Chapter 17
Spinner Dolphins of Islands and Atolls

Marc O. Lammers

Abstract Spinner dolphins, *Stenella longirostris*, occur globally in tropical and subtropical waters and form island-associated populations in many parts of the world. These populations are closely tied to island resources, relying on enhanced aggregations of mesopelagic prey and nearshore habitats to conduct a highly stereotyped daily behavioral cycle. To exploit these resources, spinner dolphins have adapted their social structure, foraging ecology, reproductive patterns, predator avoidance behavior, and communication in unique ways. Spinner dolphins are a gregarious species with individuals relying on the dynamics of the pod for nearly every aspect of their lives. Because of a daily tendency to visit the same coastal waters and engage in acrobatic displays, many populations have seen a steady rise in popular and commercial dolphin-watching by humans. This has led to management concerns about the potential impacts that chronic interactions may have on the dolphins' ability to conduct normal daily behaviors.

Keywords Island-associated · Diel cycle · Social structure · Foraging · Resting · Predator avoidance · Acoustic signaling · Acrobatic behavior · Conservation

17.1 Introduction

The spinner dolphin (*Stenella longirostris*) is one of the most common small odontocete species in tropical and subtropical waters. Several subspecies are recognized, including the globally distributed Gray's spinner (*S. l. longirostris*), the eastern tropical Pacific's (ETP) endemic eastern spinner (*S. l. orientalis*) and Central American spinner (*S. l. centroamericana*), and the dwarf spinner of central Southeast Asia (*S. l. roseiventris*) (Perrin 2009). An additional form of spinner dolphin in offshore waters of the ETP, the

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"whitebelly," is possibly a fifth subspecies. I will abbreviate the term "spinner dolphin" to "spinners" from here on to reflect common practice when discussing the species.

Spinners are generally pelagic, but coastal populations exist in the eastern Pacific, Indian Ocean, Southeast Asia, and elsewhere (Perrin et al. 1989, 1999). Pelagic populations, such as in the ETP, often occur in waters with a shallow thermocline (Reilly 1990). The thermocline concentrates pelagic organisms in and above it, upon which the dolphins feed. In certain coastal populations, such as those in Southeast Asia, dwarf spinners exploit mainly benthic and reef fishes and invertebrates (Perrin et al. 1999).

Across their global distribution, spinners exhibit an affinity for island archipelagos. In many parts of the world, island-associated populations occur that are distinct from their pelagic conspecifics, sometimes with sufficient genetic differentiation to be managed as unique stocks (Carretta et al. 2011). These island-associated populations often display high site fidelity to specific islands within an archipelago (Oremus et al. 2007; Andrews et al. 2010; Viricel et al. 2016) and even to individual coastlines (Marten and Psarakos 1999). In general, the island coastlines preferred by spinners are characterized by shallow water habitat in close proximity to steep island slopes, where the "island-mass effect" results in localized areas of biological productivity (Gilmartin and Revelante 1974; Gove et al. 2016). It is this enhanced productivity and protective nearshore habitat that tie these populations to particular islands, thereby forgoing a more pelagic existence (Andrews et al. 2010; Viricel et al. 2016).

Island-associated spinner populations have been studied in several parts of the world, including archipelagos in the south Atlantic (De Lima Silva and Da Silva 2009), south Pacific (Gannier and Petiau 2006; Oremus et al. 2007; Cribb et al. 2012), Indian Ocean (Anderson 2005; Condet and Dulau-Drouot 2016; Viricel et al. 2016), the Red Sea (Notarbartolo di Sciara et al. 2008), and other locations. However, a disproportionate amount of knowledge about behavior and ecology of island spinners has come from studies of the populations of the Hawaiian archipelago in the central north Pacific. Beginning in the late 1970s and continuing through modern times, research groups have focused efforts on studying spinners across this more than 1500-mile-long (2400 km) chain of islands and atoll. Hawaiian spinners are genetically distinct from other populations in the Pacific Ocean (Andrews et al. 2010) and occur off Hawai‘i Island, Maui, Kaho‘olawe, Lāna‘i, Moloka‘i, Oahu, Kaua‘i and Ni‘ihau in the Main Hawaiian Islands, as well as at French Frigate Shoals, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll in the Northwestern Hawaiian Islands, spanning a latitudinal range of more than 10 degrees. Genetic differentiation is present among many of these island clusters, including between the islands of Hawai‘i and Maui that are separated by only 46 km, thereby underscoring the island fidelity that characterizes some of these populations (Andrews et al. 2010).

17.2 The Daily Cycle

Island-associated spinners are characterized by a behavioral cycle first described by Norris and Dohl (1980) and later detailed by Norris et al. (1994a) for the population along the Kona coast of the island of Hawai‘i. Dolphins off the Kona coast feed in deep offshore waters at night and spend much of daytime close to shore, often in bays that tend to be sheltered by the prevailing winds. After they enter the nearshore area in the morning, they descend into rest and tend to rest for much of the day, but with intermittent bouts of social, sexual, and aerial activity. Resting groups can be as few as 20 dolphins but can also be as large as 100 or more. Groups at rest are in tight formation, tend to dive synchronously, and are relatively quiet, with only occasional sounds produced. While resting, spinner dolphins appear to rely mainly on vision. They tend to prefer sandy substrate, not bottom with coral outcroppings or rocks, presumably so that they cannot be surprised by tiger sharks (*Galeocerdo cuvier*) coming from hiding places. In the afternoon, the dolphin group becomes more active, with increasing social, sexual, aerial, and vocal activity, before moving out of the nearshore shallows and traveling to deeper offshore waters to feed. As they do so, they are often joined by other groups who spent their time in other nearshore areas, and the foraging group becomes large again. This is therefore a diel fission/fusion society, to be described later. The diel cycle is quite consistent, except that a particular nearshore area or bay is not be visited each and every day (although usually over 50% of days), and there are seasonal shifts depending on sunrise and sunset, i.e., day length (Würsig et al. 1994a). This basic cycle has since then been documented in numerous other island-associated spinner populations (Notarbartolo di Sciara et al. 2008; De Lima Silva and Da Silva 2009; Cribb et al. 2012).

Wells and Norris (1994a) suggested that availability of prey and resting habitat are the primary limiting factors to influence occurrence of spinners along the Kona coast. Other studies in Hawai‘i (Karczmarski et al. 2005; Tyne et al. 2015) but also in French Polynesia (Poole 1995; Gannier and Petiau 2006) and Reunion Island (Condet and Dulau-Drouot 2016) have similarly highlighted the relationship between shallow water habitats with light-colored bottom substrate in the proximity to deepwater prey and the occurrence of spinners. Thorne et al. (2012) used predictive modeling to establish that vicinity to deepwater foraging areas, depth, proportion of bays with shallow depths, and substrate rugosity were important factors influencing spinner occurrence in Hawai‘i, with distance to the 100 m depth contour a strong predictor of daytime resting habitat.

It would be misleading to characterize spinner occurrence as limited to coastlines resembling the one found off Kona, which is unique in its availability of numerous protected coves in close proximity to steep bathymetry and vast stretches of calm, clear leeward waters. Rather, spinners are more adaptable and often exploit habitats not considered ideal by the criteria laid out above. For example, off the island of Oahu, spinners often rest outside protected coves while transiting or milling along coastlines with little or no lee (Lammers 2004). Similarly, spinners in the Maui Nui region (Maui, Lāna’i, Kaho’olawe, and Moloka’i) rest in the channel between Maui and Lāna’i, tens of kilometers from deep offshore waters (McElligott 2018). Thus, although the general cycle of nighttime foraging and daytime socializing and resting is consistent among spinner populations, its implementation is adapted to the resources available in the habitat.

17.3 Social Structure

Spinners have high sociality, and individuals do not occur alone. Rather, they are herd animals dependent on the dynamic of the group for nearly all life functions. A spinner pod ranges in size from a minimum of three to several hundred individuals, depending on location and behavioral context. Such an obligate social lifestyle has led not only to social structure in spinner groups but also to complex social dynamics.

A pod of several dozen or more spinners is composed of multiple sub-pods. The behavior of individuals is largely regulated at the level of the sub-pod, rather than the pod as a whole. Individual dolphins reflect the behavioral state of the sub-pod they belong to, which may or may not be the same as that of other sub-pods. Thus, as an example, while a pod of ~100 animals might occupy the same area or be traveling in the same direction, it is likely that there are between three and four sub-pods of 20–40 dolphins, with individuals from sub-pods intermixing. Depending on which stage in the daily behavioral cycle the pod is in, all the sub-pods may exhibit the same behavioral state (e.g., socializing), or some sub-pods may be more or less active, coordinated, and/or synchronized than others (behavioral descriptions can be found in Norris et al. 1994a).

A likely reason for the behavioral state regulated at the level of the sub-pod is the need for coordination and synchrony during rest, which may be achieved optimally in groups of certain size. Because resting spinners rely primarily on vision for vigilance, synchronized behavior helps maximize efficiency of information transfer among pod-mates via a sensory integration system (or SIS) (Norris and Schilt 1988). An SIS is created when individuals swim in coordinated fashion as parts of a supra-individual signaling system that allows the perception, amplification, and transfer of environmental information from collective sensory windows (Norris and Johnson 1994). The SIS can provide an early warning of predators and allows for information to travel rapidly across a sub-pod, facilitating fast communal response.

Sub-pods appear to be organized around coalitions of males, with females and younger animals joining coalitions (Östman 1994). Some degree of social interaction among individuals in a sub-pod is nearly continuous, with various forms of caressing, rubbing, genital-to-genital contact, and/or chasing being the norm rather than the exception (Johnson and Norris 1994). Tactile interactions likely play important roles in establishing, reaffirming, and/or strengthening social relationships among individuals. The majority of affiliative and sexual behaviors generally occur between males and females, while overt aggressive behaviors are most common between females, suggesting that females may actively compete for access to males (Östman 1994). Associations among individuals range in longevity from momentary to lifelong, with the strongest levels of affiliation among male spinner dolphins and the lowest among females (Östman 1994; Marten and Psarakos 1999).

Associations among and within sub-pods are marked by characteristic delphinid fission-fusion dynamics (Gowans et al. 2007). Sub-pods typically aggregate into larger pods for one to several hours in the morning before fragmenting and becoming more distributed during mid-day rest. The larger pod is then typically reassembled in the afternoon prior to departing toward offshore evening feeding areas, although often with a different complement of sub-pods than in the morning (Lammers 2004). Similarly, during periods of pod assembly and presumably at night, the makeup of sub-pods is reshuffled through the intermixing of individuals. Thus, long-term affiliations among individuals, but also fluid group composition, are generally hallmarks of spinner pod dynamics.

Exceptions to the fission-fusion pattern occur in smaller, isolated populations of spinners. Karczmarski et al. (2005) reported that the population at Midway Atoll in the Northwestern Hawaiian Islands has an absence of fission-fusion dynamics for the mostly closed population occupying the atoll's lagoon during the day. Rather, spinners there live in a stable society with strong geographic fidelity, no inter-individual variation in the structure of groups, and stable associations from day to day. This difference from aforementioned spinner dolphin social patterns is thought to result from the relatively close proximity of prey resources to daytime resting areas coupled with large distances to other atolls, leading to stability rather than variability in social dynamics of the group. It is too far for dolphins to go to easily exchange with individuals of another group.

17.4 Reproduction

Reproductive strategies have been determined for the pelagic eastern and whitebelly spinner dolphins in the ETP based on comparisons of sexual dimorphism and male testes weight (Perrin and Mesnick 2003). There is great variation in sexual strategies by population. Perrin and Mesnick (2003) concluded that the eastern spinner, which exhibits a higher degree of sexual dimorphism and lower testes weight, likely has a polygynous mating system characterized by intense pre-mating competition among males. On the other hand, the more offshore whitebelly spinner dolphin is characterized by reduced sexual dimorphism and greater testes weight, indicating an emphasis on sperm competition among males and therefore a polygynandrous, or promiscuous, mating system with both males and females mating with multiple partners. This difference in mating strategies may explain the canted dorsal fin and exaggerated anal keel among mature eastern spinner males where a strong polygyny presides but comparatively absent among whitebelly spinners where multi-mate sexuality appears to occur. Perrin and Mesnick (2003) further speculated that the different mating strategies likely are tied to differences in resource availability, with eastern spinners less limited by prey abundance and therefore able to devote more energy toward competition for mates than whitebelly spinners, which occupy less productive, patchy offshore environments and therefore must devote more energy on foraging.

Island-associated spinners, such as the ones off Hawaii, are thought also to have a polygynandrous mating system, based on the prevalence of sexual behaviors among males and females and testes weights that are similar to those of whitebelly spinners (Wells and Norris 1994b; Perrin and Mesnick 2003). Like whitebelly spinners, Hawaiian spinners also exhibit a "seasonally diffuse" reproductive pattern with a slight bimodal tendency. Calving in both forms takes place year-round, but a modest peak occurs in late spring and summer and another in midwinter (Barlow 1984;

Wells and Norris 1994b). Wells and Norris (1994b) measured hormonal levels in both males and females in a small captive colony of spinners and concluded that the temporal spreading of sexual readiness among females likely explains the diffuse bimodal appearance of newborn calves in the population.

17.5 Foraging

Spinner dolphins are nocturnal feeders who exploit the nightly vertical migration of oceanic micronekton. In pelagic waters this community is termed the deep scattering layer or mesopelagic community, while around islands it is typically referred to as the mesopelagic boundary community (MBC) because it lies at the interface between coastal and oceanic ecosystems (Reid et al. 1991). The composition of MBC is diverse and varies regionally but is made up of numerous species of deepwater fish, shrimp, and squid, as well as the larval stages of pelagic and coastal organisms. The MBC community off Hawai‘i resides along island slopes at depths of 400–700 m during daytime hours and migrates to within 10 m of the surface at night (Reid et al. 1991; Benoit-Bird and Au 2004). In addition, the MBC also migrates horizontally toward shore to exploit nearshore densities of zooplankton (Benoit-Bird et al. 2001, 2008; Benoit-Bird and Au 2006), which brings elements of the MBC, particularly myctophids, into waters as shallow as 23 m and as close as 500 m from shore during the middle of the night (Benoit-Bird and Au 2006).

Spinners are specialized in feeding on members of the MBC measuring approximately 2–10 cm (Benoit-Bird 2004). Fish in the family Myctophidae typically make up more than 50% of stomach contents, and other mesopelagic fish, squid, and shrimp families compose the rest (Perrin et al. 1973; Würsig et al. 1994b). Benoit-Bird (2004) measured caloric content of spinner prey and concluded that spinners need to consume a minimum of 1.25 larger prey items per minute to meet energy needs. As a result, spinner feeding success is determined by their ability to find and exploit high densities of prey.

The spinner feeding cycle begins once the pod leaves the protection of shallow, nearshore waters used for daytime resting. The pod typically leaves resting habitat in a burst of energetic swimming and acrobatic leaping before settling into a more sustained travel speed (Würsig et al. 1994a). At this stage, larger pods often spread out widely and/or break apart, emphasizing the importance of the sub-pod and bonds among individuals in regulating group dynamics. Following a large pod of animals as they transit to their offshore feeding ground typically results in the pod gradually separating and the observer tracking only a handful of animals by the time extended foraging dives over deep waters occur. These dives generally begin within an hour of sunset, when the MBC is not yet near the surface, supporting the suggestion that spinner dolphins probably dive relatively deep (150–250 m) to meet the rising layer of prey (Würsig et al. 1994b).

How spinner dolphins find their prey remains a mystery. Au and Benoit-Bird (2008) measured the target strength of individual MBC animals using a simulated dolphin echolocation click and concluded that spinners could likely detect their prey at a range of 30–57 m, depending on the density of prey animals. It is unclear if this range is sufficient for spinner dolphins to detect concentrations of prey at depth in open waters. Afternoon tracking of pods on the island of Oahu revealed that spinners traveled to preferred locations along the coast to begin foraging, suggesting that they anticipated where prey first became available at shallower depths (Lammers 2004). These locations often coincided with areas being exploited by other odontocete species, such as spotted dolphins (*Stenella attenuata*) and common bottlenose dolphins (*Tursiops truncatus*), indicating that these were perhaps early evening hot spots of MBC prey occurrence.

Efforts to study how spinners exploit prey at night have largely relied on active acoustic methods of observation (i.e., sonar). By using vessel-based, downward-oriented sonar, Benoit-Bird and Au (2003) showed that spinners follow the diel horizontal migration of their prey toward shore, rather than feed offshore the entire night. This effectively brings spinners back into shallow, nearshore waters during the middle of the night and then offshore again during pre-dawn hours as the MBC retreats to deeper waters. The same study also showed that spinners track the vertical migration of their prey and exploit areas in the MBC that have the highest prey density. Moreover, Benoit-Bird and Au (2009) used data from a multi-beam echosounder to assert that foraging dolphin groups engage in cooperative and coordinated prey herding to help maximize prey density and therefore feeding success (Benoit-Bird and Au 2009).

17.6 Predation

Norris and Dohl (1980) reported that spinner dolphins in Hawai‘i are likely attacked by large sharks, as evidenced by scarring patterns on various parts of the body. Norris (1994) further suggested that marine mammals, including false killer whales (*Pseudorca crassidens*), pygmy killer whales (*Feresa attenuata*), short-finned pilot whales (*Globicephala macrorhynchus*), and killer whales (*Orcinus orca*), might also target spinners occasionally. However, it is presently unclear whether and how they do so. Perhaps the most common predator of spinners is the cookie-cutter shark (*Isistius brasiliensis*), a vertically migrating, small, bioluminescent squaloid shark thought to mimic squid, thereby attracting feeding dolphins to it at night (Jones 1971). It has teeth only on the lower jaw that are used to scoop out disks of blubber and flesh approximately 5 cm in diameter. Because they are generally not deadly, both fresh and healed wounds from this shark are common among spinners.

Anti-predator strategies have played a large role in shaping spinner behavioral patterns. Norris and Schilt (1988) suggested that the first line of defense is simply schooling behavior, which offers relative safety through the dilution of risks to individuals, provides early warning of an impending threat through shared vigilance, and creates a confusion effect, whereby a predator’s ability to track individual prey is confounded. The benefits of aggregation relative to predation explain not only the habit by spinners to form large pods (Norris and Dohl 1980) but also the tendency to take part in mixed-species associations in certain parts of the world (Scott and Cattanach 1998; Kiszka et al. 2011). Kiszka et al. (2011) reported that over 25% of spinner pods off the island of Mayotte in the southwestern Indian Ocean included pantropical spotted dolphins (*Stenella attenuata*), presumably to increase the size of the pod. They attributed this association to an anti-predator strategy for transiting between resting areas.

Besides aggregating into groups, spinners actively mitigate predation by carefully selecting the environment they occupy. Island-associated spinners typically seek out shallow, coastal habitats during the resting phase of their daily cycle. Because resting is characterized by reduced rates of echolocation, it is possible that spinners defend themselves against a surprise attack by reducing the dimensional properties of the environment they must monitor visually (Würsig et al. 1994a). Thus, by occupying shallow waters, they effectively eliminate the depth dimension and therefore the likelihood of an attack from below. Further, by occupying bays and/or the nearby shoreline, they reduce the threat of an attack coming from the flank facing the shore. Scarring from shark attacks is more common among island-associated populations of spinners than pelagic ones (Norris 1994). However, rather than offering this as evidence of lower rates of predation in open waters, Norris (1994) suggested that higher attack survivorship among island-associated spinner dolphins is a more likely explanation, supporting the proposed benefit of seeking nearshore resting habitats.

17.7 Communication

Spinners face the challenge of managing a life dependent on social connections in the vast open sea. Communication is the key to mediating social processes, so it is not surprising that spinners and other odontocetes with gregarious lives have evolved a complex system of signaling. Because the sea is a largely dark and opaque environment, acoustic communication plays a central role among delphinids (Lammers and Oswald 2015). This is because water is comparatively transparent to sound, which allows acoustic signals to transmit over much greater ranges than light-dependent signals and cues. As a result, highly social delphinids such as spinners have evolved a complex form of acoustic signaling using frequency-modulated whistles and short pulses or clicks (Fig. 17.1). Spinner whistles typically range in duration from tens to hundreds of milliseconds and are composed of a fundamental frequency contour with multiple harmonics (Lammers et al. 2003). Some whistles are simple frequency sweeps, while others are more complex with inflections, breaks, and steps in the contour. How whistles are used in communication among dolphins is a debated topic in the literature, but there is general agreement that they play a role in maintaining contact among dispersed pod-mates and in the identification of individuals (Lammers and Oswald 2015). Spinner dolphin clicks are only tens of microseconds long and are produced in “trains” with inter-click intervals between a few and hundreds of milliseconds (Lammers et al. 2004). They have broadband energy mostly or exclusively at frequencies above the human hearing range (i.e., >15 kHz). Click trains are differentiated into those

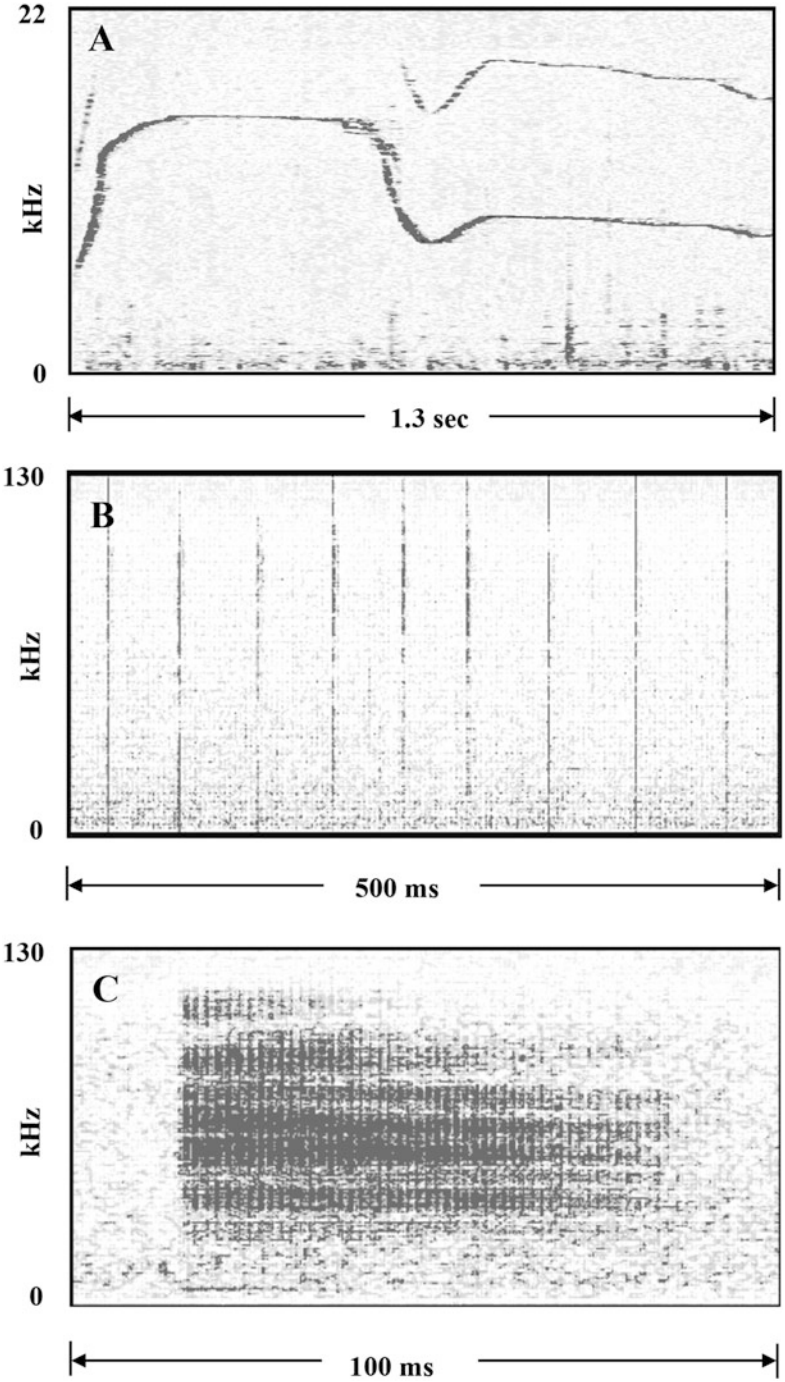

Fig. 17.1 Spectrogram examples of a spinner dolphin, *Stenella longirostris*, whistle with a harmonic (**a**), an echolocation click train (**b**), and a burst-pulse click train (**c**). From Lammers et al. 2006

used for echolocation and "burst pulses" associated with communication on the basis of their inter-click interval (Lammers et al. 2004).

Because of predictable daily behavior and accessibility to researchers, spinner dolphins have been the focus of numerous efforts to investigate acoustic communication in free-ranging delphinids. Watkins and Schevill (1974) studied spinner acoustic signals using a three-dimensional hydrophone array to acoustically localize signaling animals in a resting bay on the island of Hawai'i. Their efforts resulted in a description of exchanges of burst pulses between individual dolphins, providing an early confirmation that these signals are used in communication. Brownlee (1983) and later Driscoll (1995) showed that rates of signaling are closely tied to behavioral state, with resting spinners mostly quiet and traveling and foraging spinners exhibiting the highest rates and diversity of signaling. Driscoll (1995) further examined periods of spinner dolphin chorusing, common in the afternoon/evening, and concluded that chorusing likely helps to organize the pod during transitions between behavioral states.

Lammers et al. (2003) employed some of the earliest field-portable broadband recording technology to show that whistles and burst pulses contain substantial acoustic energy at ultrasonic (>20 kHz) frequencies. Lammers and Au (2003) used an array of hydrophones towed behind a vessel to further examine acoustic properties of whistles and concluded that high-frequency harmonics provide navigational cues that listening animals may use to infer the orientation and direction of movement of the signaler, thereby facilitating coordination of widespread animals. Lammers et al. (2006) also used a towed array to localize signaling animals as they traveled near the research vessel. They found that whistles typically originated from dolphins spaced relatively far apart, supporting the hypothesis that these signals play a role in maintaining contact between animals in a dispersed group (Brownlee and Norris 1994; Janik and Slater 1998). Burst pulses, on the other hand, usually came from animals spaced closer to one another, suggesting they function as a more intimate form of signaling between adjacent individuals. Echolocating individuals were typically spaced 10 m or more apart, with little evidence of concurrent echolocation between closely spaced individuals. The authors interpreted this as evidence that all members in a pod might not equally share the task of vigilance. Figure 17.2 illustrates the spatial context of signaling in a spinner dolphin pod.

Despite limitations of light-based signaling in the sea, visual communication is important among delphinids. Among spinners, coloration patterns, body postures, and swimming patterns strongly point to visual signaling as an important channel for communication (Würsig et al. 1990). Spinners underwater exhibit white flashes when individuals momentarily turn to expose bellies, which probably serve as a reference for animals at the edge of visual range. Distinct postures, such as open-mouth displays, are also common among socializing spinners, especially during agonistic interactions. Finally, certain swimming patterns, such as exaggerated S-turns with downward-oriented pectoral fins, have been suggested to be analogous to a similar warning signal given by certain territorial sharks (Johnson and Norris 1994).

Human observers are likely to be cognizant of only the more exaggerated and therefore unambiguous visual cues produced by dolphins. Given that individuals often swim within or very near physical contact to each other, there are likely many more subtle signals exchanged, both visual and physical, that a non-delphinid

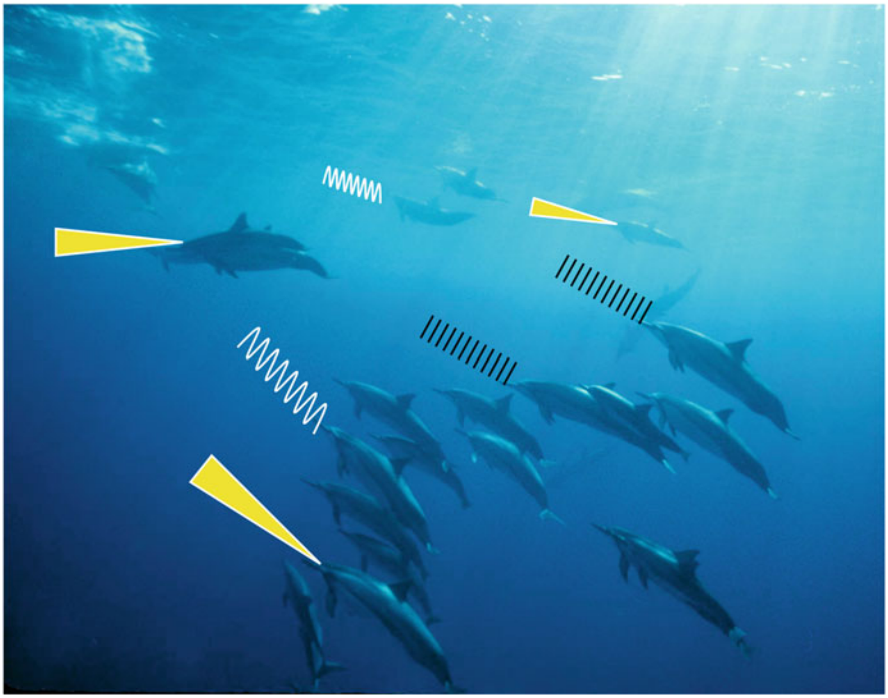

Fig. 17.2 A hypothetical representation of the spatial occurrence of acoustic signals in a spinner dolphin, *Stenella longirostris*, pod. The white sinusoids represent whistle production, the black bars represent the production of burst pulses, and the yellow cones are the occurrence of echolocation click trains (Photo courtesy of Andre Seale). From Lammers et al. (2006)

observer would not register. At times, interactions among spinner dolphins are subtle, with a fin lightly rubbing against a pod-mate or an eye partially or fully closed. Whether such cues have meaning to nearby animals is speculative, but the potential is present for a vast array of meaningful visual and physical cues to help mediate social relationships.

17.8 Aerial Acrobatics

A review of spinner dolphin behavior would be lacking without a discussion of their aerial acrobatics. Simply put, spinner dolphins are master acrobats with few rivals in the cetacean world, save perhaps dusky dolphins (*Lagenorhynchus obscurus*; see Würsig and Würsig 2010). Most odontocete species engage in some form of aerial behaviors, and some may leap higher or further than spinner dolphins, but none match them in their ability to rotate, twist, and somersault, often in extended bouts of aerial displays (Fig. 17.3).

Fig. 17.3 A collated sequence of a spinner dolphin, *Stenella longirostris*, performing a spinning leap. This sequence was taken from Twitter, with permission by the Wyland Foundation. In this compilation of a video sequence, the leap begins on the right side, and the dolphin turns on its axis two times, until it lands to the left. Leaps can be in this vertical stance, but also horizontally to the water, and can incorporate over three turns of the body axis while in-air

Spinner dolphins engage in a wide range of above-water behaviors, spanning from subtle "nose-outs," whereby the rostrum is extended just above the water's surface, to high-energy "tail-over-head" leaps, in which the dolphin throws its tail forward in a somersault (Norris and Dohl 1980). Aerial behaviors can occur at any time but are most common during periods of socializing and traveling. They are least common during periods of rest, although individuals in a resting group may leap or spin in response to an approaching vessel, as if to alert the vessel of the pod's presence. The variety, intensity, and frequency of aerial activities, combined with other behavioral metrics, can thus be used as indicators of a spinner dolphin pod's behavioral state (Lammers 2004).

Invariably, the question arises: Why do they do it? Probably the most common answer is to rid themselves of parasites, including remoras (Hester et al. 1963; Norris and Dohl 1980; Norris et al. 1994b). However, this answer alone is rather unsatisfying, as most odontocetes face the problem of parasites yet do not display the acrobatic aptitude of spinner dolphins. Thus, additional explanations are necessary that account for the spinner dolphin's distinct behavioral ecology. Norris et al. (1994b) proposed that the bubble plume produced underwater by reentering spinning dolphins would offer a strong target for echolocating pod-mates and therefore serve as a beacon of sorts to help define the envelope of the pod or perhaps act as a target to more distant subgroups. Similarly, the reentry sound produced by a leaping dolphin could serve as an omnidirectional cue to nearby animals. Still, these explanations probably cannot reconcile the large variety of aerial behaviors in the spinner dolphin repertoire. Perhaps an additional clue lies in the fact that behavioral state can be inferred from the pod's aerial displays. Thus, it may be that spinners use aerial displays to regulate the pod's state in their perpetual effort to achieve and maintain group cohesion. These acrobatic leaps are perhaps designed as a signal of group social cohesion for entering or leaving a bay, or for signaling an after-feeding "party mood" as has been suggested for dusky dolphins (Würsig and Würsig 1980).

17.9 Anthropogenic Impacts

In many places where spinner dolphins occur, humans have taken great interest in them. This is not surprising, considering spinner dolphins' propensity for visiting the same nearshore water almost daily and while there performing acrobatic feats. In some parts of the world, a steady increase in popular and commercial interest in viewing and interacting with spinners has led to management concerns (Delfour 2007; Notarbartolo di Sciara et al. 2008; Cribb et al. 2012; Heenehan et al. 2015, 2017; Tyne et al. 2015, 2017). In Hawai‘i, where long-term population estimates are available, there is evidence that the population has declined over several decades as a result of long-term, sustained anthropogenic pressure (Tyne et al. 2014).

The primary conservation concern is the disruption that chronic and sustained human attention can have on spinner dolphin abilities to enter and maintain rest during their daily cycle. In locations such as the Kona coast of Hawai‘i, spinner dolphins in resting bays are nearly always surrounded by swimmers or vessels (Courbis and Timmel 2009; Tyne et al. 2018), which is of concern because once displaced from their preferred resting bay, they are unlikely to rest elsewhere (Tyne et al. 2015). Reduced periods of rest likely impact nighttime foraging success, affect vigilance and/or raise stress hormones, which can in turn affect rates of survival and reproduction (Tyne et al. 2015; Forney et al. 2017). To the casual observer, such impacts are generally not apparent when viewing or interacting with spinner dolphin pods. This is because spinners often approach and interact with vessels or swimmers, leaving the impression that the pod welcomes the attention, which at certain times may be true, at least for a part of the group. However, these responses can be misleading, particularly when interactions with humans become frequent and chronic and are unregulated.

The potential impacts to spinners resulting from anthropogenic activities can be relayed through an (somewhat "nightmarish") analogy. Imagine living in a quiet neighborhood occasionally visited by an ice-cream truck in the afternoon hours. The children hear the distinctive jingle and excitedly rush toward the truck to indulge in a harmless ice-cream treat. As time passes, however, additional ice-cream trucks begin to visit the neighborhood but now extend their presence into the evening hours, disrupting family bedtime routines by riling up the children who now want ice cream before bed. As additional time passes, even more ice-cream trucks begin showing up in the neighborhood at all hours of the night waking up the kids and disrupting the family's sleep. Powerless to evict the ice-cream trucks, the family must decide whether to stay or find a new neighborhood. Similarly, spinners placed under increasing human pressure in their preferred resting bays eventually must decide whether to abandon the neighborhood for perhaps a less ideal habitat but one with no or fewer human disturbances (i.e., ice-cream trucks).

In many parts of the world, spinner conservation is ultimately a matter of managing interactions with people. Given adequate space, particularly during periods of rest, spinners are likely to be resilient to certain levels of interactions. As with many wildlife-viewing experiences, adapting practices to the behavioral and ecological needs of the animals is the key to making these interactions sustainable. In the case of spinners, this means ensuring they are given the opportunity to get a good day's rest, and so be ready for their all-important nighttime foraging.

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