Availability: 2 October 2013
IOTC-2013-WPTT15-INF05

Journal of Experimental Marine Biology and Ecology 440 (2013) 238–243

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Does social behavior influence the dynamics of aggregations formed by tropical tunas around floating objects? An experimental approach

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ARTICLE INFO

Article history:
Received 18 July 2012
Received in revised form 17 December 2012
Accepted 7 January 2013
Available online xxxx

Keywords:
Aggregation
Binary choice
FADs
Social behavior
Tuna

ABSTRACT

Tropical tunas associate with objects floating at the surface of the ocean, a behavior widely exploited by fishers. However, the respective roles played by environmental variables and behavioral processes (e.g., social behavior) in the formation of these aggregations remain elusive. To investigate the role of social behavior in the dynamics of such aggregations, we used the binary choice approach. The experimental design comprised two close and identical anchored fish aggregating devices (FADs) equipped with an echo sounder buoy to monitor the aggregated biomass of tuna under each device. Analysis of the results entailed characterizing whether the aggregated biomass is distributed asymmetrically (indicative of social behavior playing a role in the dynamics) or symmetrically between the two close and identical FADs, and comparing the results with theoretical distributions based on different definitions of basic units (individual fish or small schools). The results suggest that social interactions underlie aggregation processes, which represents a major advance in our understanding of these aggregations, a priority for science-based fishery management. While recognizing the logistical and technical constraints, we encourage the development of experimental studies (e.g., in which animals are presented with controlled situations) to enhance our understanding of the behavior of large pelagic fish.

1. Introduction

Aggregation patterns can be defined as the gathering of individuals at a specific point in space leading to a local density higher than that observed nearby (Camazine et al., 2001). This phenomenon has been observed in a wide range of species, ranging from bacteria to vertebrates (Ben-Jacob et al., 1998; Chowhury et al., 2004; Couzin and Krause, 2003). The ultimate causes of aggregation can be very diverse, ranging from reproduction, feeding, and sheltering, to defense against predators (Camazine et al., 2001; Krause and Ruxton, 2002; Parrish and Edelstein-Keshet, 1999; Sumpter, 2010). Aggregations can result from two mechanisms, namely attraction and/or retention processes. The inflow of individuals can essentially produce large aggregations at a specific point in space despite the individual's short residence time. In contrast, retention of individuals leads to an increase in population density even if the degree of inflow is low (Ame et al., 2006; Girard et al., 2004). Two main factors can influence these two processes. Aggregation can either be an epiphenomenon resulting from individual and independent responses to environmental stimuli, or be emergent properties resulting from mutual attraction between individuals (Ame et al., 2004; Fretwell and Lucas, 1970; Sumpter, 2006). In the case of social species, several lines of evidence indicate that the formation of aggregations usually depends on both environmental factors and mutual attraction (Bayard and Elphick, 2010; Jeanson and Deneubourg, 2009). Different vectors may be involved in the detection of heterogeneity and the information transfer among individuals (Sumpter et al., 2008) in the form of chemical (Wertheim et al., 2005), visual (Goth and Evans, 2004), or mechanical (Faucher et al., 2010; Krause and Tegeder, 1994) cues.

One example, which is the focus of this study, is the large aggregations of tropical tunas and other marine fish species below objects floating at the surface of the ocean (Dagorn et al., 2012; Hunter and Mitchell, 1967; Ritz et al., 2011). While the ultimate causes of the associative behavior of pelagic fish with floating objects have received great attention [for review, see (Castro et al., 2002; Freon and Dagorn, 2000)], relatively little research has focused on the mechanisms driving aggregation. Answering this question has gained increased importance as fishers take advantage of this evolutionary aggregative behavior by deploying man-made floating objects, also called fish aggregating devices (FADs), to increase their catch. Currently, tuna catches employing these natural and artificial floating structures account for 40% of the world tropical tuna catches (Dagorn et al., 2012; Miyake et al., 2010).

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http://dx.doi.org/10.1016/j.jembe.2013.01.005

Two main hypotheses have been proposed to explain why tuna associate with floating objects. The first one stipulates that natural floating objects might help tuna to stay in contact with rich feeding areas, as logs originate from river flows and drift within these rich water masses or concentrate in rich oceanic frontal zones [i.e., the indicator log hypothesis, (Hall, 1992)]. The second hypothesis states that such surface heterogeneities may constitute important features that enhance the encounter rate among fishes (or fish schools) and contribute to the fusion process between schools [i.e., the meeting point hypothesis, (Dagorn and Freon, 1999; Freon and Dagorn, 2000)]. These two hypotheses are not mutually exclusive.

The interplay between social behavior and response to external stimuli in the aggregation of fish with floating objects has been shown in a small pelagic fish species (Capello et al., 2011), but has not been demonstrated in tropical tunas, which are the main species exploited around FADs across the world. Although tropical tunas are known to form schools (a well known form of social behavior), in particular around floating objects (Doray et al., 2007; Moreno et al., 2007), this does not necessarily mean that social behavior plays a major role in their dynamics when they are associated with one floating object.

The objective of this study was to determine whether social behavior is involved in the dynamics of tuna association with floating objects. Such an objective can only be achieved through an experimental approach, which is usually a challenge in the pelagic realm. The binary choice approach is an experimental design used in behavioral ecology to identify the extent to which individual decisions of movement are influenced by the presence of conspecifics (Jeanson and Deneubourg, 2009). Several studies using the binary choice approach have employed arthropods (Canonge et al., 2011; Deneubourg and Goss, 1989; Dussutour et al., 2004; Jeanson et al., 2004; Seeley, 1995), and also fish, mainly from laboratory experiments on small species to investigate habitat selection strategies, influences of informed individuals on group decisions, accuracy of group decisions with increasing group size, and other phenomena in which group size and characteristics might be involved (Dill et al., 2003; Gomez-Laplaza, 2006; Krause and Godin, 1994; Svensson et al., 2000; Viscido et al., 2004; Webster et al., 2008).

2. Materials and methods

2.1. Experimental design

The experimental setup consisted of two identical anchored FADs separated by less than three nautical miles (5 km). Two pairs of FADs were used, one on the southeast coast of D'Arros Island and one on the north coast of Desroches Islands, in the Amirantes archipelago of the Seychelles (Western Indian Ocean). Those two pairs of FADs were separated by 30 km. Table 1 indicates the geographical position, the anchored depth, and the date of the FAD deployment for each setup. All FADs had the same design with the surface structure being a series of approximately 20 small buoys attached to a single rope.

Two main methods have been used in the past to estimate the biomass of tuna under floating objects: catches from purse seiners (based on the assumption that the seine operation captures the entire aggregation or the same proportion – in average – of the aggregation), and scientific acoustic surveys (Doray et al., 2008; Josse et al., 1999, 2000). Whereas the first method has an evident impact on the aggregation, the second one is limited by the obligatory presence of a vessel (equipped with a scientific echo sounder and/or sonar) at the FAD. In recent years, tropical tuna purse seine fishery has started to use echo sounder buoys attached to floating objects to monitor the amount of aggregated biomass. This equipment allows observations over several weeks or months. In this study, we used SATLINK echo sounder buoys (SATLINK, Madrid Spain, www.satlink.es) to assess the amount of tuna biomass aggregated under each FAD. Each buoy was equipped with a Simrad ES10 sounder, which operates at a frequency of 190.5 kHz with a power of 140 W. At half power (−3 dB), the half angle of the beam is 20°, whereas at −15 dB, this angle is 33° (nominal value). The range extends from 3 to 115 m, with a transducer blanking zone running from 0 to 3 m. The echo sounder provides 10 different vertical layers, each with a depth of 11.2 m. At an angle of 33°, the cone of observation under the buoy has a diameter of 5.92 m and 68.13 m at depths of 10 and 115 m, respectively. The sounder was programmed to operate for 40 s every 2 h. During this period, 32 continuous pings are sent from the transducer and an average of the backscattered acoustic response is computed and kept in the buoy. Acoustic backscatter was transformed into biomass estimates (in tons) using the algorithm developed by the manufacturer (SATLINK, Madrid Spain, www.satlink.es), based on the target strength of skipjack tuna. Two precautionary measures were taken to reduce potential bias on tuna biomass estimates. Sv lower than −45 dB were automatically removed because they likely correspond to organisms smaller than tuna (e.g. organisms of the sound scattering layers (Josse and Bertrand, 2000; Josse et al., 1998; MacLennan and Simmonds, 1992; Oshima, 2008)). We then removed acoustic signals from the first two depth layers (3–25.4 m) because these depths are mainly occupied by non-tuna species, usually forming the by-catch of purse seiners when they are set on floating objects (Lopez et al., 2010). Data were recorded every 2 h, stored in each buoy, and transmitted every day via Inmarsat-C.

Scientific acoustic observations of the tuna's schooling behavior around floating objects indicate that tuna schools commonly navigate within a radius of 400 m around the object (Doray et al., 2006; Moreno et al., 2007). Therefore, the best estimates are obtained when tuna pass under the buoy when it is in operation (40 s, 32 continuous pings every 2 h). Because it is not possible to know this information, we used the maximum biomass recorded every day as a proxy for characterizing the daily aggregated biomass of tuna.

Table 1
Experimental setup. GPS coordinate of each FAD, anchored depth, and time–date of deployment.

Setup	Latitude	Longitude	Depth	Date
Desroches FAD 1	5°34.049′S	53°40.408′E	928 m	September 30, 2009
Desroches FAD 2	5°35.303′S	53°40.918′E	936 m	September 30, 2009
D'Arros FAD 1	5°30.057′S	53°25.045′E	639 m	October 10, 2009
D'Arros FAD 2	5°32.752′S	53°25.728′E	960 m	October 10, 2009

2.2. Data analysis

Several metrics were calculated to characterize the experimental results. Let X_1 be the maximum daily biomass in tons, recorded under FAD 1 of a setup, and X_2 the maximum daily biomass in tons, recorded under the second FAD of this setup. Therefore, for each setup, X_1+X_2 represents the sum of the maximum biomass aggregated under both devices each day (hereafter referred to as the total aggregated biomass). For each observation day, we then calculated and plotted the fraction of the total aggregated biomass under one of the two FADs $[X_1/(X_1+X_2)]$, hereafter referred to as FX_1. Some errors in satellite transmissions occurred over the two-month experimentation. Combined with the experimental protocol that requires obtaining estimates of aggregated biomass for the 2 FADs of each setup on a given day, this resulted in only 19 days of observations (7 days at D'Arros and 12 days at Desroches).

Analyses of data involved characterizing how the maximum daily biomass distributes between the two FADs of each setup. A binomial and symmetrical distribution of individuals in a sequence of independent experiments suggests that the behavior is not governed by any social interaction but likely by the individual responses to environmental heterogeneities. Indeed, from a theoretical point of view of the Ideal Free Distribution related to habitat selection, individuals tend to minimize conflicts of interests, and therefore partition symmetrically under two identical and close FADs (Fretwell and Lucas, 1970; Sutherland, 1983). Therefore, in a non-social system in a homogeneous environment, $FX_{1,}$ the fraction of the total aggregated biomass under one of the two FADs, approaches 0.5. On the contrary, binary choices with a skewed partitioning of individuals between identical sites evidence the contribution of amplification processes through positive social interactions, e.g. fish around a FAD attract conspecifics and/or the individual probability of leaving a FAD decreases with the number of conspecifics around it. Such behavior leads to amplification process in the sense that a small change in the population around a FAD is amplified time step after time step, resulting in an asymmetrical partitioning of the fish between both FADs (Jeanson and Deneubourg, 2009). In a sequence of independent experiments, the corresponding distribution of individuals shows a large standard deviation and in the case of a strong inter–attraction, this distribution reaches a bimodal distribution.

The statistical analyses consisted of comparing observations with the null hypothesis of the absence of social interactions. This null hypothesis is based on a binomial distribution centered on 0.5, which leads to a symmetrical distribution of the aggregated population between the two identical FADs of a setup. Calculation of the binomial distribution requires the speciation of the total number of basic units to be distributed under FAD 1 and FAD 2 of a setup. Unfortunately, the echo sounder buoys used in the experiment only provided the acoustic energy by depth layer (no echogram with acoustic schools), precluding us from assessing the number of schools (and their respective biomass) under each FAD. Nevertheless, the total aggregated biomass (X_1+X_2 in tons) can be defined as the sum of individual tuna or by the sum of a number of schools of similar biomass. We therefore derived a sensitivity analysis by generating a binomial distribution using an individual fish as the basic unit, and a second one using schools of 1 t (200 individuals of 5 kg each) as the basic units [see (Dagorn et al., 2000; Gerlotto et al., 2010) for a similar use of school units in models].

A relevant way of summarizing the pattern observed in the experiment, especially when total aggregated biomass varies trough time, is to report the maximum daily biomass recorded under the winning FAD (the FAD that aggregates most of the biomass) against the total aggregated biomass (Astudillo Fernandez et al., 2010; Mailleux et al., 2011). Using this approach, in order to test if the observed distributions correspond to a binomial one, we computed the proportion of observations that were outside (≥) the 95% confidence interval obtained from each theoretical binomial distribution (generated using individual fish or 1–t schools). The 95% confidence intervals of the binomial distributions were calculated using the 0.95 and 0.05 quantiles (qbinom function in R).

3. Results

Maximum daily aggregated biomasses ranged from 1 to 36 t of tuna (with a mean and standard deviation of 13.5 ± 11.1 t for the D'Arros setup and 12.1 ± 9.7 t for the Desroches setup). Fig. 1 shows the histogram of the distribution of $FX_{1,}$ the fraction of the total aggregated biomass under one of the two FADs $[X_1/(X_1+X_2)]$, for each setup and for both setups analyzed jointly. The histogram of FX_1 at the D'Arros setup has a mode of approximately 0.4, indicating frequent situations in which both FADs aggregate the same amount of biomass. Nevertheless, the histogram also illustrates several days on which one of the two FADs aggregated more biomass than the other (Fig. 1a). The experimental histogram of the Desroches setup clearly indicates frequent situations in which one FAD aggregates the majority of the biomass (Fig. 1b). The distribution resulting from both setups analyzed jointly also highlights a similar pattern. The shape of the histograms of FX_1 and the raw data (Figs. 1c and 2) indicated that in each setup, each FAD was, at least one time, the FAD attracting most of the biomass (the winning FAD).

When the theoretical binomial distribution (corresponding to the null hypothesis) was calculated using the assumption of individual fish, 83%, 71%, and 78% of the observed biomasses under the winning FAD were outside the 95% confidence interval for the Desroches, D'Arros, and both setups analyzed jointly, respectively (Fig. 3a, c, e). Using the second assumption (1–t schools), the theoretical binomial distribution was over-dispersed. In this case, 50%, 29%, and 42% of the observations were outside the 95% confidence interval of the binomial distribution for the Desroches, D'Arros, and both setups analyzed jointly, respectively (Fig. 3b, d, f). A further relevant feature that can be mentioned is that differences between the observations and theoretical binomial distributions increase with increasing total aggregated biomass, suggesting an amplification phenomenon.

4. Discussion

Among the hypotheses formulated to explain why fish associate with floating objects, the meeting point hypothesis involves social behavior (Freon and Dagorn, 2000). The existence of social behavior in the aggregation process of fish with floating structures has been experimentally validated for the big-eye scad (*Selar crumenophthalmus*) using acoustic tagging and modeling (Capello et al., 2011; Soria et al., 2009). However, the influence of social interactions in the aggregation of tuna with floating objects has not been experimentally tested. This study represents the first investigation to employ a field-based and long-term binary choice experiment to study the association of tuna with floating objects.

Our results indicate that the observed distribution of the tuna biomass between two close and identical FADs supports the existence of asymmetrical distribution of tuna biomass under floating structures. Indeed, important proportion of the observations were outside the 95% confidence interval of the theoretical binomial distributions (for both assumptions of individual fish and 1-t schools), traducing a symmetrical distribution of the biomass between the FADs. Moreover, this asymmetric pattern tended to increase with increasing aggregated biomass. Two main explanations can be given to interpret the existence of both asymmetrical and symmetrical distribution of tuna biomass: a temporal environmental heterogeneity between the two FADs and/or the existence of social interactions.

The FADs used in our experiments have exactly the same design, were deployed at the same time (same life time), and were anchored on the same substrate between depths of 600 and 900 m (Table 1). Moreover, the two FADs in each setup were placed 5 km apart, a spatial scale at which we can consider that the characteristics of the water column (e.g., water temperature and dissolved oxygen) are comparable. Despite our limited knowledge on prey distribution and dynamics in the pelagic environment, we can reasonably assume that at a very small scale (e.g., 5 km), the biotic environment is homogeneous. It is therefore rather unlikely that the asymmetric distribution of biomass between the two FADs is simply the result of environmental heterogeneity, unless the attractiveness of the two FADs is inversely correlated during a few consecutive days.

In the case of a choice between identical sites, an asymmetrical distribution can only be produced through social inter-attraction (Camazine et al., 2001). A further argument favoring an underlying social process relies on the increasing differences between observations and theoretical binomial distributions with increasing aggregated biomass. This suggests inter attraction between units (nonlinear interaction), whereby an increase in the number of units leads to an amplification process. Although the schooling behavior of small pelagic fishes has been well documented (Brehmer et al., 2007; Petitgas et al., 2001; Trenkel et al., 2009), almost no information exists on the schooling behavior of tropical tunas. Our work highlights the urgent need for better knowledge of the social behavior of

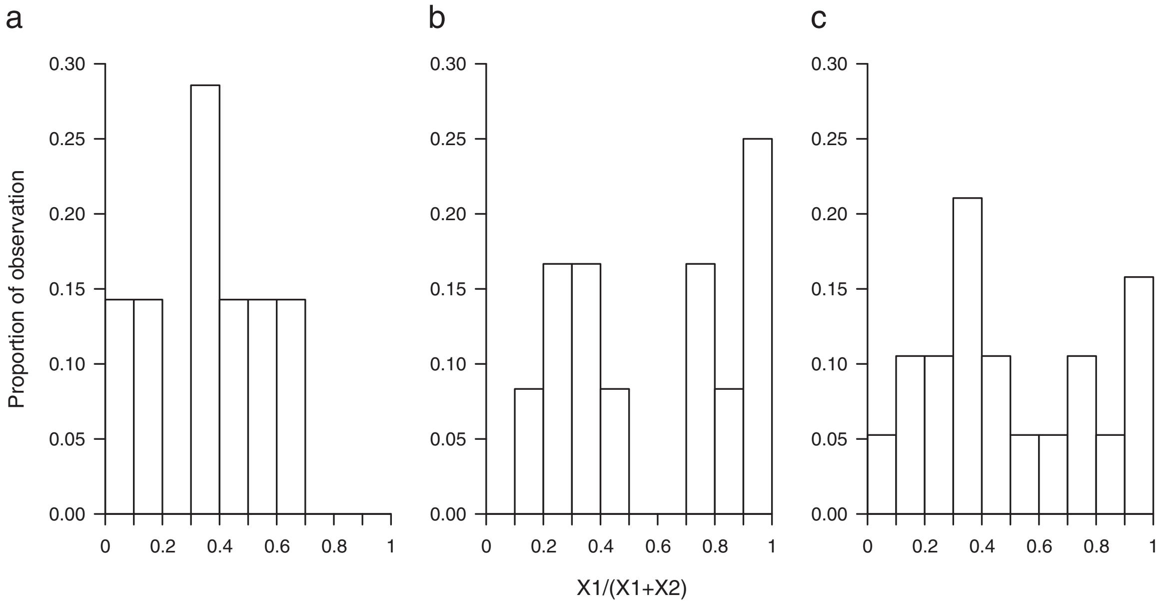

Fig. 1. Normalized histogram of FX_1, the fraction of the total aggregated biomass under one of the two FADs $[X_1/(X_1+X_2)]$, for the D'Arros setup (a), the Desroches setup (b), and both setups analyzed jointly (c).

these species. Details observation on schooling behavior and schools characteristics (number and size) that arrive at a FAD and leave a FAD are crucial for quantifying the extent to which social behavior influences the aggregation process. Indeed, the standard deviation of the binomial distribution depends on the grain of the basic units, which, in turn, influence the differences between the observed and expected distributions. The standard deviation of the binomial distribution is small when a large number of basic units are distributed between the two FADs (the assumption of individual fish leads to the distribution of 200 to 7000 units). In contrast, the resulting binomial distribution is over-dispersed when the dynamics at FADs consist of a smaller number of basic units (1 to 36 units among the two FADs). The observed symmetrical distributions do not discredit the role of conspecifics in the aggregation dynamics as several theoretical studies demonstrated that with small population sizes or stochasticity in individual decisions rules, an equal distribution between identical sites is also a solution of social systems. In contrast, in the case of a choice between identical sites, an asymmetrical distribution can only be produced through social inter-attraction (Camazine et al., 2001). Replicates of this investigation, with additional observations on the individual fish behavior and local conditions, are required to unequivocally refute the hypothesis of environmental heterogeneity being a causal factor and to confirm the role of social behavior.

We implicitly assumed that tuna could visit both FADs, considering the range of a tuna's daily excursions away from a FAD [ranging from 5 to 10 nautical miles (9–18 km)] highlighted by several active tracking experiments in the world (Cayré, 1991; Girard et al., 2004; Holland et al., 1990; Marsac and Cayre, 1998). However, coupling the binary choice experiment with acoustic tagging of individuals would provide useful information for estimating the rate of exchange between the two FADs of a setup. In addition, it appears essential to simultaneously observe the tuna prey densities in the vicinity of each FAD (through acoustic survey) and all non-tuna species associated with each FAD through underwater visual census (Taquet et al., 2007). However, these techniques require the presence of scientists on the field, and are difficult to conduct on a daily basis over long periods (e.g. two months). The development of automated instruments would considerably facilitate such experiments. The use of echo sounder buoys is currently the only possible method for frequent monitoring of the biomass of tuna around a floating object over long time periods. The huge number of buoys regularly purchased by fishers could represent one form of validation of these

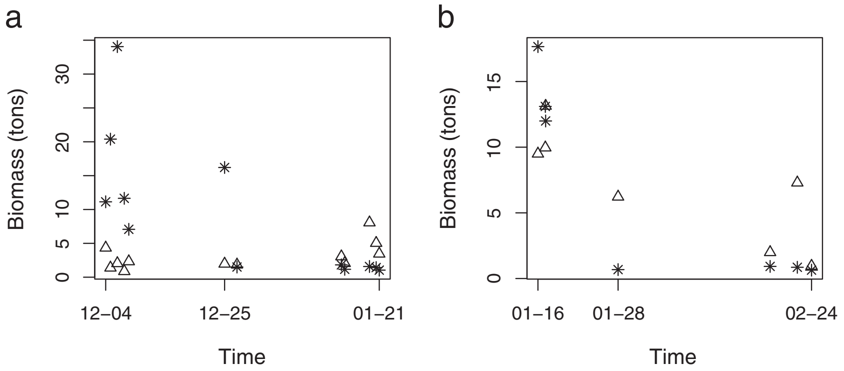

Fig. 2. Maximum daily biomass recorded under the FADs through time for (a) Desroches and (b) D'Arros setup. Black triangles and stars represent biomass recorded under the two FADs. Time is given as month–day.

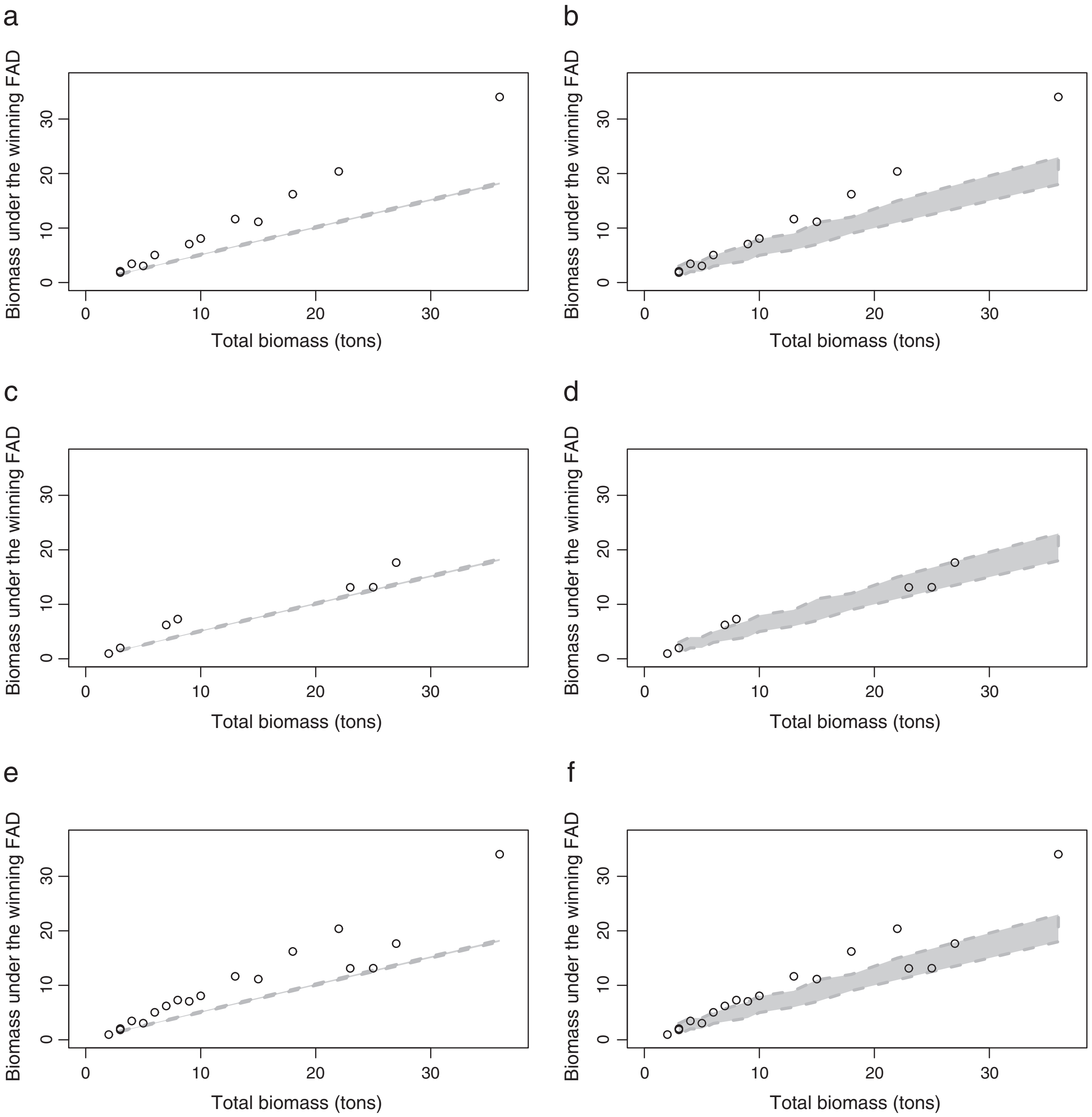

Fig. 3. Maximum daily biomass aggregated under the winning FAD (the FAD with most of the biomass) against the total aggregated biomass (X1 + X2). Dots represent the data and gray polygons, 95–50% confidence interval of the binomial distribution. Two assumptions on schooling behavior are presented. (a, c, and e), isolated fish; (b, d, and f), schools of 1 t (cluster of 200 individuals); (a and b) represent the Desroches setup, (c and d) represent the D'Arros setup, and (e and f) represent both setups analyzed jointly.

buoys. Accordingly, scientific studies should be developed to quantitatively assess the accuracy of the estimated biomass provided by these buoys.

Interpretation of field-based experiments are often more uncertain than laboratory studies, for which all additional variables are under control. However, difficulties in performing and unequivocally interpreting field-based experiments should not discourage scientists from performing these studies. Indeed, such studies can provide valuable insights into the behavioral ecology of organisms that cannot be easily maintained in captivity, or when setups require spaces that cannot be controlled.

Fishing around floating objects has become the main strategy used by tropical tuna purse seiners (Dagorn et al., 2012). Fishers are deploying increasing numbers of FADs, leading to larger catches of small tunas and by-catch (compared to fishing on free-swimming schools of tunas). Assessing the impacts of the use of FADs on the populations of tropical tunas has become a priority to ensure sustainable fisheries. In order to define efficient management measures, scientists must identify the mechanisms that drive these aggregations, and, in particular, the respective roles of ecological (e.g., environmental variables) or ethological (e.g., social behavior) processes. Experimental studies, although difficult to perform in the pelagic realm, should be encouraged to determine the processes that drive fish aggregations.

Acknowledgments

The authors are deeply indebted to John Filmalter, Fabien Forget, and the staff of the Seychelles Fishing Authority for their help in the construction and deployment of the experimental setups, and to the D'Arros Center of Research and the Desroches Hotel for logistical support. Data analysis were carried out with financial support from the Commission of the European Communities, specifically the RTD program of Framework Programme 7, "Theme 2-Food, Agriculture, Fisheries and Biotechnology," through the research project, MADE (Mitigating Adverse Ecological Impacts of Open Ocean Fisheries) and by the Alice and David Van Burren Foundation. This report does not necessarily reflect the views of the Commission and in no way anticipates the Commission's future policy in this area. **[RH]**

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