

Natural hybridization between Dall's porpoises (*Phocoenoides dalli*) and harbour porpoises (*Phocoena phocoena*)

Pamela M. Willis, Bernard J. Crespi, Lawrence M. Dill, Robin W. Baird, and M. Bradley Hanson

Abstract: Natural hybridization occurs rarely in mammals compared with other taxonomic groups of animals. Cetaceans appear unique among mammals in exhibiting striking karyological uniformity, which suggests that they have the potential to produce hybrid offspring more readily than other mammals. However, the detection and accurate identification of wild mammalian hybrids is difficult, and molecular evidence for wild cetacean hybrids is extremely limited. Here, we present molecular and morphological evidence of frequent hybridization between free-ranging Dall's, *Phocoenoides dalli* (True, 1885), and harbour, *Phocoena phocoena* (L., 1758), porpoises. The study describes a temporally and geographically concentrated case of natural hybridization in large mammals. Molecular analyses of mitochondrial and nuclear DNA revealed the species identity, sex, and direction of cross of several hybrid individuals. In concert with morphological and behavioural observations, these data confirmed the hybrid status of putative crosses in the field, including reproductive females. All crosses examined had Dall's porpoise as the maternal parent. This directionality may reflect the indiscriminate pursuit of female porpoises by male harbour porpoises. Our finding of extensive localized hybridization, despite apparently strong isolation elsewhere in their range, suggests that ecological influences on mating behaviour may be of primary importance in the reproductive isolation of these, and possibly other, cetacean species.

Résumé : Il y a rarement de l'hybridation naturelle chez les mammifères, comparativement à d'autres groupes taxonomiques d'animaux. Les cétacés se distinguent parmi les mammifères par leur remarquable uniformité caryologique, ce qui laisse croire qu'ils ont le potentiel de produire des rejetons hybrides plus facilement que les autres mammifères. Cependant, la découverte et l'identification précise des hybrides chez les mammifères sauvages sont difficiles et il y a très peu de données moléculaires qui confirment l'existence d'hybrides chez les cétacés en nature. Nous présentons ici des données moléculaires et morphologiques qui appuient l'existence de croisements fréquents en nature entre le marsouin de Dall, *Phocoenoides dalli* (True, 1885), et le marsouin commun, *Phocoena phocoena* (L., 1758). Il s'agit d'une étude de cas circonscrite dans le temps et l'espace d'une hybridation naturelle chez de grands mammifères. Les analyses moléculaires de l'ADN mitochondrial et nucléaire ont permis d'identifier l'espèce, le sexe et le sens du croisement chez plusieurs individus hybrides. Combinées aux observations morphologiques et comportementales, ces données confirment le statut hybride de croisements putatifs en nature, ainsi que celui de femelles reproductives. Dans tous les croisements observés, le parent maternel est un marsouin de Dall. Ce phénomène s'explique peut-être par la poursuite sans distinction des marsouins femelles par les mâles du marsouin commun. Notre découverte d'une importante hybridation locale, malgré apparemment un fort isolement reproductif ailleurs dans la zone de répartition géographique,

Received 8 September 2003. Accepted 29 April 2004. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 24 July 2004.

P.M. Willis,^{1,2} B.J. Crespi, and L.M. Dill. Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

R.W. Baird.³ Biology Department, Dalhousie University, Halifax, NS B3H 4J1, Canada.

M.B. Hanson.⁴ National Marine Mammal Laboratory, National Marine Fisheries Service (NMFS), Seattle, WA 98115-6349, USA.

¹Corresponding author (e-mail: pmwillis@sfu.ca).

²Present address: Ecology, Evolution and Behavior Program, Integrative Biology, 1 University Station C0900, University of Texas at Austin, Austin, TX 78712-0253, USA.

³Present address: Cascadia Research Collective, 218 West 4th Avenue, Olympia, WA 98501, USA.

⁴Present address: National Oceanic and Atmospheric Administration – NMFS – Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.

indique que les effets des facteurs écologiques sont d'importance capitale pour l'isolement reproductif chez ces espèces de cétacés et probablement aussi chez d'autres.

[Traduit par la Rédaction]

Introduction

Natural hybridization occurs rarely in mammals (Gray 1971), although it can be widespread in other taxonomic groups (Hubbs 1955; Grant and Grant 1992; Arnold 1997). The uniquely rapid chromosomal evolution of mammals is thought responsible for their relative inability to hybridize (Wilson et al. 1974; Prager and Wilson 1975). Cetaceans (whales, dolphins, and porpoises) are unusual in displaying prominent karyological uniformity (Árnason 1972, 1982), suggesting that they may have the potential to produce viable hybrid offspring more easily than other mammals (Árnason et al. 1991). Although cases of hybridization between captive cetaceans support this hypothesis (e.g., Sylvestre and Tasaka 1985; Zornetzer and Duffield 2003), only a few cases have been suspected among wild cetaceans (see review by Bérubé 2002). Molecular evidence of wild cetacean hybrids has to date been limited to only five animals: four crosses between fin, *Balaenoptera physalus* (L., 1758), and blue, *Balaenoptera musculus* (L., 1758), whales (Árnason et al. 1991; Spilliaert et al. 1991; Bérubé and Aguilar 1998) and a Dall's porpoise \times harbour porpoise, *Phocoenoides dalli* (True, 1885) \times *Phocoena phocoena* (L., 1758), fetus (Baird et al. 1998). Identification of the morphologically distinctive porpoise fetus prompted speculation regarding the possible hybrid status of numerous uniquely pigmented porpoises in the waters surrounding lower Vancouver Island, British Columbia (Baird et al. 1998), which, if confirmed, would represent the most extensive known occurrence of natural cetacean hybridization and one of the most geographically concentrated cases of hybridization in large mammals.

Mitochondrial DNA (mtDNA) studies have been useful in documenting introgression in a few mammalian species pairs in the wild, confirming the occurrence of past hybridization events (e.g., mice, Ferris et al. 1983; deer, Carr et al. 1986; voles, Tegelström 1987; wolves/coyotes, Lehman et al. 1991). However, documentation of mammalian hybrids themselves occurs infrequently because of the challenges inherent in locating and accurately identifying them. Here, we investigate the hybrid status of putative hybrid porpoises through molecular analyses of mtDNA and nuclear DNA, in concert with morphological and behavioural observations at sea. We then address the directionality (maternal species vs. paternal species), fertility, and sex-dependent viability of hybrid crosses to provide insight into the potential causes and consequences of hybridization in these species.

Materials and methods

Study species and general methods

Dall's and harbour porpoises are morphologically and ecologically distinct species, sympatric in many coastal regions of the North Pacific (Gaskin et al. 1974; Jefferson 1988). The two species diverged sometime within the last 2–

3 million years (Rosel et al. 1995) and share the same chromosome number, $2n = 44$ (Kulu et al. 1971; Árnason 1974). Both species occur regularly in the waters between southern Vancouver Island, British Columbia, Canada, and the US San Juan Islands (Baird and Guenther 1994), particularly in the study area of Haro Strait ($48^{\circ}35'N$, $123^{\circ}16'W$), but do not form mixed groups. Breeding is seasonal and overlapping between the species (Jefferson 1988; Gaskin 1992).

Boat-based data were collected within a $<60\text{-km}^2$ area of Haro Strait from June to early September 1997 and 1998 as part of a larger study of porpoise mating behaviour (Willis 2001). Putative hybrids were identified visually based on their distinctive external morphology, particularly their pale gray pigmentation (see Table 1), and photographed when possible. Skin tissue was biopsy-sampled from seven putative hybrids using either a crossbow or a pole spear equipped with custom-made sampling tips (W. Hoggard, Pascagoula, Mississippi, USA; CETA-DART, Virum, Denmark), with two additional putative hybrid tissue samples obtained via a concurrent study by Hanson (2001; M.B. Hanson, unpublished data) in the same region. Samples were stored in a sodium chloride – dimethyl sulfoxide solution. Additional samples were collected from archived tissues of locally stranded Dall's and harbour porpoises. All samples were frozen at -70°C until analyzed. Field research was conducted in accordance with the principles and guidelines of the Canadian Council on Animal Care and approved by the Simon Fraser University Animal Care Committee (project No. 514B).

DNA extraction

Small pieces ($1\text{--}2\text{ mm}^3$) of skin tissue were macerated as finely as possible using razorblades and digested in 900 μL of Lifton buffer (0.2 mol sucrose/L, 0.05 mol EDTA/L, 0.1 mol Tris/L, 0.5% w/v SDS). The homogenate was extracted with $\sim 100\text{ }\mu\text{L}$ of CHCl_3 and $\sim 100\text{--}500\text{ }\mu\text{L}$ of phenol and then precipitated with 30 μL of 7.5 mol $\text{NH}_4\text{OAc/L}$ and $\sim 500\text{ }\mu\text{L}$ of isopropanol. DNA pellets were washed with 70% ethanol, dried overnight, resuspended in 50 μL of distilled deionized water, and stored at -20°C .

Polymerase chain reactions (PCRs)

As mtDNA is maternally inherited, we identified the maternal parent of putative hybrids by amplifying and sequencing a 230 base pair (bp) portion of the mtDNA cytochrome *b* region that demonstrates species-level variation (Rosel et al. 1995). mtDNA amplification with primers designed from sequence data provided in Rosel et al. (1995) (CYTB-A 5'-CGT GGC CTA TAT TAC GGC TCC TA-3' paired with CYTB-B 5'-GTT AGT GTT GCT TTG TCT ACG G-3') was conducted in 25- μL volume reactions using ReddyMixTM PCR Master Mix (ABgene, Surrey, UK) containing 0.75 unit of *Taq* DNA polymerase, 75 mmol Tris-HCl/L (pH 8.8 at 25°C), 20 mmol $(\text{NH}_4)_2\text{SO}_4/\text{L}$, 1.5 mmol MgCl_2/L , 0.01% v/v Tween 20, and 0.2 mmol/L each of dATP, dCTP, dGTP,

Table 1. Morphological, behavioural, and genetic traits distinguishing Dall's (*Phocoenoides dalli*), harbour (*Phocoena phocoena*), and hybrid porpoises.

	Dall's	Harbour	Hybrid	Source(s)
Morphological				
Size and shape	Large, robust	Small, less robust	Intermediate	Jefferson 1990; Gaskin 1992; Baird et al. 1998; M.B. Hanson, unpublished data; P.M. Willis, personal observations
Dorsal fin size, shape	Tall, slightly falcate	Small, low, scalene	Intermediate	Jefferson 1990; Gaskin 1992; Baird et al. 1998; P.M. Willis, unpublished data
Dorsal fin pigmentation	Black with white frosting	Dark gray	Pale to dark gray, variable dark edge	Jefferson 1990; Gaskin 1992; P.M. Willis, unpublished data
Dorsal fin tubercles	Absent	Present	Present (always?)	Jefferson 1990; Gaskin 1992; M.B. Hanson, unpublished data
Body pigmentation	Black with white flank patch	Dark gray, pale ventrally	Pale to medium gray, variable dark gray to brown areas	Jefferson 1990; Gaskin 1992; Baird et al. 1998; P.M. Willis, unpublished data
Mouth-to-flipper stripe	Absent	Present	Present (always?)	Gaskin et al. 1974; Jefferson 1988; Baird et al. 1998; M.B. Hanson, unpublished data
No. of vertebrae	92–98	62–66	Approximately 75	Gaskin et al. 1974; Jefferson 1988; Baird et al. 1998
Behavioural				
Bowriding	Frequently	Never	Intermediate	Gaskin et al. 1974; Jefferson 1988; Baird et al. 1998; P.M. Willis, unpublished data
Typical surfacing	High, boxy	Low, smooth	Intermediate	Taylor and Dawson 1984; Jefferson 1988; P.M. Willis, personal observation
Rapid surfacing in "roostertail"	Yes	No	Yes	Taylor and Dawson 1984; Jefferson 1988; P.M. Willis, personal observation
Genetic				
Restriction fragment length polymorphism banding pattern affinity	(–) Harbour	(+) Harbour	(+) Harbour	Baird et al. 1998
mtDNA species affinity	Dall's	Harbour	Dall's	Rosel et al. 1995; present study
ZFX species affinity	Dall's	Harbour	Heterozygous	Present study
Intersimple sequence repeat banding pattern affinity	(–) Harbour	(+) Harbour	(+) Harbour	Present study

and dTTP. Reactions contained 10–200 µg extracted DNA/mL and approximately 100 ng of each primer. Thermal cycler parameters were 30 cycles of 60 s at 94 °C, 60 s at 47 °C, and 60 s at 72 °C.

The sex of odontocete cetaceans can be determined via amplification of a portion of the last exon in the *ZFX/ZFY* gene of the sex chromosomes (Bérubé and Palsbøll 1996). We followed the procedures outlined in Bérubé and Palsbøll (1996) using primers ZFYX0582F (5'-ATA GGT CTG CAG ACT CTT CTA-3'), ZFY0767R (5'-TTT GTG TGA ACT GAA ATT ACA-3'), and ZFX0923R (5'-AGA ATA TGG CGA CTT AGA ACG-3'). Amplification products were electrophoresed through 2% agarose gels stained with ethidium bromide and viewed under UV light.

To determine the paternal species of putative hybrids, we first used species-specific nuclear markers to identify parental DNAs in putative hybrids; these data were then consid-

ered in concert with the mtDNA data to infer the paternal species. Species markers were isolated through amplification of intersimple sequence repeats (ISSRs) and sequencing of *ZFX/Y* product (see below). ISSRs are short regions of nuclear DNA that lie between inversely oriented, simple sequence repeats (microsatellites), only recently used in the study of animal populations (Kostia et al. 2000). As spectrophotometer analysis revealed insufficient DNA in four putative hybrid extractions to carry out standardized ISSR amplifications, only five individuals were subjected to this analysis. Amplifications were conducted using primer 811 (5'-GAG AGA GAG AGA GAG AC-3'; University of British Columbia Nucleic Acid – Protein Service Unit, UBC Primer Set No. 9) in 20-µL reactions containing 0.035 µg of total DNA, 10× PCR buffer (200 mmol (NH₄)₂SO₄/L, 750 mmol Tris-HCl/L (pH 8.8), 0.2% v/v Tween 20 (TetraLink International, Amherst, New York, USA)),

lar pattern appears at a second site (position 178) where two putative hybrids and one Dall's porpoise appear as heterozygotes (Genbank accession Nos. AY257183–AY257192). These sequence data further support a hybrid classification.

Behavioural and morphological characters intermediate between harbour and Dall's porpoises or common to only one parental species have been noted for putative hybrids in the wild and documented for the hybrid fetus described previously (Baird et al. 1998) (Table 1). From these data, our observations at sea, and the results described above, we summarize the available morphological, behavioural, and molecular evidence differentiating the porpoise types and identifying hybrids in Table 1.

Discussion

This study provides strong evidence of recurrent hybridization between local populations of Dall's and harbour porpoises and is one of only a few studies identifying mammalian hybrids in the wild, including their sex and direction of descent. Our findings support the hypothesis that the slow chromosomal evolution of cetaceans enables them to produce hybrid offspring more easily than other mammalian taxa (Árnason et al. 1991). The 6.5% cytochrome *b* mtDNA divergence reported here between harbour and Dall's porpoises approaches that observed between blue and fin whales (7.6%; Árnason and Gullberg 1993), the latter species pair being among the most distantly related mammalian species pair known to hybridize (Árnason et al. 1991; Árnason and Gullberg 1993). It appears that cetacean hybridization in the wild is possible even despite substantial mtDNA divergence and long separation times. However, the porpoises studied here are only the second cetacean species pair for which strong evidence of recurring natural hybridization is available and the first for which the production of viable offspring by female hybrids in the wild has been documented. If cetaceans as a group indeed face fewer post-zygotic barriers to hybridization than other mammals, then pre-zygotic factors likely play a prominent role in reproductively isolating member species, as has been suggested for blue and fin whales (Spilliaert et al. 1991).

The evolutionary consequences of porpoise hybridization are difficult to predict without measures of hybrid fertility and viability, which are beyond the scope of the present study. However, female hybrids are at least sometimes fertile, as evidenced through observations of hybrid females with neonatal calves. The presence of a fetus in a female blue × fin whale hybrid suggests some fertility in these crosses as well (Spilliaert et al. 1991; Árnason and Gullberg 1993). Similarity between species karyotypes likely reduces meiotic incompatibility in female blue × fin whale hybrids (Árnason and Gullberg 1993) and may operate similarly in porpoises. Although the 5:4 male:female sex ratio of sampled hybrids suggests equal viability between the sexes, the predominance of male sterility in other mammalian crosses (Gray 1971; Wu et al. 1996) and the observation of probable sterility in another male cetacean hybrid (blue × fin whale; Árnason et al. 1991) suggest that male porpoise hybrids may be infertile. Porpoise hybrids may therefore be expected to exhibit reduced average fertility with respect to parentals, which should select against hybridization. However, the

presence of F₂s suggests that introgression may be occurring, presumably via female hybrids back-crossing to one or both parental species.

Examples of multiple hybridization events among large mammals in the wild are few (e.g., Carr et al. 1986; Lehman et al. 1991; Goldsworthy et al. 1999). The porpoise hybrids reported here represent a temporally and geographically concentrated case of natural hybridization in large mammals. Although we believe incidental descriptions of white or gray "Dall's" porpoises from other regions of sympatry to be misidentified hybrids (e.g., Morejohn et al. 1973; Joyce et al. 1982; Miller 1990), the present study region appears unique in hosting many hybrids over a very small area, only a small fraction of the parental species' range of sympatry. Why this localized hybridization should be occurring despite apparently strong isolation elsewhere is unclear, but it may reflect the apparent decline in local harbour porpoise numbers over the last several decades (Baird 2003). Natural hybridization events among other mammalian species almost always involve disturbed habitats where one population is in decline (e.g., Carr et al. 1986; Lehman et al. 1991). A decrease in the availability of conspecific potential mates may increase the cost of choice to individuals, so that some populations, otherwise acting as "good species", begin hybridizing (Wilson and Hedrick 1982). Harbour porpoise males may be pursuing matings indiscriminately, including matings with heterospecifics, partly in response to a lower conspecific encounter rate.

All analyzed hybrids had Dall's porpoises as maternal parents, as did the hybrid fetus reported previously (Baird et al. 1998). This directionality is among the strongest observed in hybridizing animal populations and it contradicts the recent prediction that in species displaying female choice, females of the rarer species should act as the maternal parent (Wirtz 1999). We suggest that the highly promiscuous male harbour porpoise (Fontaine and Barrette 1997) may be driving hybridization in the observed direction through the indiscriminate pursuit of females of either species. Indiscriminate and forceful or "sneaky" male mating behaviour may be common to animal hybridization events, including those occurring directionally (e.g., Lamb and Avise 1986; Spence 1990), particularly if males are of the rarer species (e.g., Goldsworthy et al. 1999). Further study of premating isolation in hybridizing animal species is needed to test these predictions.

Acknowledgements

We thank M. Vankoevinge for laboratory assistance; S. Escorza-Treviño, A. Fraser, W. Hoggard, F. Larsen, and E. Valsecchi for technical advice and assistance; S. Hazlitt, P. Miller, and numerous field assistants for field support; T. Chapman, J. Law, and S. Springer for helpful discussions and laboratory assistance; and T. Guenther and the Marine Mammal Research Group, Victoria, British Columbia, for porpoise tissues. P.M.W. was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) postgraduate scholarship and a Simon Fraser University graduate fellowship. Financial support was received from the Exploration Fund, Mountain Equipment Co-op, the PADI Foundation, and NSERC grants to L.M.D. and B.J.C.

Field research was conducted under permits issued by the National Marine Fisheries Service (permits 873, 1437, and 782-1349) and the Canadian Department of Fisheries and Oceans. Ú. Árnason and J.Y. Wang provided helpful comments on the manuscript.

References

- Árnason, Ú. 1972. The role of chromosomal rearrangement in mammalian speciation with special references to Cetacea and Pinnipedia. *Hereditas*, **70**: 113–118.
- Árnason, Ú. 1974. Comparative chromosome studies in cetacea. *Hereditas*, **77**: 1–36.
- Árnason, Ú. 1982. Karyotype stability in marine mammals. *Cytogenet. Cell Genet.* **33**: 274–276.
- Árnason, Ú., and Gullberg, A. 1993. Comparison between the complete mtDNA sequences of the blue and the fin whale, two species that can hybridize in nature. *J. Mol. Evol.* **37**: 312–322.
- Árnason, Ú., Spilliaert, R., Palsdottir, A., and Árnason, A. 1991. Molecular identification of hybrids between the two largest whale species, the blue whale (*Balaenoptera musculus*) and the fin whale (*B. physalus*). *Hereditas*, **115**: 183–189.
- Arnold, M.L. 1997. Natural hybridization and evolution. Oxford University Press, Oxford, UK.
- Baird, R.W. 2003. Update COSEWIC status report on harbour porpoise (*Phocoena phocoena*) in British Columbia. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ont.
- Baird, R.W., and Guenther, T.J. 1994. Status of porpoises in the British Columbia/Washington State transboundary area — a Canadian perspective. *Puget Sound Notes*, **34**: 5–8.
- Baird, R.W., Willis, P.M., Guenther, T.J., Wilson, P.J., and White, B.N. 1998. An inter-generic hybrid in the family Phocoenidae. *Can. J. Zool.* **76**: 198–204.
- Bérubé, M. 2002. Hybridism. In *Encyclopedia of marine mammals*. Edited by W.F. Perrin, B. Würsig, and J.G.M. Thewissen. Academic Press, San Diego, Calif. pp. 596–600.
- Bérubé, M., and Aguilar, A. 1998. A new hybrid between a blue whale, *Balaenoptera musculus*, and a fin whale, *B. physalus*: frequency, and implications of hybridization. *Mar. Mamm. Sci.* **14**: 82–98.
- Bérubé, M., and Palsbøll, P. 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Mol. Ecol.* **5**: 283–287.
- Carr, S.M., Ballinger, S.W., Derr, J.N., Blankenship, L.H., and Bickham, J.W. 1986. Mitochondrial DNA analysis of hybridization between sympatric white-tailed deer and mule deer in west Texas. *Proc. Natl. Acad. Sci. U.S.A.* **83**: 9576–9580.
- Ferris, S.D., Sage, R.D., Huang, C.-M., Nielsen, J.T., Ritte, U., and Wilson, A.C. 1983. Flow of mitochondrial DNA across a species boundary. *Proc. Natl. Acad. Sci. U.S.A.* **80**: 2290–2294.
- Fontaine, P.M., and Barrette, C. 1997. Megatestes: anatomical evidence for sperm competition in the harbor porpoise. *Mammalia*, **61**: 65–71.
- Gaskin, D.E. 1992. Status of the harbour porpoise, *Phocoena phocoena*, in Canada. *Can. Field-Nat.* **106**: 36–54.
- Gaskin, D.E., Arnold, P.W., and Blair, B.A. 1974. *Phocoena phocoena*. *Mamm. Species*, **42**: 1–8.
- Goldsworthy, S.D., Boness, D.J., and Fleischer, R.C. 1999. Mate choice among sympatric fur seals: female preference for conphenotypic males. *Behav. Ecol. Sociobiol.* **45**: 253–267.
- Grant, P.R., and Grant, B.R. 1992. Hybridization of bird species. *Science (Wash., D.C.)*, **25**: 193–197.
- Gray, A.P. 1971. Mammalian hybrids. a check-list with bibliography. 2nd ed. Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire, UK.
- Hanson, M.B. 2001. An evaluation of the relationship between small cetacean tag design and attachment durations: a bioengineering approach. Ph.D. dissertation, University of Washington, Seattle.
- Hubbs, C.L. 1955. Hybridization between fish species in nature. *Syst. Zool.* **4**: 1–20.
- Jefferson, T.A. 1988. *Phocoenoides dalli*. *Mamm. Species*, **319**: 1–7.
- Jefferson, T.A. 1990. Sexual dimorphism and development of external features in Dall's porpoise *Phocoenoides dalli*. *Fish. Bull. (Wash., D.C.)*, **88**: 119–132.
- Joyce, G.G., Rosapepe, J.V., and Ogasawara, J. 1982. White Dall's porpoise sighted in the North Pacific. *Fish. Bull. (Wash., D.C.)*, **80**: 401–402.
- Kostia, S., Ruohonen-Lehto, M., Vainola, R., and Varvio, S.-L. 2000. Phylogenetic information in inter-SINE and inter-SSR fingerprints of the Artiodactyla and evolution of the Bov-tA SINE. *Heredity*, **84**: 37–45.
- Kulu, D.D., Veomett, I., and Sparkes, R.S. 1971. Cytogenetic comparison of four species of cetaceans. *J. Mammal.* **52**: 828–832.
- Lamb, T., and Avise, J.C. 1986. Directional introgression of mitochondrial DNA in a hybrid population of tree frogs: the influence of mating behaviour. *Proc. Natl. Acad. Sci. U.S.A.* **83**: 2526–2530.
- Lehman, N., Eisenhawer, A., Hansen, K., Mech, L.D., Peterson, R.O., Gogan, P.J.P., and Wayne, R.K. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution*, **45**: 104–119.
- Miller, E.J. 1990. Photo-identification techniques applied to Dall's porpoise (*Phocoenoides dalli*) in Puget Sound, Washington. *Int. Whaling Comm. Rep. Spec. Issue*, **12**: 429–437.
- Morejohn, G.V., Loeb, V., and Baltz, D.M. 1973. Coloration and sexual dimorphism in the Dall porpoise. *J. Mammal.* **54**: 977–982.
- Prager, E.M., and Wilson, A.C. 1975. Slow evolutionary loss of the potential for interspecific hybridization in birds: a manifestation of slow regulatory evolution. *Proc. Natl. Acad. Sci. U.S.A.* **72**: 200–204.
- Rosel, P.E., Haygood, M.G., and Perrin, W.F. 1995. Phylogenetic relationships among the true porpoises (Cetacea: Phocoenidae). *Mol. Phylogenet. Evol.* **4**: 463–474.
- Spence, J.R. 1990. Introgressive hybridization in Heteroptera: the example of *Limnopus* Stål (Gerridae) species in western Canada. *Can. J. Zool.* **68**: 1770–1782.
- Spilliaert, R., Vikingsson, G., Arnason, U., Palsdottir, A., Sigurjonsson, J., and Arnason, A. 1991. Species hybridization between a female blue whale (*Balaenopterus musculus*) and a male fin whale (*B. physalus*): molecular and morphological documentation. *J. Hered.* **82**: 269–274.
- Sylvestre, J.P., and Tasaka, S. 1985. On the intergeneric hybrids in cetaceans. *Aquat. Mamm.* **11**: 101–108.
- Taylor, B.L., and Dawson, P.K. 1984. Seasonal changes in density and behavior of harbor porpoise (*Phocoena phocoena*) affecting census methodology in Glacier Bay National Park, Alaska. *Int. Whaling Comm. Rep.* **34**: 479–483.
- Tegelström, H. 1987. Transfer of mitochondrial DNA from the northern red-backed vole (*Clethrionomys rutilus*) to the bank vole (*C. glareolus*). *J. Mol. Evol.* **24**: 218–227.
- Willis, P.M. 2001. Mating system dynamics and hybridization of Dall's (*Phocoenoides dalli*) and harbour porpoise (*Phocoena phocoena*). M.Sc. thesis, Simon Fraser University, Burnaby, B.C.

- Wilson, A.C., Sarich, V.M., and Maxson, R. 1974. The importance of gene rearrangement in evolution: evidence from studies on rates of chromosomal, protein, and anatomical evolution. *Proc. Natl. Acad. Sci. U.S.A.* **71**: 3028–3030.
- Wilson, D.S., and Hedrick, A. 1982. Speciation and the economics of mate choice. *Evol. Theory*, **6**: 15–24.
- Wirtz, P. 1999. Mother species-father species: unidirectional hybridization in animals with female choice. *Anim. Behav.* **58**: 1–12.
- Wu, C.-I., Johnson, N.A., and Palopoli, M.F. 1996. Haldane's rule and its legacy: why are there so many sterile males? *Trends Ecol. Evol.* **11**: 281–284.
- Zornetzer, H.R., and Duffield, D.A. 2003. Captive-born bottlenose dolphin × common dolphin (*Tursiops truncatus* × *Delphinus capensis*) intergeneric hybrids. *Can. J. Zool.* **81**: 1755–1762.