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Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean

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Aggregations in the distribution of individuals are an almost universal phenomenon in living organisms. Groups of animals that display collective coordinated movement without forming stable social bonds such as fish schools are a special type of aggregation. In tropical tuna fisheries, aggregating behaviour is directly exploited through the use of artificial fish aggregating devices (FADs). Hence, understanding the dynamics of schooling behaviour and the potential impacts of FADs upon it may have ramifications for tuna management. As a novel way of quantifying spatiotemporal co-occurrences of animals, we applied network statistics to acoustic tracking data to identify the co-occurrences of individual yellowfin tuna, *Thunnus albacares*, in an array of FADs and determine the frequency and temporal dynamics of these co-occurrences. We observed large interannual variation in movement rates of tuna between FADs, and corresponding interannual variability in the mean number of spatiotemporal associates for each individual as well as the temporal stability of associations. When movement rates were high, associations within FAD aggregations decayed to randomness three times faster than when movement rates were lower. This raises the possibility that if FADs are sufficiently close for fish to perform frequent between-FAD movements, school mixing may be increased and cohesion reduced.

Aggregations in the distribution of individuals are an almost universal phenomenon in living organisms of all sizes, from bacteria to whales (Parrish & Edelstein-Keshet 1999). They can be considered as part of a continuum of group integration, ranging from highly territorial organisms with minimal group interaction on one end to social animal groups with strong, long-lasting bonds between individuals (Parrish et al. 2002) such as groups of primates (Flack et al. 2006) or marine mammals (e.g. Baird & Whitehead 2000) on the other. Aggregations in which animals display collective coordinated movement without forming stable social bonds such as flocks of birds, insect swarms and fish schools fall somewhere between these two extremes (Parrish et al. 2002).

The behaviour of schooling fish has been the subject of many studies, both empirical (e.g. Ward et al. 2002) and theoretical (reviewed in Giardina 2008). Yet, while the last few decades have seen a vast amount of data collected on the movement of free-ranging animals that display some degree of collective motion (Cooke et al. 2004), the analytical approaches for quantifying collective movement from these data are relatively limited. With a few exceptions (Minta 1992), the majority of studies either determine temporal synchronicity of movement parameters such as speed or movement angle through time series decomposition (Polansky et al. 2010; Polansky & Wittemyer 2010), ignoring spatial locations, or calculate home range overlap, which uses spatial locations but ignores the temporal dimension inherent in movement data (e.g. Dillon & Kelly 2008; Schuttler et al. 2012).

Network statistical analysis has emerged as a powerful tool for improving our understanding of animal interactions, particularly in fission/fusion societies, in which groups are highly dynamic and frequently split and reform (James et al. 2009). Since it relies on the temporally explicit observation of associations between individuals, to date, it has mostly been applied to determine the structure of groups of highly social species such as primates (Flack et al. 2006), insects (Fewell 2003) and marine mammals (e.g. Baird

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& Whitehead 2000). In these species associations can generally be defined by socially meaningful interactions such as grooming, performing tasks together or being sighted together in social groups. The definition of what constitutes an association, however, is open, which means that network analysis is highly flexible and adaptable to a number of applications, beyond the analysis of social networks. By defining an association as two individuals being present at the same spatial location at a given time, network analysis allows the quantification of synchronous movement, which includes both spatial and temporal information from animal location data, collected using a range of techniques from simple visual surveys to highly sophisticated acoustic telemetry. We used network analysis to determine patterns of co-occurrence of acoustically tagged yellowfin tuna, *Thunnus albacares*, in a network of fish aggregating devices (FADs) equipped with acoustic receivers.

Tropical tuna are among a number of pelagic fish species that are known to aggregate around floating objects (Fréon & Dagorn 2000; Castro et al. 2002), forming large, multispecies aggregations (Schaefer & Fuller 2005). While the biological or evolutionary advantage of the association of tuna with floating objects is not known, several hypotheses have been proposed (Fréon & Dagorn 2000; Castro et al. 2002). One of these is the meeting point hypothesis, which suggests that tuna associate with FADs to increase encounter rates with other individuals (Dagorn & Fréon 1999; Fréon & Dagorn 2000; Soria et al. 2009). If this is the case, floating objects play an important role in tuna aggregation behaviour.

The aggregation behaviour of tuna around floating objects has been exploited by tuna fishermen for decades, originally by fishing around natural floating objects such as logs and since the 1980s, by deploying both drifting and moored artificial FADs to enhance catch rates (Fréon & Dagorn 2000; Moreno et al. 2007). This practice has rapidly become an integral part of tropical tuna fisheries the world over and official numbers state that in 2009, 95% of all floating objects utilized by tuna fishermen in the Eastern Pacific Ocean were man-made and 98.5% of the total bigeye, *Thunnus obesus*, 68% of the total skipjack, *Katsuwonus pelamis*, and 15% of the total yellowfin catch were captured at FADs (IATTC 2010). Hence, understanding the dynamics of tuna aggregations at floating objects is important for determining whether this anthropogenic increase in floating object density might have a lasting impact on tuna behaviour (Soria et al. 2009).

While several studies have monitored the behaviour of individual tuna associated with floating objects (Holland et al. 1990; Cayré 1991; Marsac & Cayré 1998; Itano & Holland 2000; Girard et al. 2004; Ohta & Kakuma 2005; Schaefer & Fuller 2005; Dagorn et al. 2007), none of these studies have attempted to quantify the collective movement of tuna in FAD aggregations beyond the description of synchronous departures from and arrivals at a FAD (Klimley & Holloway 1999; Ohta & Kakuma 2005). In this study we used passive acoustic tracking to observe the presence of tropical tuna in an array of 13 FADs around the Hawai'ian island of Oahu. We analysed these data using network analysis to (1) identify the spatially and temporally explicit co-occurrences of individual tuna and (2) determine the frequency and temporal dynamics of these co-occurrences to elucidate the emergent structure and stability of the tuna aggregations. Combining the results from this novel application of network analysis with information on between-FAD movement, we attempted to identify the potential influence of artificial FADs on tuna school cohesion and mixing.

METHODS

Data Collection

The Division of Aquatic Resources of the U.S. state of Hawai'i maintains an array of 56 anchored FADs in the Hawai'ian archipelago to enhance the pelagic fishery. Thirteen of these FADs that surround the Hawai'ian island of Oahu (Fig. 1) were equipped with VR2 (Vemco, Halifax, Canada) automated acoustic receivers by the University of Hawai'i. Receivers were mounted directly to the FAD mooring system 18 m below the surface with the hydrophone element in a downward orientation. Acoustic receivers can detect uniquely coded VEMCO transmitter tags when within detection range of the receivers. Range testing showed the detection range to vary between approximately 600 and 1100 m depending on local conditions. Minimum depth at the FADs was approximately 560 m. Receivers were operational throughout the deployment period, continuously collecting and storing data of the date and time of presence of tagged individuals. The data used in this study are from 86 yellowfin tuna captured at seven of the 13 FADs (Fig. 1). Tuna were captured within 500 m of FADs using surface trolling lures or baited lines with circle hooks fished to a depth of approximately 75 m. Single hooks with crimped barbs were used to minimize damage and expedite release of the fish. Immediately after capture, fish were placed in a wetted, padded cradle where the hook was gently removed and the eyes covered with a wet artificial chamois material while a saltwater hose was inserted in the mouth to provide oxygen to the gills. Tags were only placed in healthy fish with no significant bleeding from the mouth and no injury at all to the eyes or gills. We inserted tags in the peritoneal cavity using standard fish tag implantation techniques (e.g. Meyer et al., 2000; Schaefer & Fuller 2002; Robert et al. 2012b). A scalpel was used to make a 1–2 cm long incision in the muscle of the abdominal wall 3–5 cm anterior to the anus and 2–3 cm to one side of the ventral midline. To avoid possible damage of organs by the scalpel, final entry into the abdominal cavity was made using a latex gloved finger to rupture the peritoneal lining. A coded Vemco V16 tag (69 kHz, V16-4H-R256, 5–30 s delay, rated battery life 344 days) was then inserted in the peritoneal cavity and the wound closed with two absorbable sutures. Tag weight was approximately 24 g, which constitutes an average of 0.84% and a maximum of 3.4% of

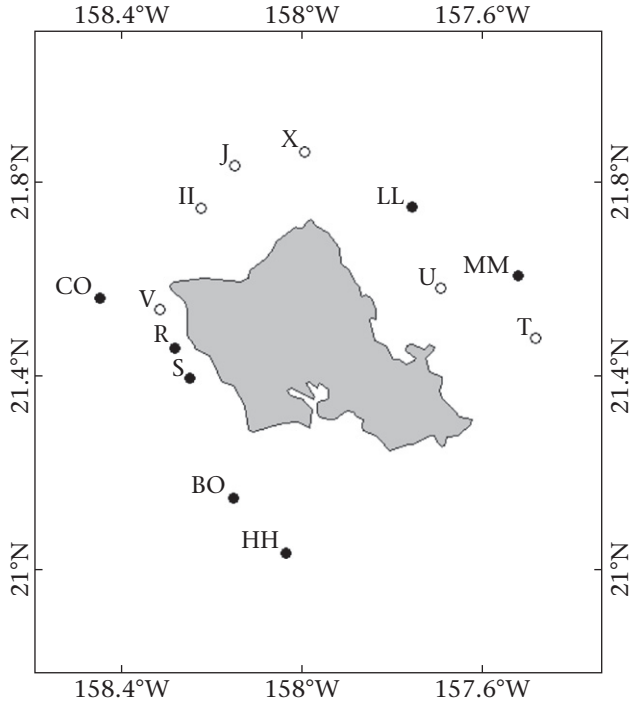

Figure 1. Map of the FAD array around the island of Oahu equipped with automated acoustic receivers. Filled circles indicate FADs where fish were tagged.