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Vertical habitat and behaviour of the bluntnose sixgill shark in Hawaii

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ABSTRACT

Bluntnose sixgill sharks are apex predators and scavengers that are near-globally distributed in slope and shelf habitats, but many aspects of their behaviour and ecology are poorly understood. A better understanding of how oceanographic variables influence sixgill shark behaviour may help predict their distribution, response to increasing anthropogenic stressors including climate change, and role in ecosystems throughout their geographic range. We used satellite telemetry to observe the vertical behaviour of four bluntnose sixgill sharks in the subtropical oligotrophic waters of Hawaii. A strong diel vertical movement cycle was observed, with sharks spending nighttime in thermocline waters and descending into the oxygen minimum zone in daytime. Depth changes generally occurred between nautical twilight and sunrise/sunset. Dive initiation and dive completion were significantly correlated with nautical dawn and sunrise, respectively. A stepwise generalised estimating equations model was used to investigate vertical speeds in the daytime and nighttime depth habitats, and this analysis revealed that photic zone light level was the primary factor correlated with vertical speed. Outside of the depth transitions, higher vertical speeds were observed when photic zone light was low, suggesting more active foraging in the shallow nighttime habitat than the deep daytime habitat.

1. Introduction

1.1. Overview

Large deep-water sharks are likely to play an important role in deep slope ecosystems throughout the world, but a thorough understanding of their ecological importance is hindered by critical knowledge gaps about their biology and behaviour. For shark species that exhibit tropical submergence, habitat and behaviour are much better documented in temperate latitudes, where they inhabit shallow water and are more accessible for study (Andrews et al., 2007; Dawson and Starr, 2009; Hulbert et al., 2006; Williams et al., 2010). There are few published studies of deep-water shark behaviour and habitat use from the tropics and sub-tropics, where species such as *Somniosus pacificus*, *Echinorhinus cookei*, and *Hexanchus griseus* inhabit shelf, slope, canyon and other deep environments (Compagno, 1984). Understanding depths of occurrence and the associated temperatures, light levels and oxygen concentrations in these deeper habitats will improve our ability to predict species occurrence and potential anthropogenic impacts throughout a species' geographic range.

Environmental parameters such as light and temperature are potential drivers of behaviour that vary depending on location, and understanding behavioural relationships with these parameters will help define a global habitat range for widely distributed deep-water species such as the bluntnose sixgill shark (*H. griseus*; hereafter referred to as the sixgill shark). Unpublished work on sixgill sharks in Hawaii has provided preliminary information on their depth range and vertical movements (Grubbs et al., 2008), but detailed information on vertical behaviour and relationship to the physical ocean environment in a deep-water habitat has been absent from the literature.

1.2. Habitat and behaviour

The sixgill shark is a Hexanchiform shark with a large geographic range. This species appears to inhabit almost all tropical and temperate continental shelves as well as islands, seamounts, and the mid-ocean ridges (Compagno, 1984; Crow and Crites, 2002). Previous research suggests that its depth range varies significantly depending on geographic location (Andrews et al., 2009; Carey and Clark, 1995; Crow et al., 1996; Yeh and Drazen, 2009).

To date, most studies of sixgill shark behaviour have been limited to productive estuarine systems where the sharks are present in shallow water (Andrews et al., 2007; Andrews et al., 2009; Dunbrack, 2008; Dunbrack and Zielinski, 2003). In the temperate estuary of Puget Sound, WA, sixgill sharks displayed diel vertical movements ranging from 15 to 250 m depth (Andrews

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et al., 2009). These sharks remained close to the seafloor most of the time, but they were also observed swimming higher in the water column (Andrews et al., 2009). In the nearby Strait of Georgia, sixgill sharks were observed moving upslope from depths of about 200–300 m and utilising habitat less than 40 m in depth, but this behaviour was only observed in summer months (Dunbrack and Zielinski, 2003). It has been suggested that the seasonality of behaviour could be due to thermal response or a reproductive cycle (Dunbrack and Zielinski, 2003)

Few studies have focused on the behaviour of specimens occurring in a deeper habitat. Two adult female sixgill sharks were tracked over short time scales (2–4 d) by active acoustics on the deep slope of sub-tropical Bermuda (Carey and Clark, 1995). The sharks showed no discernible patterns in vertical movement, and stayed close to the seafloor at about 600–700 m with deeper excursions down to 1500 m. Since the tracks were short, the stress of recent capture may have affected the behaviour of these individuals (Hoolihan et al., 2011). In Hawaii, sixgill sharks have been observed in the mid to deep-slope habitat via longline surveys (Crow et al., 1996), baited cameras (Yeh and Drazen, 2009), and satellite telemetry (Grubbs et al., 2008). Satellite telemetry has revealed diel depth shifts, a depth range of about 225–700 m, and an upper thermal limit of about 17 °C (Grubbs et al., 2008).

1.3. Potential environmental drivers of movement

Though sixgill sharks are found across a wide range of latitudes and depths, there could be common environmental drivers of their behaviour, habitat selection and movements. For example, movement patterns of fish have previously been explained by factors including light (Nakano et al., 2003), thermal habitats (Perry et al., 2005), turbulence (Bakun and Parrish, 1982), food availability (Barnett et al., 2010), and bioenergetic advantage (Sims et al., 2006). If environmental drivers of behaviour patterns such as diel vertical movements (DVM) and vertical activity levels are defined, those relationships can help predict sixgill shark depth habitat and behaviour in various ecosystems and geographic locations.

Diel vertical movement is a common behaviour pattern for a wide range of pelagic organisms (e.g., Rudjakov, 1970; Neilson and Perry, 1990; Watanabe et al., 1999; Benoit-Bird et al., 2009). While small organisms often move vertically to access food at night and avoid visual predators during the daytime (Boden and Kampa, 1967), larger-bodied apex predators may additionally use DVM to follow a migrating prey source, thermoregulate, or avoid bright light input to sensitive eyes adapted for dark conditions. For example, the basking shark *Cetorhinus maximus* has adapted to undergo vertical movements to follow the movements of its prey (Sims et al., 2005); the small-spotted catshark *Scyliorhinus canicula* hunts in warm water and rests and digests in cool water (Sims et al., 2006); and multiple species have been observed following isolumes in the ocean (Nelson et al., 1997; Nakano et al., 2003; Weng and Block, 2004, Dewar et al., 2011). In a temperate habitat, foraging behaviour was found to be an important factor associated with diel vertical movements of sixgill sharks. Foraging behaviour was more consistent with the observed vertical movements than competition or bioenergetics advantage (Andrews et al., 2009).

In this study we aimed to clarify the depth and thermal habitat of bluntnose sixgill sharks in the Hawaii region, to determine behavioural relationships with the physical variables of temperature, oxygen and light, and to elucidate which variables are most important in explaining variability in depth and vertical speed.

2. Methods

2.1. Tagging and data recovery

Sixgill sharks were captured on the southern and western slopes of Oahu, Hawaii (Fig. 1) using a bottom-set longline with 20 hooks baited with fish. The animals in the present study were captured between July 2011 and March 2012. Nighttime sets were at 300–350 m and retrieved just before dawn, while daytime sets were at 500–600 m and retrieved at sunset. Planned set times ranged from 8 to 14 h.

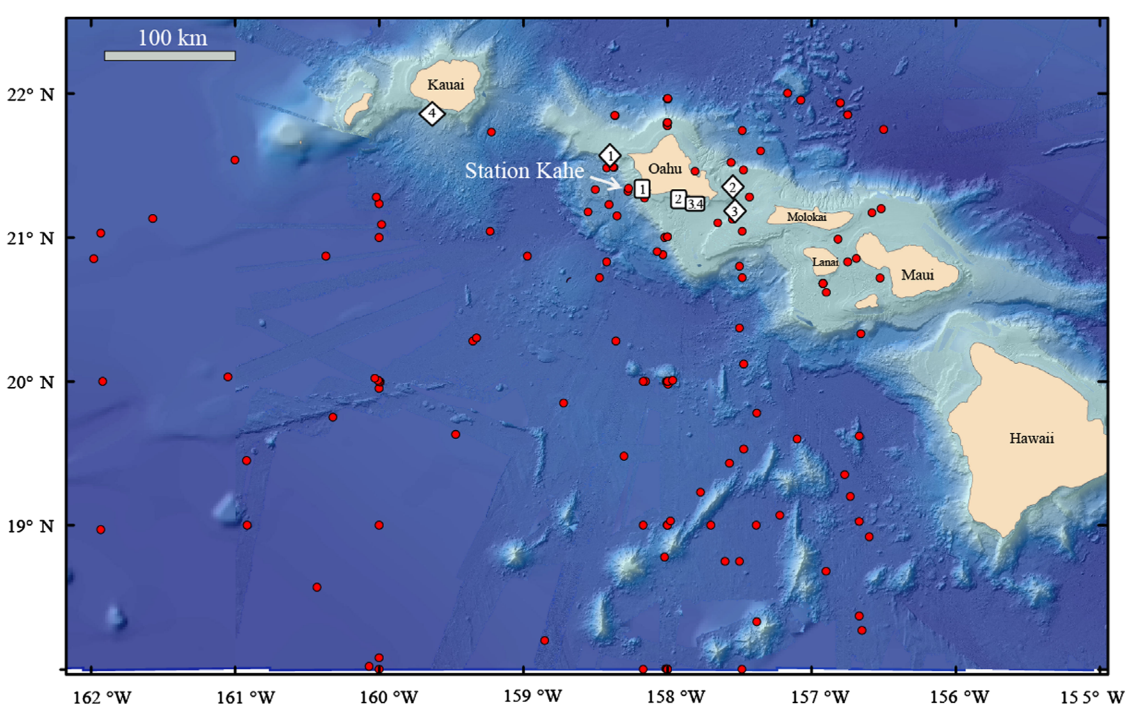

Fig. 1. Map of the study area. Squares represent shark captures; diamonds represent shark pop-up locations; red circles represent oxygen data stations from World Ocean Database and Hawaii Ocean Time-Series.