

Penis extrusions by humpback whales (*Megaptera novaeangliae*)

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Abstract

The annual winter assembly of humpback whales (*Megaptera novaeangliae*) in tropical waters has been linked to reproductive activities, including birthing, calf-rearing, and mating. However, the sexual behaviour of this species remains largely undescribed and mating has never been witnessed. We examined 121 h of underwater videotaped footage of humpback whales obtained over five winter seasons in Hawaiian waters for evidence of penis extrusions by whales engaged in various activities in a range of social groups. In 630 different pods containing videotaped males, we noted 13 penis extrusion incidents. Penis extrusions were performed by lone singers (2 incidents), by the single escort to a mother/calf pair (6 incidents), and by principal and secondary escorts in competitive pods containing a female either with a calf (2 incidents) or without (3 incidents). All penis extrusions were brief (mean=44.40 s). Body length measurements (mean=11.53 m, SD=0.46 m, range=10.64 m to 12.05 m) were obtained using underwater videogrammetry on seven penis extruders, and suggested that the majority were sexually mature. Each penis extrusion in a competitive pod coincided with the penis extruder chasing another whale, and in four of five cases appeared to be directed toward another male. In the remaining case, the extruder appeared to attempt mating with a mother. Our findings suggest that penis extrusions in humpback whale competitive pods are often a concomitant of dominance contests between males.

Key words: *Megaptera novaeangliae*, humpback whale, penis, sexual behaviour.

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Introduction

In many species, the functions of sexual behaviour extend beyond reproduction. Heterosexual behaviour often occurs in non-reproductive contexts and homosexual behaviour is common (Bagemihl, 1999). For example, Hashimoto & Furuichi (1994) determined that agonistic behaviour between adult wild male bonobos (*Pan paniscus*) was frequently followed by non-copulatory penis contact, suggesting that this 'sexual' behaviour serves in part to reduce tensions. Penis contact between immature male bonobos was often an integral part of play behaviour. In squirrel monkeys (*Saimiri sciureus*) (Ploog & Maclean, 1963) and whiptail wallabies (*Macropus parryi*) (Kaufmann, 1974), penis erections may be associated with aggression and often are performed by dominant males towards subordinates. Penis extrusion, and in some cases penetration, also can establish or reinforce intra-specific dominance relationships among male bottlenose dolphins (*Tursiops truncatus*) (Caldwell & Caldwell, 1977; Ostman, 1991) and inter-specific dominance relations between male bottlenose dolphins and male spotted dolphins (*Stenella frontalis*) (Herzing & Johnson, 1997). These examples suggest that sexual behaviour involving a male's penis can play a role in social interactions among individuals.

In this paper, we examine penis extrusions in humpback whales (*Megaptera novaeangliae*), a species whose social behaviour has been studied for over 25 years, but whose sexual behaviour remains an enigma. Most humpback whales spend summer months feeding in high-latitude waters and migrate during fall and winter months to low-latitude waters in which feeding is absent, and behaviours are related largely to reproduction (Chittleborough, 1965; Dawbin, 1966; cf. Mikhalev, 1997). Although researchers have never observed copulation in humpback whales (Mobley & Herman, 1985; Clapham, 2000), data from commercial whaling revealed seasonal increases in gonad size,

spermatogenesis, and ovulation during fall and winter months (Chittleborough, 1954, 1955; Nishiwaki, 1959; Symons & Weston, 1958).

In cetaceans, sexual behaviour can take a variety of forms (e.g., in dolphins, tail or rostrum to genital contact—Caldwell & Caldwell, 1972). However, the clearest indicant that behaviour has a sexual component is when the fibroelastic penis, which is normally concealed within the genital slit (Slijper, 1962), is extruded (Würsig & Clark, 1993). Despite decades of research on humpback whales, reports of penis extrusion are rare. Recently, Pack *et al.* (1998) described a humpback whale extruding its penis above-water adjacent to the floating body of a male humpback that died in a competitive pod shortly before. The suggested functions for the penis extrusion by the live male humpback toward the dead male humpback included dominance behaviour and sexual behaviour (Pack *et al.*, 1998). However, the unusual circumstances in which this penis extrusion occurred limited any generalization beyond this unique situation.

There are only three other reported observations of penis extrusions in humpback whales, all occurring on the Hawaiian winter grounds (Tyack & Whitehead, 1983; Glockner-Ferrari & Ferrari, 1985; Bauer *et al.*, 1993). None was described in any detail, however. Tyack & Whitehead (1983) observed the erect penis of a single male escort accompanying a mother/calf pair. They stated only that the male appeared to be urinating. Glockner-Ferrari & Ferrari (1985) described an incident in which two males, one judged by eye to be an adult and the other a subadult, rubbed against each other and touched each other with their pectoral fins. At one point, the subadult extruded its penis and rubbed it against the genital slit of the adult. No follow-up observations of the pair were reported. In an abstract, Bauer *et al.* (1993) simply noted a penis extrusion among other underwater videotape footage of humpback whales. Given that the current knowledge of humpback whale penis behaviour is limited to these brief reports, there is a clear need for more detailed data. Such data should increase understanding of the contexts in which penis extrusions occur, their functional characteristics, and their significance in humpback whale social or reproductive interactions.

Unlike the penis extrusions of right whales (*Eubalaena australis*) and grey whales (*Eschrichtius robustus*), which frequently occur at the surface (e.g., Payne & Dorsey, 1983; Swartz, 1986), humpback whale penis extrusions occur primarily under water (Clapham, 2000). If so, the lack of documented penis extrusions by humpback whales may reflect the infrequency with which their underwater behaviour has been studied. Although a few researchers have published observations of selected

underwater behaviours of humpback whales (e.g., Glockner & Venus, 1983; Baker & Herman, 1984; Glockner-Ferrari & Ferrari, 1985; Pack *et al.*, 1998), to date there have been no comprehensive reports of subsurface behaviours. Most published studies of humpback whale behaviour have concentrated on either behaviours observed above the surface (e.g., Mobley & Herman, 1985; Clapham *et al.*, 1992; Helweg & Herman, 1994; Smultea, 1994) or vocalizations occurring below the surface without accompanying underwater observations (e.g., Silber, 1986; Au *et al.*, 2000).

In this study, we examined videotape records of underwater behaviours and accompanying descriptions of surface behaviours of different types of humpback whale pods containing at least one male obtained over five seasons on the Hawaiian winter grounds for evidence of penis extrusions. On the winter grounds, individual male humpbacks can occupy different social roles. They may 'escort' single females with calf or without calf (Herman & Antinaja, 1977). 'Competitive pods' consist of multiple escorts competing for the position closest to a lone female, either with a calf (M), or without (NA) (Tyack & Whitehead, 1983; Baker & Herman, 1984). The escort defending this favoured position has been termed the principal escort (PE) (Tyack & Whitehead, 1983). His ability to maintain this position may permit mating access and/or constitute mate guarding from secondary escorts (SE) (Herman & Tavolga, 1980; Clapham, 1996). Although humpback whales do not appear to form enduring dominance hierarchies (Frankel *et al.*, 1995; Clapham, 1996), a PE can be viewed as occupying a temporary position of dominance relative to the SEs in the group. Another social role occupied by males on the winter grounds is that of singer. The hypothesized functions of song include sexual advertisement (Payne & McVay, 1971; Glockner-Ferrari & Ferrari, 1985; Medrano *et al.*, 1994), spacing of individuals (Winn & Winn, 1978; Tyack, 1981; Frankel *et al.*, 1995), and display towards other males (Frankel *et al.*, 1995; Darling & Berube, 2001). Males also may be observed as singles and, finally, as calves accompanied by their mothers.

For each of these social roles, we report the frequency and duration of penis extrusions, and the different types of pods and contexts within which penis extrusions occurred. Finally, we discuss the probable functions of penis extrusions suggested by these observations.

Materials and Methods

Our whale surveys took place between January and April of 1996 through 2000 in waters off West Maui, Hawaii. This area contains one of the

highest concentrations of humpback whales in the Hawaiian Islands during the winter season (Herman & Antinoya, 1977; Herman *et al.*, 1980; Mobley *et al.*, 1999). Both surface and underwater observations of humpback whales were conducted almost daily from one or two small boats (*ca.* 5.2 m) equipped with outboard engines. Whales were sighted initially from their blows or surface activities. After approaching a group of whales, we recorded their surface behaviours, group composition, and individual social roles. In conjunction with recording the behaviour of observed whales, we photographed the ventral surface of each whale's tail flukes opportunistically using 35-mm cameras equipped with 100- to 300-mm lenses. Individuals were identified from the white and black patterns on the ventral surface of the flukes, along with the pattern of the trailing edge (Katona *et al.*, 1979). Fluke photographs were matched against the Kewalo Basin Marine Mammal Laboratory's (KBMML) 25-year catalogue of North Pacific humpback whale fluke photographs, a portion of which appears in Perry *et al.* (1988).

If the whales were stationary, milling, or moving slowly, we deployed a swimmer equipped with mask, snorkel, fins, and a video camera in an underwater housing fitted with a hydrophone. A Hi-8 video camera was used in 1996 and 1997, and a digital video camera was used in all other years. The swimmer recorded all whale behaviour and social interactions on videotape, and when possible determined the sex of individual whales from the presence (in females) or absence (in males) of a hemispheric lobe just caudal of the genital slit (True, 1904; Glockner, 1983). As noted earlier, behaviour involving a male humpback's penis was clearly definable because the penis, as in all cetaceans, is normally concealed within the genital slit (Slijper, 1962). In 1999 and 2000, in addition to recording underwater whale behaviours, we used an underwater videogrammetric technique developed by Spitz *et al.* (2000) to measure the lengths of individual humpback whales.

Results

Table 1 summarizes the number of whale pods filmed and duration of film footage per year for all pods of humpback whales containing at least one male. A mean of 17.40 h of video footage was obtained for seven types of pod commonly observed in Hawaiian waters ($SD=17.17$, range=0.80–50.36 h). These pod types were: mother/calf pair (MC), mother/calf accompanied by a single escort (MCE), mother/calf with more than one escort (MC2E+); singleton (1A), pair of adults (2A), group of three or more adults (3A+), and

lone singer (S).¹ Sampling differences among pods, as shown in Table 1, most likely reflected not only their frequency of occurrence, but also a bias towards stationary or slow-moving pods to facilitate underwater observation.

Although 630 different pods were videotaped under water for over 120 h, as well as observed from the surface, there were only 13 observed penis extrusion incidents, all of which occurred under water. Table 2 lists each incident of penis extrusion along with supplementary data.² Penis extrusions were filmed in four different years, three different months, and at several times-of-day. In 12 of 13 cases, the penis was extruded only once. In Incident 4, two separate extrusions (by the escort in an MCE group) were documented, the second occurring 66.32 min after penis retraction. In Incidents 9 and 11, the whale's ventral side was hidden from view for a short period (<1 min) between views of its extruded penis. For these incidents, we assumed a single penis extrusion that continued while the whale's genital area was not in view.

Penis extrusions were brief. The duration of the 14 separate penis extrusions ranged from 19.80 s to 100.80 s (mean=44.40 s, $SD=30.00$ s). These times should be considered minimums because either the video record of each extrusion captured a whale with its penis already extruded, and/or we were unable to determine the exact time of penis retraction (e.g., because the whale's ventral surface turned away from the camera's view). Nevertheless, in most incidents the total duration of penis extrusion was a small percentage of the total video record for that incident (mean=4.90%, $SD=8.10\%$).

Penis extrusions were observed in 4 of 7 types of pod listed in Table 1, and were performed by humpback whales occupying four different social roles in several different competitive and non-competitive contexts (Table 2). Two of 55 lone singers (3.6%) extruded their penis either in concert with song production or between bouts of singing (Incidents 6 and 13). Seven penis extrusions were performed by single escorts in 6 of 263 MCE pods (2.3%) (Incidents 2, 3, 4, 5, 7, and 10). Additionally, a SE and a whale which had recently attained the position of PE extruded their penis (Incidents 1 and 9, respectively) in 2 of 52 competitive pods containing a mother/calf pair (3.8%). We also observed both SEs and PEs extrude their penis in 3 of 154 (1.9%) competitive pods in which no calf was present (Incidents 8, 11, and 12). Overall however,

¹Singing escorts also were videotaped, but were counted as escorts.

²The 1996 observation of the penis extrusion from a live humpback whale toward a dead humpback male published by Pack *et al.* (1998) is not reported again here.

Table 1. Underwater videography effort in surveys of humpback whales off Maui for humpback whale pods containing at least one male (1996–2000).

Year	Number days	Number of pods videotaped under water (total duration of recordings (h:m:s))									
		MCE	MC2E+	1A	2A	3A+	S	MC	TOTAL		
1996	61	48 (11:14:32)	13 (02:49:58)	0 (00:00:00)	2 (02:32:22)	25 (05:08:52)	5 (00:26:07)	1 (00:06:28)	94 (22:18:19)		
1997	58	48 (11:07:05)	7 (00:30:07)	1 (00:01:44)	5 (01:18:50)	17 (04:09:48)	2 (00:27:03)	6 (02:05:22)	86 (19:39:59)		
1998	60	36 (07:44:41)	7 (00:59:20)	1 (00:05:40)	8 (01:20:15)	25 (03:31:23)	10 (01:08:07)	5 (00:42:12)	92 (15:31:38)		
1999	80	63 (10:27:33)	8 (01:46:50)	3 (00:25:11)	21 (03:44:05)	34 (04:19:31)	17 (03:35:33)	8 (01:28:55)	154 (25:47:38)		
2000	84	68 (09:47:38)	17 (01:17:51)	2 (00:19:13)	39 (08:53:55)	53 (11:37:59)	21 (05:21:52)	4 (01:13:46)	204 (38:32:14)		
Total	343	263 (50:21:29)	52 (07:24:06)	7 (00:51:48)	75 (17:49:27)	154 (28:47:33)	55 (10:58:42)	24 (05:36:43)	630 (121:49:48)		

Note: M=mother, C=calf, E=escort, A=adult, S=singer, '+'=groups containing indicated number of animals or greater. For MC pods, calf was identified as male. Whales were identified as males either through direct observation of their genital areas or inference from their social role (i.e., escort=male, singer=male, Glockner, 1983).

Table 2. Incidents and contexts of underwater penis extrusions by humpback whales in Maui (1996–2000).

Incident	Date	Time observed	Total duration video record**	Duration of penis extrusion (min)			Penis extruder			% males mature from whaling data that bracket our whale size		
				Extrusion 1	Inter-extrusion interval	Extrusion 2	Post-extrusion period	Group Type	Context		Social role	Identity
1	10 Mar 1996	10:47–13:49	29.20	>0.33	—	—	—	MC7E	Competitive	SE	13 739	—
2	15 Mar 1997	15:42–18:02	33.87	>0.70	—	—	6.33	MCE	Non-competitive	E	10 982	—
3	29 Mar 1997	15:03–16:27	52.20	>0.82	—	—	45.93	MCE	Non-competitive	E	11 096	—
4	23 Jan 1999	16:55–18:34	50.27	>0.52	<66.32*	>0.83	15.77	MCE	Non-competitive	E	184	11.65
5	25 Jan 1999	13:09–14:07	17.42	>1.33	—	—	5.38	MCE	Non-competitive	E	184	11.65
6	18 Mar 1999	10:23–11:09	18.75	>0.60	—	—	4.38	S	Singing	S	1559	11.97
7	31 Mar 1999	9:37–10:59	52.65	>0.62	—	—	25.23	MCE	Non-competitive	E	13 477	11.43
8	14 Jan 2000	11:45–13:23	46.96	>0.22	—	—	2.38	NA2E	Competitive	PE	15 024	10.64
9	18 Jan 2000	17:09–17:30	5.48	>1.66	—	—	7.78	MC3E	Competitive	PE	13 886	—
10	2 Feb 2000	9:14–10:40	24.77	>0.55	—	—	10.53	MCE	Non-competitive	E	14 075	11.45
11	9 Feb 2000	13:18–14:23	33.98	>0.40	—	—	3.87	NA4E	Competitive	PE	14 160	12.05
12	18 Feb 2000	14:44–16:24	13.85	>0.08	—	—	5.87	NA11E	Competitive	SE	15 025	—
13	30 Mar 2000	10:45–12:22	17.68	>1.68	—	—	6.35	S	Singing	S	14 676	11.53

Note: NA = adult-sized female unaccompanied by a calf in competitive pod, M = mother, C = calf, E = single escort, A = adult, PE = principal escort, SE = secondary escort, S = singer.

**includes behaviour recorded prior to first extrusion.

*interval included period of underwater observation while videotape was being changed at surface. Whaling size data are from Nishiwaki (1959; 1962) and Omura (1955).

Table 3. Synopses of videotaped penis extrusion incidents by male humpback whales in competitive contexts.

10 March 1996 (MC7E). SE 9924 blew a linear bubble trail (LBT) and was physically blocked by the PE. After 30 s, SE 9926 struck 9924 on the abdomen with its rostrum. SE 13739 approached 9924 on its right side, and wrapped its pectoral fins around 9924's lower body. 13739 partially extruded its penis, and probed it along 9924's peduncle. After 10 s, 9924 broke contact with 13739's penis. However, 13739 maintained its pectoral grasp on 9924. 9924 then struck 13739 with its flukes, deflecting away 13739's penis and left pectoral fin. 9924 turned away from 13739 and dived steeply in synchrony with 9926.

14 January 2000 (NA2E). NA 13810 rested below the surface. PE 15024 remained close to NA, its rostrum often positioned perpendicular to 13810's abdomen. SE 13811 was approximately 40 m from the NA and was singing. When SE moved closer to NA, PE positioned its tail flukes toward SE. Occasionally, PE turned to chase SE away. During one chase sequence, PE turned its genitals towards SE and partially extruded its penis as it dived. PE then returned to a position near NA.

18 January 2000 (MC3E). A pair of males (E 13886 and E 13884) approached an MCE (M 15023 and E 13885). M travelled rapidly with E 13886 closest to her and an unidentified E further away. With penis extruded, E 13886 approached M and positioned itself vertically head-up with its pectoral fins spread wide as it pressed its ventral surface against M's right side. M pumped its tail flukes vigorously as E 13886 grasped M with its left pectoral fin around the back and attempted to contact M with its penis. All three whales disappeared behind a curtain of bubbles. After 24 s C, (a male) swam into view. C milled rapidly in front of the bubble curtain and high-pitched vocalizations were heard. C swam into the bubble mass. After 13 s, E 13886 and M emerged from the bubble curtain. E 13886's penis was extruded as it chased M. At the surface, C trailed M. E 13886 positioned itself with pectoral fins spread wide on top of M's dorsal surface. Grunting sounds were heard. E 13886's penis no longer visible as all three whales surfaced with E 13886 positioned between M and C. M and E 13886 dived followed by E 13884 (from the pair). Approximately 6 min later, E 13884, M, and C swam into view. E 13884 dived toward M and pressed its ventral side against M's dorsal side. With pectoral fins spread wide, E 13884 blew a stream of bubbles and then swam rapidly toward C at the surface. M blew a stream of bubbles and swam rapidly up toward E 13884 and C. E 13884 maintained its position between M and C. After milling in a tight circle, M retrieved C with E 13884 in close pursuit. M, C, and E 13884 traveled out of view.

9 February 2000 (NA4E). NA14156 rested below the surface. NA surfaced synchronously with PE14160 who blew a LBT. SE 14158 surfaced several whale lengths behind NA. After diving, NA and PE were again observed stationary approx. 25 m. below surface. PE surfaced and dived towards NA. It positioned itself with its tail pointed toward SE who was less than 15 m away from NA. After 6 min PE surfaced and urinated without extruding its penis. About 1 min later, PE logged at the surface approximately 20 m from SE, also logging at the surface, positioned parallel to PE. After 30 s, as PE and SE dived, PE extruded its penis and turned its genital region towards SE. After chasing SE away from the vicinity, PE returned to NA. NA and PE surfaced together, but PE quickly dived and chased SE who was surfacing from below NA. PE turned back toward NA and performed a LBT as he followed her. SE surfaced behind the pair and all three whales swam out of view.

18 February 2000 (NA11E). SE 15025 had its penis already extruded and dangling as it closely chased another SE. Loud grunt sounds were heard. A third whale was observed in the background as all three swam out of view. Additional recordings revealed numerous bouts of aggression between escorts.

Note: M=mother, C=calf, PE=principal escort, SE=secondary escort, NA=nuclear single female (gender confirmed visually) unaccompanied by calf in competitive group, E=single escort.

penis extrusions were rare across all pod types, and were never observed from calves, or within pairs of adults, although these groups were well represented in our survey efforts (Table 1).

A detailed chronology of each penis extrusion incident for competitive pods and non-competitive pods is presented in Tables 3 and 4, respectively. There were five competitive pods of varying composition in which penis extrusions occurred. No extrusions were associated with urination, although in one instance urination by a male occurred in the absence of penis extrusion.

Each penis extrusion in a competitive pod was coincident with the penis extruder chasing another

whale. Penis extrusions, therefore, appeared to be directed toward particular individuals in each pod. In four of the competitive pods, it appeared that penis extrusions were directed toward another male, even though a female was present. In Incidents 1 and 12, SEs directed penis extrusions to other SEs. In Incident 1, SE 13739 actually contacted SE 9924 with its penis while grasping 9924's body with its pectoral fins (Figure 1). In Incident 12, SE 15025 had its penis extruded as it closely chased SE 15026. In Incidents 8 and 11, the PE directed its penis extrusion to the SE challenger that approached the NA, closely attended by the PE. In each incident, the PE's penis extrusion was coincident with

Table 4. Synopses of videotaped penis extrusion incidents by male humpback whales in non-competitive contexts.

15 March 1997 (MCE). M 10983 was stationary 20 m below the surface with head raised and peduncle arched. Less than 15 m away E 10982 was positioned horizontally, and oriented with its head pointing toward M's peduncle. As M and C surfaced, E rolled slightly along its longitudinal axis. Its penis was already extruded, erect and bowed pointing towards its abdomen. E slowly trailed M and C. Its penis pointed downward as it swam out of view.

29 March 1997 (MCE). M 11097 and C were stationary and positioned horizontally 20 m below the surface. E 11096 was approximately 15 m from M with its head oriented toward M. As C and M surfaced, E's already extruded penis came into view. It appeared erect and bowed with the tip pointing at E's abdomen. As E slowly trailed M and C, its penis pointed downward and remained in view until the whales were out of video range.

23 January 1999 (MCE). E 184 trailed M 1560 at the surface, its penis partially extruded with urine emanating from the tip for 22 s. After 44 s, E's penis was no longer visible and MCE dived, MC to 15 m and E to 20 m. M and E were stationary, oriented horizontally. E faced M's peduncle. C began nursing as E observed closely from behind. After 1.55 min, E adopted a near-vertical head-up posture, its pectoral fins spread wide. After 29 s, E turned toward MC as they surfaced. After diving, C nursed again, then surfaced, opened its mouth and briefly inflated its ventral pleats. About 10 min later, E angled its head upward towards M from below. E's penis was extruded and erect. E rose to a near-vertical posture below M. E's penis pointed at an angle perpendicular to its body, the tip curled upward. E sculled its pectoral fins, flashing the white ventral surface upward toward M. After 50 s E's penis was no longer visible as it surfaced behind MC.

25 January 1999 (MCE). E 184 was positioned horizontally below the surface 15 m from M 1560 and C. E's penis was extruded, erect and bowed, and moved toward and away from its abdomen 7 times in 10 s. E then adopted a head-up vertical posture with its penis still extruded, now pointing at an angle perpendicular to the body. E sculled with both pectoral fins, flashing the white ventral surface upwards. After 80 s E's penis retracted completely.

18 March 1999 (S). S 1559 sang loudly 20 m below the surface with its head pointed down. After 14 min 19 s, S's already-extruded penis came into view. It was erect and bowed, pointing toward its abdomen. S continued to sing. After 36 s the penis was no longer visible. S sang for 5 min, 35 s more before going silent. No other whales were observed in the vicinity.

31 March 1999 (MCE). M 13476 rested below E 13477. C repeatedly swam to and rested under E. E sculled with its pectoral fins, ventral-surface-down. After 10 min, M travelled around E's head and was joined by C. MC surfaced together. As E trailed MC, its penis was extruded. It was erect and pointed perpendicular to its body. After 37 s, E's penis retracted. After diving, both E and M were stationary, E positioned perpendicular to M at a distance of approximately 15 m. C consistently dived to E under its arched peduncle and remained there. On each occasion when M surfaced it swam around E and was joined by C.

2 February 2000 (MCE). M 14074 rested 20 m below the surface with its body angled upwards. E was oriented vertically, behind and below M. After about 10 min, MC began to surface. E began surfacing approximately 25 m to M's right. E's penis was extruded and pointed downward as E swam forward of M. E urinated for 5 s, after which its penis remained extruded. E continued travelling forward of M and began to urinate again for several sec. After urination ceased, E's penis remained extruded as E continued to travel. E's penis appeared to retract as E moved out of view.

30 March 2000 (S). S 14676 sang loudly 20 m below the surface with its head pointed down. After 8.60 min, singing stopped, S surfaced and began travelling. After 45 min, travelling ceased and S rested silently below the surface. Its peduncle was cocked slightly downward and its erect penis was faintly visible for 1.68 min. After 7.48 min S surfaced and approximately 3 min later singing resumed.

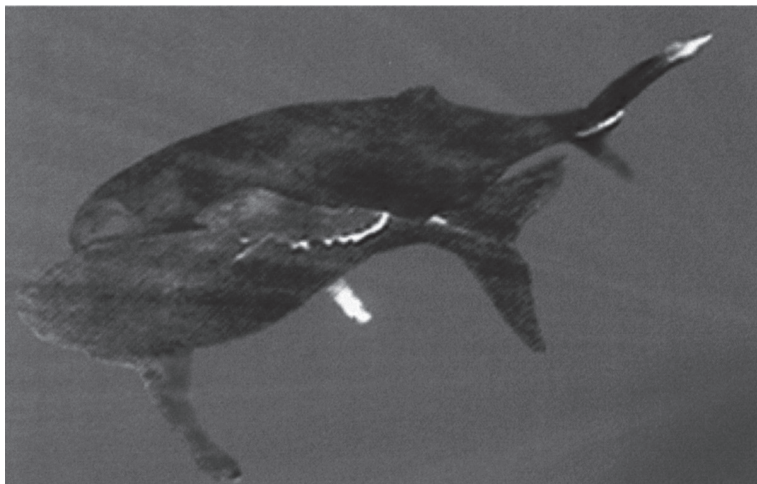
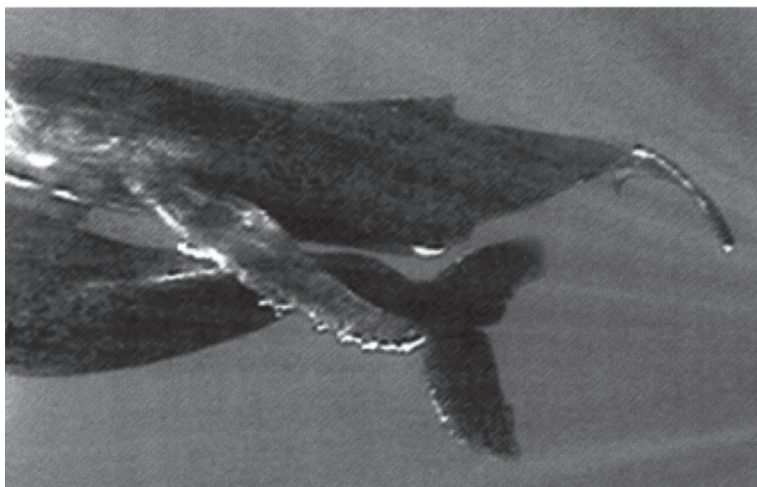
Note: M=mother, C=calf, E=single escort, S=singer.

and/or closely followed by the PE chasing the SE challenger, after which the PE returned to the NA. Penis extrusions were never observed while a PE was in close proximity to the NA.

The only other incident of penis extrusion in a competitive pod occurred as a pair of males affiliated with an MCE pod (Incident 9). One of the males from the pair approached the M and initiated penis contact with her while grasping her with his pectoral fin. This male, as well as the other from the pair, then chased after the M.

Nine penis extrusions occurred in non-competitive contexts. Two of the 9 extrusions were by lone singers and occurred concurrently with either the production of song, or between bouts of singing. We observed no other whales in the immediate vicinity during these penis extrusions, and neither singer altered its behaviour following penis extrusion. Neither extrusion was associated with urination.

Seven of the 9 penis extrusions in non-competitive pods were by single males escorting



mother-calf pairs. Urination occurred during 2 of the extrusions. Single escorts extruded their penis both while stationary and while traveling slowly with their bodies oriented both vertically and horizontally. Figure 2 shows Whale 184 in two of these positions with its penis extruded. Single escorts extruding their penis were typically located within a body-length (*ca.* 15 m) of the mother. The escort often adopted a position with its head oriented toward the mother's lateral or ventral abdominal or peduncle region. Occasionally, the escort extruded its penis after adopting this position (Figure 2 top). Although a single escort in an MCE pod sometimes extruded its penis while slowly trailing the mother/calf pair, there was no evidence of the escort chasing the M or grasping her with its pectoral fin. Indeed, MCE groups in which penis extrusions occurred appeared no different in their behaviour after the escort extruded its penis from MCE groups in which no penis extrusions occurred, within the limits of our observations (mean duration = 27.49 min, SD = 24.14 min, range = 6.33 to 66.32). However, the relatively passive behaviour of the single escorts in these groups during penis extrusion contrasted sharply with the behaviour of the penis-extruding escort toward the MC in Incident 9.

Table 2 presents the mean body length for each measured whale followed, in parentheses, by the percentage of mature males from pooled North Pacific whaling data (Nishiwaki, 1959, 1962; Omura, 1955) whose sizes bracketed our measurements. These whaling data are useful in assessing the maturity of each whale we measured. Whales 184, 1559, 13477, 15024, 14075, 14160, and 14676 were measured each at least two independent times on each sighting date. Coefficients of variation for each mean were small, ranging from 1.29% to 4.23%. Whale 184's mean length was based on the mean of measurements on two different days. Fifty of 54 (92.59%) commercially caught males whose lengths bracketed the lengths of Whales 1559, 14160 and 14676, were sexually mature. Of 46 commercially caught males whose lengths bracketed our measured length of Whale 184, 37 (80.43%) were sexually mature. In contrast, only 27 of 42 (64.29%) commercially caught males whose lengths bracketed the lengths of Whales 13477, 14075, and 14676 were sexually mature, and none of the 17 commercially caught males whose lengths bracketed the length of Whale 15024 were sexually mature.

Photographic sighting histories of individual humpbacks based on matches to the KBMML catalogue confirmed the maturity of Whale 184 only. Whale 184 was first photographed in the summer feeding grounds in Frederick Sound, Alaska on 20 August 1979, and classified by eye to be of adult size. Assuming conservatively that at its first sighting Whale 184 was 1.5 years old, it would have been at least 21 years old in 1999.

Discussion

Overall, our findings demonstrated that, as in other mammalian species (Bagemihl, 1999), male humpback whales extrude their penis in a variety of contexts, some of which are not related directly to reproduction or urination. For the first time, penis extrusions were documented as occurring in 6 different contexts: singing alone, singly escorting a mother/calf pair, acting as either a secondary escort or a principal escort in a competitive pod with a mother/calf pair, and acting as either a principal escort or a secondary escort in a competitive group with a lone female unaccompanied by a calf. We also documented, for the first time, a male humpback whale contacting a female humpback with its penis, although copulation was not observed.

What function(s) does a penis extrusion serve? Obviously, with 13 observations of penis extrusions in different contexts, there are limitations to any strong inferences about function. However, a cursory consideration of those extrusions, for which we have several examples within the same context and with consistency of behaviour, suggests some possibilities, allows us to discount alternatives, and helps guide future inquiries. With this in mind, it seems clear that the penis extrusions by lone singers did not have any apparent intra-species social function because no whales were within visual contact of the extruder. Additionally, unlike other lone male cetaceans that extrude their penis to masturbate on various objects (e.g., bottlenose dolphins, Caldwell & Caldwell, 1972), no such behaviour was exhibited by the singers. It is possible that these singers extruded their penis in response to the divers, as has been observed occasionally in dolphins (personal observations). However, if this were the case, we would expect this behaviour to occur more frequently than was recorded given that we

Figure 1. Sequence of still photographs captured from underwater Hi-8 video recording of Whale 13739 (male humpback whale acting as a secondary escort) extruding its penis and performing 'pectoral-grasp' behaviour toward Whale 9924 (another male humpback whale acting as a secondary escort). From top to bottom: Whale 13739 with penis extruded and left pectoral fin extended, approaching Whale 9924's right side; Whale 13739 with penis pointing backwards, extending left pectoral fin over Whale 9924's back; Whale 13739 wrapping both pectoral fins around Whale 9924 and making penis contact.



videotaped a total of 55 singers. Better evidence for a social function of penis extrusions comes from our observations of extrusions within pods of more than one whale.

Penis extrusions directed toward males

In all five instances of penis extrusion in competitive pods, the extrusion occurred within approximately 15 m of another humpback. Four extrusions were in close proximity to another male humpback and were accompanied by chasing and/or blocking of the male. One possibility is that these extrusions were simply reactions of excitement due to the competition. However, this seems unlikely given that we have observed numerous competitive behaviours and contests between males under water and relatively few have been in conjunction with penis extrusions.

Alternatively, penis extrusions could help convey aggression like other behaviours performed by male humpbacks in competitive pods, such as head lunges, linear bubble trails or strikes with the pectoral fins, tail flukes, or head (e.g., Baker & Herman, 1984). In this case, the co-occurrence of chasing and penis extrusion/contact between male humpback whales in competitive groups could be similar to agonistic/sexual interactions between male bottlenose dolphins and male spotted dolphins in the Bahamas (Herzing & Johnson, 1997). Although spotted and bottlenose dolphins sometimes forage together, on other occasions male bottlenose dolphins chase and side-mount male spotted dolphins. The mounting position, which sometimes results in penetration, is different from the typical intra-species ventral-to-ventral copulatory position observed between males and females. Furthermore, side-mounting between males occurs only from bottlenose towards spotted males, suggesting that these penis extrusions convey dominance. In our observations, penis extrusions between PEs and SEs ($N=2$) were observed also occurring in one direction, from the former group to the latter. As noted above, a PE can be regarded as occupying a temporary position of dominance relative to the SEs in the group. The PE is closest in proximity to the female in the pod and may have the best chance of mating if the female is receptive. Additionally, Spitz (1999) found that PEs were on average larger than SEs, suggesting that size confers an advantage in competing for proximity to the female.

Penis extrusions directed from one SE toward another SE also may reinforce temporary dominance relations within competitive pods. There is some evidence that SEs are not necessarily of equivalent status within competitive pods and aggress selectively towards each other. For example, not all SEs become challengers to PEs, many remaining on the fringes of competitive pods with little or no aggressive behaviours (personal observations). Spitz (1999) found that approximately 40% of SEs were of sexually immature size. Additionally, Tyack & Whitehead (1983) noted several instances of SEs 'fending off' advances towards PEs by other SEs. In the current study, SE 9926's body strike on SE 9924 was followed within seconds by SE 13739's pectoral grasping and penis contact on SE 9924. However, no aggression was displayed between SE 9926 and SE 13739, suggesting that SE 9924 had a subordinate role and perhaps, that SE 9926 and SE 13739 were acting as a 'coalition' (e.g., Clapham *et al.*, 1992, see also below interpretation of Incident 9).

Penis extrusions directed toward females

Of the 13 instances of penis extrusions, 8 (61.5%) were by males escorting MC pairs, of which 6 (46.2%) were by single escorts. This relatively large proportion of incidents was unexpected given that lactating female humpback whales are less likely to ovulate than are mature females without calf (Chittleborough, 1958). What might account for the large proportion of penis extrusions in mother/calf pods? In theory, these penis extrusions (other than perhaps those associated with urination) were related to the receptivity of the female, and to the escort's level of maturity. The presence of a calf in these groups indicated that the mothers were all sexually mature. However, they may not all have been sexually receptive. Interestingly, there was no apparent reaction by a mother to an escort's penis extrusion or retraction even though the mother often appeared to be in a favourable position for viewing the male's penis (e.g., see Figure 2 top).

Our length measurements and photo-identification data suggested that at least some of the single escorts observed with extruded penises were sexually mature. However, none of these escorts physically contacted the mothers with whom they associated. In most cases, the escort was positioned with its rostrum oriented towards the mother's peduncle region, a potentially favourable

Figure 2. Underwater still frames from digital video recording of Whale 184 (male humpback whale acting as single escort to a mother/calf pair) in two different orientations with penis extruded. Top—Whale 184, located below Whale 1560 (humpback whale mother), orients vertically head-up with penis extruded. Whale 184's pectoral fins are spread, the white undersides flashing upwards; Bottom—Whale 184 oriented horizontally with penis extruded.

position for chemoreception of pheromones that might provide information about her reproductive state (see Yablokov *et al.*, 1972; Herman & Tavalga, 1980; Norris & Dohl, 1980). Accurate detection of a female's reproductive condition should enhance a male's reproductive success, and a recent study showed that male humpbacks preferentially escort females with high reproductive potential for the following year (Craig *et al.*, in press). Possibly, the detection of a female humpback in oestrus stimulates a male to extrude his penis.

The only case in which penis extrusion in a competitive pod appeared to be clearly related to mating occurred on 18 January 2000 (see Table 3), when a male-male dyad joined an MCE and a male from the dyad initiated penis contact with the mother. Although actual copulation between the male and the mother was not observed, the actions of the male whale obviously were directed toward the mother and were probably an attempt at copulation. As a side note, the participation of both males from the original dyad in apparently 'securing' access to the mother and interacting closely (and indeed sexually) with her in the absence of aggression towards each other is interesting, and suggests some level of cooperation between pairs of male humpbacks. Although coalitions of males have been reported in other mammalian species (e.g., in baboons, Bercovitch, 1988; in dolphins, Conner *et al.*, 1992), Mobley & Herman (1985) reported that escorts often changed their associations on their winter grounds and that pod membership was largely transient. Nonetheless, Clapham *et al.* (1992) reported pairs of males joining and leaving competitive pods together and exhibiting aggression towards other whales in the pod but not towards each other. Clapham *et al.* raised the possibility that cooperative behaviour between male humpbacks could occur on the winter grounds (see also Brown & Corkeron, 1995). As noted above, in our observations cooperative behaviour could have occurred on 10 March 1996 between SE 9926 and SE 13739 in their aggressive and sexual behaviour toward SE 9924. The only other instances of reported cooperation between humpbacks have concerned foraging behaviour on the summer feeding grounds (e.g., Jurasz & Jurasz, 1979; D'Vincent *et al.*, 1985) by unrelated individuals (Sharpe *et al.*, 2001), many of whom appear to be female (Baker, 1985; Mobley *et al.*, 1988).

Co-occurrence of penis contact and pectoral grasp behaviour

It is striking that each instance of penis contact between humpbacks occurred in competitive contexts and was accompanied by pectoral grasping by the extruder. Similar pectoral grasping behaviour and accompanying penis extrusion by a live male

humpback whale toward a dead male humpback floating at the surface was documented by Pack *et al.* (1998). However, at the time the significance of this combination of behaviours was unclear. The only other report of a pectoral-grasp-like behaviour was by Herman *et al.* (1980) who described a humpback whale in Hawaii resting its ventral surface against the side of a northern right whale (*Eubalaena glacialis*) and then wrapping its pectoral fin partially around the back of the whale. Although no extruded penis was visible, Herman *et al.* (1980) stated that 'the type and sequence of interactions . . . between humpback whale and right whale give the strong impression that the humpback whale was engaging in courtship behaviour' (p. 274). Our observation of simultaneous penis contact and pectoral grasping by a male towards a female (Incident 9) suggests that the pectoral grasp behaviour could play a significant role in mating behaviour between humpbacks as proposed by Edel & Winn (1978). However, the co-occurrence of pectoral grasping and penis contact or extrusion between male humpbacks in competitive groups also suggest that pectoral grasping could serve a broader function.

Why are observations of penis extrusions by humpbacks so rare?

We set out to investigate whether the rarity of documented sexual behaviour by humpback whales was due to a paucity of underwater observations of this species. Although we observed penis extrusions from males in several different pod types and in a variety of contexts, the instances of penis extrusion constituted a mere fraction of the underwater video footage. Why then, with humpback whales spending considerable amounts of time during the winter reproductive season in relatively shallow, clear, coastal waters (Herman & Antinoya, 1977; Mobley *et al.*, 1999), is sexual behaviour observed so infrequently?

The rarity of observed penis extrusions in humpback whales stands in sharp contrast to numerous observations of this behaviour in southern right whales (*Eubalaena australis*) (e.g., Donnelly, 1967; Cummings, 1985), bowhead whales (*Balaena mysticetus*) (Würsig & Clark, 1993; Würsig *et al.*, 1993), and grey whales (*Eschrichtius robustus*) (Wolman, 1985; Swartz, 1986). In some cases in these species, behaviours involving a whale's penis appeared to be unrelated to reproduction. For example, although female grey whales typically come into oestrus during the winter months, copulation has been observed year-round, including on the feeding grounds and along the migration route (Rice, 1983; Wolman, 1985). Similarly, Würsig *et al.* (1993) observed copulation that was unlikely related to reproduction in bowhead whales in the fall in the

eastern Beaufort Sea. They speculated that some whales involved in this sexual activity were sexually immature, and consequently, that the behaviour was related to 'play' (p. 108). Homosexual behaviour also has been observed in these species. Würsig & Clark (1993) reported two incidents of a male bowhead whale inserting its penis into the genital slit of another male bowhead. Several reports have documented penis extrusions in all-male grey whale groups on their feeding grounds (Newman, 1976; Darling, 1977 as cited by Brownell & Ralls, 1986).

Several factors could account for the difference in frequency of observations of penis extrusions in humpback whales as compared with right, bowhead, and grey whales. In these latter species, testes size is greater and penis length longer relative to body size than in other mysticetes, and interactions between males are relatively non-aggressive, suggesting that male reproductive success is determined largely by sperm competition (Brownell & Ralls, 1986). In contrast, male humpback whales have smaller testes than would be predicted from body size, a relatively short penis (Brownell & Ralls, 1986), and often are physically aggressive towards each other while competing for proximity to females (Tyack & Whitehead, 1983; Baker & Herman, 1984). These findings, together with the dearth of penis observations, support the hypothesis that male humpbacks compete primarily by physically preventing other males from gaining mating access to females, rather than through sperm competition (Brownell & Ralls, 1986).

Additionally, it is conceivable that most sexual behaviour occurs at night. If this were true, the absence of light at night would imply that vision plays a minimal role in sexual activities. This seems unlikely given the apparent importance in competitive groups of physical displays (Baker & Herman, 1984). Other factors that could limit observations of sexual behaviour on the winter grounds include Craig & Herman (1997)'s suggestion that some females become pregnant en route to the winter grounds and then return to higher latitudes before completing the migration (see also Pack *et al.*, 2001). Also, the presence of many immature males on the winter grounds (Nishiwaki, 1959; Omura, 1955; Spitz, 1999) could decrease opportunities for observing sexual activities. It is also possible that copulation in humpbacks, as in other mammals with a fibroelastic penis, is rapid (Slijper, 1962). Supporting this conjecture, we found that penis extrusions were relatively brief (*ca.* <1 min). Furthermore, it may be that much of what is observed underwater in competitive groups is actually post-copulatory mate guarding by the PE (Clapham, 1996). Finally, it is possible that some sexual behaviour on the winter grounds occurs at depths beyond observer visibility. For example, using suction-cup

attached time-depth-recorder/VHF tags, Baird *et al.* (2000) determined that some escorts in humpback whale competitive groups and dyads off the West Coast of Maui regularly dove to >100 m (maximum dive recorded = 176 m from an SE). In light of these potentially limiting factors, future studies of socio-sexual behaviour of humpback whales should continue to emphasise underwater observations using both traditional videographic techniques, as well as new technologies, that allow for increased tracking abilities (e.g., Francis *et al.*, 2001).

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