# Altered swimming gait and performance of dolphin mothers: implications for interactions with tuna purse-seine fisheries

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ABSTRACT: Physical constraints while carrying an infant represent one of many reproductive costs. For bottlenose dolphins *Tursiops truncatus*, near-term pregnancy and 'carrying' a calf in echelon position (calf alongside mother's mid-lateral flank) alter maternal swimming gait and performance. As calves mature an alternate form of 'carrying', infant position (calf underneath mother's tailstock) dominates. To complete our understanding of locomotion during motherhood in dolphins, kinematics (peak-to-peak stroke amplitude, $A$, and tailbeat oscillation frequency, $f$) and performance (swim speed, $V$) while 'carrying' a calf in infant position were quantified. The relationship (slope) for $A$ and $V$ differed between solitary swimming and swimming with a calf in infant position ($Z = -1.706$, p = 0.088) as did the relationship (slope) for $f$ and $V$ ($Z = -3.699$, p < 0.001). Compared to solitary swimming ($2.17 \pm 0.02$ m stroke$^{-1}$; n = 166), mothers 'carrying' a calf in infant position had diminished distance per stroke ($1.82 \pm 0.07$ m stroke$^{-1}$; n = 27, $t = 5.209$, df = 191, p < 0.001; means ± SE) concomitant with a significant reduction (54 %) in average swim speed (n = 27, 166, $T = 629.00$, p < 0.001). These results have implications for dolphins that interact with tuna purse-seine fisheries in the Eastern Tropical Pacific (ETP). Dolphins 'carrying' a calf may be unable to achieve speeds sustained by groups evading fishermen. To maintain proximity with the group, mothers may become separated from their calf. Permanently separated dependent calves represent unobserved mortality events, which may partially explain the non-recovery of depleted ETP dolphin populations.

KEY WORDS: Kinematics · Locomotion · Eastern Tropical Pacific · Maternal investment · Cetacean

## INTRODUCTION

Maternal investment in mammals includes gestation, lactation, and other forms of parental care. Carrying an infant is considered to be the most costly form of parental care after lactation (Altmann & Samuels 1992, Kramer 1998) and has been described in 6 of 19 eutherian mammalian orders (for review see Ross 2001). This behavior provides a solution for mothers of diverse taxa that must maneuver within their environment to forage and avoid predators while accompanied by their young offspring (Ross 2001), which are handicapped by small body size, physiological immaturity, and inexperience (Carrier 1996). Infant carrying behavior was only thought to evolve in aerial and arboreal environments (Ross 2001), as for young primates which must accompany their mothers yet are encumbered by underdeveloped locomotor performance (Altmann & Samuels 1992, Doran 1992, Wells & Turnquist 2001).

Recent research has provided evidence of 'carrying' an infant in an aquatic environment. Although cetaceans (whales and dolphins) cannot physically carry their performance impaired calf (Noren et al. 2006), the mothers escort their calf in either echelon position or infant position (Fig. 1). Early in life, echelon position is the dominant behavior displayed by cetacean mother–calf dyads (McBride & Kritzler 1951, Norris & Prescott 1961, Au & Perryman 1982, Taber & Thomas 1982, Krasnova et al. 2006); it enables neonatal cetaceans to maintain close proximity to their mothers during travel (Norris & Prescott 1961, Lang 1966) by increasing the swimming efficiency of the infant (Kelly 1959, Weihs 2004, Noren et al. 2008). As cetacean offspring increase in size, infant position becomes the dominant formation swimming strategy for mother–calf dyads (Taber & Thomas 1982, Mann & Smuts 1999, Xian et al. 2012). For example, bottlenose dolphin *Tursiops truncatus* calves are observed in this position 38% of the time
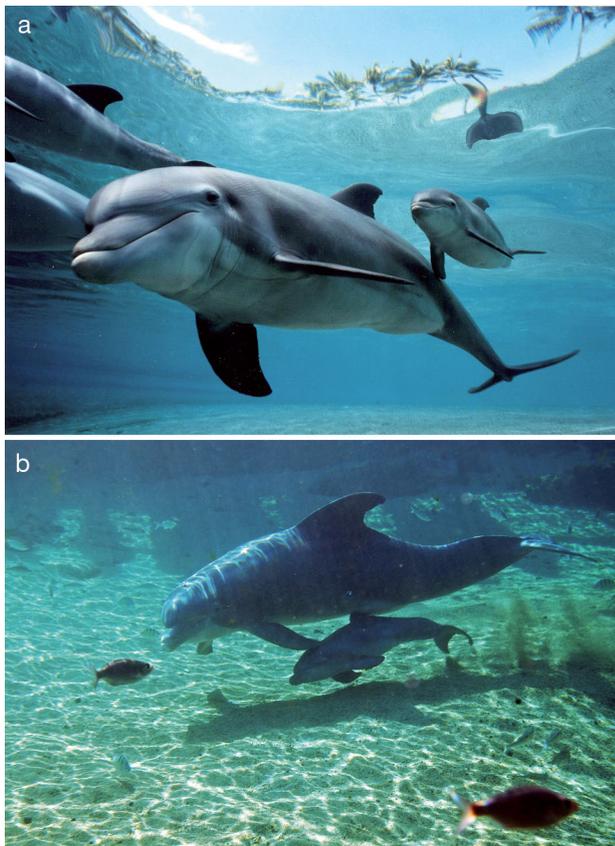


Fig. 1. *Tursiops truncatus.* Bottlenose dolphin mother 'carrying' its calf. (a) Echelon position: calf in close proximity to its mothers' mid-lateral flank. (b) Infant position: calf in very close positioning underneath its mother's tailstock. Photo credit: Dolphin Quest

by 1 yr postpartum (Gubbins et al. 1999), and this behavior remains important for calves up to 4 yr old (Gibson & Mann 2008). Indeed, dolphin calves tend to assume infant position when they are startled or tired (Gubbins et al. 1999) or traveling (Mann & Smuts 1999).

Like echelon position (Weihs 2004, Noren et al. 2008), infant position improves the swimming capabilities of calves (Weihs 2004, Noren & Edwards 2011). However, empirical studies demonstrated that the hydrodynamic benefits afforded by calves in infant position are not as great as those gained by calves in echelon position (Noren & Edwards 2011). Noren & Edwards (2011) suggested that older, stronger swimming calves are predominately in infant position because by relinquishing some hydrodynamic benefits of echelon position they gain other important benefits of infant position (Gubbins et al. 1999), including camouflage from predators. Nonetheless, there are maternal costs associated with swimming with a calf in echelon position (Noren 2008), and it is likely that there are maternal costs associated with swimming with a calf in infant position, although this remains to be quantified.

Current interactions between dolphins and tuna-purse seine fisheries in the eastern tropical Pacific Ocean (ETP) make the study of swimming abilities in dolphin mothers especially timely. These fisheries capture schools of yellowfin tuna *Thunnus albacares* by locating, chasing and encircling herds of associated dolphins. As a result of this fishery, eastern spinner *Stenella longirostris oreintalis* and northeastern offshore spotted *Stenella attenuata attenuata* dolphins are only at 29% and 19%, respectively, of their pre-1959 abundance levels when the yellowfin tuna purse-seine fishery initiated setting on dolphin schools (Wade et al. 2007). Despite a reduction in observed dolphin mortality associated with this fishery, dolphin populations that were depleted are not recovering, and the lack of recovery may be attributable to some unobserved mortality (Gerrodette & Forcada 2005). Archer et al. (2004) observed a deficit of dolphin calves in the historical bycatch, and suggested that separation of calves during fishery induced chase may represent unobserved mortality events. They recommended that research efforts should focus on how mother–calf pairs could become separated during tuna purse-seine fishery interactions to elucidate the magnitude of unobserved calf mortality and the effect that this may have on dolphin populations.

In view of this, I examined the kinematics and performance of dolphin mothers swimming with their

calf in infant position (Fig. 1a) and compared this to periods of solitary swimming by the mother (>1 m from their calf and all other dolphins) to aid in completing our understanding of how 'carrying' an infant affects maternal swimming in dolphins. The morphology and swimming kinematics of dolphins are characteristic of the thunniform mode, which is typical of some of the fastest marine vertebrates, including scombrid fishes, laminid sharks, and cetaceans (Lighthill 1969). Dolphins generate thrust exclusively with a high aspect-ratio caudal hydrofoil (tailflukes; Fish & Hui 1991). Thus, a qualitative assessment of swim effort was obtained by considering both tail movement amplitude and beat frequency; higher amplitudes and frequencies are associated with greater energy expenditure (Kooyman & Ponganis 1998). Performance was also examined quantitatively by comparing swim speeds. These data can help elucidate how mother–calf pairs may become separated during fishery induced chase. Understanding the effects of carrying an infant are important because this type of maternal investment (infant carrying) has received little attention to date.

## MATERIALS AND METHODS

### Experimental dolphins

Behavioral and physiological development of delphinid calves are generally similar across species (Noren & Edwards 2007). The bottlenose dolphin served as a model because its prevalence in human care provided trained individuals for the experimental protocols. We studied 4 adult dolphin mothers in a large, oblong semi-natural lagoon at Dolphin Quest Hawaii (high tide dimensions: $43 \times 53 \times 7$ m deep, low tide dimensions: $37 \times 46 \times 5$ m deep). The dolphin mothers had been held at the facility for a minimum of 4 yr, thus they were acclimated to their environment. Dolphins were fed a mixed diet of capelin, herring, and squid supplemented with vitamins. Studies occurred from October 2003 to November 2005, which corresponded to the time when the calves were 1 wk to 2.5 yr of age. Data were collected during 1 wk intervals on a quarterly basis for the first year, and during 1 wk intervals on a semi-annual basis for the second year of the study. Infant position swimming was represented by mothers swimming with a calf ranging in age from 8 to 318 d (mean ± SE: 71 ± 17 d, median: 31 d). Water temperature during the experimental period ranged from 24.0 to 26.7°C (25.3 ± 0.4°C).

### Swimming trials

During each data collection interval, the swimming motions of the dolphins were recorded daily throughout daylight hours. A submerged SCUBA diver, sitting stationary on a wide ledge on one side of the enclosure, used a digital video camcorder (Sony Hi-8 in an underwater housing; Amphibico Dive Buddy, Amphibico) to film the dolphins as they passed by. The SCUBA diver kept the video camera stationary such that the dolphins were only filmed when they were in the field of view of the camcorder. The animals swam ~1 to 3 m below the surface of the water and swam in a straight line path within 7 to 8 m parallel to the SCUBA diver. Experimental swim sessions included both opportunistic (no reward) and directional between 2 trainers (reward based). For opportunistic trials, the SCUBA diver was positioned in an area of the lagoon where the dolphins passed in a stereotypic straight-line path. For directional trials, the trainers were positioned across the lagoon from each other in a way that forced the dolphins to swim a straight-line path. Rewards (tactile stimulation, toys, and food) were based on the intensity of the swimming provided. Standard operant conditioning was used to train the directional swimming.

### Video analysis

Short (2 to 6 s) video clips of the dolphins swimming were extracted from the videotapes using digital video editing software (Pinnacle Studio 8, Pinnacle Systems). Distinct morphological features including the rostrum tip, cranial insertion of the dorsal fin, and the fluke tip were digitized at a rate of 60 fields per second of video using a motion-analysis system (Peak Motus 6.1, Peak Performance Technologies) following methods similar to Skrovan et al. (1999) and Noren et al. (2006). To correct for any slight deviations in the dolphins' vertical angle in the water column, all coordinates were transformed so that the starting position of the cranial insertion of the dorsal fin (digitized point closest to the center of mass) represented the zero position on the y-axis. The measured body length (beak tip to fluke notch) of the dolphin mothers, which did not change during the study interval because the females had already attained mature body length, provided a scalar so that the system could calculate instantaneous transformed coordinates, velocity, and acceleration for each digitized point. Only video clips where dolphins swam steadily, maintained a parallel path to the camera

lens, and had no qualitatively apparent acceleration were included in the analyses. In addition, a rock within the field of view of the camcorder was also digitized to ensure that the camera was held steady throughout the entire pass of the individual. Digitized video clips that indicated that the reference point moved were excluded from the analyses.

## Swimming kinematics, Strouhal number, and swim performance

The video clips were divided into 2 swimming behavior categories: (1) infant position (calf underneath mother's tailstock; Fig. 1b), and (2) solitary swimming (mother >1 m away from calf and all other dolphins). A quantitative assessment of gait was obtained by calculating peak-to-peak fluke stroke amplitude ($A$; in m) and tailbeat oscillation frequency ($f$; in strokes s$^{-1}$) from the data. Multiple sequential strokes were used to calculate the mean stroke amplitude and tailbeat oscillation frequency for each video clip. Distance per stroke was also calculated so that any differences in stroke frequency between swimming behaviors could be detected without the compounding effect of swim speed, since tailbeat frequency increases significantly with swim speed in odontocetes (Fish 1993, 1998, Skrovan et al. 1999, Fish et al. 2003, Noren et al. 2006). The principal wake parameter, a dimensionless number called the Strouhal number (St), was calculated according to Triantafyllou et al. (1993):

$$St = f \times A / V \qquad (1)$$

where $f$ = tailbeat oscillation frequency in strokes s$^{-1}$, $A$ = peak-to-peak fluke stroke amplitude in m, and $V$ = the average of the instantaneous swim speed (m s$^{-1}$). A quantitative assessment of swim performance was possible by comparing swim speeds across swimming behaviors.

## Statistics

We examined 4 adult females with dependent calves. Each performed numerous swim trials and the swim speed for each trial varied. A mixed model regression approach was used to determine the effect of swimming behavior (B, categorical variable) and peak-to-peak stroke amplitude ($A$, continuous variable) on swimming speed ($V$, continuous variable). Likewise, a mixed model regression approach was used to determine the effect of swimming behav-

ior (B, categorical variable) and tailbeat oscillation frequency ($f$, continuous variable) on swimming speed ($V$, continuous variable). An interaction term was included to test the homogeneity of slopes assumption; this was used to determine if the relationship (slope) between $A$ (or $f$) and $V$ varied as a function of B. In all cases, 'individual' was treated as a random term. The full models were:

$$V = B + A + B \times A \qquad (2)$$

$$V = B + f + B \times f \qquad (3)$$

These standard statistical analyses were performed using Sigma Stat version 2.03 and SYSTAT version 13.1 (Systat Software). All means are denoted with ±1 SE.

## RESULTS

The random term 'individual' did not affect any of the relationships noted in the statistical analyses section (mixed model p > 0.2). For both models, the interaction term was significant (we used p ≤ 0.10 as the critical p-value based on low sample size). The relationship (slope) for $A$ and $V$ differed across swim behaviors ($Z = -1.706$, p = 0.088) as did the relationship (slope) for $f$ and $V$ ($Z = -3.699$, p < 0.001; see Fig. 2).

Given that 'individual' did not affect the parameters being tested, all dolphins were combined to determine the relationships for $A$ and $V$ and $f$ and $V$ for each swimming behavior. Least squares linear regression analyses were used and the significance of these regressions were determined using $F$-tests. The results are shown in Table 1 and allow for comparisons to other studies on dolphin swimming kinematics that utilized least squares linear regressions to report the influence of $A$ and $f$ on $V$ (Fish 1993, Skrovan et al. 1999, Fish et al. 2003, Noren et al. 2006, 2008, 2011, Noren 2008, Noren & Edwards 2011).

Comparisons of distance per stroke, Strouhal number, and swim speed were also made across swimming behaviors. Because individual did not have an effect, data were pooled across individuals and differences between the 2 swimming behaviors were determined using student's test or Mann-Whitney rank sum test when normality or equal variance failed. Normality was determined using the Kolmogorov-Smirnov test and equal variance assumption testing with the Levene median test. Distance per stroke was less for mothers with a calf
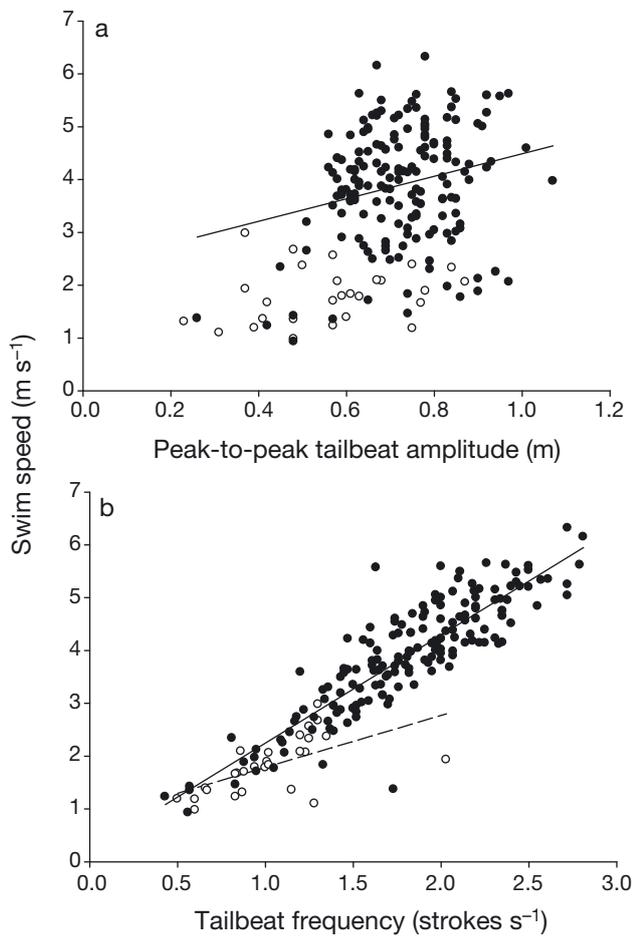
Fig. 2. *Tursiops truncatus*. Kinematics in relation to swim speed for 4 mothers during solitary swimming (●) and with their calf in infant position (○). Individual did not affect either relationship (mixed model p > 0.2). (a) The relationship for peak-to-peak stroke amplitude (*A*) and swim speed (*V*) differed across swim behaviors ($Z = -1.706$, p = 0.088). Solid line: relationship for *A* and *V* for solitary swimming. The relationship for *A* and *V* was not significant for infant position swimming. (b) The relationship for tailbeat frequency (*f*) and swim speed (*V*) differed across swim behaviors ($Z = -3.699$, p < 0.001). Solid and dashed lines: relationship for *A* and *V* for solitary and infant position swimming, respectively. See Table 1 for the statistics for the linear regressions

Table 1. *Tursiops truncatus*. Swimming kinematics of mothers during solitary swimming and when accompanied by their calf in infant position. *A* = peak-to-peak stroke amplitude; *f* = tailbeat oscillation frequency; *V* = swim speed

| Kinematic | Maternal solitary swimming | Maternal infant position swimming |
|---|---|---|
| *A* | $V = 2.13\ A + 2.36$ r = 0.23, *F* = 9.49, p = 0.002, n = 166 | Not correlated r = 0.24, p = 0.227, n = 27 |
| *f* | $V = 2.05\ f + 0.20$ r = 0.88, *F* = 582.56, p < 0.001, n = 166 | $V = 0.98\ f + 0.81$ r = 0.60, *F* = 13.93, p < 0.001, n = 27 |

achieved during solitary swimming (3.91 ± 0.09 m $s^{-1}$, n = 166, *T* = 629.00, p < 0.001). Similarly, the maximum performance of dolphins accompanied by a calf in infant position (2.98 m $s^{-1}$) was approximately half of that achieved during solitary swimming (6.32 m $s^{-1}$).

## DISCUSSION

Although carrying an infant is considered costly (Altmann & Samuels 1992, Kramer 1998), and it is evident across arboreal, aerial, terrestrial, and aquatic environments, only a few studies have examined the energetic and locomotor consequences of 'carrying' for the carrier. These studies have predominately focused on terrestrial species, primarily primates (Altmann & Samuels 1992, Schradin & Anzenberger 2001) and marsupials (Baudinette & Biewener 1998). Nonetheless, Noren (2008) provided evidence of locomotor consequences for dolphin mothers swimming alongside a calf, but only investigated the effect of 'carrying' when the dolphin mothers swam with their calves in echelon position (Fig. 1a), because echelon position was considered to be the primary formation of mother–calf pairs. Yet observations of wild dolphins have shown that from 1 to 2 mo post-parturition the frequency of echelon position decreased from 69% to 11% while infant position increased from 8% to 18% of the time (Mann & Smuts 1999). Infant position appeared to remain important, as calves up to 4 yr old were observed in this position 39% of the time (Gibson & Mann 2008). Captive dolphins have shown similar trends. During the first year of life, the frequency of echelon position decreased from 67% to 23% while infant position increased from 7% to 38% of the time (Gubbins et al. 1999). Given the predominance of infant position as the calves mature, an examination of the locomotor

in infant position (1.82 ± 0.07 m $stroke^{-1}$; n = 27) compared to periods of solitary swimming (2.17 ± 0.02 m $stroke^{-1}$; n = 166, *t* = 5.209, df = 191, p < 0.001), yet Strouhal numbers were similar across the 2 swim behaviors (swimming with calf in infant position: 0.316 ± 0.0161; solitary swimming: 0.341 ± 0.005; *T* = 2351, n = 27, 166, p = 0.320). Nonetheless, the average speed of dolphin mothers swimming with a calf in infant position (1.81 ± 0.10 m $s^{-1}$, n = 27) was significantly lower than the average speed

consequences of maintaining a calf in infant position (Fig. 1b) is needed to fully elucidate the maternal costs of 'carrying' cetacean calves.

## Dolphins 'carrying' a calf in infant position

Although formation locomotion is vital to the calf's survival by ensuring that mother–infant dyads remain intact during travel, it does not come without a cost for the mother. The presence of the calf may disrupt the boundary flow around the mother causing it to separate, which would increase turbulent flow (Weihs 2004, Weihs et al. 2006). Meanwhile, the entrained calf could increase the surface area of the mother. This would effectively increase the drag of the swimmer and require more power to overcome increased turbulent flow and drag (Webb 1975). As a greater proportion of maternal power output is needed to accommodate increased turbulent flow and drag, there will be less energy available to propel the individual because total work is limited by its metabolic scope (Weibel et al. 1987). Indeed, the results suggest that dolphins swimming with a calf in infant position must exert more effort compared to solitary swimming, as evidenced by a reduction in speed per a given tailbeat frequency (Fig. 2b).

In addition, the presence of the calf appears to alter the swimming gait of the mother. Mothers with a calf in infant position exhibited a size-specific stroke amplitude of $0.23 \pm 0.01$ body lengths (mean $\pm$ SE, n = 27) that was lower in magnitude than the mean size-specific stroke amplitude ($0.30 \pm 0.00$ body lengths, n = 166) exhibited during periods of solitary swimming. The reduced stroke amplitudes for mothers swimming with a calf in infant position may be due to a mechanical constraint as the mothers avoided bumping their calf with their tailflukes. Because power output per stroke is limited by mechanical constraints (Fish & Hui 1991) this undoubtedly alters locomotor performance.

Indeed, the combination of increased drag and altered gait in dolphins swimming with a calf in formation resulted in reduced performance. Mothers swimming with a calf in infant position had a 16% decrease in distance covered per stroke compared to when the mothers swam alone. In addition, mean and maximum swim performance was reduced by 54% and 53%, respectively, when the mothers swam with their calf in infant position compared to periods of solitary swimming. These results are comparable to the observation that dolphin mothers swimming with a calf in echelon position had a 13% reduction in dis-

tance per stroke, 46% reduction in mean swim performance, and 24% reduction in maximum swim performance compared to periods of solitary swimming (Noren 2008).

Interestingly, even though maternal gait and performance is altered by formation locomotion, the principal wake parameter (termed the Strouhal number) seems to be unaltered by the mode of locomotion. The Strouhal number for mothers swimming with a calf in infant position (means $\pm$ SD: $0.316 \pm 0.0161$; this study), mothers swimming with a calf in echelon position ($0.310 \pm 0.00571$; calculated using unpubl. data from Noren 2008), and mothers swimming alone ($0.341 \pm 0.005$; this study) all fell within the range where efficiency is considered to be maximal (0.25 to 0.35; Triantafyllou et al. 1993). In addition, the Strouhal numbers calculated in this study were in agreement with values determined previously for adult dolphins swimming alone (0.32 and 0.30; Triantafyllou et al. 1993). This implies that even though dolphins swimming with a calf in formation have an altered gait and reduced swim performance, efficiency remains optimized.

## Dolphins interacting with ETP tuna fishery

Diminished performance of dolphins swimming in formation with their calf could have important consequences for dolphins that interact with the yellowfin tuna fishery in the ETP. Yellowfin tuna are frequently found swimming under schools of spotted or spinner dolphins. For the past 5½ decades this fishery has chased and encircled dolphins in purse-seines to capture the associated tuna (see NRC 1992 for a review of these fishing techniques). Fishery interactions are prolonged; chase and release may last for several hours during which dolphins elevate routine speeds to chase and burst speeds of 2 to 4 m s$^{-1}$ and 5 to 8 m s$^{-1}$, respectively (Au & Perryman 1982, Au et al. 1988, Chivers & Scott 2002). Although the swim performance of dolphin mothers that interact with this fishery has yet to be quantified, the average speed (2.1 m s$^{-1}$) of adult spotted dolphins in the ETP (Scott & Chivers 2009) is similar to the routine speed (2.1 m s$^{-1}$; Williams et al. 1993) of adult bottlenose dolphins. This makes the bottlenose dolphin a viable model for predicting outcomes for dolphins that interact with the tuna purse-seine fishery.

Our experimental approach likely captured the swimming performance of wild dolphins. Average swim speeds of satellite monitored bottlenose dolphins reached 2.4 m s$^{-1}$ (rate of travel calculated from

straight-line distance between 2 sampled locations; see Klatsky et al. 2007 for review), and falls within the range of speeds measured for the dolphins in this study (see Fig. 2) and other studies on dolphin mother swimming kinematics and performance (Noren 2008, Noren et al. 2011). Therefore, the data compiled from dolphins in human care were utilized to formulate predictions for wild dolphins. Maximum swim performance of bottlenose dolphin mothers trained for speed swimming was diminished when accompanied by a calf in infant (2.98 m s$^{-1}$; present study) and echelon (4.39 m s$^{-1}$; Noren 2008) position compared to periods of solitary swimming (6.32 m s$^{-1}$; present study). The maximum swim speed (3.54 m s$^{-1}$) of 0–2 wk pre-parturition near-term pregnant dolphins was also diminished (Noren et al. 2011). The extra drag associated with formation locomotion (Weihs 2004) and pregnancy (Noren et al. 2011) reduces swim performance during motherhood. Thus, dolphin mothers in the ETP may be unable to achieve the burst speeds required to maintain proximity with their group during fishery interactions.

Dolphin mothers that are left behind during the chase may attempt to reunite with their group after the fishery interaction is terminated. However, unlike the stealthy, short duration chases associated with natural predators like sharks, tuna purse-seine chases are noisy and long in duration, including 20 min of chase and a 100 min escape response after being released from the net (Myrick & Perkins 1995). If wild dolphin mothers are only capable of achieving the maximum swim speeds exhibited by the trained dolphins in the kinematic studies, then mothers with a calf in echelon position, mothers with a calf

in infant position, and near-term (0–2 wk pre-parturition) pregnant females, will be separated from the group by 0.73, 2.42, and 1.75 km, respectively, at the end of a 20 min 5 m s$^{-1}$ chase (Fig. 3). These groups will be separated by an additional 3.66, 12.12, and 8.76 km, respectively, after 100 min of escape behavior. The noise, prolonged duration, and expansive combined chase and escape distances of 4.39 to 14.54 km separating dolphin mothers from the group may preclude a reunion.

Alternatively, females may become separated from their drafting calf during fishery induced chase. The presence of a calf does not appear to deter maternal herd-conforming behavior during the flight response as evident in photographs of an ETP dolphin school evading a vessel (Weihs 2004). It was hypothesized that chase may permanently separate mother–calf dyads (Noren & Edwards 2007). Indeed, examination of data collected from dolphins incidentally killed during fishing operations revealed that 74% of lactating spinner and 82% of lactating spotted dolphins were not associated with calves (Archer et al. 2001) and 0–1 yr old eastern *Stenella longirostris orientalis* and whitebelly *S. longirostris* spinner dolphins were underrepresented in the nets (Larese & Chivers 2008). The relatively slow maximum swim speeds of solitary calves <1 yr old (Noren et al. 2006) would preclude them from staying with the group during chase. Because this age group is not yet weaned (Myrick et al. 1986, Archer & Robertson 2004), the abandoned dependent calves are not likely to survive without their mothers for nourishment, protection, and social learning, and could represent an unobserved mortality event (Noren & Edwards 2007).
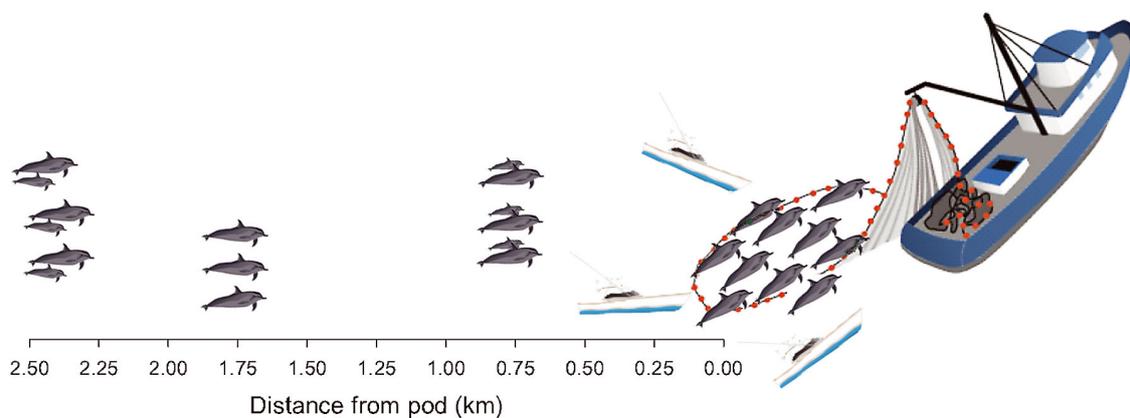


Fig. 3. Distances that dolphin mothers would be separated from the group after a hypothetical 20 min fishery induced chase at 5 m s$^{-1}$. The maximum swim performance of pregnant females 0–2 wk pre-parturition and mothers accompanied by a calf in infant or echelon position precludes them from maintaining proximity with the pod. This figure was constructed using the *Stenella longirostris* (spinner dolphin), powerboat, and purse seine images by Tracey Saxby, IAN Image Library (http://ian. umces.edu/imagelibrary/)

Overall, there has been a decrease in the proportion of eastern spinner and northeastern pantropical spotted *Stenella attenuata attenuata* dolphin females observed with calves, which was attributed to a decrease in birth rate or calf survival (Cramer et al. 2008). If near-term pregnant dolphins are separated from the group during fishery interactions and are unable to reunite with their group (or any other groups in the vicinity), then the birth rate for these populations will be lowered. Meanwhile, if dependent calves are separated during fishery induced chase and subsequently die, then the calf survival rate for these populations will be decreased. These events are likely to contribute to the non-recovery observed for dolphin populations that interact with the tuna purse-seine fishery in the ETP.

## SUMMARY

This study provides further empirical evidence of consequences for dolphin mothers 'carrying' an infant. Regardless of a calf's positioning alongside its mother, the drafting calf alters the mother's swimming performance. This may make dolphin mothers vulnerable to separation from the group during interactions with tuna-purse seine fisheries in the ETP. Even in the absence of fishery interactions, 'carrying' an infant in an aquatic environment is associated with maternal costs, and this behavior could affect maternal energy budgets, foraging efficiency, and predator evasion.

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