Evidence for Sleep in Sharks and Rays: Behavioural, Physiological, and Evolutionary Considerations

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Abstract

Sleep is widespread across the animal kingdom. However, most comparative sleep data exist for terrestrial vertebrates, with much less known about sleep in amphibians, bony fishes, and invertebrates. There is an absence of knowledge on sleep in cartilaginous fishes. Sharks and rays are amongst the earliest vertebrates, and may hold clues to the evolutionary history of sleep and sleep states found in more derived animals, such as mammals and birds. Here, we review the literature concerning activity patterns, sleep behaviour, and electrophysiological evidence for sleep in cartilaginous (and bony) fishes following an exhaustive literature search that found more than 80 relevant studies in laboratory and field environments. Evidence for sleep in sharks and rays that respire without swimming is preliminary; evidence for sleep in continuously swimming fishes is currently absent. We discuss ways in which the latter group might sleep concurrent with sustained movement, and conclude with suggestions for future studies in order to provide more comprehensive data on when, how, and why sharks and rays sleep.

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Introduction

Sleep is often a conspicuous behaviour, distinguishable from wakefulness by immobility and postural relaxation, and accompanied by reduced awareness of the local environment. This sleep-related reduced responsiveness can be reversed (to wakefulness) with sufficient stimulation. The propensity to sleep is influenced by the time-of-day (circadian regulation) and prior sleep-wake history. Circadian oscillators (e.g., pineal gland, eyes) are entrained by environmental cues, commonly natural light-dark cycles, to act as pacemakers for the adaptive timing of sleep and wakefulness [Kazimi and Cahill, 1999; Falcón et al., 2007]. Sleep is also homeostatically regulated with lost sleep recovered by sleeping longer and more deeply [Borbély, 1982; Tobler, 2011].

In addition to the behavioural correlates of sleep, sleep is also a brain state. Analysis of brain activity, recorded by the electroencephalogram (EEG), reveals multiple sleep states in mammals and birds, called non-rapid eye movement (non-REM) sleep and REM sleep. Non-REM sleep is associated with high-amplitude, EEG slow waves, while REM sleep is characterised by a wake-like pattern of low-amplitude, high-frequency activity. REM sleep is also associated with signs of reduced skeletal muscle tone, eye movements under closed eyelids, and increased cardiores-

spiratory variability [Aserinsky and Kleitman, 1953; Jouvet et al., 1959; Siegel, 2016]. Unequivocal non-REM and REM sleep have yet to be identified outside of mammals and birds, although some other animals appear to engage in two sleep states, including reptiles [Shein-Idelson et al., 2016; Libourel et al., 2018], zebrafish [Leung et al., 2019], cuttlefish [Iglesias et al., 2019], and flies [van Alphen et al., 2013]. However, the homology of these states (if any) to those in birds and mammals is unclear.

Elasmobranchs: Sharks, Rays, and Kin

Sharks and rays are cartilaginous fishes and living representatives of the earliest jawed vertebrates [Compagno, 1999; Fuss et al., 2014]. They are members of the Elasmobranchii of which approximately 1,000 species are extant today. Fossil records from 450 million years ago suggest that their basic morphology has changed little since their evolutionary appearance [Budker, 1971]. They mostly inhabit marine (and occasionally freshwater) habitats. In contrast to their popular image as mindless killing machines, they have demonstrated cognitive capabilities to match those of other vertebrates [Graeber and Ebbesson, 1972; Hart et al., 2006; Lisney et al., 2012; Fuss et al., 2014].

The variable mechanisms for ventilation are typically used to separate sharks and rays into two physiological groups. In both groups, oxygen-rich water is forced over the gills for gas exchange. However, how this flow comes about differs between these two groups and is directly linked to metabolism and lifestyle. Sharks and rays that rely predominantly on buccal pumping, such as members of the Heterodontiformes and Rajiformes, facilitate respiration by lowering and raising the floor of the buccal cavity. Lowering the floor increases buccal volume and draws oxygenated water into the mouth. The floor is then raised while the mouth is closed, decreasing buccal volume, which pushes the fresh seawater over their gills. This mechanism is also used by many bony (teleost) fishes. By ventilating the gills in this manner, buccal pumping sharks and rays, generally benthic species, can remain stationary for extended periods of time [Roberts, 1978; Carlson and Parsons, 2001; Carlson et al., 2004].

Conversely, more active pelagic species, such as those found in the taxonomic orders Myliobatiformes and Carcharhiniformes (families Mobulidae, Carcharhinidae, and Sphyrnidae) use ram ventilation. That is, these animals maintain forward motion to push oxygenated water into the mouth and over the gills, making these animals obligate swimmers [Brown and Muir, 1970; Wardle,

1985; Carlson et al., 2004]. Some ram ventilating benthopelagic species, including members of the Lamniformes, Squaliformes, and Carcharhiniformes (families Odontaspidae, Squalidae, and Carcharhinidae) are capable of brief periods of inactivity, during which time buccal pumping takes over as the method of ventilation [Brett and Blackburn, 1978; Carlson et al., 2004; Barker et al., 2011; Tomita et al., 2018]. Similarly, more sedentary species, whose primary method of respiration is buccal pumping, may ram ventilate while swimming. These differences, and combinations, in respiration raise interesting questions about sleep in these animals. Notably, when and how do obligate ram ventilating sharks and rays sleep? To begin, we first establish what is known about sleep and circadian rhythms in bony fishes. We then provide a thorough review on the evidence for sleep in sharks and rays. By doing so, we identify the gaps in our understanding about sleep biology in these cartilaginous fishes. We end with a discussion of the hypothetical possibilities for the form sleep might take in sharks and rays, and suggest areas for future research.

Sleep in Bony Fishes

Before moving onto sharks and rays, there is value in a brief review of sleep in the other class of fully aquatic vertebrates, the bony fishes. Studies on sleep in bony fishes are few, and, for the most part, have relied on behavioural criteria to determine the presence or absence of sleep [Campbell and Tobler, 1984; Hartse, 2011; but see Leung et al., 2019]. More is known about sleep in zebrafish (*Danio rerio*) than any other teleost [Zhdanova, 2011]. Sleeping zebrafish do not swim, and instead stay immobile near the bottom, or top, of the aquarium. Like humans, zebrafish are diurnal and respond to extended periods of wakefulness by increasing sleep duration [Yokogawa et al., 2007; Sigurgeirsson et al., 2013; Singh et al., 2017; Pinheiro-da-Silva et al., 2018]. Sleep is also regulated by circadian mechanisms [Zhdanova et al., 2001]. Sleep behaviour is associated with reduced and irregular respiratory rates [Árnason et al., 2015]. A recent report has described two sleep states in young zebrafish [Leung et al. 2019]. The second state is associated with muscle atonia and increased heart rate variability, similar to that observed during REM sleep in mammals; however, unlike mammals, this state occurs in the absence of eye movements [Árnason et al., 2015; Leung et al., 2019]. Thus, the relationship between these states and mammalian and avian REM and non-REM sleep is unclear. Pharmaceuticals that promote,

or inhibit, sleep in humans have similar effects on sleep in zebrafish [Zhdanova et al., 2001; Appelbaum et al., 2009; Sigurgeirsson et al., 2013; Leung et al., 2019], such that the neurochemical pathways regulating sleep appear to be conserved across these distantly related vertebrates.

Behavioural studies on several species of Bermuda reef fishes, and other freshwater fishes, reveal that these species also sleep. Tauber and Weitzman [1969] and Tauber [1974] report that blueheads (*Thalassoma bifasciatum*), Spanish hogfish (*Bodianus rufus*), and many species of wrasse (family Labridae) could be easily handled and lifted to the surface at night, perhaps owing to elevated arousal thresholds while sleeping. Sleep, at least in the form of a circadian rest-activity cycle, has also been observed in rainbow wrasse (*Coris julis*), with animals burying themselves in the sandy substrate, where they remain inactive from dusk till dawn [Videler et al., 1986]. Three-spot wrasse (*Halichoeres trimaculatus*) maintain an endogenous circadian rhythm under a 12:12 h light:dark photoperiod and under constant darkness; sleep-like behaviour (such as decreased locomotor activity and respiratory rates) was induced with melatonin, a sleep-promoting hormone in other diurnal animals [Hur et al., 2012]. Sleep behaviours have been reported in parrot fishes (family Scaridae) with animals retiring under corals [Dubin and Baker, 1982] or secreting a mucus cocoon in which they remained inactive throughout the night [Starck and Davis, 1966]. Perch (*Cichlasoma nigrofasciatum*) [Tobler and Borbély, 1985], goldfish (*Carassius auratus*) [Tobler and Borbély, 1985; Iigo and Tabata, 1996], walleye (*Stizostedion vitreum*) [Ryder, 1977], brown bullhead (*Ameiurus nebulosus*) [Titkov, 1976], and banded knifefish (*Gymnotus carapo*) [Stopa and Hoshino, 1999] ostensibly were sleeping as they could be handled or touched on the tail without eliciting a response.

As eye movements during sleep are a behavioural correlate of REM sleep in mammals, birds, and perhaps lizards, some observations of eye movements during periods of sustained quiescence in Bermuda reef fish raise the possibility of a REM sleep-like state in bony fishes [Tauber and Weitzman, 1969]. Subsequent studies have failed to observe the same phenomenon however [Peyrethon and Dusan-Peyrethon, 1967; Shapiro and Hepburn, 1976]. A novel form of sleep behaviour has been reported in a group of reef fishes (*Dascyllus marginatus*, *D. aruanus*, and *Chromis viridis*) that spend the night in live, hard corals. These fish exhibit an unusual sleep-swimming behaviour characterised by an increased fin stroke frequency to ventilate the coral, while maintaining a stereotypic nocturnal posture [Goldshmid et al., 2004].

Early research into sightless, cave-dwelling species of fishes [Pavan, 1946] suggested that these animals might be sleepless as they show evidence of continuous swimming and lack activity-based circadian rhythmicity. More recent studies, however, contradict this idea. Specifically, while cavefish (*Astyanax mexicanus*) do sleep, they in fact sleep very little, relative to their surface-dwelling conspecifics [Zafar and Morgan, 1992; Duboué et al., 2011, 2012; Yoshizawa et al., 2015; Jaggard et al., 2017, 2018]. Since the transition from a surface-living to cave-dwelling existence has consistently been associated with a large reduction in sleep across several populations, this may suggest that cave-living causes a reduction in the need for sleep. Reduced sleep among populations might arise if less neurologically demanding forms of wakefulness in the simplified cave environment reduce that need. This could be somewhat akin to the local decreases in sleep intensity that have been observed in the human sensorimotor cortex [Huber et al., 2006] and pigeon hyperpallium [Lesku et al., 2011; Rattenborg et al., 2019] following brain disuse during prior wakefulness.

Due to the difficulties recording brain activity in water, very few studies have focused on the electrophysiological correlates of sleep behaviour in bony fishes [Hartse, 2011]. What information is available is limited and warrants replication. A study that focused on modulating brain activity using sound and light in tethered, awake codfish (*Gadus morhua*) found that EEG recordings from the midbrain were dominated by 8–13 Hz waves, which appeared as spindles 0.5–5 s in duration, a pattern that was most pronounced under dark and silent conditions, and suppressed under light and noisy conditions [Enger, 1957]. A study on tench (*Tinca tinca*) found no evidence of a distinctive electrophysiological pattern with sleep behaviour [Peyrethon and Dusan-Peyrethon, 1967]. Conversely, EEG spikes and slow waves from the mid- and forebrain were accompanied by cardiac arrhythmia in sleeping catfish (*Ictalurus nebulosus*) [Karmanova et al., 1981; Karmanova and Belich, 1983].

Clearly, more study is needed to characterise the brain activity correlates of sleep behaviour in bony fishes, and a recently developed method of measuring neural activity using fluorescence in young zebrafish is particularly promising [Leung et al., 2019]. The central nervous system of these transparent animals alternates between synchronous flashes of activity and periods of silence. Interestingly, a second sleep state was also observed in which a burst of neural activity propagates across the neuroaxis. Whether these sleep states are homologous to mammalian and avian non-REM and REM sleep is unclear.

Table 1. Studies containing evidence (or lack thereof) for sleep in sharks and rays

Order	Family	Species	Common name	Evidence			Ref.
				immobility	stereotypic posture	reduced awareness	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus amblyrhynchos</i>	Grey reef shark				1
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus falciformis</i>	Silky shark				2
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus leucas</i>	Bull shark	+		+	3
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus perezi</i>	Caribbean reef shark	+		+	3–5
Carcharhiniformes	Carcharhinidae	<i>Galeocerdo caviar</i>	Tiger shark				5–7
Carcharhiniformes	Carcharhinidae	<i>Negaprion brevirostris</i>	Lemon shark	+		+	3, 8–12
Carcharhiniformes	Carcharhinidae	<i>Prionace glauca</i>	Blue shark	+		+	3, 13, 14
Carcharhiniformes	Carcharhinidae	<i>Triakodon obesus</i>	Whitetip reef shark	+			15–18
Carcharhiniformes	Carcharhinidae	<i>Cephaloscyllium ventriosum</i>	Swell shark	+			19
Carcharhiniformes	Scyliorhinidae	<i>Scyliorhinus canicula</i>	Small-spotted catshark	+			20–23
Carcharhiniformes	Scyliorhinidae	<i>Scyliorhinus stellaris</i>	Nursehound	+			24
Carcharhiniformes	Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead shark		+		25–29
Carcharhiniformes	Sphyrnidae	<i>Sphyrna tiburo</i>	Bonnethead shark	+			30
Carcharhiniformes	Triakidae	<i>Galeorhinus galeus</i>	School shark	+			31
Carcharhiniformes	Triakidae	<i>Mustelus canis</i>	Smooth dogfish	+			32
Hexanchiformes	Hexanchidae	<i>Notorynchus cepedianus</i>	Sevengill shark	+			33
Hexanchiformes	Hexanchidae	<i>Hexanchus griseus</i>	Bluntnose sixgill shark	+			34, 35
Heterodontiformes	Heterodontidae	<i>Heterodontus francisci</i>	Horn shark	+			19, 36
Heterodontiformes	Heterodontidae	<i>Heterodontus portusjacksoni</i>	Port Jackson shark	+			37
Lamniformes	Alpiidae	<i>Alopias superciliosus</i>	Bigeye thresher shark				38, 39
Lamniformes	Cetorhinidae	<i>Cetorhinus maximus</i>	Basking shark		+	+	40, 41, 24
Lamniformes	Lamnidae	<i>Carcharodon carcharias</i>	Great white shark				42–44
Lamniformes	Lamnidae	<i>Isurus paucus</i>	Shortfin mako				45, 46
Lamniformes	Megachasmidae	<i>Megachasma pelagios</i>	Megamouth shark				47
Lamniformes	Odontaspidae	<i>Carcharias taurus</i>	Grey nurse shark		+		48–50
Myliobatiformes	Dasyatidae	<i>Dasyatis pastinaca</i>	Common stingray	+			51
Orectolobiformes	Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	Nurse shark	+		+	5, 24, 52
Orectolobiformes	Rhincodontidae	<i>Rhincodon typus</i>	Whale shark	+			53, 54
Orectolobiformes	Stegostomatidae	<i>Stegostoma fasciatum</i>	Zebra shark	+			55
Squaliformes	Centrophoridae	<i>Centrophorus granulosus</i>	Gulper shark				35
Squaliformes	Etmopteridae	<i>Etmopterus piasius</i>	Smooth lanternshark				35
Squaliformes	Squalidae	<i>Squalus acanthias</i>	Spiny dogfish	-			52
Squaliformes	Somniosidae	<i>Somniosus microcephalus</i>	Greenland shark				56
Squatinaformes	Squatinae	<i>Squatina californica</i>	Pacific angel shark				57

Evidence for sleep has been broken down into seven categories covering both the behavioural and physiological characterisation of sleep. This includes periods of immobility, a sleep-like (relaxed) posture, reduced awareness (or increased arousal threshold) during that state, reversibility of the restful condition to unequivocal wakefulness, the circadian organisation of consolidated immobility (including cyclic, diel diving behaviour), and whether restfulness is homeostatically regulated and associated with changes in brain activity. The absence of a "+" reflects the absence of data for that criterion for that species; the presence of a "-" indicates the lack of evidence for that criterion following an investigation, as seen in the spiny dogfish. In the case of the great white shark, conflicting evidence for circadian organisation has been reported. This table highlights the paucity of comprehensive sleep data for any elasmobranch. References: (1) McKibben and Nelson, 1986; (2) Clarke et al., 2011; (3) Clark, 1973; (4) Chapman et al., 2007; (5) Randall, 1967; (6) Springer, 1963; (7) Tricas et al., 1981; (8) Cortés and Gruber, 1996; (9) Gleiss et al., 2009; (10) Gruber et al., 1988; (11) Morrissey and Gruber, 1993; (12) Nixon and Gruber, 1988; (13) Carey et al., 1990; (14) Scariotta and Nelson, 1977; (15) Barnett et al., 2016; (16) Fitzpatrick et al., 2011; (17) Nelson and Johnson, 1980; (18) Randall, 1977; (19) Nelson and Johnson, 1980; (20) Metcalfe and Butler, 1984; (21) Sims et al., 1993; (22) Sims et al., 2006; (23) Sins et al., 2001; (24) Weber, 1961; (25) Clarke, 1971; (26) Holland et al., 1992; (27) Holland et al., 1993; (28) Klimley et al., 1988; (29) Klimley and Nelson, 1984; (30) Myrberg and Gruber, 1974; (31) West and Stevens, 2001; (32) Casterlin and Reynolds, 1979; (33) Ebert, 1991; (34) Andrews et al., 2009; (35) Clark and Kristof, 1990; (36) Finstad and Nelson, 1975; (37) McLaughlin and O'Gower, 1971; (38) Nakano et al., 2003; (39) Weng and Block, 2004; (40) Shepard et al., 2006; (41) Sims et al., 2005; (42) Bruce and Bradford, 2013; (43) Carey et al., 2007; (44) Weng et al., 1982; (45) Carey et al., 1981; (46) Holts and Bedford, 1993; (47) Nelson et al., 1997; (48) Meffert, 1968; (49) Pollard et al., 1996; (50) Smith et al., 2010; (51) Karmanova et al., 1976; (52) Bigelow and Schroeder, 1953; (53) Gleiss et al., 2013; (54) Rowat et al., 2007; (55) Dudgeon et al., 2013; (56) Stokesbury et al., 2005; (57) Standora and Nelson, 1977.

Fig. 1. Sleep-like behaviours in buccal pumping sharks. Species capable of ventilating the gills via buccal pumping can remain inactive for extended periods of time. A nurse shark (a) and a Port Jackson shark (b) resting in a rocky cave. c Whitetip reef sharks often rest in large, intraspecific congregations. d Lemon sharks are known to sit motionless on the sandy bottom for extended periods of time. Photographs by Yann Hubert/Shutterstock.com (a), Dirk van der Heide/Shutterstock.com (b), Janos Rautonen/Shutterstock.com (c), and Nicolas Voisinn/Shutterstock.com (d).

Evidence for Sleep in Buccal Pumping Sharks and Rays

Sharks and rays are inherently shy and elusive animals, often inhabiting hard-to-reach environments, which are rarely appropriate for sleep-based, experimental research [Heithaus et al., 2002; Papastamatiou et al., 2010]. Replicating the appropriate housing and husbandry to facilitate such studies in captivity also presents its own series of logistical complications. It is no surprise, therefore, that what information is available on this topic is anecdotal or incomplete (Table 1). Moreover, studies involve few animals, of limited phylogenetic diversity, often reaching conclusions only tangentially related to sleep.

With this preface in mind, a number of buccal pumping sharks have been observed either in the wild or in aquaria to have a sleep-like state, or at least a diel activity pattern. The eyelids of a captive nursehound (*Scyliorhinus stellaris*) appear to be half-closed during periods of sustained restfulness when the animal is propped up on

its pectoral and tail fins, and its head rested against a rock or substrate [Weber, 1961]. A captive nurse shark (*Ginglymostoma cirratum*; Fig. 1) is able to spend extended periods of the 24-h day immobile in caves and becomes active only in the evening. Moreover, this species failed to react to scuba divers swimming nearby, at least until one diver pulled its tail, which evoked an escape response [Weber, 1961]. Such behaviours are consistent with observations by Randall [1967] who described wild nurse sharks as “sluggish,” spending much of the daytime resting on the seafloor. Similar to nocturnal nurse sharks, two benthic species, the horn (*Heterodontus francisci*) and swell (*Cephaloscyllium ventriosum*) shark, seemingly sleep during much of the day in both the wild and in captivity [Nelson and Johnson, 1970] (Fig. 2). Night-time swimming and feeding begins with the onset of darkness; *C. ventriosum* maintains diel rhythmicity under constant light and constant dark photoperiodic conditions, whereas *H. francisci* does not. Subsequent work found that *H.*

Fig. 2. Activity patterns of two buccal pumping sharks. Mean activity levels of horn and swell sharks recorded during 8 days of underwater observation at Santa Catalina Island, California. The activity levels of individual sharks were coded as: 0 – complete immobility; 1 – movement but no swimming; 2 – swimming along the bottom; 3 – swimming above the bottom. Although the absence of horn shark data during the day could be due to a lower incidence of daytime sightings, this was not the case for swell sharks, which were observed across the day and night. Reprinted from Nelson and Johnson [1970], with permission from The American Society of Ichthyologists and Herpetologists.

francisci maintains rhythmicity under constant dim light in captivity [Finstad and Nelson, 1975].

Many other sharks also apparently sleep during the day, and exhibit either crepuscular or nocturnal activity, including the small-spotted catshark (*S. canicula*) [Metcalfe and Butler, 1984; Sims et al., 1993, 2001, 2006], the Port Jackson (*H. portusjacksoni*) [McLaughlin and O’Gower, 1971], the zebra (*Stegostoma fasciatum*) [Dudgeon et al., 2013], the Pacific angel (*Squatina californica*) [Standora and Nelson, 1977], the Caribbean reef (*Carcharhinus perezii*), and whitetip reef shark (*Triaenodon obesus*) [Randall, 1967, 1977; Nelson and Johnson, 1980; Chapman et al., 2007; Fitzpatrick et al., 2011; Barnett et al., 2016]. An accelerometry and respirometry-based study found that wild whitetip reef sharks swim up to three times more at night and have a higher metabolic rate at night compared to that during the day under laboratory conditions [Whitney et al., 2007].

Increased activity and feeding rates have been observed in wild lemon sharks (*Negaprion brevirostris*), both during the night and twilight [Gruber et al., 1988; Cortés and Gruber, 1990; Morrissey and Gruber, 1993]; similarly, metabolic rate is higher in captive lemon sharks at night [Nixon and Gruber, 1988]. Using accelerometry, Gleiss et al. [2009] observed extended periods of resting behaviour in wild lemon sharks (*N. brevirostris*). The common stingray (*Dasyatis pastinaca*) reduces its motor

activity at night in captivity [Karmanova et al., 1976], which, to our knowledge, is the only report of a sleep behaviour in a ray. Lastly, we are not aware of any study looking at sleep homeostasis or sleep/wake recordings of brain activity in any cartilaginous fish (Table 1).

Evidence for Sleep in Ram Ventilating Sharks and Rays

Ram ventilating species show more modest (if any) changes in activity patterns. For example, the spiny dogfish (*Squalus acanthias*; Fig. 3) swims continuously in captivity, showing no obvious changes over a 24-h period [Karmanova et al., 1976]. However, a circadian activity pattern does exist in some ram ventilating sharks. Basking sharks (*Cetorhinus maximus*) engage in cyclic diving migrations [Sims et al., 2005; Shepard et al., 2006]. In the wild, they can be observed idly gliding at the surface, basking in the sun (at times ventral-side-up), and can be touched without disturbance [Weber, 1961]. Similar suggestive evidence of increased arousal thresholds has also been reported in four species of wild requiem sharks (*C. leucas*, *C. perezii*, *Prionace glauca*, *N. brevirostris*), two of which (the bull and blue shark) are thought to be obligate ram ventilators, found in an underwater cave off the coast of Mexico. These animals exhibit extended periods of in-

Fig. 3. Ram ventilating sharks. **a** A spiny dogfish shows no evidence of sleep-like behaviour in captivity, and instead swims without interruption. **b** The basking shark may have an elevated arousal threshold during periods of less intense swimming. **c** The great white shark, a known obligate constant swimmer, has shown conflicting evidence regarding any circadian rhythmicity in its activity patterns. **d** Scalloped hammerhead sharks, although never inactive, engage in cyclic, diurnal periods of foraging at night. Photographs by Greg Amptman/Shutterstock.com (**a**), Martin Prochazkacz/Shutterstock.com (**b**), Palomba/Shutterstock.com (**c**), and Tomas Kotouc/Shutterstock.com (**d**).

activity and respond only after rough and excessive handling [Clark, 1973]. Milling behaviour (a form of low level activity, where sharks swim slowly within the same area with frequent directional changes) has regularly been observed in wild grey nurse sharks (*C. taurus*), with animals spending up to 85% of the daytime engaged in this behaviour, with more active swimming and foraging throughout the night [Meffert, 1968; Pollard et al., 1996; Smith et al., 2010]. Milling quickly transitions to rapid avoidance behaviour when approached by divers [Pollard et al., 1996; Smith et al., 2010]. Nocturnal activity patterns have been seen in laboratory studies of the smooth dogfish (*Mustelus canis*) [Casterlin and Reynolds, 1979], and in field studies of the sevengill shark (*Notorynchus cepedianus*) [Ebert, 1991], and the grey reef shark (*C. amblyrhynchos*) with the mean rate of movement doubling at night [McKibben and Nelson, 1986].

Although not compelling evidence of sleep, cyclic diel vertical migrations (DVMs) have been recorded in the

shortfin mako (*Isurus oxyrinchus*) [Carey et al., 1981, 1990; Holts and Bedford, 1993], the blue (*P. glauca*) [Scariotta and Nelson, 1977; Carey et al., 1990], the megamouth (*Megachasma pelagios*) [Nelson et al., 1997], the school (*Galeorhinus galeus*) [West and Stevens, 2001], the bigeye thresher (*Alopias superciliosus*) [Nakano et al., 2003; Weng and Block, 2004], the Greenland (*Somniosus microcephalus*) [Stokesbury et al., 2005], the bluntnose sixgill (*Hexanchus griseus*) [Andrews et al., 2009], the whale (*Rhincodon typus*) [Rowat et al., 2007; Gleiss et al., 2013], and the tiger (*Galeocerdo cuvier*) [Springer, 1963; Randall, 1967; Tricas et al., 1981] shark, and may be evidence of an endogenous circadian rhythm (Fig. 4). These species inhabit greater depths during the day (60–400 m and as deep as 600 m in some species) than during the night (surface to 100 m) (although Gleiss et al. [2013] observed the opposite pattern in whale sharks) and engage in DVMs at dusk and dawn. Descents and ascents do not appear to involve “fly-glide” behaviour (rapid ascents,

Fig. 4. Example of DVMs in a ram ventilating shark. DVMs of a bigeye thresher shark across 4 days. DVM data are superimposed on a 1°C isotherm plot produced from expendable bathythermograph casts. Dark photoperiods are indicated by black, bold lines along the top, horizontal axis. Reprinted from Nakano et al. [2003], with permission from Inter-Research Science Publisher.

slower acute angle descents) [Weihs, 1973], but appear to be powered behaviours due to the angles and speed of ascents and descents [Carey et al., 1990; Nakano et al., 2003]. It is thought that these migrations may be driven by a light-entrained, endogenous rhythm as animals may be following preferred light zones [Nelson et al., 1997].

A number of hypotheses have been proposed around diel migration, including an attempt to reduce predation pressure by avoiding light environments, thermoregulation, hunting tactics, and the following of prey movements. However, the selection of a bioenergetic advantageous environment to facilitate rest may play a role, as seen in the buccal pumping small-spotted catshark (*S. canicula*) which hunts in prey-rich, warmer waters at night and rests in cooler waters during the day, to best facilitate digestion [Sims et al., 2006]. Similar diel patterns of territory occupations have been observed in the silky shark (*C. falciformis*) [Clarke et al., 2011]. One telemetry study of a single, juvenile great white shark (*Carcharodon carcharias*) in the wild found no obvious diel activity patterns [Carey et al., 1982], while later studies found a nocturnal increase in swimming rates [Weng et al., 2007; Bruce and Bradford, 2013]. A study on three species of wild deep-sea sharks (the bluntnose sixgill [*H. griseus*], the gulper [*Centrophorus granulosus*], and the lantern shark [*Etmopterus pusillus*]) also revealed vertical migrations between the euphotic and aphotic zones [Clark and Kristof, 1990].

Wild scalloped hammerhead sharks (*Sphyrna lewini*) gather around a seamount, maintaining a state of relatively low activity during the day, during which time they do not feed, even in the presence of suitable prey. At night, the hammerheads disperse to hunt and feed [Klimley and Nelson, 1984; Klimley et al., 1988]. In the wild, hammerhead pups engage in diurnal refuging behaviour and remain in murky bay water during the day, while venturing out onto reefs to forage at night [Clarke, 1971; Holland et al., 1992; Holland et al., 1993]. Conversely, captive bonnethead sharks (*S. tiburo*) “patrol” throughout the day, and swimming levels (speed and distance covered) decrease at night [Myrberg and Gruber, 1974], although daytime activity may be influenced by daytime feeding. As with buccal pumping sharks and rays discussed above, there have been no systematic sleep studies on any ram ventilating fish. Owing to the absence of comprehensive sleep data on elasmobranchs, we consider next what form sleep could take in these largely unstudied animals.

Hypothesis: Buccal Pumping Sharks and Rays Sleep, Ram Ventilating Fishes Do Not

It has been suggested that buccal pumping sharks and rays sleep, an ability afforded to them by extended periods of restfulness [Compagno, 1988], but that ram ventilating fishes have secondarily lost the need for sleep, due to their

Fig. 5. Unihemispheric non-REM sleep in a bottlenose dolphin (*Tursiops truncatus*). Electrodes were placed over the left (1–3) and right (4–6) cortical hemispheres. The left hemisphere shows an awake EEG (red) while the other hemisphere concurrently shows the high amplitude, slow waves of non-REM sleep (blue). Modified from Mukhametov et al. [1977], with permission from Elsevier.

continuously swimming lifestyle [Kavanau, 1998]. This hypothesis may have stemmed from the fact that animals living in more simplified environments have independently evolved reductions in the amount of sleep, including in cave-living fishes [Duboué et al., 2011; Yoshizawa et al., 2015] and subterranean mole rats [Kruger et al., 2016]. The sensory-impoverished environment of cave-fishes and fossorial rats might foster reduced brain use during wakefulness, thereby reducing the need for sleep. This argument led Kavanau to suggest that obligate ram ventilating sharks might not sleep at all, owing to the reduced visual input experienced for the majority of their lives in open, barren seascapes [Kavanau, 1998].

In our view, the possibility that ram ventilating sharks and rays do not sleep, seems unlikely. Many species of shark, including pelagic species, are known to have excellent visual capabilities [Sabbah et al., 2010; Collin, 2018], playing a role in predatory behaviour, orientation and navigation [Lisney et al., 2012], communication, and social behaviour [Hart et al., 2006]. Moreover, at least some species of sharks show complex learning, similar to that observed in teleost fishes [Fuss et al., 2014].

Importantly, the evolutionary persistence of sleep also makes it unlikely that only some species of shark and ray would have secondarily lost the need for sleep. Sleep is widespread across animals [Lesku et al., 2019], having been found in all species studied by sleep researchers, including several species of arthropods and molluscs, and

even roundworms, flatworms, and jellyfish [Lesku and Ly, 2017; Nath et al., 2017; Omond et al., 2017]. Furthermore, species that routinely sleep little [Ruckebusch, 1972; Gravett et al., 2017] or hardly sleep at all when their ecology demands sustained waking performance [Lesku et al., 2012; Rattenborg et al., 2016], still sleep. Even animals experiencing a heightened risk of predation [Lima et al., 2005], as well as flying birds [Rattenborg et al., 2016, 2019], swimming mammals [Lyamin et al., 2008, 2016], and humans driving motor vehicles [often to unproductive ends; Tefft, 2018], all sleep. The remarkable evolutionary (and ecological) longevity of sleep indicates that it must serve some ancient and important function. Consequently, ram ventilating sharks and rays likely also sleep. What form might that sleep take?

Hypothesis: Buccal Pumping Sharks and Rays Sleep Bihemispherically, Ram Ventilating Fishes Sleep Unihemispherically

In the earliest known study on sleep in sharks, Weber [1961] commented that while not all fishes display conspicuous behavioural changes between day and night, such animals might instead sleep while swimming. Similar to ram ventilating sharks and rays, many marine mammals also swim continuously, and yet sleep. In terrestrial mammals, non-REM sleep is accompanied by an almost

complete behavioural shutdown while slow waves occur in both cerebral hemispheres. Conversely, cetaceans swim while sleeping with one-half of their brain at a time, or unihemispherically (Fig. 5). Unihemispheric non-REM sleep is the main form of sleep in cetaceans, and each hemisphere is independently capable of showing wake-related or non-REM sleep EEG activity. During unihemispheric sleep, the eye neurologically connected to the hemisphere showing slow waves is typically closed, while the other eye remains open. Cetaceans use the open eye to visually monitor the local environment [Goley et al., 1999; Sekiguchi et al., 2006]. In this way, cetaceans, and perhaps some sharks and rays, can obtain the benefits of sleep while swimming.

Other marine mammals, including otariid seals, walruses, and manatees [Lyamin et al., 2008], are also capable of generating interhemispheric differences in brain activity during sleep. Interestingly, in seals there are phylogenetic and respiratory differences that might have relevance to understanding how buccal pumping and ram ventilating sharks and rays obtain a daily amount of sleep. Earless seals (family Phocidae) retain the bihemispheric non-REM sleep patterns of their terrestrial ancestors, even when sleeping in seawater. However, eared seals (family Otariidae) sleep predominantly bihemispherically while on land but exhibit more asymmetric (more cetacean-like) non-REM sleep in the water [Lyamin et al., 2016]. Otariid seals use this interhemispheric asymmetry to keep their nares above the surface of the water to breathe. The flipper neurologically connected to the more awake hemisphere remains in the water, paddling slowly, while the other flipper is motionless. This interesting situation between the sleep patterns of phocid and otariid seals raises the possibility that buccal pumping sharks and rays might retain a bihemispheric form of sleep, whereas ram ventilating sharks and rays might have evolved the ability to sleep unihemispherically. By advancing this idea, we do not mean to suggest that sharks and rays engage in non-REM sleep per se, but rather that one hemisphere might show a shark sleep-related EEG pattern, while the other shows the signature of wakefulness.

Instead of sleeping with an interhemispheric difference in brain state in the case of unihemispheric sleep, sharks and rays might sleep with an *intra*hemispheric difference in brain activity. In humans and rats, sleep and wake-like brain activity can occur simultaneously in different parts of the brain in an outwardly sleeping animal [Nir et al., 2011; Nobili et al., 2011; Vyazovskiy et al., 2011]. In humans with epilepsy who have been implant-

ed with deep brain electrodes for chronic recordings, the motor cortex appears to reveal wake-like activity, while the dorsolateral prefrontal cortex exhibits non-REM sleep [Nobili et al., 2011]. As non-REM sleep accrues across the night (and the need for sleep diminishes), the occurrence of “local wakefulness” increases. Similar results have been found in recordings of the healthy rat brain [Vyazovskiy et al., 2011], indicating that this phenomenon in humans is unrelated to epilepsy, but rather reflects a general feature of the mammalian brain. This mix of wake and sleep EEG activity might provide clues to how sharks and rays sleep. Interestingly, a small group of neurons control the lateral movements of the tail to maintain forward propulsion in bony fishes [Thiele et al., 2014]. If this were true in sharks and rays, then they might sleep in a piecemeal manner, wherein much of the telencephalon can sleep, while the few pathways that control the tail remain awake. Of course, it is also possible that all sharks and rays sleep with their whole-brain at a time, but ventilate passively using favourable water currents.

Hypothesis: Ram Ventilating Fishes Sleep in Currents

It is possible that currents play a role in permitting restfulness and sleep in ram ventilating sharks and rays. Animals facing into currents would have oxygenated water passively pushed over their gills facilitating respiration and allowing the animals to remain motionless or maintain a low level of, or indeed no, swimming activity. This may explain reports of normally obligate ram ventilating sharks resting on the seafloor off the coast of Mexico [Clark, 1973]. It was reported by local divers that strong currents could be felt at the times when large numbers of sharks were found to be inactive; however, the orientation of the sharks relative to the direction of the current was not reported. Furthermore, the sharks were observed passively pumping water over their gills rather than allowing the current to passively do so. Klimley and Nelson [1984] found no evidence that milling hammerheads changed their position or swimming direction at a seamount in response to changes in current direction. Similarly, Carey et al. [1990] reported that blue sharks did not swim against currents when recording their vertical and horizontal movements in the water column. To our knowledge, no other observations have been reported regarding inactivity in ram ventilating sharks associated with currents. Hence, although plausible, this idea requires further investigation.

Conclusion

For a taxon of vertebrates consisting of over 1,000 species, studies on only 33 species of sharks, and on a single ray, contain data potentially related to sleep. Furthermore, no single study has focused specifically and comprehensively on sleep, but rather often on the circadian organisation of swimming or anecdotes about responsiveness to stimulation. It is also clear that the fundamental biology of elasmobranchs is poorly understood. Specifically, the degree to which buccal pumping and ram ventilating sharks and rays exist as distinct categories is unclear. Some species thought to be obligate swimmers can show reduced activity, or even become inactive for short periods of time by switching their mode of ventilation. Thus, more research is needed to understand how many species are in fact obligate constant swimmers, and when and why swimming sharks and rays become quiescent. Furthermore, it remains unknown whether extensive periods of restfulness in buccal pumping sharks and rays can be considered sleep or simply quiet wakefulness. Unfortunately, none of the studies covered in this review answer these questions. To do so, future work must include a systematic investigation into the presence or absence of sleep, preferably on a broad range of elasmobranchs. This would include investigating the persistence of circadian activity patterns in both buccal pumping and obligate swimming species, along with measuring arousal thresholds, and testing for the homeostatic regulation of restfulness to distinguish sleep from quiet wakefulness in sedentary species. The inclusion of other measurements, such as respiration rates, oxygen consumption, and heart rate also should be included in any description

of sleep in sharks and rays. Finally, there has never been a study investigating sleep/wake changes in EEG activity in cartilaginous fishes. Identifying sleep using measures of brain activity is the most reliable method available, as behaviour alone can sometimes be misleading, or at least, incomplete [Aulsebrook et al., 2016]. Among living vertebrates, sharks and rays best resemble the earliest jawed vertebrates, and so describing sleep in these animals may provide new insight into the evolution of sleep in other, more derived vertebrates.

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