49, 95, 49; number of species: 5, 8: including all species also occurring in the North Atlantic, 5) for the three sets of diet variables, respectively (Table 5).

The 'best' models for the small Delphinoidea of the North Pacific included the variables average group size, body length and diet PC 4 for diet set 1, the variables average group size, body length and diet PC 3 for diet set 2 and the variables warmth, specificity and body length for diet set 3.

Body length was also the most important variable for discriminating the small Delphinoidea in the North Pacific (on its own reaching misclassification errors of 10, 20 and 14 % for the three sets of diet variables, respectively). The best models included again some variables of the physical environment and some of the diet PCs without it being obvious how these measures helped in the discrimination. Some details of the model using set 2 of the diet PCs are (this model includes more cases and more species): Group size seems to differentiate between some similarly sized species. Given a similar body length the Pacific white-sided dolphins are found in smaller groups than the common dolphins, Dall's porpoise in smaller groups than spotted dolphins and northern right whale dolphins in smaller groups than the striped dolphins.

Discussion

Delphinoidea species membership can be predicted based on population typical group size, physical environment, diet and life-history information in a step-wise procedure using discriminant analysis. First all species are split in three body length groups. One group only contains the largest killer whales. The small Delphinoidea have to be split additionally according to region (North Atlantic and North Pacific) to enable a successful classification.

All these categorisations seem to be mainly based on body length reflected in the fact that all models with similar low misclassification errors include the variable body length, whereas the additional variables included in such models are more variable and in the fact that most misclassifications occur between species of adjacent body length.

Misclassifications in a model of all species are not more common within than between the families Delphinidae, Monodontidae and Phocoenidae (Table 2) nor are they more common within than between the subfamilies of the Delphinidae (Tables 2, 5; for the most recent suggestion of subfamilies see: LeDuc *et al.*, 1999) as could be expected due to the phylogenetic relationships. If the Monodontidae are separated from the larger Delphinoidea due to their geographically different distribution, the larger Delphinoidea coincide with the Globicephalinae as suggested in LeDuc *et al.* (1999, see there: Fig. 2). Phylogeny of the Delphinoidea based on morphology and on DNA samples is not well reflected in the variables used in the present analysis.

The success in classification in the present analysis relies mainly on body length. This is surprising in at least two respects. Firstly, body length seems to correlate roughly with body shape in that larger species are more heavily built. One would assume that this is a reflection of different ecological niches. This, in turn, would suggest that these species also differ in their ecology measured by the physical environment and the diet. This is not supported by the current data. Secondly, one would assume that similarly sized species are capable of similar mobility, have a similarly sized potential prey spectrum and face similar threats from predators. These constraints suggest that species similar in size would try to fit into very similar niches. Such a process would increase competition and species would be thought to specialise rapidly into more specific and less overlapping niches. Again, the question remains open why such a process is not reflected in the variables of the physical environment and the diet in the present study.

All small Delphinoidea species together can be classified only with a high misclassification rate. Misclassification decreases if small Delphinoidea are split by ocean region even though the same species occur in the North Atlantic and the North Pacific. This indicates that the same species in different oceans inhabit slightly different or narrower niches in response to the other species that occur in the same region.

It is of course possible that the parameters of the physical environment and diet do not reflect the niches detailed enough but one would assume niches to be so different that at least some aspects are caught in the variables used in the present evaluation.

The huge niche overlap may not be so surprising if we consider on the one hand that species such as bottlenose dolphins (Dowling and Brown, 1993), white-sided dolphins (Lux *et al.*, 1997), harbour porpoises (Andersen, 1993; Rosel *et al.*, 1995b; Wang *et al.*, 1996; Wang and Berggren, 1997; Börjesson and Berggren, 1997; Gao and Gaskin, 1996, 1998), Hector's dolphins (Pichler *et al.*, 1998) and beluga whales (Maiers *et al.*, 1996; Palsbøll *et al.*, 1997; Brennin *et al.*, 1997; Brown Gladden *et al.*, 1997) differ morphologically and genetically within quite small areas (*e.g.*, along the coast of an ocean) and / or differ markedly between oceans implying the existence of morphologically similar subspecies. On the other hand, at least in some regions and species, such as bottlenose dolphins (Hersh, 1990; Hoelzel *et al.*, 1998) common dolphins (Rosel *et al.*, 1994), and killer whales (*e.g.*, Morton, 1990; Ford *et al.*, 1994) sympatric populations occur which differ genetically and ecologically (forming sub-species). This suggests that the current species might not be good entities for comparison because they actually consist of several ecotypes which leads to great within species variation in the variables studied here.

Another interpretation is possible though: some of the variables (especially the ones on reproduction) might not vary much over the whole superfamily of Delphinoidea whereas other variables (such as group size) might be very variable within the families or even within the species. The former would be a reflection of strong evolutionary constraints within the whole superfamily (or a too short period for change since speciation) whereas the latter rather points to a high ontogenetic adaptability of these species to their current environment.

This would lead to the conclusion that, on the whole, Delphinoidea species might be pretty similar and that their niches largely overlap. It remains open how specifically adapted these species are to their environment, why so many species would have evolved and how competition works between these species.

The use of single observations of different Delphinoidea species instead of population means and continuing detailed studies on the behavioural ecology of the Delphinoidea species might shed more light on these questions, as either more finely tuned specialisations to the environment or the ontogenetical flexibility of these species might become apparent.

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