Facultative river dolphins: conservation and social ecology of freshwater and coastal Irrawaddy dolphins in Indonesia

Kreb, D.

Citation for published version (APA):

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
CHAPTER 11

Freshwater distribution of Irrawaddy dolphins based on river “vagrancy” or allopatric “speciation”? 

The *pesut* has adapted to the riverine habitat and has become skilful in catching various prey items from large catfishes to smaller cyprinid fishes and bottom-dwelling river shrimp.
ABSTRACT

Freshwater and coastal Irrawaddy dolphins in East Kalimantan are currently separated from each other, which is obvious from a hiatus in their distribution. This raises the issue of whether separation is a recent process due to degradation of intermediate habitat, or results from a historic process due to allopatric speciation during the last glacial maximum. If we hypothesize that separation is a recent process, it is assumed that prior to the habitat degradation gene flow still existed between coastal and riverine populations and that the riverine population is built up of groups or individual coastal “river vagrants”. To determine the likelihood of each hypothesis the most relevant variables were examined in terms of finding differences between both populations, i.e., dolphin distribution, morphology, social ecology, vision, physiology, acoustics and comparisons with other “facultative” river dolphins. Most evidence supports a separation of coastal and riverine populations over a larger time scale, although one cannot be definite about the time of separation unless there is genetic data. Collection of tissue samples of coastal Irrawaddy dolphins therefore has a high priority. Nevertheless, whatever hypothesis reflects the actual process of separation, it is clear that this riverine population is critically endangered and in need of conservation. If the river vagrant theory prevails, conservation effort should focus on restoring degraded intermediate habitat; if the population appears to be obligate riverine the entire riverine habitat is a priority. It is recommended to continue collecting genetic tissue sample to assess the genetic variation of the riverine population and to determine whether it is necessary to translocate isolated groups in the river to join the main breeding population.

RINGKASAN

Lumba-lumba air tawar dan laut di Kalimantan Timur terpisahkan satu dan lainnya, dimana ternyata terdapat kekosongan dalam penyebarannya. Hal ini menjadi pertanyaan apakah proses pemisahan ini terjadi sebagai proses baru karena adanya penurunan kualitas habitat antara, atau sebagai hasil proses sejarah karena untuk menyelidiki proses perpisahan seiring penurunan habitat lanjutan atau penyebab dari proses sejarah pemisahan selama jaman es terakhir. Jika kita membuat hipotesa bahwa pemisahan adalah proses yang baru terjadi, ini diasumsikan karena penurunan kualitas habitat, kesamaan gen tetap ada antara populasi lumba-lumba laut dan sungai dan bahwa populasi sungai terbentuk dari individu lumba-lumba laut yang masuk ke areal sungai (penjelajah sungai). Untuk menentukan kesamaan dari tiap hipotesis, variabel yang dapat dipercaya diui dengan tujuan untuk menemukan perbedaan antara kedua populasi, antara lain penyebaran lumba-lumba, morfologi, ekologi sosial, daya pandang, fisiologi, akustik dan perbandingan dengan lumba-lumba sungai fakultatif lainnya. Banyak bukti lainnya mendukung pemisahan populasi laut dan sungai terjadi dalam jangka waktu lama, meski tidak ada satupun yang memastikan tentang waktu
DISCUSSION

The taxonomic separation of a freshwater and coastal form within the Irrawaddy Dolphin has been debated since Gray first described the species *Orcaella brevirostris* in 1866 based on a specimen described by Owen in Gray, 1866, as *Phocaena brevirostris*. This description was based on a specimen from the east coast of India in the harbour of Vishakhapatnam. Anderson described a freshwater form of the species in 1871 based on a specimen collected in 1868 at 1500 km from the mouth in the formerly named Irrawaddy River in Burma (presently named Ayeyarwady River, Myanmar) and assigned it a different species name *Orcaella fluminalis*. Later, in 1878 he reduced the status of the river form to a subspecies, *O. b. fluminalis*, but Loze (1973), and Pilleri and Gihr (1974) found no consistent differences between both freshwater and marine specimens stating that both forms belong to the same species *Orcaella brevirostris*. Until now, this is the general consensus (Rice, 1998). Analysis of the skull morphology of Irrawaddy dolphins throughout much of their range indicated specific or sub-specific differences in the height of the temporal fossa, number and width of nasal bones/ossicles, development of mesethmoid plate, and pterygoid hamuli between animals from Australia and South Asia (Beasley et al., 2002). However, data was insufficient to investigate the question freshwater and coastal separation. Nevertheless, in this study we found that at least at present the freshwater Irrawaddy dolphin population in the Mahakam River is separated from the coastal population based on a hiatus of 160 km in their distribution between the mouth and further upstream the river due to degradation of habitat (see chapter 6, results, abundance & distribution), and based on ecological differences related to salinity. Coastal Irrawaddy dolphins were always associated with brackish water and they only entered the delta at high tide. The most in-shore observation was made at 10 km upstream the delta but they may move until 20 km upstream the mouth according to interviews with fishermen. The freshwater population, on the other hand was never sighted lower than 180 km upstream from the mouth, although some local residents claimed that they sighted dolphins very occasionally 90 km from the mouth. In the early 1980s the dolphins were still
commonly sighted by residents in Samarinda at 60 km from the mouth, after which they became increasingly rare, and they vanished completely from the area in the mid 1990s.

In this study, I investigate whether the separation of coastal and freshwater Irrawaddy dolphins in East Kalimantan has occurred recently due to degradation of intermediate habitat, or has an evolutionary origin related to the changing sea levels during the Pleistocene resulting in an allopatric speciation process. The possible short-term and long-term separation processes and the origin of the freshwater population may be explained by the following two hypotheses:

Hypothesis 1- “river vagrancy”: The freshwater population has its origin in the accumulation of individuals or small groups of occasional, coastal “river vagrants” (see chapter 1), which have adapted to the freshwater ecosystem. The process of river vagrancy may have a historic origin but is an ongoing process and would still be continued if the intermediate habitat between the coastal and freshwater populations had not been degraded, because the behaviour is supposed to be inherent to the dolphins exploring and adaptive biology. Conservation and upgrading intermediate habitat may then be very essential in terms of maintaining genetic exchange.

Hypothesis 2- “allopatric speciation”: The freshwater population has its origin in the last glacial maximum during the Pleistocene when sea levels were low and Sundaland, the landmass of South East Asia, was above sea level delineated by the 200-m isobath (Tomascik et al., 1997). During this period, land was continuous from peninsular Southeast Asia across to Sumatra, Java and Borneo, and the western shallow part of the South China Sea as far east as the Natuna Islands (Hutchison, 1989). Shelf seas, e.g., the Java Sea, had disappeared and freshwater aquatic species may have dispersed throughout the major ancient rivers that connected different islands (Fig. 1) (Haile, 1975; Verstappen, 1975). Coastal Irrawaddy dolphins of South and West Borneo, North Java, East Sumatra, and South East Asian continental mainland may also have dispersed in this aquatic habitat intermediate of present islands, which became sea again c. 10,000 years ago when water levels started to rise (MacKinnon et al., 1996) and coastal dolphins re-colonized the shallow coastal areas. The three major river systems, Ayeyarwady, Mekong, and Mahakam form an exception. These rivers claimed the shallow waters off their mouths during the last glacial period and directly opened into the deep waters (> 200 m). Coastal Irrawaddy dolphin populations, which were adapted to the brackish, shallow delta areas are more likely to have adapted to the freshwater habitat than they would to the deep, offshore waters, which would have required a greater adaptation of their biology. Therefore, I hypothesize that the current riverine populations in the three major rivers in South East Asia have been separated from their coastal conspecifics at least since the Late Pleistocene during Sunda Shelf formation. Current coastal populations along the coast of East Kalimantan most likely represent migrants after the glacial period from South Borneo. Conservation of freshwater populations have a high priority because they represent unique, isolated populations.
Figure 1. The Sunda Shelf showing present coastlines (unshaded), the area of Sundaland exposed at times of lowest sea level (dark shade) delineated by the 200-m isobath during the last glacial about 12,000 years ago, and past and present river systems (After Tjia, 1980 and MacKinnon, 1996).

Step by step we will look for support for each of both hypotheses based on Irrawaddy dolphin distribution, morphology, social ecology, vision, physiology, acoustics and comparisons with other “facultative” river dolphins. Although genetic material is available of the Mahakam population, unfortunately no genetic material of coastal Irrawaddy dolphins in East Kalimantan is available. Looking at the Irrawaddy dolphin distribution, we find that they are distributed along shallow coasts, bays, brackish water lakes (lagoons), and in river mouths throughout much of the tropical to sub-tropical Indo-Pacific (Stacey and Leatherwood, 1997). In addition, they occur in three major river systems, i.e., the Ayeyarwady (Myanmar), the Mekong (Vietnam,
Cambodia and Laos) and the Mahakam (Kalimantan, Indonesia). If river vagrancy would be inherent to the dolphins biology, we would expect to find Irrawaddy dolphins in more river systems. And indeed, the dolphins were also observed to move further upstream the mouth of some rivers, i.e., the Rajang River in Sarawak, where they were regularly seen in Tg Mani, 33 km from sea (Mörzer Bruyns, 1966). Several sightings were made by crew of a coal barge and one carcass was retrieved between 72 km and 85 km the mouth in the Brisbane River, and a bit upstream of the junction with the Bremen River at 77 km from the mouth (Paterson et al., 1998). However, all these sightings were regarded as unusual by the crew because the dolphins were rarely observed further upstream than 10 km from the mouth of the Brisbane River. The dolphins observed in the Rajang, Brisbane, and Bremer Rivers are nevertheless not typical freshwater vagrants since their occurrence was still within the limit of tidal influence. Similarly, if coastal Irrawaddy dolphins were to explore the riverine environment of the Mahakam, one would expect that they would do so at high tide, but the dolphins presence in the lower areas is associated with high or medium water levels according to semi-structured interviews with local residents, which makes it more likely that these belonged to the freshwater stock. Lloze (1973) suggested that the Irrawaddy population in the Mekong river is not an isolated population. He mentioned that the dolphins left the lakes (e.g. the Tonle Sap) at low water levels together with some large fishes (ranging from 1 to 3 metres) and joined the Mekong River. Further he suggested that after the dolphins arrived there, some individuals would swim upstream and others move downstream and progressively gain the delta regions of south Vietnam and the South China Sea. The problem is that the dolphins have only been followed downstream until the Vienamese border. Therefore it is not known whether they move further downstream and whether any interbreeding exists between these dolphins and the Irrawaddy dolphins in the delta region, whose presence have been recorded by Gruvel (1925). Another sighting, which may suggest the existence of “true” river vagrants (exceeding the tidal limit) was reported by Mörzer Bruyns (1971) and was made 110 km up the Pussur River in Bangladesh. Since there was no date specified or any further information, nor are there any other records in the river, the record is identified as tentative. In South Kalimantan Delsman (1922) reported the occurrence of Irrawaddy dolphins at c. 380 km upstream the Barito River below Puruk Cahu. However, no further details were given about his sighting. According to Westerman (1939) no positive records through observations or interviews exist, which indicates the presence of dolphins in the larger rivers of South Kalimantan including the Barito. Therefore, the sighting below Puruk Cahu most likely represented an occasional river wandering.

In this study we found that the river dolphins had a high site fidelity during the 3.5 years study period and that their overall home ranges were limited to a maximum of 180 km river strip (see chapter 9, results, spatial distribution). Since clear evidence for regular river vagrancy is lacking, we find the allopatric speciation hypothesis more plausible to explain the origin of freshwater Irrawaddy dolphin populations. Although occasional river wanderings may occur, this does not seem to be regularly enough to explain the
existence of relatively large river populations.

With regards to their morphology, we observed in the field that the river dolphins seemed to have larger body sizes, displayed a greater sexual dimorphism as expressed in a large neck crest for males, which are absent in females (see chapter 9, results, sexual dimorphism). Lastly, body skin of coastal dolphins had a much rougher texture with many scratches. The first two differences between coastal and river populations favour hypothesis 2, since these variables may have evolved over a longer time-scale. The last characteristic more reflects differences in habitat ecology and at least implies that dolphins remain in their own habitat during their life-time.

The social ecology differs in a number of aspects, i.e., groupsize, nature and frequency of inter-group interactions, spatial distribution, breeding period, mating strategies (see chapter 9). As the term social ecology implies, the differences in social structures reflect differences in their ecology and are adaptations to their environments, i.e., the geographical shapes of habitat, the temporal abundance and spatial distribution of food resources. Although ecological adaptations do not necessarily require a historic time-scale, adaptations to fit in another social system probably exceed a life-time and makes river vagrancy therefore a less suitable hypothesis because of the presumed lack of successful adaptations. However, river vagrancy of Irrawaddy dolphins may still occur in other rivers, which are not occupied by a well-adapted riverine population.

Other differences, which may have arisen as a result of the separation may be reflected in their visual capacities such as is the case with obligate river dolphin species such as the Indus susu, *Platanista gangetica gangetica*, Ganges susu, *Platanista gangetica minor*, the Amazon River dolphin (*Inia geoffrensis* and the Yangtze dolphin (*baiji*), *Lipotes vexilfer* for which an increasing regression of the eye has been demonstrated as an adaptation to a turbid and fluviatile environment (Herald *et al.*, 1969; Purves & Pilleri, 1973; Best & Da Silva, 1989; Zhou *et al.*, 1980). The first two (sub)species are blind, whereas the eyes of the boto and the baiji, although reduced, still appear functional (Leatherwood & Reeves, 1983). Irrawaddy dolphins do not have reduced eyes and like other delphinids appear to have good eyesight, which was also observed in the field during this study when river dolphins were observed to spy-hop for a great deal of the time. However, some reduced use of eyesight has been described for captive freshwater Irrawaddy dolphins from the Mahakam, which would not take a fish in plain view that was thrown in the basin less than 100-150 cm away as if it was unnoticed. Instead they would first scan the near environment by sonar and only then capture their prey (Kamminga *et al.*, 1983). This habit would indicate that they have probably spent their entire life in a turbid environment (mean clarity in the Mahakam is 23 cm) and have developed feeding strategies that rely exclusively on the use of their sonar. However, in order to use this argument to prove that coastal and freshwater Irrawaddy dolphin populations are seperate, similar tests are required with coastal Irrawaddy dolphins. Since clarity in the bay is much higher, i.e., 170 cm, one would expect differences in feeding strategies. In this study, we found that coastal Irrawaddy dolphins did not continuously emit click trains while fishing, which may indicate that they would partially
prey on sight or by listening (see chapter 10). Nevertheless, differences in use of eyesight have not been satisfactorily determined yet to use as an argument for a short-term or long-term coastal/freshwater separation.

The physiology of the freshwater form of the Irrawaddy dolphin does not seem to support a long evolutionary separation event from coastal populations. For four specimens of *Orcaella brevirostris* in the Mekong River in Cambodia it has been found that each kidney contains about the same number of adrenal bodies as *Delphinus delphis*, i.e., 380 and 400 respectively. This large number is in contrast with the low number of 80 adrenal bodies found in *Platanista gangetica* (Lloze, 1973; Harrison & King, 1968). Lloze (1973) therefore suggests that the small ‘lobulation’ as is apparent from the low number of adrenal bodies in *Platanista* is characteristic for odontocetes that are living in freshwater environments. He also explains the small lobulation in terms of the absence of any necessity for dolphins in freshwater to separate the salt and freshwater from seawater, which marine dolphins gulp down together with fishes. According to Slijper (1962), there is a direct relation between the degree of lobulation and the degree of marine life. The large lobulation for the freshwater Irrawaddy dolphin thus seems to indicate that this should not be an obstacle for changing its river habitat for a marine habitat. For further research it may be useful to compare the number of adrenal bodies, representing the degree of lobulation, of the freshwater forms with that of the marine forms of the Irrawaddy dolphin. If a lower number is found for the freshwater populations, then this may indicate that there is no gene-flow between both populations as a result of a long historical separation process. Based on the current data both hypotheses may hold since lobulation in freshwater populations may be a remnant trait of their marine descent.

With regards to the acoustic behaviour of the coastal and freshwater Irrawaddy dolphin populations in this study we found many differences (see chapter 10): pod-specific whistle dialects; vocalizing intensity; size of vocal repertoire. Vocal repertoire was less varied for coastal Irrawaddy dolphin populations in East Kalimantan and Australia compared with the Mahakam River and may be determined by ecological conditions. The vocalizations rates (numbers per time unit) seem to be determined by social structures. Since these two “plastic” variables may involve ecological and social adaptations to each environment or stock, this does not favour hypothesis 1 but instead favours hypothesis 2 since vagrants may not be able to successfully adapt to other stocks because its dialect may not be recognized. On the other hand, sound types including whistle structures were more similar between the likely more genetically related, coastal and freshwater populations in East Kalimantan than between coastal populations of Australia and East Kalimantan. This does not necessarily imply that there is still gene-flow (although it is possible) if sound types are formed during a slow evolutionary process (and is a non-plastic variable) and may only indicate a genetic relatedness although at distance.

In addition, I would like to investigate whether the basic sonar system, i.e., echolocation clicks of freshwater dolphins exhibits some degree of adaptation to the riverine habitat and whether this is an irreversible adaptation of having lost their ability
of using low-frequency-signals. This information would be very important for conservation purposes, as the lost of this capability would restrict these dolphins to their riverine habitat. When looking at dominant frequencies of echolocation signals, however, this present study cannot make any comparisons due to limitation of the recording equipment, which only made effective recordings of sounds up to 24 kHz. It has been generally argued that both pelagic and river odontocetes have basic or one-component sonar signals while the littoral and estuarine species use two-component sonar signals. Fast swimming pelagic species require low frequency sonar signals for long range navigation in the open water, whereas river species require high frequency sonar signals in order to detect close objects. The littoral and estuarine species require the use of both signals as they are faced with both kinds of situations (Dudok van Heel, 1981). Estuarine harbour porpoises, *Phocaena phocaena*, the beluga, *Delphinapterus leucas*, and estuarine form of *Sotalia fluviatilis guianensis*, which were studied in captivity, all displayed the two component signals (Dudok Van Heel, 1981; Kamminga & Wiersma, 1981; Wiersma, 1982). However, in captivity no need rises to use this low frequency signal for long-range navigation. A study on free-ranging cetaceans showed that botos produced echolocation clicks with dominant frequencies around 100 kHz, whereas the sympatric riverine tucuxi produced clicks of 80 to 95 kHz. However, captive studies on the riverine tucuxi revealed that they produced clicks with dominant frequencies of 8-15, 30 and 95 kHz. Also clicks of high-frequency (95 kHz) and low-frequency (30 kHz) were recorded simultaneously (Norris et al., 1972). These lower frequencies between 8 and 15 kHz were also recorded in an earlier captive study, in which a hydrophone was used, which could only detect frequencies up to 20 kHz (Caldwell & Caldwell, 1970). The results would indicate that lower frequencies can still be used by riverine *Sotalia*, although it is not clear whether these same dolphins, when released in the wild, would emit a sonar signal of similar dominant frequencies. As the use of the lower frequencies is generally associated with long range-navigation, the recordings of lower frequencies as well is rather surprising for these riverine dolphins which were held in a pool in which the emittance of low frequencies would seem of no use just as in the studies with belugas and harbour porpoises mentioned earlier. Possibly, the emittance of echolocation clicks of low frequency might also serve another function, e.g. communication. Conclusively, coastal and riverine *Sotalia* can use both high and low frequencies for echolocation, although in the wild only dominant high frequency sounds are used.

The high-frequency component of riverine *Orcaella brevirostris* is similar to that of *Sotalia fluviatilis* and its vocalising intensity has similarities with *Inia geoffrensis* (Kamminga et al., 1983). The main sonar signal of *Orcaella* held in captivity after being caught in the Mahakam River was elementary, consisting of only a few cycles of a dominant frequency of around 60 kHz with small deviations. No low-frequency components could be distinguished (Kamminga et al., 1983). No recordings of echolocation clicks, which used equipment covering the entire bandwidth are available on estuarine or coastal *Orcaella*. It could be argued that the dolphins from the Mahakam have either lost the ability of using low frequencies for echolocation or that there was no need for them
emitting low frequencies in the small holding pool (in which they contrast Sotalia, if this is the case). An alternative hypothesis might be that all Irrawaddy dolphins, coastal as well as riverine, are only able to use high frequency sonar signals, which would seem unlikely though when comparing with other estuarine species. Generally, it can be argued that the river habitat does not call for a complicated sonar but rather for basic one-component high frequency signals suitable for short-range navigation and functioning in a turbid environment (Kamminga et al. 1983). Although acoustics do not solve the question if the freshwater Irrawaddy dolphin populations represent different (sub) species or merely geographical forms, acoustics may help to define stock s as separate management units. We have evidence that the riverine population seems very well adapted to its environment as it is able to use high frequency signals. Also, the distinction in vocalization intensity, vocal repertoire, and whistle dialects makes a strong case for a historic separation of coastal and freshwater dolphin populations (hypothesis 2) as it would seem likely that river vagrancy would diminish these differences in vocalizations.

When examining the origin of two other “facultative riverine” species, i.e., the tucuxi, Sotalia fluviatilis, and finless porpoise, Neophocaena phocaenoides, it appears that coastal and river populations are well distinguished based on body size, number of teeth in the upper row, and skull characters in the tucuxi (Borobia, 1989; Hendriks, 1984; Monteiro-Filho et al., 2002), and skull morphometric, meristic data, and mitochondrial DNA polymorphism in the finless porpoise (Pilleri & Gihr, 1972; Gao, 1991; Gao & Zhou, 1995a, b, c; Jefferson, 2002). Although their genera are considered monospecific, subspecies or separate freshwater populations are recognized (Rice, 1998; Borobia & Sergeant, 1989). Another evidence of support for a separate freshwater population of the facultative riverine tucuxi may be the fact that the tucuxi (regarded as relatively recent immigrant of the freshwater system) and obligate riverine boto share rather similar clicks with regard to dominant frequencies and time duration, which are attributed to the adaptation of their riverine environment (Kamminga et al., 1993). Since there appears to be no gene flow between coastal and river populations, which would have reduced the distinct differences, river populations of both species more seemed to have evolved because of allopatric speciation rather than through river vagrancy or sympatric speciation, which increases the likelihood that a similar case prevails (hypothesis 2) within the facultative Irrawaddy dolphin.

After examining all variables, only one variable related to visual capacities possibly may be in favour of hypothesis 1. However, since eyesight of the boto and the baiji are still functional, as well as that of two other facultative river dolphins, the tucuxi and finless porpoise, which are considered to have distinct river populations (see below), perhaps this variable is not such a good character upon which to make any distinctions between (sub)species or geographically variable populations. Also, the Mahakam is likely to have greatly increased in turbidity in only a few decades due to increased erosion and sedimentation. Most evidence is in support of a separation of coastal and freshwater populations over a longer time scale. We recommend further sample collections for DNA analysis to reconstruct the time of separation. Conclusively, the
term facultative as proposed in (Leatherwood & Reeves, 1994) may be a bit misleading as it implies that these dolphins may have a choice to move between coastal and freshwater habitat, which they more than likely do not have. Although genetic analysis may be able to shed more light on which historic or actual processes are involved in the existence of riverine populations of Irrawaddy dolphins or species with a similar ecology, it is clear that many species or populations depend on the river habitat and are in need of protection whether it is because they are restricted to this habitat for their entire or part of their life, or because of their occurrence in estuaries. Each hypothesis to explain the coastal and freshwater dolphin separation in occurrence, implies a need for conservation of riverine habitat in order to maintain viable populations or subspecies. Recommendations for conservation are in chapter 6. In addition, we recommend further sample collections for DNA analysis to determine the genetic variation within the freshwater population. If the genetic variation is very low, a translocation of an isolated group, “trapped” between two rapid streams may be considered an option to increase the genetic variation and breeding population.

REFERENCES


