Karen Pryor and Ingrid Kang on the bridge of the tuna purse seiner Queen Mary, *1500 miles from land in the Eastern tropical Pacific, with speedboats keeping pace off the bow.*

CHAPTER NINE

Social Structure in Spotted Dolphins *(Stenella attenuata)* in the Tuna Purse Seine Fishery in the Eastern Tropical Pacific.

***by Karen Pryor and Ingrid Kang Shallenberger*[1,2]**

Introduction

Along the west coast of South America, reaching north from the Galapagos and 1,500 miles out toward Tahiti, lies a million-square-mile area of ocean known as the eastern tropical Pacific, or ETP. A peculiarity of the ETP is that while in this region the

[1]Reprinted with permission from *Dolphin Societies: Discoveries and Puzzles,* K. Pryor and K.S. Norris, Eds., University of California Press, 1991.

[2]This study was undertaken as a portion of the 1979 Dedicated Vessel Program, under the joint direction of the Marine Mammal Commission, the National Marine Fisheries Service, and the U.S. Tuna Foundation. The research was supported by National Marine Fisheries Service Contract No. 01-78-027-1043.

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sea floor is thousands of meters below, the warm, productive surface water is shallow, sometimes only 10 m deep. This surface layer, in which temperatures are typically greater than 24.5°C, is cut off from the water beneath by a thermocline, a "floor" or discontinuity, below which the water is not only colder but higher in salinity and unusually low in oxygen. Therefore, the sea life that in other tropical oceans is often spread through a much deeper water column, is here concentrated in the shallow surface layer (Au et al. 1979). Vertical discontinuities and confluences of water bodies along and within this surface layer attract enormous concentrations of prey and predator, most conspicuously, dolphins, tuna, and tuna fishing vessels.

Schools of dolphins in the ETP, principally of the genus *Stenella,* are often accompanied by schools of yellowfin *(Thunnus albicares)* and skip-jack tuna *(Katsuwonus pelamis)*. The association, which appears to be involuntary on the part of the dolphins, is probably due to the behavior of the tuna, which tend to join up with dolphin schools in the daylight hours. Presumably, this increases their foraging efficiency; while dolphins do not eat everything tuna eat (e.g., pelagic portunid crabs), tuna eat dolphin prey (Perrin et al. 1973). The association may also include several species of seabirds, sharks, and other fast-swimming predators such as marlin. Such mixed-species foraging groups are a phenomenon related to areas of rich but patchy resources (McArthur and Pianka 1966).

Tuna fishermen, using hooks and poles, had long known that the "porpoise," as they call all species of small cetaceans, could be an indicator of the presence of tuna. After World War II, the American tuna fleet, based in San Diego, developed techniques for using large purse seine nets to surround tuna and dolphins both, gathering in the tuna and releasing the dolphins. Initially, dolphin mortality was extremely high: pelagic animals are not behaviorally adapted to avoiding or surmounting obstacles, and the nets were fatal to hundreds of thousands (Pryor and Norris 1978).

Although the ETP dolphin populations were postulated to consist of many millions, they could not sustain this kind of loss for long (Perrin et al. 1982). Techniques were developed and adopted by the industry for safe release of encircled dolphins; the federal government established detailed regulations governing the fishing procedure; and by 1982, mortality caused by the U.S. fleet dropped to biologically acceptable levels (unfortunately, annual mortality caused by domestic and foreign fleets had climbed again to an estimated 120,000 by 1986). Meanwhile, the National Marine Fisheries Service undertook extensive research into the biology of the dolphins. In 1978, a consortium was formed between the U.S. tuna industry, the National Marine Fisheries Service, and other interested groups to use a tuna purse-seining vessel exclusively for scientific research on the tuna-porpoise problem. The *Elizabeth C.J.*, a large seiner, was chartered experimentally. Then a middle-sized seiner, the *Queen Mary,* (150 ft., 500-ton capacity) was refitted to accommodate up to six scientists for a full year of research during 1979, the "Year of the Dedicated Vessel." Six research voyages of four to six weeks each were accomplished in the eastern tropical Pacific. During these voyages, the vessel located and encircled schools of tuna and dolphins, in the usual manner called fishing "on porpoise," but scientific tasks and requirements took precedence over fishing success.

In January 1979, the authors contracted with the Southwest Fisheries Center to join one voyage of the Dedicated Vessel to study the behavior of encircled dolphins by making underwater observations within the net. The principal species of dolphins involved in the tuna fishery are the Pacific spotted dolphin (*Stenella attenuata*) and the spinner dolphin (*Stenella longirostris,* so-called for its behavior of leaping into the air and spinning on its long axis). Spotted and spinner dolphins have been maintained successfully in captivity only at Sea Life Park in Hawaii. Karen Pryor was head trainer and curator at this oceanarium from before its opening, in 1963, until 1971. Ingrid Kang Shallenberger was second-in-command from 1965 until 1971 and was head trainer and curator from 1971 until 1990. Both authors were also trained as ethologists, Shallenberger at the University of Stockholm and the University of Washington, Pryor at Cornell, New York University, and Rutgers University.

Between 1963 and 1979, the authors personally adapted to captivity, maintained, and trained many individuals of several pelagic species of cetaceans, including over forty spinner and spotted dolphins (Pryor 1973, 1975). Spinner and spotted dolphins were maintained as performing and research animals, in groups of two to eight individuals, throughout this period.

Training as a tool for the ethologist

George Schaller has been widely quoted as saying that to describe the behavior of any species of animals in the field, one needs "5,000-hour eyeballs," meaning that it takes considerable looking before one can understand or indeed even notice the crucial but often small events that constitute social communication. If this is true of terrestrial animals, whose signals—a growl, a threatening posture—are often at least partly familiar to us, it is much truer of the cetaceans. For example, the lay literature abounds with egregious accounts of dolphins "laughing," "smiling," and "acting playful," when what the author witnessed were the gaped jaw and head movements that in dolphins signify aggressive intent (Nollman 1987).

We had, individually, considerably more than Schaller's requisite 5,000 hours of looking at the behavior of spinner and spotted dolphins as well as several other species (Pryor 1973, 1975; Defran and Pryor 1980). Furthermore, we had looked at these animals from the special viewpoint of the trainer.[3] Training animals in a group, as we did with spinner and spotted dolphins, provides excellent opportunities for learning about social relationships and the nature of social signaling (Lorenz 1975; Pryor 1981, 1987). For example, we dolphin trainers have a straightforward technique for identifying an animal's place in the dominance hierarchy: if a fish falls between two dolphins, who gets it? The dominant animal (barring the rare gesture: a dominant male spotted dolphin at Sea Life Park, named Hoku, sometimes deliberately gave a fish to his female con-specific, Kiko; see Pryor 1975).

[3]For detailed discussions of dolphin training methods, see Karen Pryor's *Lads Before the Wind* (Harper & Row, 1975; Sunshine Books, 1987) and *Don't Shoot the Dog.* (Bantam Books, 1985).

Knowledge of the dominance hierarchy is of practical importance to the trainer.[4] It also opens a window to the ethologist. Knowing which animal in a pair or group is dominant, one can then learn to identify aggressive and submissive displays and other indications of relationships, often in rather fine detail. As an example, a common threat gesture in spotted dolphins (not seen in bottlenose dolphins) is a rapid nodding of the head, sometimes with jaws open, and sometimes accompanied by burst-pulse sounds (dubbed "snitting" by Sea Life Park trainers). The male spotted dolphin mentioned above, Hoku, routinely used this threat to force an adult female false killer whale *(Pseudorca crassidens)* ten times his weight to give him some of her fish. When we looked at wild spotted dolphins underwater, at sea, and saw groups of males "snitting" at each other, we knew this to be an exchange of threats, not, say, affiliative greetings, however much it might have looked like "nodding and smiling."

Social organization in captivity

Studying our captive animals, we learned to identify many individual behavioral events, from postures and gestures to stylized bubble releases, and to recognize their significance at least in part (Defran and Pryor 1980, Pryor and Kang 1980). Of major importance in our captive school was the dominance hierarchy, to which the animals devoted much time. Behavioral indications of this hierarchy are many: we have observed that the dominant animal often swims slightly in advance of the others, or above them; subordinate animals in a group tend to swim closer to equals and a bit farther away (wider interanimal distance) from animals dominant to them; subordinate animals move aside from dominant animals and can be displaced from feeding or work stations. Gregory Bateson found that our *Stenella* group sometimes rested in "rank order," with the superior animals cruising at the surface and the most subordinate at the bottom of the school (Bateson 1974). He also observed that changes in the hierarchy (introduc-

[4]All too often, novice trainers dismiss a nonperforming animal as "untrainable" when it is merely at the bottom of the hierarchy, being prevented from earning reinforcement by more dominant animals. These animals may actually go hungry if not given special attention.

tion of new animals) or transgressions by subordinates (stealing fish, for example) sometimes produced open conflict, blows, and ramming attacks that could be quite severe.

In any established group of captive dolphins, a network of affiliative connections is, as it were, thrown across the dominance hierarchy. Affiliative relationships can be expressed by unison swimming and respiration; by close interanimal distances; by frequency and duration of swimming together; and most conspicuously, by contact, especially by animals petting, touching, or rubbing each other with fins, flukes, rostrum, or body (Defran and Pryor 1980, Norris et al., 1985). We observed repeatedly that in the Sea Life Park *Stenella* group, individuals newly introduced into the school were not included in affiliative exchanges. In fact, a stranger, unless highly dominant, was likely to be shunned and avoided for days or even weeks before becoming part of the affiliative network (Defran and Pryor 1980; Pryor 1973, 1975).

Research goals

Of primary interest to the National Marine Fisheries Service in our research at sea were evidences of stress that might or might not be evinced by encircled animals. Their hypothesis was that animals encircled by tuna nets might be undergoing hazardous levels of stress, perhaps leading to mortalities additional to those observed during the fishing process.

Of primary interest to us, however, was the question of social organization. At sea, these species can be found in aggregations of hundreds or even thousands of animals. It seemed likely that some sort of finer-grained social organization continues to be maintained in these large schools. Subgroups of two to perhaps six or eight animals or so could sometimes be seen even in aerial photographs of these aggregations. But what might the nature of those subgroups be? And how might they relate to each other? The brief confinement of whole schools of these ever-traveling pelagic animals in a purse seine was an unprecedented opportunity for behavioral observation. We hoped our familiarity with the interactions between individual captive animals would help us investigate the next step up the ladder of social behavior:

the nature of the subgroups and the interactions and relationships between them.

METHODS

The fishing method

A tuna purse seiner cruises until a school of dolphins is sighted (some larger vessels carry helicopters to spot schools). Several speedboats are then lowered overboard which chase, turn, and herd the dolphins, like cattle, back toward the ship. Tuna accompanying the school usually remain with it during this process. The captain directs the herding by radio from the top of the mast.

The seine net, which is 200 m deep and sometimes nearly a mile long, is stacked on the back deck of the ship, fan-folded so that it will run into the water smoothly. The location of winches and other gear requires the net to be set on the left or port side of the vessel. When the dolphins reach the port side of the ship, a heavy open boat, the net skiff, is dropped off the stern of the vessel, pulling one end of the seine net after it. The fishing vessel then travels in a circle until the net is paid out, or set, around the animals.

Once the circle of net is complete, a cable running through steel rings around the bottom of the net is drawn tight, thus pursing or closing the net underwater. The top of the net, or cork line, is kept open in a circle, by the way in which the net is set relative to the wind and current and if necessary, by speedboats pulling the cork line outward; this allows the dolphins room to swim and breathe. The vessel is now temporarily immobilized by the inertia of the net in the water.

The dolphins usually cluster at or near the water surface and as far from the vessel as possible. The tuna, meanwhile, move constantly about in the net throughout the time the net is in the water. Unlike the object-shy dolphins, if the tuna find a hole in the net, they will rapidly escape.

The net is then "rolled," or pulled back aboard the vessel, through a power winch at the top of the boom. Crew members

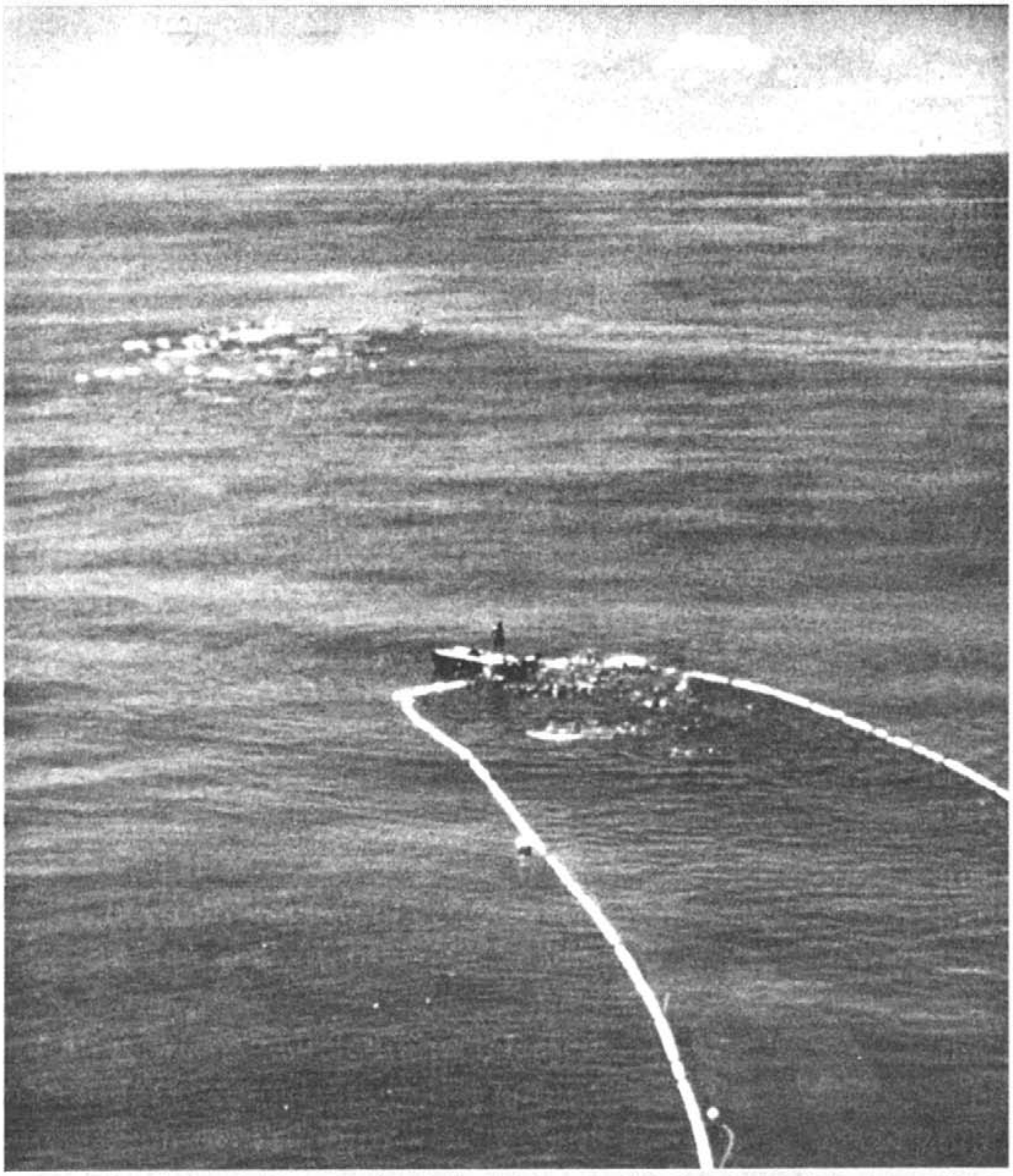

Fig. 1. Taken from the mast of the fishing vessel, this photograph shows the completion of the backdown procedure. The vessel has pulled the net until the cork lines at the far end sank, passing under the dolphins. White splashes in the distance are made by the released dolphins. A school of tuna "boil" inside the cork line, which is now at the surface again. The speedboat driver is examining the area to make sure all dolphins have been released. (Photo courtesy of the United States Tuna Foundation.)

restack the net below the winch on the deck. When approximately three-quarters of the net is back aboard, the vessel starts its engines and begins backing up, hauling the remaining bowl-shaped net through the water. The net elongates, and in due course, the cork line in the portion of the net farthest from the boat is pulled underwater. This area of the net is lined with special fine-meshed net, the "Medina panel," which prevents accidental entanglement of dolphin fins or beaks. When the cork line sinks, the backward movement of the vessel slips the net out from under the dolphins, releasing them unharmed. (Figure 1.) Many dolphins appear to have learned to expect this procedure, called "backing down;" they wait quietly in the backdown area and swim out or allow themselves to be sluiced out.

When all the dolphins have been released, the remainder of the net is rolled aboard. The tuna are "sacked up" in the last of the net and scooped aboard the vessel to be frozen in tanks of brine in the hold. Sharks and other unwanted animals in the catch are disposed of overboard. Cleaning and other processing of the fish is done later by canneries onshore. A single set of the net may take two or more hours to complete, requires a crew of about twenty, and may catch no tuna, a few fish, or 30 tons or more (Orbach 1977).

Investigators' procedures during a set

The fishing procedure allowed a period of one to two hours, during pursing and rolling of the net, when the seiner was stationary and underwater observations were possible. Once the seiner had halted and the two ends of the net had been drawn together, we lowered an inflatable, outboard-powered rubber raft over the side, climbed into it, and crossed the cork line into the net. It was usually possible to approach the school very closely by moving slowly and by flanking the school rather than heading right at it. A third member of the scientific party, Phillippe Vergne, launched and handled the raft for us and dove with us as shark guard. First mate Ralph Silva, Jr., also dove with us when duties permitted, and other members of the scientific party sometimes assisted us from the surface. (Fig. 2.)

We then entered the water using snorkeling gear and collected data and photographs and made observations until backdown was about to begin. The clarity of the water and the approachability of the dolphins made SCUBA gear unnecessary. The water temperature, approximately 80°F, was not a limitation on observation time. (Fig. 3.)

Fig. 2. Investigators make observations in a school of spotted dolphins, near the corkline. One shark guard swims behind them while another watches from the surface.

Fig.3. Ingrid Kang Shallenberger taking data underwater, using a plastic slate and ordinary lead pencils. The pair of spotted dolphins directly behind her are "columning," or diving vertically after surfacing to breathe. Bubbles, at left, were released by a whistling animal.

During backdown, as the dolphins were released from the net, we tied the raft to the cork line in the backdown area, next to the release point. We continued observations underwater until ordered into the raft (to avoid being sluiced out into open sea; Pryor did get backed out of the net once). We then returned to the vessel, transferred and recorded our data and observations, and prepared for the next set.[5]

Species, age, and sex recognition

Spotted and spinner dolphins in the ETP are easily separated by coloration, spotters having a dark cape and in adult animals, light and dark speckles or spots, while spinners are unspotted and either all gray or gray with white bellies. Also, spotted dolphins have falcate or sickle-shaped dorsal fins, and spinner dolphins have triangular fins, making them easily separable even in silhouette or at a distance.

Conveniently for the investigator, spotted dolphins change their color pattern as they age. William Perrin, studying specimens taken during tuna fishing, divided spotted dolphins into five maturation stages, based on size and on the degree of spotting: neonatal (gray with ivory belly), two-toned (dark gray above, light gray below), speckled (with a few dark ventral spots), mottled (spotted all over, with spots overlapping below), and fused (heavily spotted, with a black mask, and spots below fused and faded; Perrin 1969). We divided the spotted dolphins in the nets, by size, into five age groups—neonate, calf, juvenile, young adult, and large or fused-pattern adult—that corresponded to the differences in coloration as defined by Perrin (Table 1). While transitional animals undoubtedly existed, in practice, we found we could readily assign animals to their age groups based on Perrin's five color pattern groups and on size relative to nearby animals.

[5]Care must be taken if the tuna come into the backdown area while the dolphins are being released. Speedboat drivers are assigned to signal if the tuna head toward the opening, whereupon the vessel halts temporarily and the cork lines pop to the surface until the tuna swim away. Crew members also assist any dolphins that may be in difficulties and inspect the net underwater for stragglers.

*Table 1. Color Pattern Changes with Age in Pacific Spotted Dolphins**

Age group	*Size*	*Coloration*	*Pattern type*
Neonate 1–2 weeks	80–110 cm	gray and ivory	neonatal
Calf 2 weeks–1 year or 3/4 adult	100–160 cm	dark gray above, light gray below	"two-tone"
Juvenile 1–3 years	150–180 cm	dark above, light below with a few ventral spots	"speckled"
Young adult 3–6 years	160–190 cm	spotted all over	"mottled"
Large adult 6 or 7+ years	170–200 cm	black mask, heavily spotted, spots fused and faded below	"fused"

*Age estimates are based on sizes and color patterns of captive spotted dolphins of known ages. Size estimates are adapted from Perrin *et al.,* 1976, based on measurements of animals killed during fishing. Pattern type is derived from Perrin, 1969.

Sex identification was usually possible in large adult spotted dolphins. In fused-pattern adults, the sexes are dimorphic: the most conspicuous difference is that males have a postanal bulge, or keel, and a thickened caudal peduncle (Perrin 1975). Since this keel is more pronounced in ETP spotted dolphins than in Hawaiian spotted dolphins, the keel on large male dolphins in the nets seemed quite conspicuous to our eyes; it is not, however, as conspicuous as the keel in large male ETP spinners, which is almost grotesque. Nevertheless, to verify that the individuals we identified as males were indeed males, we tested our assumptions on a group of fused-pattern animals that was resting at the surface (rafting) by verbally agreeing on the presumed sex of an animal and then taking turns visually checking its genital area. Those with postanal keels were indeed males, and those without were females. In addition, adult animals closely associated with a calf were usually assumed to be female, based on behavior.

Solitary animals and younger animals could not be sexed unless circumstances provided a close look at the genital area (males have two visible swellings, at the anus and penis, while females have a single genital slit, flanked, in adults, by two small mammary slits). We never succeeded in sexing a calf or a juvenile.

Recording data

We recorded data underwater on lightly sanded plastic slates made of 3/16-inch Lucite, cut into 9-inch-by-12-inch sheets and painted white on the reverse side to improve legibility (the white surface was then painted over again with black to reduce visibility to sharks). The writing tools were ordinary No. 2 soft lead pencils. Each slate was drilled with two 1/4-inch holes, one for a string to tether the slate to the investigator, and one to tether the pencil to the slate. About twenty extra pencils and slates were carried in the raft for each dive.

We used Focal Animal Sampling as one data collection method (Altmann 1974). Based on our experience with captive animals,

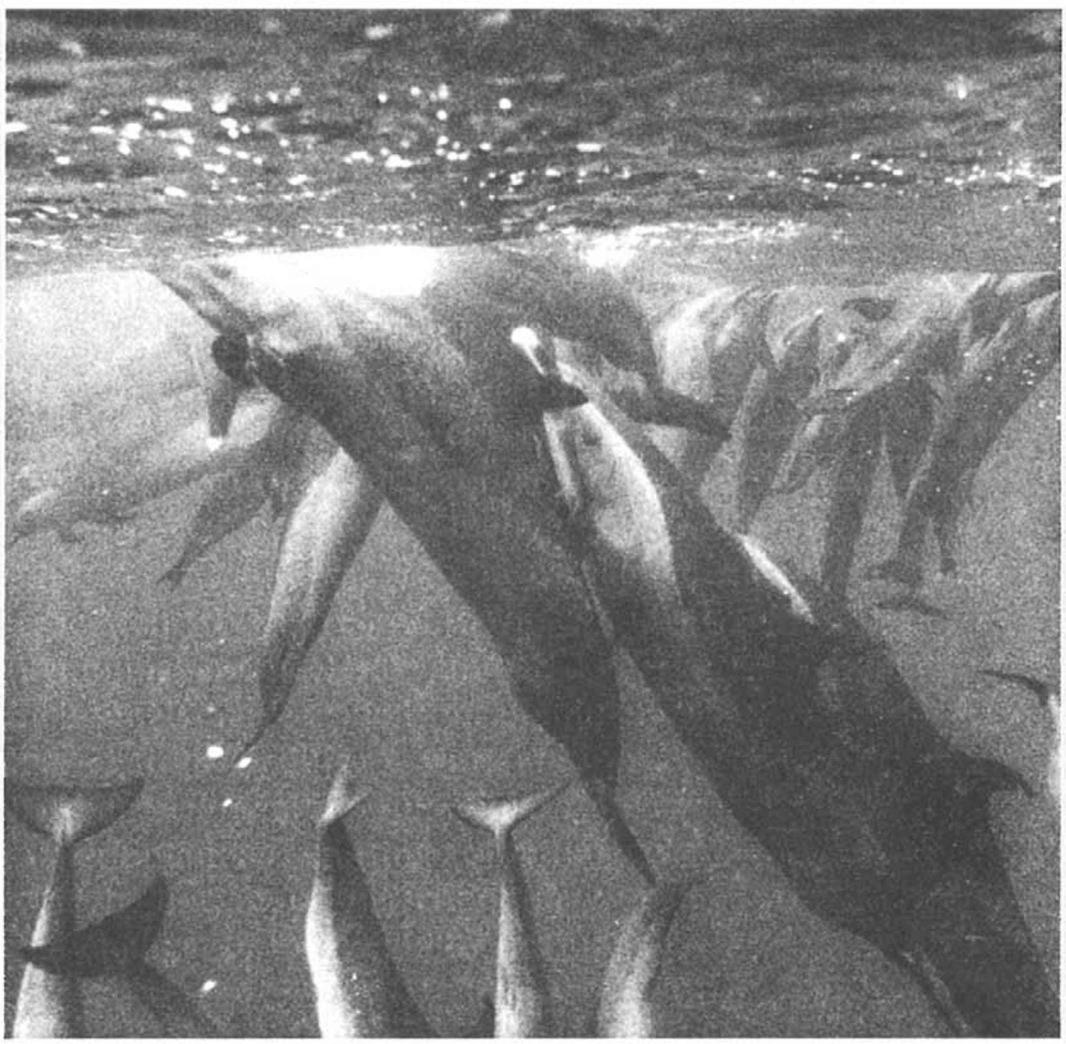

Fig. 4. a. Surfacing to breathe, two fused-pattern Pacific spotted dolphins exhibit the postanal keels of mature males. The third animal accompanying them is an adult female. Rafting animals are visible in the background.

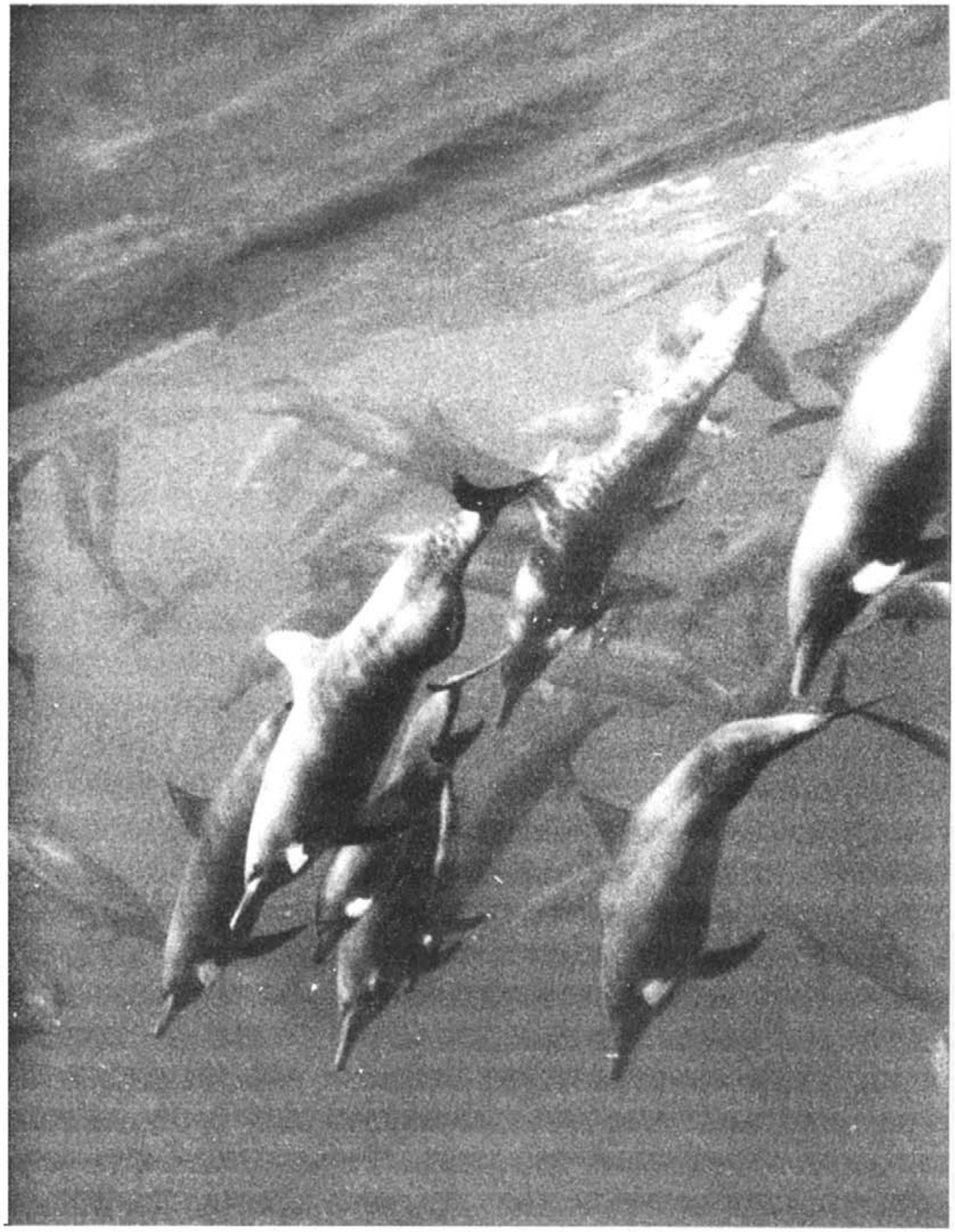

Fig. 4. b. In a group of spinner dolphins of mixed ages and sexes, the nearest animal shows the "backward" dorsal fin and exaggerated postanal keel of mature male spinners in the eastern tropical Pacific.

we selected five minutes as a representative sample of an animal's activity when viewed underwater. Insofar as possible, we spread our focal animal selection over both sexes, all age groups, and over active, inactive, solitary, and grouped animals. To record focal animal samples without taking our eyes off the animals, we listed events vertically, moving the hand down the edge of the slate after each entry. If two animals were interacting or swimming in unison, we could sometimes watch two focal animals at a time.

Each set also provided a wealth of observational data other than the behavior of focal animals. We tape recorded our other observations and discussion immediately on returning to the ship after each set. Written field notes and taped observations were also made whenever possible during the chase and the early part of the set, from shipboard on sets in which we did not dive, and during and after backdown. Weather, location, time at start of chase, and shipboard school size estimates were taken from the ship's log.

Recognition and labeling of behavior

Before going to sea, we constructed a "dictionary" of all the behavioral events known by us to occur in spotted dolphins in captivity and the social or communicative significance of these events when known (based on a previous survey of senior trainers: Defran and Pryor 1980). We used standard terms where they existed and coined terms if they did not, especially for behavior specific to these species, such as certain leaps and aggressive displays. Each behavior was assigned a two-letter, mnemonic code (BR for "breathe," DV for "dive," TS for "tailslap," etc.) to facilitate data taking underwater and subsequent computer analysis of focal animal samples. We augmented the dictionary and codes in the field as needed (Pryor and Kang 1980.)

Sets made

Between July 23 and August 13, 1978, the M.V. *Queen Mary* made seventeen sets of the net in the eastern tropical Pacific. (Fig. 5.) The investigators dove in the net on fourteen sets (omitting two night sets and one set in which sharks were visible

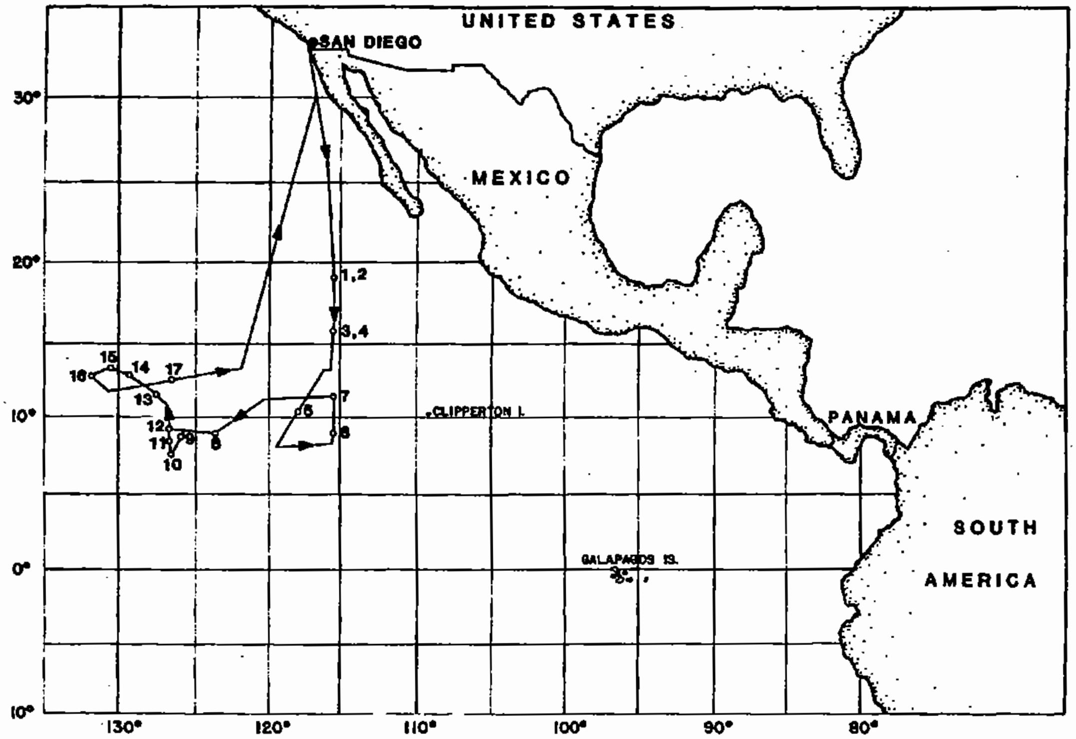

FIGURE 1: CRUISE TRACK AND SET LOCATIONS

Fig. 5. Cruise track and set locations.

in the net). In two more sets, data could not be collected under water because of rough seas, though the attempt was made. Details of each set are given in Table 2.

A total of over 4,000 dolphins were encircled and released during the voyage; three mortalities occurred. Spotted dolphins were present in all seventeen sets; spinner dolphins were present only in nine sets. A total of 119 focal animal samples were completed (table 3).

Table 2. Set-by-Set Overview

Set	Spinners present	School size	Time (at chase start)	Agitation levels[a]	Social activity[b]
1		23	12:36 P.M.	1,1,2	III
2		60	3:30 P.M.	2,2,4	II
3		60+	9:45 A.M.	1,1,1	III
4		45	1:00 P.M.	1,1,1	II
5	✓	180	7:12 A.M.	1,1,3	III
6		300+	4:58 P.M.	4,4,4–5	II
7	✓	300–500	2:21 P.M.	2,3,3	—
8	✓	—	11:19 A.M.	2,1,3	—
9	✓	300+	11:22 AM.	1,1,2–3	III
10	✓	500+	11:18 A.M.	1,1,2	IV
11	✓	100	6:23 P.M.	2,1,2	—
12	✓	220	7:59 A.M.	2,1,2	IV
13		120	12:51 P.M.	1,1,2	—
14	✓	350	9:15 A.M.	1,1,2	III
15		50–100	12:37 P.M.	2,3,3	—
16	✓	1000	4:40 P.M.	3,3,3	—
17		450+	7:45 A.M.	3,3,2	III

[a]Types of surface activity during pursuing, rolling, and backdown. See text for details.
[b]Degree of social interaction underwater. See text.

Table 3. Focal Animal Samples

	Spotted Dolphins	Spinner Dolphins
Adult male	26	13
Adult female	16	2
Adult, sex unknown	5	1
Juvenile	23	—
Calf	5	—
Females and calves in pairs	22	6

FINDINGS AND DISCUSSION

Dolphin aggregations underwater

Excellent visibility prevailed on most dives during our cruise (30-75 m, gauged by the distance at which the net walls and floor were visible). We could often view the aggregation of animals as a whole, at least until the crowded conditions before backdown.

We follow Norris in defining a school as any aggregation of animals that swim together as a unit, separated from other aggregations (Norris and Dohl 1980). If spotted and spinner schools were both present, they occupied the same general area in the net but did not mingle; no social interactions were observed between species. The aggregations of each species in the net might be further divided into several separate groups containing from 20+ to 100+ individuals. For example, Set 3 initially contained three groups of spotted dolphins that stayed separate for half an hour. Set 9 contained two separate groups of spotted dolphins, a cluster of about 30 mostly stationary animals and another of about 60 actively swimming animals, as well as three separate groups of spinners. In these multiple-school sets, the groups kept to themselves as neatly as if they were contained in invisible plastic bags, what Norris aptly calls "the school envelope" (Norris et al. 1985).

Once within the net, spinners have been reported to group themselves in a circle, with animals in the middle engaged in "rafting" (floating in a somewhat vertical posture near or at the surface) and more active animals moving protectively in a "ring of aggression" around the central group—what one might call the musk-ox model. But spotted dolphins did not, in our underwater observations, appear to arrange themselves in this manner. In nine of the eleven sets in which we could see the whole school, spotted dolphins were arranged in a truncated cone (likened by Norris to an upside down tea cup). The top of the cone, the smallest portion, was the area at the surface, where rafting animals, if present, were indeed gathered; rafting animals might be of any age, including large adult males, except neonates. Here, also, other animals in the school surfaced to breathe.

Meanwhile, most of the rest of the group, including large and small adults and juveniles, circled and cruised below this apex, in a pyramidal mass that might extend 20 or more m downward and widen to 30 m or more at the base. In the center of this mass, a column of animals were moving upward and downward vertically, rising to breathe and diving again in a column, and then joining the animals cruising horizontally at various depths.[6]

Rather than staying in the middle of the school , a la musk-ox, females with calves under one-year size tended to remain, during rolling and pursing of the net, at the outside perimeter of the bottom of the mass of animals. Female-calf pairs on which focal animal samples were taken in this location surfaced to breathe, of course, but then returned to the bottom rim of the school, staying, as it were, out of the crowds.

Fear and stress

While social organization and the role of males in spotted dolphin schools is our principal topic, it seems appropriate to discuss, first, the question of fear and stress in the nets, so as to respond to the not uncommon supposition that one could observe little or no normal social behavior in such frightening circumstances.

When each dolphin school was finally driven into the net by the pursuing speedboats, the animals were certainly agitated and, if the chase had been a long one, probably severely fatigued. All schools, when set on, took up a similar position in the net, described as a "node" of minimum fear, as far from the ship as possible without coming into actual contact with the net (Norris et al. 1978). Whether aggregation in the net consisted of a single group or of two or more separate groups, all the animals

[6]The picture was very different in spinners (present in 9 of 17 sets), which seldom rafted and which surfaced to breathe in long, horizontal arcs rather than vertical columns. Spinners also moved faster and over a wider area throughout the sets (Pryor and Kang 1980).

We saw only two neonates, identifiable by visible fetal folds, on this cruise; in both cases, the mother and neonate, viewed repeatedly by both observers during the set, were moving rapidly, continuously and well beyond the perimeter of the school.

responded to any alarming stimulus, such as a speedboat motor, by moving away.

At the beginning of some sets (9 out of 17), we saw signs of agitation at the surface, such as headslaps, tailslaps, thrashing, and "bunching" (animals traveling rapidly, grouped tightly together, and breathing in sharp puffs). In captive *Stenella* spp., these are all signs of fear, stress, excitement, or frustration (Pryor 1973, 1975; Norris and Dohl 1980). In most sets, these agonistic displays diminished partially or entirely during pursing and rolling but sometimes increased again just prior to backdown (Table 2).

Presence or absence of behavioral events can be used as an index of the state of an organism, as is done in many physiological assessment scales (King-Thomas and Hacker 1987). Norris and his associates observed that some types of surface behavior in spinner dolphins increased in frequency prior to the school's traveling from a rest area to offshore feeding sites. Ranking of these behaviors enabled them to predict when the departure was imminent (Norris et al. 1985).

Similarly, we created an agitation scale, using surface-visible behavior related to fear and stress in *Stenella* in captivity, to rank the evidences of stress in the schools (Table 4). We rated each school on the Agitation Scale three times, at the beginning, middle, and end of the set (Pryor and Kang 1980). Schools varied from being highly agitated throughout (Set 6) to being very calm, with no surface displays even at backdown (Sets 3 and 4; see Table 2).

Table 4. Agitation Levels

Level 1:	No aerial behavior, Animals moving quietly.
Level 2:	Rapid swimming; rolling or leaping across surface ("porpoising"); loud exhalations ("chuffing").
Level 3:	Level 2 plus some headlaps, tailslaps,rostrums in air.
Level 4:	Level 2 and 3 activity plus fluking, tailwaves, sideswipes, charging; whistling audible in air.
Level 5:	Level 2, 3, and 4 activity plus panicky dashing about, charging the net, struggling.

Except for the animals in Set 6, we saw no panicky dashing about or blundering into the nets, scenes that had been described by many observers in previous years. We also saw no "sleepers," animals lying on the bottom of the backdown channel (Norris et al. 1978), though we were able to scan the backdown area through face masks in most sets. It is our surmise that this difference was a result of experience on the part of the animals we happened to observe. There seems to be no doubt that some dolphins in the ETP have learned what to expect when set on and can develop accommodating behavior (Stuntz and Perrin 1979). We think it probable that those schools showing the most agitation were those with the least experience; highly agitated schools also showed the most incompetence at backdown, going out of the net sideways, swimming back into the net, and so on, whereas calmer schools sometimes left the net very efficiently, some individuals even slithering over the cork lines before they sank.

As the intensity of fear and agitation varied from school to school, so did evidences of fear and stress in individuals. Some cruised slowly as captive animals do when resting or engaged in social activity; others showed signs of stress, such as sinking briefly or whistling repeatedly. One individual, a large adult male, caught our eye by lashing out in all directions for about 10 seconds. The other animals gave him a wide berth (this was the only event of its kind that we observed in 11 underwater sets).

Rafting

The behavior of rafting, or hanging at the surface with just the blowhole exposed, was recorded in animals of both sexes and in all age groups except neonates and small calves (which, according to Sea Life Park staff, never lie still at the surface in captivity, either). Percentage of animals rafting varied from none to over half the animals in a given set; there was no correlation between agitation levels and the percentage of animals rafting.

It is our guess that rafting may combine elements of both fear and adaptation in individually varying amounts. Nearby rafting animals appeared alert and could be seen inspecting us and our equipment attentively; yet in several sets, we swam among rafting animals, touched them, and even moved them about. At Sea Life Park, newly captured *Stenella* specimens are often extremely passive, allowing themselves to be caught, force-fed, and even inoculated without resistance, until they learn to feed, whereupon they become hard to catch again. Some rafting animals may be exhibiting this "learned helplessness." However, in captivity, spotted dolphins that are not otherwise occupied sometimes loaf or rest in the rafting position. It is possible that some animals were doing so by choice. And some animals may have been rafting simply in mimicry of others. One focal animal case describes a juvenile repeatedly nudging its rafting mother (a play invitation). When the female gaped (a threat display), the calf finally gave up and rafted beside her.

Social activity levels

The *Stenella* school at Sea Life Park tended to engage in abundant social interaction in intermittent bouts, alternating with rest periods (in spinners, aerial displays often occurred at night and were reported by night watchmen). Bouts of leaping and social interaction in the dusky dolphin *(Lagenorhynchus obscurus)* commonly occur following feeding episodes (Würsig and Würsig 1981). The social activity observed by us in spotted dolphins in the net also appeared to be occurring in bouts. Either a lot was going on or very little. Whatever the state of socializing in a particular set happened to be, that level of activity remained constant throughout the set until just before backdown.

While actions of individual animals—leaps, tailslaps, and so on—can be seen from the surface, one needs to be under water to see and record the small but significant interactions between two or more animals, such as a pectoral pat or a gape and the reaction to it. Therefore, we can report on spotted dolphin social activity only in the eleven sets we observed underwater. We created a scale for assessment of the intensity of social activity, similar to our scale for agitation levels, as shown in table 5.

In three sets, social activity was at a minimum. In six sets, social activity was commonplace. The remaining two sets were very high in social activity. The social activity level for each set seen underwater is given in Table 2.

Table 5. Social Activity Levels

Level I:	No apparent social activity; animals *not* in visible subgroups.
Level II:	Animals in subgroups, rafting, columning, and/or cruising. Social interactions not conspicuous.
Level III:	Level II activity plus social interaction between individuals, such as affiliative exchanges, aggressive display, and adult-calf play.
Level IV:	Level II and III activity, plus extensive social interactions of long duration or involving several animals.

Social activity levels, agitation levels, and time of day

If spotted dolphins feed at dawn and dusk, and if social activity normally follows feeding as in the dusky dolphin, we might expect time of day to affect social activity levels. All sets observed underwater before 1:00 P.M. were ranked for social activity at Levels III or IV; the two sets observed after 1:00 P.M. were low (Level II) in social activity. Given our limited data, there is nevertheless a significant visible trend toward social activity in the morning. (Fig. 6a.) We also compared agitation levels for all seventeen sets to time of day and to size of school and found a random scatter and no correlation. (Fig. 6b.)

It has been suggested that some of what we considered to be normal social activity, particularly male-male aggression, was a by-product of fear and stress. We compared social activity levels to agitation levels for the eleven sets observed underwater. We found a highly significant inverse correlation of social activity to agitation levels: sets with higher levels of agitation showed less incidence and less variety of social activity; sets with high levels of social interaction (including male-male conflict) were, conversely, low in surface signs of agitation (Spearman rank correlation = 0.84; n =11; 0.002 < P < 0005; Zar 1984).

Spotted dolphin subgroups: general observations

We define subgroups as a relatively small (<20) group of animals oriented and traveling in the same direction, maintaining close interanimal distances (usually <2 m), and, typically, separated from their neighbors by a wider gap (>3 m). Subgroups usually surfaced to breathe all together. Some subgroups moved in physical contact and in complete unison, tailbeat matching

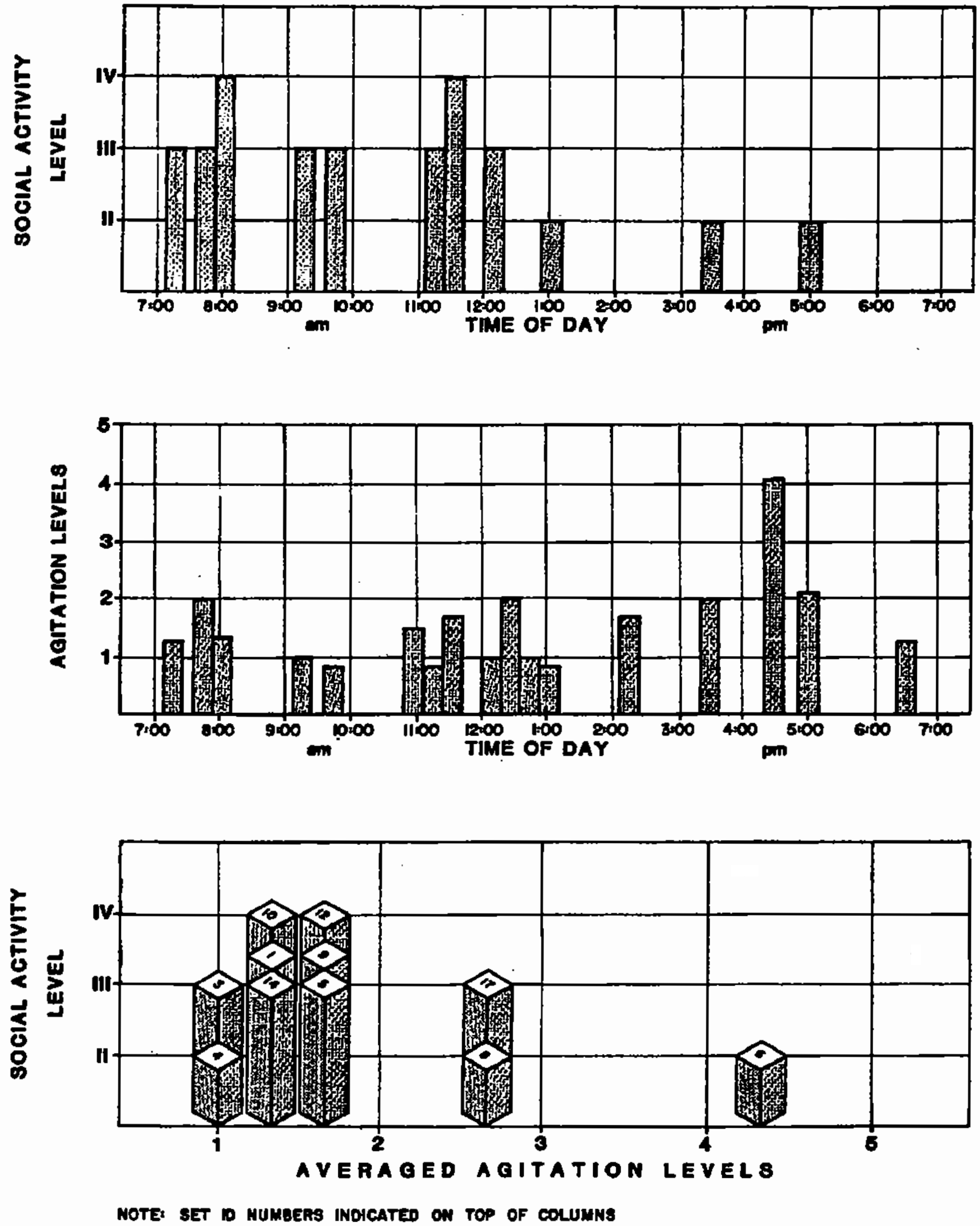

Fig. 6 a. Social activity levels compared to time of day.
Fig. 6 b. Agitation levels compared to time of day.
Fig. 6 c. Social activity levels compared to agitation levels.

tailbeat. In the schools we observed, subgroups constituted about half the animals; most of the remaining half moved in a single loose congregation.[7]

[7]A few animals moved about individually but rarely for long: of 14 focal animals selected for being solitary, only 4 failed to join another animal or group even in the brief five minutes of case study.

Female-calf pairs

Focal animal sampling was the technique that helped us tease apart the subgroup structure. We began by taking five-minute study cases on the most obvious and identifiable animals, the female-calf pairs that stayed in one location on the perimeter of the school. These pairs were easily recognizable not only by their size difference but also by behavior; rather than cruising or resting side by side as adult pairs might, they often oriented toward each other, rubbing heads or fins or bodies, even when cruising or surfacing to breathe. Studies of the reproductive tract indicate that female spotted dolphins do not normally have a new calf every year but may keep a single calf with them for two, three, or even four years. Therefore, we could expect that some females would be accompanied by quite large young, even juveniles in the speckled state (Kasuya et al. 1974; Hohn et al. 1985). In fact, we did occasionally see the somewhat irregular swimming pattern and the frequency and types of contact that characterized females and calves in pairs consisting of a mottled or fused-pattern adult and a speckled juvenile. Based on these behavioral patterns, we considered these to be mother-young pairs, even though the size difference might no longer be appreciable. It is possible, however, that such pairs may also be siblings (Perrin pers. comm.)

Female-young subgroups

Female-calf pairs did not always remain alone; sometimes they joined other animals or were joined by them. We noted the animals female-calf pairs associated with and thus identified another type of subgroup—female-young. These groups, when inspected animal by animal, consisted of adult females in the mottled or fused pattern, each accompanied by a calf or two-tone or speckled juvenile. Sometimes female-young groups did include a single, large, fused-pattern female without a youngster. Spotted dolphin schools sometimes contain a few (> 1%) truly postreproductive females (Myrick et al. 1986). It seems at least possible that, as in many terrestrial animals, older females that are neither pregnant nor lactating may remain in social association with their daughters and their offspring.

Female-young groups were by no means static organizations: the numbers in such groups changed constantly as animals joined and

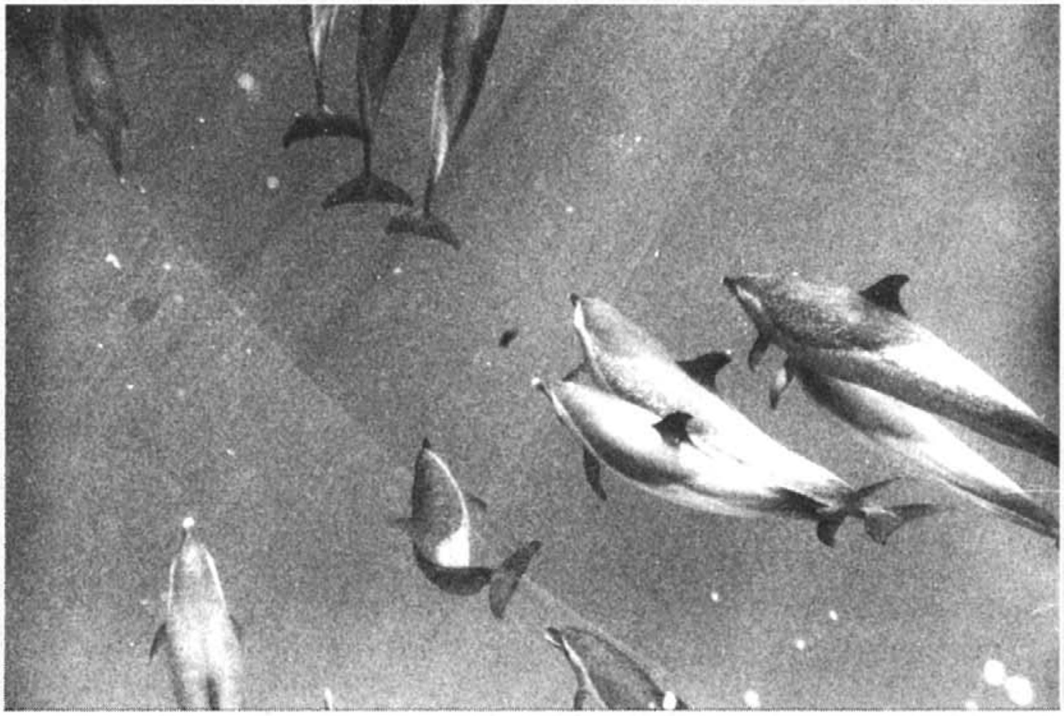

Fig. 7. A female-young subgroup. The calf in the center is traveling from the adult female at left to the two female-calf pairs at right. The net floor is visible below these animals as they in turn pass below the investigator floating at the surface.

left. However, the separation of the group from other nearby animals and the composition of the group remained constant. Female-young groups never seemed to contain any other classes of animals, such as independent juveniles, young adults, or large adult males, and the presence of even one calf seemed diagnostic. Whenever we inspected all the animals in a group with a calf in it, all appeared to be adult females with associated young[8] (Fig. 7).

Juvenile subgroups

Juvenile subgroups, which were not seen in every set, consisted of three to six two-tone individuals, smaller than adult size and quite without spots, characterized by minimum interanimal distances and near-perfect synchrony of breathing and swimming. In fact, the behavior of these juvenile subgroups was strikingly similar to that of adult male subgroups: both swam shoulder to shoulder in precise formation, both moved through the schools at a constant speed and on their own course, and both appeared to remain intact throughout sets, neither gaining

[8]In examining photographs of schools in the nets, Norris et al. (1978) found that any group with a calf in it had smaller interanimal distances, overall, than groups without calves.

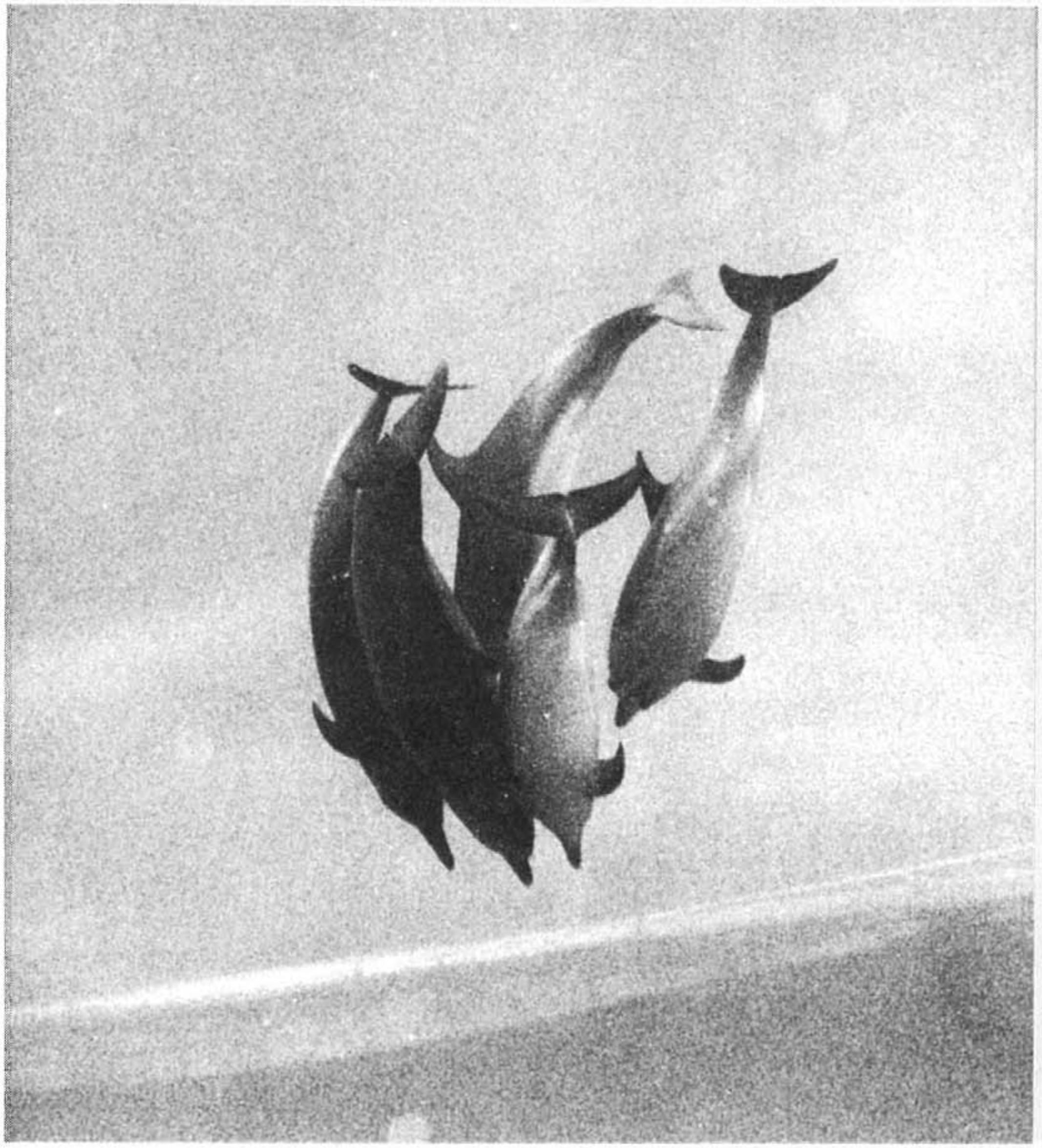

Fig. 8. A juvenile subgroup "rafting head-down" near the bottom of the net. These five juveniles persisted in this behavior, exhept when surfacing to breathe, throughout the set until backdown. Two adult male subgroups were seen rafting head-down in other sets.

nor losing individuals. Also, a peculiar behavior we called rafting head-down was seen only in juvenile and adult male subgroups (Pryor and Kang 1980) (Fig. 8).

Juvenile subgroups were never seen to join other subgroups, although once a juvenile subgroup was joined by an adult female that exchanged body rubs and pectoral pats with one of the juveniles. Juvenile subgroups did not appear to gain or lose animals; focal animals in a juvenile sub-group studied in Set 10 were seen repeatedly, their behavior and numbers unchanged,

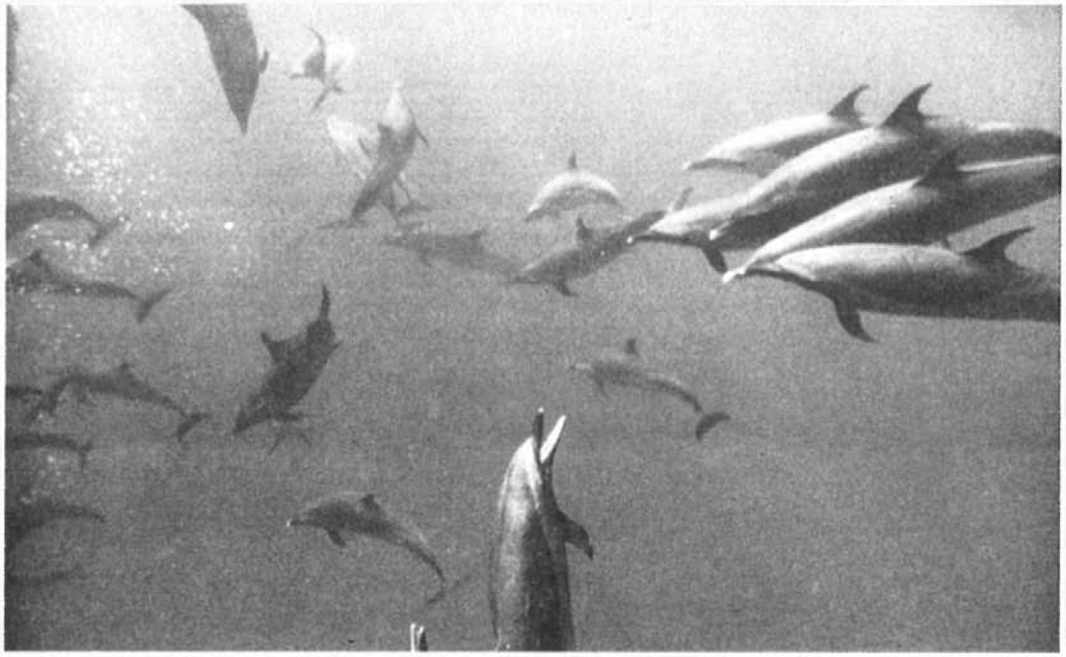

Fig. 9. An adult male subgroup crusing through the school. An individual in another male subgroup rising from below gapes his jaws in a threat gesture at the group passing over him.

until backdown. We had no explanation for why some juveniles formed these closely associated subgroups, while others, as large or larger, were still paired with adult females.

Adult male subgroups

The most conspicuous subgroups, seen in every school, were made up of adult males. These were groups of three to eight large, fused-pattern males, all with heavy keels, dark coloration, black facial masks, and white rostrum tips, the fully developed mature pattern of the largest animals in Perrin's scale (Table 5.1; Perrin 1969). These animals characteristically moved in unison, often shoulder to shoulder with pectoral fins overlapping and no individual in advance of another. They cruised slowly through the school without swerving or altering speed, while a path opened up before them; even rafting animals bestirred themselves to move aside when these dominant animals passed through (Fig. 9).[9]

[9]We identified similar subgroups of large, heavily keeled males in some (not all) spinner schools; they did not exhibit the tight unison of spotted male groups but swam in loose clusters and echelons, as has been reported for Hawaiian spinners (K. Norris pers. comm.)

Every school observed contained at least one adult male subgroup. If the aggregation in the net was divided into separate schools, each such school contained one or more of these conspicuous groups. In Set 12, among 200+ spotted dolphins, we counted eight adult male subgroups.

These subgroups did not seem to fluctuate in numbers as, for example, female-young subgroups did. We sometimes recorded a fused-pattern female (slender and keelless) joining an adult male subgroup to exchange affiliative gestures (patting, body rubbing) with one (or in one case, two) of the males, but the visit was always brief; conversely, an individual male might leave its subgroup, perhaps to interact with another individual or to investigate one of us, but in all recorded observations these individuals returned to the subgroup they came from, usually in less than one minute. In three sets, we noted an adult male subgroup containing a marked or scarred individual that could be positively identified throughout the set; in each case, the numbers of males in that subgroup remained the same.

Young adults

The rest of the school, the amorphous mass of animals that were not in clear-cut subgroups, proved to consist of speckled juveniles and mottled-pattern young adults. We never saw fused-pattern animals or calves in these larger aggregations. Young adult gatherings differed from the smaller subgroups in size, up to fifty or more individuals, but they were similar to the smaller groups in that interanimal distances were small (about 1 body width), and exchanges of affiliative displays were abundant.[10]

Other associations

In addition to the subgroup types recognized above, we observed many kinds of transient associations between two or more animals that we did not consider as subgroups, such as male-female pairs, animals engaged in aggressive interchanges, and triads, two adults with a young calf sandwiched tightly between them.

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[10]Again, the picture was very different in spinners. In some spinner schools we saw large, heavily keeled males, females, half-grown animals, and calves jumbled together in a big mass of animals throughout the set.

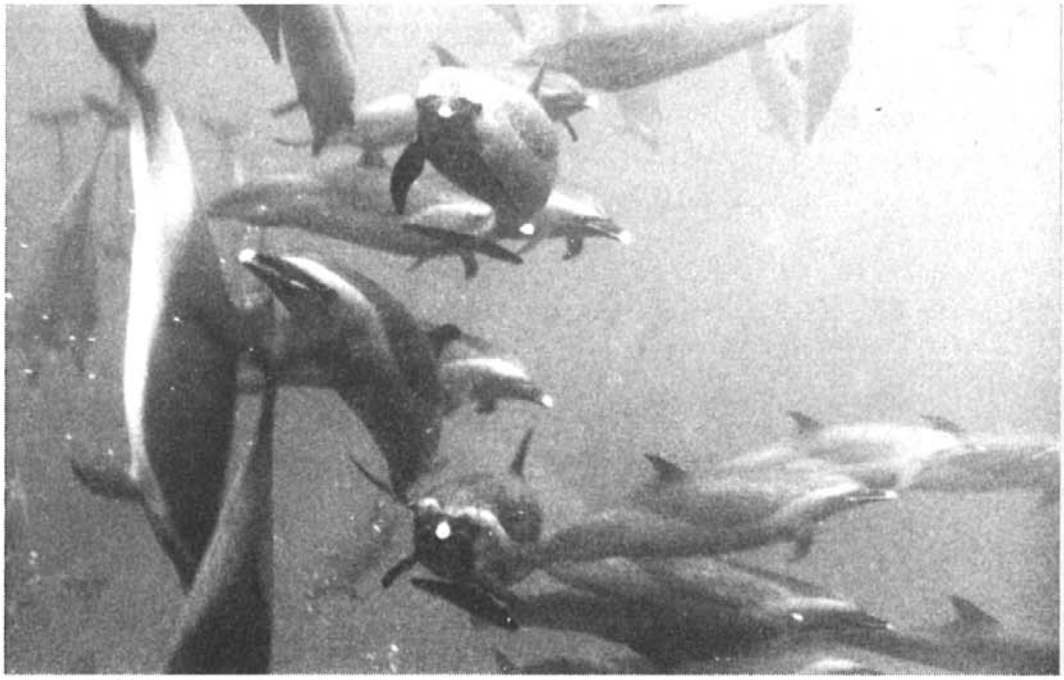

Fig. 10. An adult male subgroup positions itself between the main part of the school and the investigators. Another adult male subgroup of four animals cruises behind these three. Two of the first group cock their heads stiffly to study us with both eyes; these pelagic dolphins do not have the head-neck mobility of coastal bottlenose dolphins. Note the conspicuous white rostrum tips of the mature males, also visible on a large, fused-pattern female in a female-calf subgroup, lower right.

The behavior of adult male subgroups

The behavior of adult male subgroups differed from the behavior of all other animals in the school, perhaps most conspicuously in the way they carried out so much of their activity in synchrony. Synchronized behavior is a particular skill of dolphins, and episodes of unison breathing, leaping, and so on, are not uncommon. Usually, however, this unison behavior is a transient event. These adult male subgroups took it to extremes. In unison, they rose to breathe, and dived again. Together, they investigated us; an adult male subgroup was often our first sight, positioned between us and the school, when we entered the water. (Fig. 10.)

If one adult male subgroup met another, they made threat displays in unison.[11] Often, we could identify adult male

[11]Senior male subgroups even scouted out the unknown together. In Set 13, just before backdown, we observed a group of four make a simultaneous high-speed excursion 200 m back toward the ship to investigate some research gear being hauled up from the net floor; together, they circled the gear tightly, twice, before returning to the school.

subgroups, even at considerable distance underwater, by the stereotyped precision of their swimming formation. This "military" unanimity, which has been remarked on by other observers, seems to us to be peculiar to this species (James Coe pers. comm. Brower and Curtsinger 1981).

Social aggression

We feel that it is important to differentiate between noninteractive agonistic behavior (such as headslaps and breaching), which is often fear or stress related, and agonistic behavior directed at another specific individual animal (such as a threat display or actual blow), which constitutes social aggression.

Social aggression in captive animals is usually related to dominance disputes. As such, we consider it normal social behavior. We were not surprised, therefore, to see episodes of social aggression occurring, along with many other sorts of social behavior, in schools engaged in social activity. The principal aggressive behavior we recorded in focal animal sampling was gaping. Females sometimes gaped at calves. Solitary animals, whether adults or juveniles, sometimes gaped at other animals investigating or approaching them. Animals in young adult subgroups occasionally gaped at newcomers (but in reviewing data from all sets, young adults were about three times more likely to greet animals joining them with a pectoral pat). We recorded only one instance of threat between males in an adult male subgroup; two males in a subgroup of five exchanged two rounds of gapes and head noddings. Even including this modest exchange of threats, in data compiled from all sets, aggressive signaling was recorded less often within adult male subgroups than in female-young and young adult subgroups.

Outside of focal animal sampling, however, we collected numerous observations of more extensive episodes of social aggression, almost entirely between adult males. There were three exceptions: once a female reprimanded a lively calf in the backdown area by knocking it into the air with her head three times before it settled at her side; in Set 10, a female drove another female out of an adult male subgroup with gapes; and in Set 12, three pairs of young adults engaged in noisy and bubbly bouts of toothraking, which may or may not have been aggressive behavior.

We saw three interchanges between spotted dolphins which we would describe as fights, each time between a fused-pattern male and a younger individual (a juvenile in the speckled phase in Set 1 and mottled-phase young adults in Sets 3 and 8). The animals exchanged threat signals and burst-pulse sounds and whirled around each other head to tail, until the younger animal swam away (with the older male, in one case, in aggressive pursuit). These episodes took place in clear water and about 4 to 5 m from the observer, so the color pattern differences were distinct, but the sex of the younger animal could not be identified positively.

In Set 12, Pryor recorded a confrontation between two adult male sub-groups. An adult male subgroup of four animals and another of three met face to face, came to a halt, and exchanged open-jawed burst-pulse threat displays for about 10 seconds before the smaller subgroup ducked under and both continued on their previous courses. In Set 14, two fused-pattern males, with a fused-pattern female between them, fenced with open jaws across her bows as they cruised; the clash of teeth was audible.

Little aggression was manifested toward divers. On seven occasions, a male spinner or spotted dolphin directed a loud click train and sharp eye contact at an investigator, a signal pairing that in captivity is sometimes followed by a feint or a blow. Once, in Set 17, the nearest animal in a subgroup of four adult males threatened an observer with jaw shaking and burst-pulse sounds but deflected his course when threatened back.

Affiliative behavior in spotted dolphin schools

Much of the typical behavior of individuals within subgroups, such as unison breathing, unison swimming, close interanimal distances, and body contact, could be characterized as affiliative. Therefore, the very existence of subgroups might be considered to be affiliative behavior. In captive spotted dolphins, such affiliative activities are engaged in largely or exclusively by individuals that recognize each other and have established relationships. One may deduce that the animals seen in spotted dolphin subgroups in the nets are well acquainted with each other.

In addition, we observed many occurrences of affiliative behavior between animals that were not in the same subgroups. The most frequently recorded events might be termed greeting behavior and consisted of an individual briefly joining another individual or group and exchanging body rubs or pectoral pats. Specific instances were recorded between calves and other calves, between calves and more than one adult female, between adult males on meeting (in Set 4, two large adult males exchanged pectoral pats), between solitary juveniles encountering each other (rostrum touches, Set 4), between young adults, between large adult males briefly joining females in female-young groups, and between females and individual males in adult male subgroups. In summary, we saw greeting and affiliative behavior between every category of sex and age in the school except adult males and young adults and adult males and calves.

One unusual example of affiliative behavior occurred in Set 17, shortly before backdown. Both investigators were recording animals in adult male subgroups when a speedboat engine started up suddenly nearby, alarming the animals (the boat was attempting to drive animals away from a pocket in the net). Each group of males bunched together and speeded up, and each was simultaneously joined by females, calves, and young adults, crowded above, below, and beside the males. One group thus increased briefly from three males to ten individuals and the other, from eight males to seventeen individuals.

Conclusions

The sample size of this study is small—seventeen sets, of which only eleven were studied underwater. Nevertheless, we feel that subgroup identification was reliable, thanks to the focal animal sampling approach. The wealth of observational material allows some hypotheses on spotted dolphin organization.

Each autonomous aggregation of spotted dolphins in a set contained female-calf pairs, female-young subgroups, young adult subgroups, and adult male subgroups; some also contained juvenile subgroups. Because of the frequency and widespread nature of affiliative exchanges, we suspect that the spotted dolphin groups that we saw, or at least most of the animals in those groups, knew each other and had been in association for prolonged periods.

The adult male subgroups, in particular, exhibited unusually uniform behavior and constancy. In captivity, we have seen spotted dolphins (but not spinners) form fixed, long-term associations that excluded other individuals (Pryor 1975). We suspect that adult male subgroups will eventually prove to be neither temporary nor opportunistic but long-term associations of particular individuals.

What could be the function of such an alliance? Perhaps it facilitates breeding. In spotted dolphins, anatomical studies have demonstrated that fused-pattern males are the breeding animals (Hohn et al. 1985). About 50 percent of the females are reproductively mature in the mottled stage (and 4 percent in the speckled stage), but the testes size and function in many hundreds of samples show that mottled-pattern males are reproductively immature (Perrin et al. 1976; Perrin and Reilly 1984; Hohn et al. 1985). Therefore, what we identify as adult male subgroups are likely to be the principal reproductive males in their schools.

In examining specimens collected from four different schools, Perrin found several variations of color pattern between schools. For example, in one school, the darkish band from jaw to flipper, seen in all age groups, was narrow and simple, and in another, it was wide and complex; in one school, the adults had white rostrum tips, and in another, they did not (Perrin 1969). Behavioral evidence suggests to us that spotted dolphin schools could be stable enough to provide an environment favoring the perpetuation of genetic relatedness. Males within such a school might not need to compete with each other physically for dominance or access to mates. And, indeed, the amount of status conflict within adult male subgroups seemed to us to be very low. One can speculate, however, that defense of the group against other adult male sub-groups, or maturing, younger males, would confer reproductive advantage. Again, our glimpses of social aggression by fused-pattern males and adult male subgroups are consonant with this premise.

There are many successful species of pelagic cetaceans. Spinners and spotted dolphins are among the most numerous. Their behavioral ecology is probably similar in some respects and different in others. For example, in the ETP in a year, spinners may travel no more than 300 miles, while spotted dolphins may move 1,000 miles or more, traveling 30 to 50 miles a day (Perrin et al. 1979). Possibly, a more rigid school structure is beneficial to the more nomadic spotted dolphins.

Several studies in progress at the Southwest Fisheries Center suggest that there are two kinds of spotted dolphin schools in the ETP. Some schools are breeding schools, generally numbering under 300 animals (Barlow and Hohn 1984, Myrick et al. 1986). These schools (which are the kind we saw in our research) are characterized by the presence of fewer males and more females and young than would be expected by chance and by a partly *missing* age class consisting of prepubescent animals (Hohn and Scott 1983). These juveniles are sometimes completely absent from the records of a given school, although young adults, the next age group, are present in expected proportions (Perrin and Myrick 1980).

The missing age class apparently forms the bulk of the second sort of spotted school: these are small groups, mostly male and mostly juvenile, which are often found in association with very large schools of spinners (Barlow and Hohn 1984, Hohn and Scott 1983). Since very large groups of spinners rarely carry tuna, they are seldom set on by tuna vessels; thus, fewer records exist of these animals that seem to have left the parental association. How and when (and if) these juvenile schools rejoin the breeding groups is at present only a matter for speculation.

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