A comparison of pectoral fin contact between two different wild dolphin populations

Kathleen Maria Dudzinski, Justin David Gregg, Christine Ann Ribic, Stan Abraham Kuczaj

1. Introduction

“Flipper rubbing” behaviour, when physical movement occurs between one dolphin’s body or pectoral fin and another dolphin’s pectoral fin, has been observed in wild and captive individuals of various odontocete species. Wild species include Indo-Pacific bottlenose dolphins (Tursiops aduncus) (Mann and Smuts, 1998, 1999; Sakai et al., 2003, 2006a, 2006b) spinner dolphins (Stenella longirostris) (Johnson and Norris, 1994), Atlantic spotted dolphins (Stenella frontalis) (Dudzinski, 1996, 1998), belugas (Delphinapterus leucas) (Smith et al., 1992), rough-toothed dolphins (Steno bredanensis) (Kuczaj and Yeater, 2007), and sperm whales (Physeter macrocephalus) (Whitehead and Weilgart, 2000). Captive dolphins observed engaging in flipper rubbing include common bottlenose dolphins (Tursiops truncatus) (Tavolga and Essapian, 1957; Samuels and Tyack, 2000) and wild Atlantic spotted dolphins in The Bahamas and described “petting” and “petting/rubbing” where one dolphin rubs its pectoral fin over another dolphin’s pectoral fin or body, respectively. Samuels et al. (1989) analyzed and defined “gentle rubbing” in captive bottlenose dolphins where one dolphin rubs the length of its body or a specific body part against the immobile, outstretched pectoral fin of a partner. “Petting” was defined by Samuels et al. (1989) as one dolphin giving a rub to another by moving its pectoral fin back and forth against another’s body, while the term “pec touches” was used by Johnson and Moewe (1999) to describe the use of the leading edge of the pectoral fin to contact any part of another individual’s body for Commerson’s dolphins. In addition to rubbing, static contact behaviour involving the pectoral fin but without rubbing motions has been observed in both captive (Tavolga and Essapian, 1957; Samuels and Tyack, 2000) and wild dolphins (Richards, 1996; Connor et al., 2006; Mann and Smuts, 1999; Connor et al., 2000; Paulos et al., 2007). Connor et al. (2006, p. 631) termed this behaviour “contact swimming”, and described...
Table 1

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th># Min. Effort</th>
<th># Min. video</th>
<th>% yr-old calves</th>
</tr>
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<tbody>
<tr>
<td>Mikura</td>
<td>1997</td>
<td>2,475</td>
<td>79</td>
<td>4.96</td>
</tr>
<tr>
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<td>1998</td>
<td>5,604</td>
<td>273</td>
<td>7.97</td>
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<tr>
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</tr>
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<td>87</td>
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<tr>
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<tr>
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<td>1994</td>
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<td>41</td>
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<tr>
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<td>~9,000</td>
<td>13</td>
<td>2.14</td>
</tr>
<tr>
<td>Bahamas</td>
<td>2001</td>
<td>~12,000</td>
<td>222</td>
<td>2.14</td>
</tr>
</tbody>
</table>

The minutes of effort relates to time spent looking for dolphins during boat trips. The percent of the total population comprised of calves ≤ one year old for each study site annually is also presented.

the behaviour as follows: “one dolphin rests its pectoral fin against the flank of another dolphin, behind the other dolphin’s pectoral fin and below or just posterior to the dorsal fin.” Dudzinski (1996, 1998) labeled this behaviour as “contact position” though the definition was the same as Connor et al. (2006).

Although the literature is still sparse with respect to research on pectoral fin contact exchanges, and the definitions of the behaviours involved are highly variable, possible function(s) for flipper rubbing/touching have emerged. Samuels et al. (1989) analyzed gentle rubbing among four captive bottlenose dolphins and suggested that this contact served both social and hygienic functions. The authors suggested a social function because preferential rubbing relationships persisting for many months were observed between certain individuals. They also speculated that this behaviour could help in the removal of ectoparasites and old epidermal cells based on observations that one particular dolphin, which received infrequent rubbing from other dolphins, often rubbed its body against objects. Norris et al. (1994) who studied Hawaiian spinner dolphins, Sakai et al. (2006a) who studied Indo-Pacific bottlenose dolphins, and Dudzinski (1998) who studied Atlantic spotted dolphins all suggested that flipper rubbing is a kind of affiliative behaviour similar to grooming observed in primates, and so may have both hygienic and social functions. Some researchers have suggested that flipper rubbing is a type of sexual behaviour: Tavolga and Essapian (1957) studied captive bottlenose dolphins and suggested that pectoral fin rubbing is a passive or inaction form of sexual behaviour. They termed what they observed as “stroking” because it appeared primarily as a pre-copulatory behaviour. Norris et al. (1994) also reported that pectoral fin contact among captive spinner dolphins was observed during their “caressing bout” and was oriented specifically to the abdomen and the genital area. Caressing was observed both for captive spinner dolphins and their wild counterparts in Hawaii (Norris et al., 1994) with rubbing by a dolphin’s pectoral fins or flukes observed predominantly when dolphins swam in the mating posture (i.e., belly-to-belly). Norris et al. (1994) also discussed a more active behavioural pattern among spinner dolphins: “pectoral whetting” (originally defined by Bateson, 1974 but cited in Norris et al., 1994) was when two dolphins swim belly-to-belly with mutual pectoral fin rubbing. Connor et al. (2006) discussed a number of hypotheses to explain the function of contact swimming as observed between female dyads within male-biased groups, including reduced male harassment, assisted locomotion and reduced stress.

We investigated flipper contact behaviours in two populations of wild dolphins: Indo-Pacific bottlenose dolphins from Mikura Island, Japan, and Atlantic spotted dolphins from Little Bahama Bank, The Bahamas. A comparison between the two sites allowed us to discuss in more detail the possible function of pectoral fin contact behaviour by considering the similarities and differences between two species in two disparate geographic locations. These two populations were chosen because each research site allowed access to long-term video data collected in water that allowed for consistently good visibility, where each population was habituated to the presence of researchers and their recording equipment. We investigated the type, quantity, frequency, and location of flipper contact between the two sites, as well as the body parts, postures, age, gender, and individual identification of the dolphins involved in these behavioural exchanges.

2. Materials and methods

Data collected on both study populations were part of a long-term, longitudinal and comparative examination of dolphin communication and signal exchange (e.g., Dudzinski, 1996, 1998; Dudzinski et al., 2003; Gregg et al., 2008).

2.1. Study sites and populations

Data were gathered at two locations over a total of 12 years on the Little Bahama Bank, The Bahamas and around Mikura Island, Japan. The Atlantic spotted dolphins were found near the White Sand Ridge of the Little Bahama Bank, located ~64.5 km north of West End, Grand Bahama Island. This area ranges from 6 to 10 m in depth with a white sandy bottom and good visibility to at least 30 m. Dolphins are most often sighted in the northwest section of this sand bar. Data for this study on this group of dolphins were collected from 1993–1995 and 2000–2001. Approximately 150 individual spotted dolphins were identified with relative age categories and sex determined for all individuals (Dudzinski, 1996; Herzing, 1997; Brunnicke, 2000). The Indo-Pacific bottlenose dolphin group is a population resident to the area within 300 m of Mikura Island, Japan. Mikura Island is a dormant volcanic island roughly 200 km south of Tokyo with a circumference of 16.4 km, and is characterized by a boulder-strewn seafloor with depths ranging from 2 to 60 m at 2 to 250 m from shore, respectively. DNA analysis confirms that the dolphins around Mikura are aduncus-type (Kakada et al., 2002). The Mikurajima Bandouriruka Kenkyukai (M.B.K.) conducted a photo-identification research study on this group of dolphins between 1994 and 2004 (Kogi et al., 2004): the identified population consisted of approximately 165 dolphins. Video data from 1997 to 2002 and from 2004 were used to examine pectoral fin contact between dolphins in this study group. Both study sites are adjacent to fish-productive, deep waters (Gulf Stream for The Bahamas and Marianas Trench for Mikura Island, Japan).

2.2. Data collection

Dolphin behaviours and sounds were recorded with a mobile video/audiosonic system that permits real-time synchronous video and audio recordings under water (Dudzinski et al., 1995). Underwater swims were video-documented opportunistically with limiting factors including poor weather, sea, and visibility conditions. Behavioural data were collected using focal animal and all-occurrence sampling (Altmann, 1974). Identified individuals were opportunistically observed, based upon which dolphins were near the vessel. Follows and recordings of individual dolphins began as soon as the video camera and observer were in a favorable underwater position and group composition was assessed. An individual was selected and recorded until it was no longer within the field of view. Pectoral fin contact behaviours was coded only from videotaped segments (for reliability and repetition).

Event sampling for pectoral fin contact between individual dolphins was conducted from all video data gathered during 1993 to 1995, 2000, and 2001 from The Bahamas on spotted dolphins.
and from 1997 to 2002 and 2004 for Indo-Pacific bottlenose dolphins around Mikura Island, Japan. Each contact event between one dolphin’s pectoral fin and another dolphin’s body (including the pectoral fin) was documented. Other relevant, recorded information included: date of occurrence, “real” time of contact, initiating dolphin identification, age and sex, receiving dolphin identification, age and sex, each dolphin’s posture, duration of contact, whether contact was a touch or rub, group behaviour and composition, and identification of the departing dolphin. In addition, whether the initiating and receiving dolphins were the rubber or rubbee and which body part was contacted on the rubbee were documented.

2.3. Definitions

Definitions of rubbing behaviour in general or the contact between pectoral fins or a pectoral fin and the body of a second dolphin more specifically vary considerably in the published literature (see Sakai et al., 2006a for an overview). For this study, we defined rubbing as the active movement between one dolphin’s (i.e., the rubber’s) pectoral fin and another dolphin’s body (i.e., the rubbee). We defined petting as pectoral fin-to-pectoral fin rubbing where active movement between pectoral fins of two dolphins is observed. Touches were defined as physical contact between the pectoral fin of one dolphin and another dolphin’s body without active movement of either the pectoral fin or the area of the body being touched. The term contact is used to denote all pectoral fin contact behaviour including rubbing, petting and touching.

Pectoral fin tactile exchanges were begun by one dolphin (either the rubber or rubbee) approaching and physically contacting another dolphin and were ended by one of the dolphins departing from the other. We defined this behaviour unit between the start of contact and the departure as a flipper contact episode. In addition, either the rubber or the rubbee can be the initiator or the receiver of the contact. For example, the rubbee may initiate contact with the rubber by approaching the rubber and soliciting a rub by placing part of its body in contact with the rubber’s pectoral fin. Subsequently, the rubber in this scenario is considered the receiver, and the rubbee is the initiator.

To record the dolphin body part in contact with a pectoral fin, we divided the body surface of the dolphin into 11 parts (Fig. 1). Dolphin posture during pectoral fin contact exchange was categorized into the following types: horizontal (HOR), side-down left (lOSD), side-down right (rOSD), upside down (VUD), head down (HDO) and head up (HUP). Horizontal was defined as a posture in which the dolphin’s ventral side is parallel to the sea floor and “facing” down. A posture in which one pectoral fin is kept up and the other is parallel to the sea floor was classified as side-down. An upside down posture was defined as the dolphin horizontal with the ventral side up and the dorsal side toward the sea floor. Head down or head up postures related to the dolphin in a vertical position in the water column with its head down or up, respectively.

Four dolphin age classes (i.e., adult, subadult, juvenile and calf) were identified and used to categorize dolphins at each study site. Atlantic spotted dolphins age classes were defined according to the development of pigmentation along their bodies (Perrin, 1970; Dudzinski, 1996; Brunnick, 2000), as well as girth and length. For spotted dolphins, calves have no spots and are roughly half the size of an adult. Juvenile spotted dolphins have begun to develop spots ventrally, have reached one half to two-thirds the size of an adult, and no longer regularly associate with their mothers. Subadult spotted dolphins have spot pigmentation over the entire body, except the pectoral fins, flukes and dorsal fin, and have reached two-thirds to equal size of an adult spotted dolphin. Adult spotted dolphins are covered in spot pigmentation and are roughly 2 m in length. Age classification of the Indo-Pacific bottlenose dolphins from Mikura follows from the definitions outlined by Kogi et al. (2004). Calves are roughly half the size of an adult, have no spots, minimal to no scarring, and are regularly observed in the company of their mothers. Juveniles are roughly two-thirds the size (length and girth) of an adult, have not yet begun to develop spots, have begun to acquire scars, are frequently observed with their mothers, and are a light-gray color. They are classified as juveniles typically one year after first being observed. Subadults are roughly similar in length to an adult but with less girth, have begun to develop spots ventrally, and no longer associate with their mothers. Adults have larger girth, spots covering the ventral area, posses many scars, and are a darker gray color. Female adults are classified as such once they have given birth to a calf.

2.4. Statistical analyses

In order to ensure independence and randomness of the data, we only included one contribution per identified dolphin in the role of rubber and one contribution per identified dolphin in the role of rubbee per encounter, even though a single animal might have contributed multiple pectoral fin contacts in an encounter. Thus, from the total number of pectoral fin contacts per site per year of study, we limited our examined sample size to individual adjusted contacts as defined above. Sampling in this way facilitated an avoidance of pseudo-replication of the data. Comparison of the stability of pectoral fin contacts between sites was compared as rates where the total number of individual adjusted contacts per year per study site was divided by the total effort (i.e., minutes of underwater video per site per year). A comparison by location of exchanged pectoral fin contact behaviour was examined (using individual adjusted sample sizes) with a t-test with two samples assuming unequal variances. Body part preference for both rubber and rubbee in the role of initiator (using individual adjusted sample sizes) was examined with Spearman’s rank correlation. Chi-square analysis was used to examine fin-to-fin versus fin-to-body contact, to assess variation in posture assumed when the initiator was rubber versus rubbee, to examine identification of sex/age in partner preference during contacts, rubbing versus touching for contacts, and initiator versus receiver roles. All chi-square analyses were conducted with individual adjusted contact data.

3. Results

Twelve years of video data were examined to understand how dolphins use their pectoral fins in the exchange of contact behaviour (Table 1). A total of 512 min of video data provided the basis for analyses from 5 years of data collected from The Bahamas and 1208 min from 7 years of data from Mikura Island, Japan.

3.1. Comparison of contact frequency between research sites

A total of 139 contact episodes were recorded from The Bahamas, and 450 from Mikura. The mean rate of contact (rubs, including petting, and touches) per minute for each year was calculated for
3.2. Pectoral fin to pectoral fin vs. pectoral fin to body

We examined the data to determine if the dolphin initiating contact prefers petting (i.e., pectoral fin to pectoral fin contact) or rubbing (i.e., pectoral fin to body contact) while in the role of either the rubber or the rubbee. For The Bahamas, the dolphin initiating contact was more likely to engage in rubbing behaviour, than petting behaviour \( (X^2_1 = 6.09, P = 0.014) \). A similar trend was found at Mikura, where the dolphin initiating contact was more likely to engage in rubbing behaviour, than petting behaviour \( (X^2_1 = 4.40, P = 0.036) \).

3.3. Initiator vs. receiver

In contrast to the results reported by Sakai et al. (2006a), we found that the rubber was significantly more often the initiator of contact episodes at Mikura Island, Japan \( (P < 0.001, 74.41\% \text{ of 340 episodes}) \), as well as in The Bahamas \( (P < 0.001, 73.73\% \text{ of 118 episodes}) \). There was no significant difference found between the two sites in terms of how often the rubber was also the initiator \( (X^2_1 = 0.001, P = 0.98) \), suggesting that in our study the rubber tends to initiate contact behaviour at nearly identical rates for both study populations.

3.4. Body parts contacted

We documented 141 rubs and touches between dolphins from The Bahamas, and 370 from Mikura with respect to identification of body part contacted. These episodes were scored according to the frequency with which body parts were contacted by the initiator in the role of the rubber and the rubbee (Table 2). In order to determine if the rubber and the rubbee initiate contact on similar body parts between the two research sites (see Fig. 4 for contact rates), the body parts were rank ordered from least to most likely to be contacted for each of these two conditions for each site; a Spearman rank correlation was performed. Episodes where multiple body parts were contacted throughout the episode were eliminated from this test. When the initiator was in the role of the rubber, a significant correlation was seen between the two sites \( (r_s = 0.66, N = 91, P < 0.05) \). Similarly, when the initiator was in the role of the rubbee, a significant correlation was seen between the two sites \( (r_s = 0.71, N = 308, P < 0.01) \). These correlations demonstrate that the identified preferential choice of body part to contact (touches and rubs) by the rubber and the rubbee is consistent between the two species at each of the field sites.

3.5. Body postures

Body posture assumed by the initiator in both the rubber and rubbee roles was examined for each field site. For both Mikura Island and The Bahamas, a strong preference was shown for the HOR position for both the rubber and rubbee roles when combined for all contact types \( \text{(Japan: } X^2_2 = 804.77, P < 0.001; \text{ The Bahamas: } \)
Fig. 4. Frequency of pectoral fin contact by rubber (R) and rubber (E) for each body part from The Bahamas and Mikura Island.

\[ X^2_1 = 192.49, P < 0.001. \] When HOR was removed from the analyses to assess relative preferences for the remaining five postures, there were no significant differences in preferences for these five postures at either Mikura Island or The Bahamas.

We examined the data to determine whether the two dolphins involved in a contact episode assumed the same or different roles. At Mikura Island, dolphins were found in the same posture significantly more often than a different posture during a rubbing episode when the initiator was in the role of rubber \( (X^2_1 = 22.58, P < 0.001) \). Touching episodes at Mikura Island when the initiating dolphin was the rubber did not result in both dolphins in the same posture more often than was the case when the initiating dolphin was the rubber \( (X^2_1 = 2.17, \text{NS}). \) The pattern for The Bahamas was the exact opposite. Rubbing episodes in The Bahamas when the initiating dolphin was the rubber did not result in both dolphins in the same posture more often than was the case when the initiating dolphin was the rubber \( (X^2_1 = 0.87, \text{NS}). \) However, the dolphins were found in the same posture significantly more often during a touching episode when the initiator was in the role of rubber \( (X^2_1 = 12.04, P < 0.001). \)

### 3.6. Sex and age

For both Mikura Island and The Bahamas, strong preferences for same-sex rubbing partners were found for both the rubber and rubber (Table 3). Same sex preferences occurred when the initiator was the rubber \( (X^2_1 = 45.94, P < 0.001) \) and when the initiator was the rubber \( (X^2_1 = 24.81, P < 0.001). \) The same trend was found in The Bahamas: rubber \( (X^2_1 = 24.34, P < 0.001), \) rubber \( (X^2_1 = 7.86, P = 0.005). \) No differences were observed between Mikura Island and The Bahamas when examining the rate at which males choose other males in the role of rubber \( (X^2_1 = 0.11, P = 0.74) \) or rubber \( (X^2_1 = 2.81, P = 0.094), \) nor when females choose other females in the roles of rubber \( (X^2_1 = 1.98, P = 0.16) \) or rubber \( (X^2_1 = 0.11, P = 0.14) \) (Table 3). There was no difference in the rates at which males or females were found in the role of rubber vs. rubber as either the initiator or receiver at the same frequency for each condition (initiator or receiver) for both Mikura Island and The Bahamas.

For each of the two field sites, dolphins were categorized according to four age classes: adult, subadult, juvenile, and calf. At Mikura Island, no differences were found for the rates at which animals in each of the four age classes assumed the role of rubber vs. rubber as either the initiator \( (X^2_1 = 6.28, P = 0.099) \) or the receiver \( (X^2_1 = 5.10, P = 0.165) \) (Table 4). In The Bahamas, no difference was found for the rates at which animals in each of the four age classes assumed the role of rubber vs. rubber as the receiver \( (X^2_1 = 6.18, P = 0.103). \) However, significant differences were observed for the rubber vs. rubber when in the role of the initiator \( (X^2_1 = 14.55, P = 0.002) \) (Table 4). For The Bahamas, the initiator was the rubber 50% of the time for adults, 83% for subadults, 58% for juveniles and 84% for calves. This suggests that subadults and calves tend to initiate rubs in the role of the rubber in The Bahamas more frequently than is observed for other age classes and conditions; as rubber, juvenile, and calf spotted dolphins initiated pectoral fin contact more with other juveniles \( (n = 16) \) and calves \( (n = 15) \) (respectively) than with the other age classes, excluding mother/calf pairs (Table 4). As a rubber, calves initiated pectoral fin contact with adult females \( (n = 22) \), likely their mothers, almost twice as often as with other calves (Table 4). As a rubber initiator, calves at both sites initiated more contact with adults than with all other age classes, even calves (Table 4). Similarly, as rubber, adults in The Bahamas initiated much more pectoral fin contact with calves \( (n = 10) \) than with adults, subadults or juveniles (Table 4); also in the role of rubber, calves initiated more contact with adults than with other calves, and not at all with subadults or juveniles (Table 4).

When the frequency at which each age class assumed each role (i.e., rubber vs. rubber) for each condition (i.e., initiator or receiver) was compared between the two sites, the only significant difference found was between adults as initiators: in The Bahamas, the adult initiator was the rubber in 50% of episodes, whereas around Mikura Island the adult initiator was the rubber in 75% of episodes \( (X^2_1 = 5.55, P = 0.019). \) Overall, this suggests similarity within and between field sites in terms of the rate at which animals of different age classes assume various roles (i.e., rubber, rubber, initiator, receiver), with a significant exception in The Bahamas where it appears that adults tend to assume the role of rubber/rubber more uniformly.

### Table 3

<table>
<thead>
<tr>
<th>Initiator</th>
<th>Mikura Island</th>
<th></th>
<th>Bahamas</th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Male receiver</td>
<td>Female receiver</td>
<td>Male receiver</td>
<td>Female receiver</td>
</tr>
<tr>
<td>Male rubber</td>
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<td>6</td>
</tr>
<tr>
<td>Female rubber</td>
<td>15</td>
<td>62</td>
<td>6</td>
<td>38</td>
</tr>
</tbody>
</table>

Values in bold font highlight the same sex/same age partner preferences.
when initiating contact than is observed for other age classes, and when compared to their counterparts around Mikura Island.

When comparing the frequency with which the four different age classes initiated contact with each of the other four age classes in both the role of rubber and rubbee (Table 4), significant differences between contact rates were observed for both sites: Mikura Island with the initiator as the rubber ($X^2 = 168, P < 0.001$); Mikura Island with the initiator as the rubbee ($X^2 = 92.7, P < 0.001$); The Bahamas with the initiator as the rubber ($X^2 = 41.7, P < 0.001$); and The Bahamas with the initiator as the rubbee ($X^2 = 32.1, P < 0.001$). These trends suggest that the initiators (of any age class) appear to have strong preferences for individuals of specific age classes when choosing a receiver. It should be noted that some of these trends are likely to be explained by bias in the proportion of animals of a certain age class observed at each study site. For example, the majority of animals observed around Mikura Island are subadults (Kogi et al., 2004; Dudzinski, unpublished data 1997–2004); this would bias the number of observations of subadult-to-subadult contacts around Mikura Island. Still, in the role as rubber, adults initiated two to three times more pectoral fin contact with other adults, than with all other age classes (Table 4). Similarly, subadult rubbers at Mikura initiated contact with other subadults five to 25 times more than with all other age classes (Table 4). When subadults were in the role of rubbee, they initiated contact five times more with other subadults than with adults and never with juveniles or calves (Table 4). Juvenile dolphins at Mikura initiated flipper contact with other juveniles when acting as rubber or rubbee more than with adults, subadults or calves. In fact, juveniles at this location never initiated pectoral fin contact with subadults or calves when in the role of rubbee (Table 4). One observed trend, however, cannot be explained by age class bias, namely the scarcity of calf-to-calf contacts observed around Mikura Island. The average proportion of calves less than a year old from within the study population observed at Mikura Island was 5.76%, while calves of the same age range at The Bahamas represented an average 34.4% of that population (see Table 1 for annual percentages per study site). Even given the larger percent of calves within the population recorded around Mikura Island, no calf-to-calf contacts were observed in either the role as rubber or rubbee. In The Bahamas, the number of calf-to-calf contacts was much greater. When the rate at which calves initiate contact with each of the four age classes is compared between the two sites (with the calf as rubber), significant differences between the two sites are observed ($X^2 = 23.4, P < 0.001$, Table 4). Calves around Mikura Island were significantly less likely to seek contact with other calves when compared to calves in The Bahamas. Rates per site were as follows: Mikura Island—calf-to-adult 92%, calf-to-subadult 8%, calf-to-juvenile 0% calf-to-calf 0%; The Bahamas—calf-to-adult 48%, calf-to-subadult 6%, calf-to-juvenile 13%, calf-to-calf 54%.

3.7. Individual dolphin IDs

A complete examination of the individual pairs and reciprocity of pectoral fin contact exchanges is beyond the scope of this paper (though it is being examined for future discussion of individual variation); however, several dolphin pairs are included to illustrate the nature of the age and sex pair preferences previously presented.

3.7.1. The Bahamas

Three sets of individual pairings were examined in greater detail; these pairings represented one adult male (SfdID018) with two subadult males (SfdID055, SfdID025), a juvenile female (SfdID061) with several peers of varying age class representing both sexes (e.g., juvenile females: SfdID109, SfdID111; subadult female: SfdID30; calf male: SfdID112), and three juvenile males (SfdID084, SfdID094, SfdID03). For the adult/subadult males, SfdID018 initiated both touch and rubbing contacts as the rubber with SfdID025 along the lateral side, belly and pectoral fin for durations lasting between 3 and 17 s. SfdID025 reciprocated by rubbing the lateral side of SfdID018 and also initiating contact to SfdID055’s pectoral fin and belly about a minute after contact with SfdID018. After these observations, all three males swam out of the observer’s view. These three males were traveling together across the shallow sandbar of the White Sand Ridge on two consecutive afternoons in July 1993. On the second day of our observations, we documented SfdID055 initiating a 4 s rub to SfdID025’s belly. The underwater observations of these 3 males over these 2 days totaled 31 min and it is likely that we did not record all of the reciprocal pectoral fin or other rubbing contact exchanged between these individuals as they traveled through the study area. SfdID061 was often observed exchanging tactile contact with other spotted dolphins: as rubber, she initiated 7 and received 3 pectoral fin contacts during 4 underwater sessions with a subadult female, a male calf and 2 juvenile females (SfdID109 and SfdID111) spotted dolphins. As rubber, SfdID061 initiated or received an additional 4 pectoral fin contacts with SfdID109 and SfdID111. Contacts with the subadult female and male calf were brief, averaging 1 or 2 s, primarily along the side, dorsal fin, or face and were seemingly not reciprocated; however, pectoral fin contact exchanged between SfdID061, SfdID109 and SfdID111 was strongly reciprocal (n = 38 exchanges between these 3 individuals), longer in duration (median = 3 s, range between 1 and 24 s), and covered more of the body (e.g., dorsal fin, rostrum, face, side, belly, pectoral fin). In comparison, the 3 juvenile male spotted dolphins all exchanged relatively brief pectoral fin contacts (only 1 or 2 s) only with other male juveniles, which were only mildly reciprocal (2 sets of exchanges between SfdID084 and SfdID03). Also, these 3 juvenile males exchanged touches and rubs with equal frequency whereas the juvenile and calf females exchanged primarily rubbing contact.

3.7.2. Mikura island

Interactions between a few subadult male bottlenose dolphins highlight the significance in same-sex, same-age partner preferences observed among individuals around Mikura Island. TalID053 and TalID240 initiated (n = 5) and received (n = 5) an equal amount of pectoral fin rubs with each other during our observations, which ranged from 1 to 7 s (median = 1 s) and focused on their faces (40% of rubs) and backs (40%). TalID053 also exchanged pectoral fin contact with four other subadult males (TalID043, TalID230, TalID263, TalID358) in reciprocal fashion; both rubs and touches were exchanged and the body focus for contact was the side, back and belly during these exchanges. Most contacts were 1 s in duration though exchanges of 2–8 s were recorded. TalID240 also initiated and received pectoral fin contact with 2 other subadult male bottlenose dolphins that we documented: 5 contacts with TalID263 and 4 contacts with TalID226. More rubs (n = 6) than touches (n = 3) were recorded but the duration (median = 1 s, range 1–7 s) and body part (67% to lateral side) were consistent with the other exchanges observed between subadult males from this study population.

4. Discussion

This study has revealed a number of similarities between the two study sites in terms of contact behaviour involving the pectoral fin. The rates of observed contacts between sites are nearly identical. Species at both sites engage more frequently in tactile and both species prefer same sex rubbing partners.
Contrary to the findings of Sakai et al. (2006a), we found that the rubber is significantly more likely to be the initiator than the receiver for both Mikura and The Bahamas. Sakai et al. found that for Mikura dolphins, 73.1% of initiators (of 67 episodes) were the rubber. For this study, we found that 74.41% (of 340 episodes) of initiators were the rubber, not the rubber. This discrepancy in findings is surprising given that both studies used similar definitions, and coded data in a similar fashion. The frequency of observed dolphins from the defined age classes and gender involved in each study were roughly similar as well. It is not the case that the differences between the two studies reflect the fact that Sakai et al. (2006a) focused on active rubbing, while we included all forms of pectoral fin to body contact in our analyses (e.g., touches). When we only include active rubbing in our analyses, the rubber was still more likely to initiate a contact event than was the rubber (X² = 6.99, p < 0.01). One possible explanation is the difference in sampling sizes: N = 67 for Sakai et al. (2006a), whereas N = 340 for this study.

Overall, there is much similarity within and between each field site in terms of the rate at which animals of different age classes assume various roles (i.e., rubber, rubber, initiator, receiver). The initiators (of any age class) appear to have strong preferences for individuals of specific age classes when choosing a receiver. For both sites and for all roles, adults tend to primarily contact other adults, and occasionally calves and juveniles, and subadults almost exclusively tend to contact other subadults. The only exception appears to be that in The Bahamas, subadults and calves tend to initiate rubs in the role of the rubber more frequently than do the other age classes. An important and striking difference between the two sites is the observation that calves in Mikura are significantly less likely to seek contact with other calves when compared to calves in The Bahamas. This suggests that calves (and to some extent the other age classes) in The Bahamas are less inhibited when seeking a rubbing partner, and often leave their mother’s side to seek contact with other individuals. Calves in Mikura on the other hand were never observed leaving their mother's side to seek out contact with another calf or juvenile. Perhaps there are social or ecological pressures in Mikura that are absent in The Bahamas that require a calf to ‘stick close’ to its mother during the first few years of its life. These pressures may include increased predation from sharks, the need for tactile stimulation resulting from contact with conspecifics. Moreover, the observation that the rubber is the initiator of contacts in the majority of cases for both sites is inconsistent with the notion that the primary function of contact is self-stimulation. The fact that dolphins engage in contact behaviours at similar rates despite differences in water clarity suggests that the function of contact behaviour has a social component. However, given that the vast majority of contact occurs with same sex partners, it is unlikely that rubbing is a pre-coitalatory behaviour, as has been previously suggested (e.g., Tavolga and Essapian, 1957). Furthermore, as has been pointed out by Sakai et al. (2006a), the reciprocal nature of rubbing bouts (i.e., switching rubber/rubber roles during a bout) suggests that rubbing serves an affiliative function.

Delphinid rubbing behaviour is potentially analogous to grooming behaviour observed in terrestrial mammals. The grooming of other individuals (termed ‘allogrooming’ or simply ‘grooming’) has been documented in many primate species (e.g., chimpanzees (Pan troglodytes) (Hemelrijk and Ek, 1991), patas monkeys (Erythrocebus patas) (Muroyama, 1994), Japanese macaques (Macaca fuscata) (Muroyama, 1991), as well as other mammalian species (e.g., squirrels (Halleran and Bekoff, 1995) and horses (Equus caballus) (Rho et al., 2007)). Grooming in primates leads to increased support during future agonistic encounters (Seyfarth and Cheney, 1984), as well as increased food sharing (de Waal, 1997). These kinds of exchanges involve a system of reciprocal altruism where individuals’ behaviour towards conspecifics is based upon a history of interaction with that individual or the individual’s close kin (Seyfarth and Cheney, 2007). de Waal (1997) describes the trade-off of grooming ‘services’ for food sharing ‘services’ a ‘service economy’ in chimpanzees. In these studies, the recipient of the grooming (i.e., the groomee) was shown to alter/increase sharing and aid giving behaviour as a result of the grooming. Consequently, the groomee could be considered to have accumulated a ‘social debt’ for the grooming services provided that would be re-paid during future interactions with the groomer. The ‘services’ model may help explain our observation that the majority of dolphin rubbing episodes involved same sex partners. In many documented dolphin societies, agonistic encounters between the sexes involves mate guarding (Willis and Dill, 2007), herding (Connor et al., 1992), and infanticiete (Dunn et al., 2002). As a result, long-term social bonds between same sex partners have developed (Connor, 1992). In the absence of ‘grooming’ as the currency in the dolphin services economy, rubbing may be a commodity that is traded for future assistance in agonistic encounters, such as male conflicts. This possibility is consistent with the notion of reciprocal altruism (Connor and Norris, 1982).

Recent research, however, has challenged the notion that grooming in primates should always be considered a ‘service’ that benefits the groomee. In a study of stress in Barbary macaques (Macaca sylvanus), individuals who spent more time grooming in the role of the groomee had reduced stress hormone levels in their feces, whereas the groomee’s stress hormone levels were unaffected by the amount of grooming they received (Shutt et al., 2007). This finding suggests that the groomee may receive assurance of his/her position within a social network by engaging in grooming behaviours directed at conspecifics, leading to a drop in stress levels. For this explanation, the potential benefits received by the groomee (e.g., parasite removal) play a less important role in the
function of the interaction, and a discussion of future agonistic support or other forms of reciprocal altruism must be re-focused on the groomer. If we apply a similar explanation to rubbing behaviour in dolphins, then it may be that the rubber receives the greatest benefit during a rubbing bout, which may partly explain why in this study the rubber tends to initiate such bouts. For this explanation, it would then be the rubber who has accumulated a ‘social debt’, and would be expected to reciprocate to the benefit of the rubberbee—either by allowing him/herself to be rubbed in the future, or to come to the rubberbee’s aid during agonistic encounters.

There are potential pitfalls in suggesting an analogy between grooming in primates and rubbing in dolphins. Unlike primate grooming, the rubberbee seems to more actively participate in the rubbing act, often by moving the body part being rubbed—it is not a case that the rubberbee should be understood as exclusively ‘receiving’ the behaviour in question. The rubberbee often moves the body part being rubbed in conjunction with the movement of the rubber’s flipper (Sakai et al., 2006a). In such cases, the rubberbee is participating in the rubbing act. For dolphin rubbing then, both animals could be considered as active participants in the act.

For dolphin rubbing, it is not yet clear which of the individuals is receiving the most benefit in the case of an imbalanced ‘social debt’ (i.e., the rubber or the rubberbee), or if any social debt arises at all. Especially in the case of petting, the behaviour itself does not necessarily provide clues as to its social significance for each of the participants, making the distinction between mutualism and reciprocal altruism difficult to establish. If the benefits of rubbing are not weighted toward either the rubber or the rubberbee, then rubbing may itself be an act of mutualism, and not altruism. A study by Tamaki et al. (2006) suggests that contact behaviour may be used by dolphins to restore alliances, and reduce tensions in post-conflict encounters for bottlenose dolphins, similar to one of the proposed functions of genito-genital rubbing in bonobos (Blount, 1990). If we assume that there may be multiple functions and manifestations of rubbing behaviour within dolphin societies, then explaining the function of rubbing behaviour in dolphins requires that we determine who exactly is receiving benefits from the acts involved.

This study provides only an initial direct comparison of the pectoral fin contact behaviour of two species at two study sites. Continued long term study of wild dolphin populations, as well as the addition of new focus species at other study sites are required to form a consistent picture of the kinds of rubbing behaviours used by various dolphin species. Comparison of environmental and ecological factors between sites, as well as the social structure of these species involved will shed further light on the likely function and ontogeny of pectoral fin contact behaviour. For this to be accomplished, and to allow for easier meta-analysis of the results reported in the literature by different research groups, we urge that rubbing nomenclature conventions be adopted. Currently, the evidence points toward a social component being the driving force behind the evolution of rubbing behaviour, possibly similar in function to grooming in primates, but further study is required to confirm this hypothesis.

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