Abstract—Size-related differences in power production and swim speed duration may contribute to the observed deficit of nursing calves in relation to lactating females killed in sets by tuna purse-seiners in the eastern tropical Pacific Ocean (ETP). Power production and swim-speed duration were estimated for northeastern spotted dolphins (*Stenella attenuata*), the species (neonate through adult) most often captured by the fishery. Power required by neonates to swim unassisted was 3.6 times that required of an adult to swim the same speed. Estimated unassisted burst speed for neonates is only about 3 m/s compared to about 6 m/s for adults. Estimated long-term sustainable speed is about 1 m/s for neonates compared to about 2.5 m/s for adults. Weight-specific power requirements decrease as dolphin calves increase in size, but power estimates for 2-year-old spotted dolphin calves are still about 40% higher than power estimates for adults, to maintain the same speed. These estimated differences between calves and adults are conservative because the calculations do not include accommodation for reduced aerobic capacity in dolphin calves compared to adults. Discrepancies in power production are probably ameliorated under normal circumstances by calves drafting next to their mothers, and by employing burst-coast or leap-burst-coast swimming, but the relatively high speeds associated with evasion behaviors during and after tuna sets likely diminish use of these energy-saving strategies by calves.

Duration of unassisted swimming activity for spotted dolphin (*Stenella attenuata*) calves: implications for mother-calf separation during tuna purse-seine sets

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Dolphin calves draft in echelon position next to their mothers for the first few weeks after birth and continue to return to drafting in echelon position frequently throughout at least their first year (Edwards[1]). "Echelon position' is the physical positioning of the calf within a few centimeters of the mother, near her mid-section, with fin motions reduced or absent (e.g., Norris and Prescott, 1961). This position takes advantage of the mother's flow field, reducing or effectively eliminating the energy cost to the calf of moving forward through the water (Weihs, 2004). Because drafting appears to be ubiquitous among dolphin calves, particularly during the neonate stage, it appears likely that drafting is an essential factor in maintaining physical association between calves and their mothers, especially when the calves are small.

In the eastern tropical Pacific Ocean (ETP) a situation occurs in which it becomes important to consider the consequences for calves of losing their drafting association with their mother. In this area, a tuna purse-seine fishery targets schools of large yellowfin tuna that associate closely with schools of dolphins, primarily the spotted dolphin (*Stenella attenuata*) (NRC, 1992). The associated schools of tunas and dolphins are located by a helicopter sent out from the purse-seine vessel and are subsequently captured through the actions of several high-powered speedboats, which are released from the purse-seiner to overtake and herd the associated animals into the closing arc of the purse-seine (NRC, 1992). Examination of the dolphins found dead in the net has revealed that 75% to 95% of the lactating females killed in the sets are not killed with an accompanying calf (Archer et al., 2004). This observed calf deficit is a potentially important factor in the lack of recovery of ETP dolphin populations despite over a decade of very low fishery mortality (Wade et al.[2]), but little is known about why or how the separation of mothers and calves occurs (Archer et al., 2004).

The chase, encirclement, and release procedure of purse-seine fishing operations tends to be relatively prolonged—chases averaging about 30 minutes, capture and confinement about 90 minutes, and postrelease swimming at least 90 minutes (Myrick and Perkins, 1995; Chivers

[1] Edwards, E. 2002. Behavioral contributions to separation and subsequent mortality of dolphin calves chased by tuna purse-seiners in the eastern tropical Pacific Ocean. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-28, 33 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.
[2] Wade, P., S. Reilly, and T. Gerrodette. 2002. Assessment of the population dynamics of the northeastern offshore spotted and eastern spinner dolphin populations through 2002. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-13, 58 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

and Scott[3]). The set procedure also tends to induce relatively high, sustained swimming speeds in the dolphins. Swimming speeds of two spotted dolphins carrying velocity tags during and after tuna purse-seine sets in the ETP averaged 1.7–2.8 m/s during chase and 2.6–3.1 m/s after release, compared to undisturbed speeds of 1.2–1.9 m/s (Chivers and Scott[3]). Compared to adults, dolphin calves have smaller, less-coordinated muscles and lower aerobic capacity, especially at birth but persisting through the first year or more (Dolar et al., 1999; Dearoff et al., 2000; Noren et al., 2001; Noren et al., 2002; Eitner et al., 2003; Noren et al., 2004). Therefore, it appears possible that the observed calf deficit in the kill may result at least in part from energetics-related separation of calves from mothers during the chase or after release, as well as the inability of calves to maintain speed with adults while swimming alone.

The present study examines the possibility of energetics-related separation, by estimating the length of time (duration) during which spotted dolphin calves of different sizes ranging from neonate through two years of age can swim unassisted at various velocities. These velocity-durations are then compared to adult swimming capacities, in order to determine whether calves swimming without assistance may experience energy-based difficulty keeping up with adult dolphins during evasion from tuna purse-seine sets.

Materials and methods

Duration limits for unassisted swimming by spotted dolphin calves were calculated by combining estimates of mass-specific energy cost of steady, submerged, unassisted swimming by neonate through adult spotted dolphins, with reported swimming speed durations of adult dolphins of various species (Table 1). Swimming duration for adults was used because this information was not available for dolphin calves. The data were combined based on the assumption that the duration a given unit of dolphin muscle can sustain a given mass-specific energy cost is the same for both adults and calves within any species of dolphin. It is much more likely that swimming capacity of calves within any dolphin species is significantly lower than that of adults and that differences are particularly pronounced at birth (Dolar et al., 1999; Dearoff et al., 2000; Eitner et al., 2003; Noren et al., 2001, 2002, 2004), but the exact differences are unknown. The swimming duration estimates presented in this study therefore represent maximum durations. It is also possible that species differ in power production capacities, based on observations of blood chemistry differences between species (Ridgway and Johnston, 1965), but it is not unreasonable to assume that relative

differences between species are maintained throughout the size ranges of individuals within a species, so that younger dolphins are probably less adept than adults in any particular species. Thus, although it is not yet possible to quantify differences between calf and adult swimming-duration capacities in *Stenella attenuata* in nature, they are likely greater than estimated in the present study, so that problems apparent from this study are likely greater during actual tuna purse-seine sets.

The energy cost of a steady, submerged, unassisted swimming rate was estimated in this study for velocities ranging from 1.5 to 6.0 m/s in order to encompass speeds from slow undisturbed swimming to the maximum likely to occur during attempted evasion from tuna purse-seine sets. Average velocities observed during tracking of dolphins before and after experimental sets varied from about 1.5 m/s m to about 3 m/s (Chivers and Scott[3]) but short term speeds attained during evasion maneuvers were likely to have exceeded these averages (Table 1). Total body energy costs were estimated first and then converted to mass-specific costs by dividing total estimated energy costs by the estimated total muscle weight of each size of modeled dolphin. Muscle-mass-specific measures are more appropriate than simply dividing by total body weight for comparisons between sizes because muscle fraction of body weight increases with body weight in *Stenella attenuata* in the ETP, from 35–40% in neonates to 55–60% in adults (Edwards, 1993).

Data sources

Total body energy costs were estimated for eight modeled *Stenella attenuata* ranging in size (age) from newborn through adult. Sizes were selected to emphasize changes during the early months (Table 2). Size-at-age to two years old was estimated from Hohn and Hammond (1985). Size of an adult reproductive female was estimated from Perrin and Reilly (1984). Total body wet weight, wetted surface area of body, fins, and flukes, maximum body diameter, and fraction of total body weight composed of muscle were estimated for each size of modeled dolphin by using regression equations developed from morphological measurements of ETP dolphins (Edwards 1993, Edwards[4]).

The morphological measurements were taken from 35 spotted dolphins ranging in size from 0.71 to 2.1 m total length (tip of rostrum to fluke notch). This size range encompasses all life-history stages (near-term fetus through mature adult) of the spotted dolphins found in the eastern tropical Pacific Ocean. Spotted dolphins are about 0.8 m total length at birth (Hohn and Hammond, 1985). Specimens included 22 females and 13 males (Edwards, 1993). Male specimens included

[3] Chivers, S., and M. Scott. 2002. Tagging and tracking of *Stenella* species during the 2001 Chase and Encirclement Stress Studies cruise. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-33. 23 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA. 92037.

[4] Edwards, E. 2002. Energetics consequences of chase by tuna purse-seiners for spotted dolphins (*Stenella attenuata)* in the eastern tropical Pacific Ocean. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-29, 32 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

three fetuses, six immature, and four mature individuals. Female specimens included three fetuses, six immature, one mature resting, one mature lactating, and 11 mature pregnant individuals. All specimens were killed during tuna fishing operations in the eastern tropical Pacific Ocean. Two of the specimens were collected in February 1980, one in July 1983, nine in July 1985, two in August 1985, seventeen in December 1985, and four were collected without a date noted (Edwards, 1993). All specimens were processed according to the same procedures prior to dissection. Immediately after the sets, the dolphin specimens were brought on board the vessel and frozen whole in the brine wells of the vessel. The specimens were transported frozen to port and then transported frozen to the Southwest Fisheries Science Center. Specimens were kept frozen until thawed in fresh water (about 27°C) just prior to dissection. Not all measurements were made on all specimens; therefore sample sizes differ between the regression equations presented below.

Energetics model   The energetics model used to estimate total body cost of swimming was taken from Edwards (1992, based on Magnuson, 1978), except that 1) new data were used to estimate dolphin body parameters and 2) the estimate of fin plus induced drag was replaced by the multiplier 3 (see below). The model used standard hydrodynamic equations and methods (Hoerner, 1965; Hertel, 1969; Webb, 1975) to estimate hydrodynamic drag on a fully submerged streamlined body of revolution moving steadily in turbulent flow. Body surface area was increased to specifically include the surface area of fins and flukes (Fish[5]), and drag estimates were increased to account for body and fin movements. Because energy to move forward (thrust energy) must exactly balance the drag experienced by a steadily swimming animal, estimating total drag energy is equivalent to estimating thrust energy, i.e., the energy cost to swim (Fish and Rohr, 1999).

Model formulation   Total power (P_t, in watts) required to overcome drag during steady, submerged swimming (Hertel, 1969) by a modeled dolphin of a given total length (L, rostrum to fluke notch) was estimated as

$$P_t = P_c / (E_m E_p),$$

where P_c = mechanical power (in watts) required to overcome hydrodynamic drag;
E_m = muscle efficiency; and
E_p = "propeller efficiency" (efficiency of propulsion by flukes).

E_m was assumed to be 0.2 from studies of muscle efficiencies in terrestrial animals (e.g., Goldspink 1988), man (Alexander, 1983; quoting Dickinson, 1929) and dolphins (Fish, 1993, 1996). E_p was assumed to be 0.85 based on

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studies by Fish (1998), Webb (1975), and Yates (1983). P_c was estimated as a function of total hydrodynamic drag (D_t, in dynes) and velocity (V, in m/s) as

$$P_m = D_t V / 10^7,$$

where the factor 10^7 converts ($D_t V$) to watts.
   Total drag was estimated as a function of drag due to body, fins, and movements of body parts as

$$D_t = 0.5 \rho V^2 S_w C_{d3} = 1.5 \rho V^2 S_w C_d,$$

where ρ = density of seawater (1.025 g/cm³);
   S_w = wetted surface area;
   C_d = coefficient of total drag; and
   3 = drag augmentation factor.

S_w includes surface area of body plus fins and flukes, where estimated planar area of fins was increased by 6% to account for the curvature of the fins, based on measurements of individual slices from fins and flukes from one small and one large dolphin, 1.32 m and 1.93 m in length, respectively (Edwards, unpubl. data). Drag augmentation factor generally varies between 3 and 5 (e.g., Lighthill, 1971; Fish, 1993) and was assumed equal to the value of 3 in the present study, based on studies of gliding vs. actively swimming dolphins (Skrovan et al., 1999). The factor 3 accounts for the increase over gliding drag caused by body movements during active swimming. Use of a squared relationship between V and D_t is supported by the observed relationship between total drag and velocity in free swimming *Tursiops truncatus* (Skrovan et al. 1999, Eq. 6). Use of a cubic relationship between V and P_t is supported by observations of swimming kinematics of *Tursiops truncatus* swimming between 1 and 6 m/s (Fish, 1993).
   S_w (in cm²) was estimated as

$$S_w = 0.299 L^{2.05},$$

based on measurements from 19 *Stenella attenuata* ranging in size from 0.71 to 2.01 m, where L is total length (in cm).
   C_d was estimated from the formula for drag of submerged streamlined bodies of revolution moving at constant velocity (Hoerner, 1965; Hertel, 1969; Webb, 1975) as

$$C_d = C_f \left[1 + \left(1.5(d/L)^{3/2} \right) + 7 \left((d/L)^3 \right) \right],$$

C_f = the coefficient of friction drag; and
d = 0.12

where d = maximum body diameter (in cm) based on measurements from 24 *Stenella attenuata* ranging in size from 0.71 to 2.01 m.

C_f was estimated from the formula for submerged streamlined bodies of revolution moving at constant velocity in turbulent flow (e.g., Webb, 1975) as

Table 1

Reported duration of various swimming speeds for several species of dolphins.

Velocity (m/s)	Duration	Publication	Species
	Burst (seconds)		
11.2	leap	Rohr et al. (2002)	*Tursiops*
11.1	2	Lang (1975)	*Stenella*
10.6	2	Lang (1975)	*Stenella*
10.3	2	Lang (1975)	*Stenella*
9.7	leap	Rohr et al. (2002)	*Tursiops*
8.8	<2	Rohr et al. (2002)	*Delphinus*
8.8	leap	Rohr et al. (2002)	*Tursiops*
8.3	7.5	Lang (1975)	*Tursiops*
8.2	<3	Rohr et al. (2002)	*Tursiops*
8.2	<120	Au et al. (1988)	*Stenella*
8.0	7.6	Lang and Norris (1966)	*Tursiops*
8.0	<3	Rohr et al. (2002)	*Delphinus*
7.8	2	Lang (1975)	*Lagenor*
7.7	2–3	Lang and Prior (1966)	*Stenella*
7.5	leap	Lang (1975)	*Tursiops*
7.4	leap	Lang (1975)	*Tursiops*
7.3	leap	Au and Weihs (1980)	*Stenella*
6.8	10	Lang and Norris (1966)	*Tursiops*
6.7	1.4	Rohr et al. (2002)	*Delphinus*
6.7	<3	Rohr et al. (2002)	*Delphinus*
6.3	10	Lang and Norris (1966)	*Tursiops*
6.4	240	Au and Weihs (1980)	*Stenella*
6.2	<2	Rohr et al. (2002)	*Tursiops*
5.9	50	Lang and Norris (1966)	*Tursiops*
6.0	2	Rohr et al. (2002)	*Delphinus*
5.6	<10	Rohr et al. (2002)	*Tursiops*
5.3	6.6	Lang and Norris (1966)	*Tursiops*
	Maximum (minutes)		
4.7	11	Au and Perryman (1982)	*Stenella*
4.4	21	Au and Perryman (1982)	*Stenella*
4.2	<8.5	Rohr et al. (2002)	*Delphinus*
	Prolonged (hours–days)		
3.5	1 hour	Au and Perryman (1982)	*Stenella*
3.2	9.3 hour	Leatherwood and L. (1979)	*Stenella*
3.1	extended period	Lang and Norris (1966)	*Tursiops*
3.1	90 min	Chivers and Scott[3]	*Stenella*
3.0	1.5 hours	Au and Perryman (1982)	*Stenella*
2.8	15 min	Chivers and Scott[3]	*Stenella*
2.6	106 min	Chivers and Scott[3]	*Stenella*
2.1	days	Chivers and Scott[3]	*Stenella*
1.9	hours	Chivers and Scott[3]	*Stenella*
1.8	hours	Chivers and Scott[3]	*Stenella*
1.7	32 min	Chivers and Scott[3]	*Stenella*
1.6	4 days	Hui (1987)	*Delphinus*
1.6	hours–days	Chivers and Scott[3]	*Stenella*
1.5	hours	Chivers and Scott[3]	*Stenella*
1.2	hours	Chivers and Scott[3]	*Stenella*
1.2	<50 hours	Perrin et al. (1979)	*Stenella*

No. of animals	Length (m)	Weight (kg)	Swimming location	Swimming condition
3			tank	maximum observed leap velocity
1	1.86	52.7	lagoon	accelerating, 25 m course
1	1.86	52.7	lagoon	accelerating, 25 m course
1	1.86	52.7	lagoon	accelerating, 25 m course
3			tank	average maximum leap velocity
1			wild	maximum observed speed
3			tank	average leap velocity
1	1.91	89	lagoon	61 m course in 300 m lagoon
6	2.6	197	small tank	maximum speed, 8 m course
300			wild	evading helicopter
1	1.91	89	lagoon	61 m course; maximum speed observed
1	1.83	105	tank	5 or 8 m course
1	2.09	91	tank	accelerating, long narrow tank
1			captive	70 m circular pool; maximum speed
1	1.91	89	ocean	swimming in speedboat waves
1	1.91	89	ocean	swimming in speedboat waves
not specified			wild	during chase by speedboats
1	1.91	89	ocean	swimming in speedboat waves
"A school"			wild	average maximum observed speed
1	1.83	105	captive	mean high swim speed
1	1.91	89	lagoon	61 m course; maximum observed speed
not specified			wild	after escaping purse seine
6	2.6	197	tank	mean high swim speed
1	1.91	89	ocean	swimming in speedboat waves
41			wild	average maximum speed evading aircraft
4			wild	maximum speed after release
1	1.91	89	ocean	swimming in speedboat waves
school no. 5			wild	maximum observed speed and duration
school no. 5			wild	swimming with ocean swells
"A school"			wild	average maximum velocity evading aircraft
school			wild	average speed evading vessel
1	2.05		wild	average speed estimated from radiotag
1	1.91	89	ocean	swimming in speedboat waves
D230			wild	postrelease velocity
school no. 2			wild	average speed evading vessel
D230			wild	velocity during chase by seiner
D19			wild	postrelease velocity
12			wild	average speed, 1992, 1993
D230			wild	average nonchase velocity, night
D230			wild	average nonchase velocity, day
D19			wild	velocity during chase by senior
2	1.76	95	tank	small, shallow round tank
2			wild	average speed, 2001
D19			wild	average nonchase velocity, day
D19			wild	average nonchase velocity, night
26			wild	minimum distance traveled, radiotag

Table 2

Dolphin model parameters. See text for formulas and rationale.

Dolphin no.	Age	Total length (cm)	Body weight (kg)	Muscle weight (kg)	Wetted surface area (cm²)	Maximum diameter (cm)	Fineness ratio
1	new born	85	6.40	2.62	2700	13.5	6.30
2	1 week	87	6.85	2.81	2832	13.8	6.29
3	1 month	90	7.58	3.18	3036	14.3	6.28
4	3 months	98	9.76	4.29	3615	15.7	6.24
5	6 months	110	13.76	6.33	4581	17.7	6.20
6	1 year	129	22.08	11.04	6351	21.0	6.14
7	2 years	154	37.37	20.18	9131	25.4	6.07
8	adult	190	69.73	41.84	14045	31.7	5.99

$$C_f = 0.072R^{-0.2},$$

where R is Reynold's number, estimated here as

$$R = LV / v,$$

where v = kinematic viscosity (=0.01 Stokes).

The calculations above generated estimates of the power required for a whole dolphin of a given size to swim at a given velocity (P_t, in watts). Power required per kilogram of wet weight muscle (P_m), for a given velocity was estimated as

$$P_m = P_t / M_m,$$

where M_m = total *muscle* mass (wet weight in kg), estimated from total *body* mass (M_t, wet weight in kg) as

$$M_m = -2.97M_t^{0.468}$$

based on ln-ln regression of measurements from a sample of 26 *Stenella attenuata* from the ETP ranging in size from 0.71 to 2.06 m. Total muscle was used rather than some portion of measured musculature because the complex and interconnected muscle and connective tissue of dolphins makes it difficult to isolate any particular portion as uniquely responsible for locomotion (Pabst, 1990). M_t was estimated from total length (L, in cm) as

$$M_t = 0.0000119L^{2.97}$$

based on ln-ln regression of measurements from a sample of 23 *Stenella attenuata* from the ETP ranging in size from 0.71 to 2.01 m.

Results

Model corroboration

Model estimates of the cost of swimming compared reasonably well with the cost of swimming in published reports for other species of dolphins swimming 1–6 m/s, in cases where the published reports can be appropriately compared with the present model. Although a number of studies present a variety of estimates of drag, thrust power, and metabolic power at various swimming speeds for a variety of dolphins (reviewed by Fish and Rohr, 1999), comparisons of present results with many of these earlier studies would be inappropriate because either the estimates were derived from completely different models from the one used in the present study or from generally similar models but where different assumptions were made about model parameters, such as propulsive efficiency, metabolic efficiency, drag formulation, and body structure (Edwards[4]). Only appropriately comparable published results are discussed in the present study.

All weight-specific measurements in the following paragraph refer to total body mass. At estimated optimum velocities ranging from about 1.2 m/s in neonate spotted dolphins to about 1.7 m/s in adults (Edwards[4]), model estimates are approximately 3 W/kg for all sizes of spotted dolphin, compared to measurements (derived under various methods) of about 2.5–5.5 W/kg for adults of various species of dolphins, either resting or swimming about 2 m/s (Hui, 1987; Worthy et al., 1987; Williams et al., 1992; Fish, 1993; Yadzi et al., 1999). Observed average total metabolic rates calculated from oxygen consumption by two *Tursiops* (average weight 162 kg), swimming 2 and 3 m/s, were approximately 2.5 and 3.7 W/kg (Yadzi et al., 1999), compared to model estimates of approximately 2.9 and 5.9 W/kg for an adult spotted dolphin (about 70 kg) swimming at the same speeds. Model estimates of thrust power output for an adult spotted dolphin (about 70 kg) also compared well with thrust power estimated as a function of velocity from videos of five *Tursiops* swimming between 1 and 6 m/s (Fish, 1993). Given an average adult *Tursiops* weight of 230 kg, average estimated thrust power for *Tursiops* swimming 1, 3, 5, and 6 m/s was 1, 3, 14, and 23 W/kg, compared to spotted dolphin model estimates of 1, 3, 13, and 21 W/kg, respectively. These comparisons refer to mechanical power output

only, because Fish's (1993) analysis does not include metabolic efficiency. Assuming the same metabolic efficiency of 0.2 for the *Tursiops* in Fish's study as used in the present model, an estimate of total power by his *Tursiops* swimming 6 m/s is 115 W/kg (i.e., $23 \times (1/0.2)$), compared to the model estimate of about 125 W/kg for the adult spotted dolphin.

Mass-specific cost of swimming

Model estimates of mass-specific power requirements (watts per kilogram muscle, W/kg_m) for unassisted swimming by spotted dolphins in the ETP increase quickly with velocity, regardless of dolphin size, but increase much more quickly for smaller dolphins (Fig.1). Model results indicated that a neonate (85 cm) spotted dolphin must produce 3.6 times more power per kilogram of muscle than an adult swimming at the same speed. The factors are 3.5, 3.3, 2.8, 2.4, 1.8, and 1.4 times adult power for 87-, 90-, 98-, 110-, 129-, and 154-cm spotted dolphins. The factors do not vary with velocity because the relative differences between body dimensions in dolphins of different sizes remain constant regardless of swimming speed.
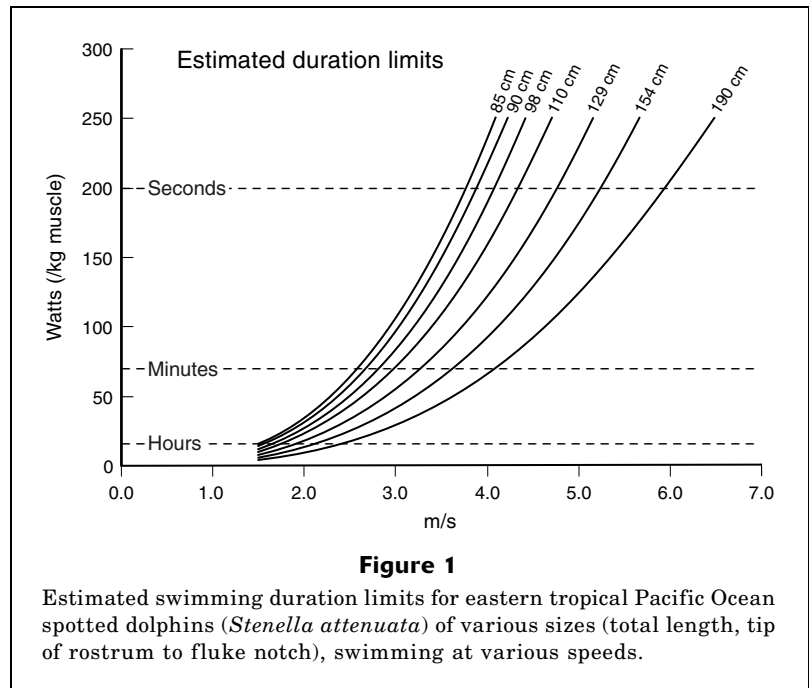
For example, at speeds typical of ETP dolphins attempting to evade speedboats during an impending tuna-purse-seine set or during escape from the net after release (about 3 m/s) (Chivers and Scott[3]), the model predicts that an 85-cm neonate swimming unassisted by its mother would require a muscle power of about 105 W/kg_m versus 30 W/kg_m for a 190-cm adult. The difference is still relatively marked even for two-year-old calves (154 cm), which would require an estimated 42 W/kg_m to maintain a steady submerged unassisted swim speed of 3 m/s, i.e., 1.4 times adult power requirements.

Velocity duration limits

Velocity duration limits for adults, drawn from literature sources, appear to range from a few seconds for burst speeds above about 5 m/s, to several minutes for maximum speeds of about 4 m/s, to hours at prolonged speeds below about 3.5 m/s (Table 1).

Estimated mass-specific muscle power required of adult spotted dolphins to achieve these speeds ranges from 208 W/kg_m for burst speeds of 6 m/s greater, to 67 W/kg_m for maximum sustainable speeds around 4 m/s, and 4–10 W/kg_m for prolonged duration speeds between 1 and 2 m/s (Fig.1).

If one assumes that these power-duration limits apply also to dolphin calf muscle, neonate dolphins (85 cm) for example, could generate a burst duration power of about 200 W/kg_m for a few seconds at unassisted swimming speeds of about 3.0 m/s, maximum duration power

Figure 1

Estimated swimming duration limits for eastern tropical Pacific Ocean spotted dolphins (*Stenella attenuata*) of various sizes (total length, tip of rostrum to fluke notch), swimming at various speeds.

of about 70 W/kg_m for some minutes at about 2.2 m/s, and prolonged duration power of about 5–10 W/kg_m for hours at about 1.0 m/s (Fig.1). For two-year-old spotted dolphins (154 cm), estimated swimming duration limits were about 5 m/s for burst effort at 200 W/kg_m, about 3.5 m/s for maximum effort at 70 W/kg_m, and about 2 m/s for prolonged effort at 5–10 W/kg_m. Intermediate ages produced intermediate results.

Discussion

Model results demonstrated clearly that swimming capability of dolphin calves is much lower than that of adults. The especially pronounced difference between neonates and adults appears a likely basis for development of the ubiquitous drafting behavior observed in both captive and wild neonates. Given the large difference in swimming capacities, it is difficult to imagine how small dolphin calves could maintain any long-term association with the mother without the hydrodynamic benefits of drafting, even under normal circumstances.

During the relatively fast-paced evasion swimming associated with tuna purse-seine sets in the ETP, it appears that spotted dolphin calves swimming unassisted are likely to have serious difficulty maintaining the same speed as adults—difficulties being especially pronounced for younger dolphins. It is also likely that the differences in swimming capacity presented in this study are underestimates because they do not include effects such as positive bouyancy (Cockroft and Ross, 1990; Mann and Smuts, 1999) and soft, flexible fins and flukes that are present for several hours after birth (McBride and Kritzler, 1951; Tavolga and Essapian,

1957; Wells, 1991). Other differences persist for weeks or months, including undeveloped musculature (Eitner et al., 2003) and uncoordinated swimming and respiratory movements (Tavolga and Essapian, 1957; Taylor and Saayman, 1972; Reiss, 1984; Cockroft and Ross, 1990; Peddemors, 1990; Herzing, 1997; Mann and Smuts, 1999). Aerobic capacity is also likely to be reduced throughout the first few months, and not likely to reach adult levels until two to three years of age (Dolar et al., 1999; Dearoff et al., 2000; Noren et al., 2001, 2002, 2004). The results presented in this study also do not include the added costs of increased drag due to swimming near the surface, and repeatedly piercing it, which will occur much more often during evasion of tuna sets than during normal swimming. These other effects increase the likelihood that dolphin calves, particularly the younger individuals, will have problems coping with the swimming conditions induced during tuna purse-seine sets.

Difficulties with unassisted swimming for dolphin calves may be ameliorated to some extent by employing drafting (Weihs, 2004), burst and coast (Au and Weihs, 1980), or leap-burst-coast swimming behaviors (or a combination of these behaviors) (Weihs, 2002). Theoretically, these strategies could significantly reduce the cost to calves of moving through the water. However, it is not clear that any of these energy-saving strategies will be consistently attainable by spotted dolphin calves during herd movements associated with evading or escaping sets by tuna purse-seiners in the ETP.

Drafting can only be sustained through respiratory leaps if mother and calf leave and reenter the water with equal speed and efficiency (Weihs, 2004). Because evasion of tuna purse-seine sets involves sustained high-speed swimming characterized by repeated full-body respiratory leaps from the water (Au and Wiehs, 1980), calves are likely to tire and lose coordination more quickly than adults, and the smallest calves will be the first to experience problems. These factors may have contributed to the observed failure of a neonate dolphin calf in the ETP to successfully maintain a drafting relationship with its assumed mother during a respiratory leap while attempting to evade a vessel (Weihs, 2004).

Once the drafting relationship is disrupted, the calf appears likely to fall behind because of its physical limitations, unless its mother alters her speed so that the calf can reestablish the drafting relationship. However, review of dolphin mother-calf behavior indicates that the mother is not likely to voluntarily leave other adults during attempted evasion of tuna purse-seine sets in the ETP (Edwards[1]). Thus, the faster or longer the chase or postrelease escape period (or combination of all three factors), and the younger the calf, the more likely it appears that the calf will become separated from its mother and be left behind during periods of fast swimming by the adults. Although fast swimming for a few minutes may not pose a great problem for many calves, longer periods appear increasingly likely to lead to significant calf loss in purse-seine operations.

The duration of the high-speed period is at least as important as the speed maintained during the period, given the power-duration relationship. If fast swimming is concluded quickly, it is more likely that calves could achieve the required power during the short time required. As fast-swimming persists, power capacity decreases rapidly (Fig. 1), so that more and more calves are likely to be lost because they have exceeded their ability to keep up with the adults in their school.

Even under normal circumstances, burst and coast, or burst-leap-coast, swimming patterns are not likely to provide sustained benefits to free-swimming calves until they approach adult size, coordination, and swimming capacity, because the calves will still tire more quickly than their associated adults. In the case of tuna purse-seine set evasion, sustained use of these swimming patterns may not be employed even by adults because these behaviors become less efficient as swim speed increases (Weihs, 2002). Video studies of swimming behaviors of adult *Tursiops* have shown that burst and coast periods decrease with increasing drag and cease altogether if the drag is large (Skrovan et al., 1999). In a study of dolphin gaits, an adult *Tursiops* experiencing increased drag due to an instrument pack did not use burst and coast propulsion during horizontal swimming speeds and depths at which four other adult *Tursiops* (without instrument packs) did employ short periods of burst and coast swimming. Even animals swimming without instruments at 1.5–3.7 m/s incorporated only short periods of burst and coast, and glide periods rarely exceeded 2 seconds. At the speeds characteristic of tuna purse-seine sets, dolphins tend to swim steadily or employ burst-leap-coast swimming behaviors (Weihs, 2002, Au and Weihs, 1980). With their smaller power production capacities, calves will need to shift into leap-burst-coast mode at slower speeds than will adults (Weihs, 2002), and again will tire more quickly.

A potential shortcoming of the results presented in the present study is that the model produces absolute values from single calculations, without any associated statistics or sensitivity analyses. It is more likely that a range of values for morphological, physiological and behavioral characteristics occurs within real spotted dolphin populations in the ETP, so that a range of responses is much more likely than a single response for a given size, swimming speed, and duration of chase. Lack of statistical and sensitivity analyses can be a problem where responses tend to be subtle and therefore difficult to discern. However, the model results presented in this study with respect to estimated size-related differences in power production capacities of spotted dolphins in the ETP are far from subtle, and model results are reasonably similar to energy measures derived from observations on real dolphins indicating that these model results are not unrealistic. In general, results presented here imply that older calves may be able to swim unassisted as fast and for as long as their associated adults during or after most sets (or during and after most sets) by tuna purse-seine vessels in the ETP. The markedly smaller energy production

capacities of younger calves, particularly neonates and infants, compared to adults appears to be a reasonable factor contributing to mother-calf separation during or after sets by tuna vessels in the ETP.

Management and research implications

From these observations, it appears that energetic limitations may contribute significantly to the observed calf deficit in the retrieved purse-seine by facilitating mother-calf separation during purse-seine set activity. Separation risk appears to increase strongly with decreasing calf size and with increased speed and duration of evasion-related swimming. If separation is prolonged, subsequent mortality of milk-dependent calves appears likely due to predation or starvation because adoption by a surrogate mother is unlikely in the ETP (Edwards[1]). Examination of existing aerial photographs of spotted dolphins attempting to evade helicopters and research vessels, as well as directed future experiments in which aerial observations are conducted specifically to identify and monitor mother-calf pairs over time during various chase scenarios, would be very helpful in evaluating the extent to which calf size effects predicted here occur during relatively high-speed evasion behaviors by ETP spotted dolphin schools. Estimation of the rate at which dolphins of various ages are likely to encounter tuna purse-seine sets will be another important factor in relating the results of this analysis to potential calf loss during purse-seine sets.

Assuming that power limitations are a significant factor in calf loss during evasion of tuna purse-seine sets, management strategies that could be implemented to minimize calf loss include 1) avoiding setting on schools that contain calves, particularly young calves, 2) minimizing the speed or duration of chase, and 3) minimizing the length of time dolphins are retained in the net so that mothers and calves separated during the set may reunite more quickly, if possible. Minimizing the length of time in the net is already a desired fishery goal, related to minimizing cost and the potential for dolphin mortality in the net. Minimizing chase duration is also already a desired fishery goal, because shorter chases are both less expensive and tend to be more successful. Minimizing chase speed is not a realistic goal because it would likely lead to the escape of the dolphins and the targeted tuna. Thus, the only potential improvement that might be made under current conditions (i.e., while setting on dolphin calves is permitted) would be to concentrate effort on identifying and avoiding dolphin schools with calves, presumably by scrutinizing the school from the vessel's helicopter prior to initiating a set. This may or may not be possible, depending on the ability of observers in helicopters to spot calves from the air.

Given the model results presented here, it appears that further research and perhaps management actions should be implemented to better understand and reduce the risk of separation of mothers and calves during sets by tuna purse-seiners in the ETP.

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