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The aggregation of tuna around floating objects: What could be the underlying social mechanisms?



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HIGHLIGHTS

- Identify which mechanisms are most likely to reproduce fish aggregations dynamics under FOBs.
- Dynamics and distributions of populations of behavioral models were compared to observations.
- Results challenge the common vision these aggregations.
- Social interactions should be incorporated to reproduce the temporal patterns observed.
- The characterization of these mechanisms is a priority for science-based fishery management.

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ABSTRACT

Several empirical and theoretical studies have shown how the exploitation of food sources, the choice of resting sites or other types of collective decision-making in heterogeneous environments are facilitated and modulated by social interactions between conspecifics. It is well known that many pelagic fishes live in schools and that this form of gregarious behavior provides advantages in terms of food intake and predator avoidance efficiency. However, the influence of social behavior in the formation of aggregations by tuna under floating objects (FOBs) is poorly understood. In this work, we investigated the collective patterns generated by different theoretical models, which either include or exclude social interactions between conspecifics, in the presence of two aggregation sites. The resulting temporal dynamics and distributions of populations were compared to in situ observations of tuna behavior. Our work suggests that social interactions should be incorporated in aggregative behavior to reproduce the temporal patterns observed in the field at both the individual and the group level, challenging the common vision of tuna aggregations around FOBs. Our study argues for additional data to further demonstrate the role of social behavior in the dynamics of these fish aggregations. Understanding the interplay between environmental and social factors in the associative behavior of fish with FOBs is necessary to assess the consequences of the widespread deployment of artificial FOBs by fishermen.

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1. Introduction

Understanding the spatiotemporal distribution and dynamics of wild animals remains a challenge for biologists. A particular question concerns the high densities of animals observed at certain specific points in space, e.g., aggregations (Camazine et al., 2001). A substantial literature is dedicated to the study of these patterns that appear in the wild for a wide range of taxa from

bacteria to humans (Sumpter, 2010). The ultimate behavioral causes of an aggregation can be very diverse and include feeding strategies, reproduction and resting (Krause and Ruxton, 2002; Parrish and Edelstein-Keshet, 1999). Several lines of evidence indicate that the underlying mechanisms often result from the interplay between environmental and social factors (Canonge et al., 2011; Capello et al., 2011; Camazine et al., 2001). To disentangle these driving factors (social and environmental), both experimental and modelling approaches are usually carried out. Through multi choice experiments (Canonge et al., 2011; Dussutour et al., 2004; Jeanson et al., 2004a), the role of social behavior is demonstrated when one option is selected by the population, while a scattering of individuals among the distinct options rather

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suggests responses to environmental stimuli (including competition for resources). In parallel, models taking into account social interactions and environmental preferences allow the identification of individual mechanisms that can generate the observed collective patterns (Jeanson et al., 2004b; Meunier et al., 2006).

In our study, we focus on one type of aggregation that is widely utilized by fishermen to enhance their catches: the aggregation of pelagic fish species under objects floating at the surface of the ocean (hereafter called FOBs). Thousands of individuals from several species can be found under a single piece of wood (such as a log) (Castro et al., 2002; Hunter and Mitchell, 1967; Taquet et al., 2007b). Among these species, tropical tunas (skipjack—*Katsuwonus pelamis*, yellowfin—*Thunnus albacares*, bigeye—*Thunnus obesus*) have received great attention in the last two decades, as more than half of the tropical tunas landed in the world by purse seine fisheries are caught when they are associated with FOB's (see Dagorn et al., 2013 for a review). The use of electronic tags (acoustic tags and archival tags) has allowed the investigation of the behavior of tunas in an array of FOBs (Bach et al., 2003; Brill et al., 1999; Cayré, 1991; Cayré and Marsac, 1993; Dagorn et al., 2000a, 2007; Girard et al., 2004; Govinden et al., 2013; Holland et al., 1990; Klimley and Holloway, 1999; Marsac and Cayre, 1998; Mitsunaga et al., 2012; Ohta and Kakuma, 2005; Robert et al., 2012; Schaefer and Fuller, 2002, 2010; Taquet et al., 2007a), showing in particular that a tuna alternates between associative and unassociative phases (Dagorn et al., 2007; Govinden et al., 2013; Robert et al., 2012; Schaefer and Fuller, 2010). Individual residence times around floating objects (associative phase), as well as the times between two consecutive associations with a FOB (unassociated phase), are highly variable, ranging from a few minutes up to several months (Dagorn et al., 2007; Ohta and Kakuma, 2005; Mitsunaga et al., 2012). This variability is found at the individual level, as the same tuna can switch between short (few days) and long (few weeks) residence times depending on the local conditions around the FOB (e.g., prey availability, presence of conspecifics, abiotic conditions) (Robert et al., 2013a). The reasons why tuna associate with these structures and the underlying mechanisms are still poorly understood (see Freon and Dagorn, 2000 for a review). This behavior might rely on environmental cues, and one hypothesis often mentioned in the literature proposes that tuna use drifting objects to stay in contact with food-rich water masses. Indeed, natural floating objects are abundant in river mouths or concentrate in frontal zones offshore, two areas known for their high biological productivity (indicator log hypothesis—Marsac et al., 2000). A second hypothesis, the “meeting point hypothesis”, indicates that such surface heterogeneity could enhance the encounter rate between individuals or schools, allowing the formation of schools or increasing their sizes (Dagorn and Freon, 1999; Freon and Dagorn, 2000). In this scenario, floating objects would have an important role in the process of fusion between schools. Recent experiments support the existence of social interactions in the aggregation processes of fish with FOBs. The meeting point hypothesis has been experimentally validated for small pelagic species such as bigeye scad (Soria et al., 2009). In tuna, a first trial of a field-based binary choice experiment has highlighted the asymmetrical distribution of the population between two close and identical FOBs (Fig. 1), suggesting the existence of social interactions (Robert et al., 2013b). In terms of the dynamics, this experiment has indicated an alternation of the winning FOB (the FOB that aggregated most of the biomass) over time. Temporal variation of the winning FOB in an array of FOBs has also been observed for other species that aggregate under FOBs (Capello et al., 2012). The departure of substantial numbers of tuna from a FOB has been observed by fishermen (Moreno et al., 2007), and acoustic tagging has highlighted synchronicity in the departure of several fish associated

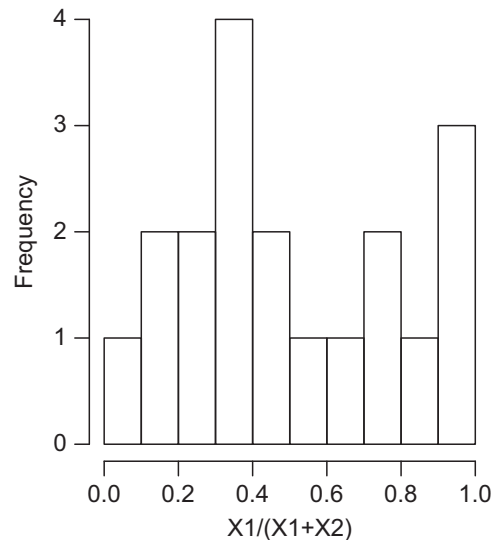


Fig. 1. Frequency of the distribution of populations between two close and supposed identical FOBs ($X_1/(X_1+X_2)$) observed in a binary choice experiment (Robert et al., 2013b).

with the same floating object (Klimley and Holloway, 1999; Dagorn et al., 2007; Govinden et al., 2013). Those observations suggest (but do not demonstrate) social synchronization in the departure process of fish from FOBs.

The objective of this work is to identify which mechanisms are most likely to reproduce the behavioral patterns of tuna aggregations around FOBs at both the individual (highly variable residence times and alternate of associated and unassociated phases) and the group levels (asymmetrical alternate distribution and synchronicity in departure), mentioned above (See Table S1 which summarized the information described above in the form of actual targets for the modeling outcomes). Several modeling approaches co-exist in the literature: from detailed descriptions of individual mechanisms to population level modeling, and from short (e.g., minutes) to long time-scales (years). We developed a model at an intermediate time-scale (e.g., days and weeks) where the overall objective is to link individual behavior to collective patterns. Generally, in such cases, individuals are considered as “black boxes” with transition probabilities between different states where their behavior is modeled from a phenomenological point of view (e.g., no emphasis on the underlying sensory systems of detection), with the objective of exploring the resulting emergent collective pattern.

We developed a theoretical approach where the mechanisms proposed in the literature to explain the aggregative behavior of tuna around FOBs are translated into phenomenological functions. We first applied a non social model, which was the common vision of tuna behavior around FADs (Hilborn and Medley, 1989). Second, the application of a well-known retention model (model which has been mainly studied by entomologists (Ame et al., 2006; Jeanson and Deneubourg, 2009)) constitutes a first attempt to involve social interactions in the aggregative behavior of tuna around FOBs. The objective of the third model is to identify the condition to observe synchronism in departure from the FOBs. The synchronization pattern is a main characteristic of the meeting point hypothesis (Dagorn and Freon, 1999; Freon and Dagorn, 2000). Previous works, mainly on vertebrates, have focused on short time-scale modeling (second, minute) of the synchronization in departure observed in sheep and primates (Petit and Bon, 2010). In such a short time-scale description, the departure is isolated from the global dynamics. Here we developed another phenomenological model of synchronous departures where the dynamics (departures and returns) are integrated into the global dynamics of

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