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First field-based experiment supporting the meeting point hypothesis for schooling in pelagic fish

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Aggregations of fish around fish aggregation devices (FADs) have been widely described in the literature; most commercial catches of tuna by surface fisheries are performed around FADs, taking advantage of this behaviour. The meeting point hypothesis (MPH) suggests that fish could make use of FADs to increase the chance of encounters between conspecifics, helping individuals to form larger schools. To attempt a validation of the MPH, we performed an experiment in the field to test the following predictions: (1) fish spend more time at FADs than at any other random points and therefore aggregate around FADs, and (2) fish arrive at FADs as isolated individuals or in small groups and leave them in larger groups. Our investigation involved acoustic telemetry techniques commonly used to observe fish at FADs. The study was carried out on a small pelagic fish species, the bigeye scad, *Selar crumenophthalmus*, in Saint-Paul's Bay (Reunion Island). Our results validated our two predictions: FADs acted as retention points, increasing the encounter rate of fish and enhancing schooling behaviour, thereby supporting the meeting point hypothesis. FADs could be beneficial to the fitness of the associated fish, promote increased school size and hence confer the advantages of being in a larger group. The impact of the deployment of large number of FADs in some ocean regions is reinterpreted in light of our results.

Group formation is a widespread phenomenon throughout the animal kingdom. This social behaviour can be a permanent trait or occur only during some seasons or some parts of the life cycle. Swarming insects, schooling fish, flocking birds and herd mammals all illustrate this behaviour. Different reasons for grouping have been proposed, including decreasing the predation risk, promoting optimal foraging, increasing reproductive success and facilitating migration and learning. There is a large body of literature on the dynamics of group size (including optimal group size) based on experimental observations and modelling (Mangel 1990; Giraldeau & Caraco 1993; Zemel & Lubin 1995; Parrish & Hamner 1997; Bonabeau et al. 1999; Fréon & Misund 1999; Krause & Ruxton 2002). However, the processes responsible for the dynamics of group formation and dispersion in the wild are poorly documented. Splitting or dispersion of a group can come from individual decisions or result from processes linked to predation, foraging activity, loss of sensory contact or habitat features. The homogeneous and expansive nature of certain habitats, such as the marine pelagic domain, favours dispersion. Hence, for gregarious fish species some processes must enhance the gathering of individuals. The simplest way to meet is to go to the same place at the same time, which is trivial for territorial species, but not so obvious for nomadic animals such as pelagic fish. This matter has led to studies of the impact of fish aggregating devices (FADs) on fish behaviour and biology (Gooding & Magnusson 1967; Castro et al. 2002; Dempster & Taquet 2004). The use of FADs in tropical ocean fisheries is massive and, in the last 10 years, has been responsible for 50–70% of the total purse-seine catch of tuna in the western Indian Ocean (Fonteneau 2003). At any given time in this region, 2500 FADs are estimated to be in use (Moreno et al. 2007). This led to the hypothesis that FADs may act as ecological traps (Marsac et al. 2000; Schlaepfer et al. 2002; Hallier & Gaertner 2008). Under this hypothesis, the proliferation of FADs could cause fish to stay too long around FADs even when local conditions are unfavourable for feeding, affecting their biology (e.g. growth).

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Dagorn & Fréon (1999) proposed the meeting point hypothesis (MPH) to explain how tropical tuna could enhance the aggregation of isolated individuals or small schools in vast environments. This hypothesis suggests that fish could make use of floating objects to increase the chance of encounters between conspecifics, helping individuals to form larger schools. Fréon & Dagorn (2000) generalized this hypothesis to other marine species and other types of associations. However, thus far, no field data have been obtained to validate it. Here, we investigated the MPH through the study of the spatial dynamics of individual fish around FADs. Using a small pelagic fish species, the bigeye scad, *Selar crumenophthalmus*, in Saint-Paul's Bay (Reunion Island), we aimed to test the following predictions: (1) fish spend more time at FADs than at any other random points, and (2) fish arrive at FADs as isolated individuals or in small groups and leave them in larger groups. If fish spend more time at FADs than around any random point, and if simultaneity of departure from a FAD is higher than that of arriving at a FAD, one could consider that FADs increase the encounter rate of fish and enhance schooling behaviour. Our investigation involved acoustic receivers and coded transmitters, a technique commonly used for observing associated fish (Klimley et al. 1988; Ohta & Kakuma 2005; Dagorn et al. 2007; Girard et al. 2007; Taquet et al. 2007).

METHODS

Species and Study Site

Bigeye scad is a ubiquitous cosmopolitan species that occurs mostly in clear coastal waters in tropical and subtropical regions and naturally aggregates around coastal FADs (Roos et al. 2007). This carangid is an obligate schooling fish species, travelling in compact groups of hundreds or thousands of fish (Soria et al. 2007). As such, this species appears to be an appropriate candidate for investigating the MPH.

The study took place in Saint-Paul's Bay, Reunion Island, an open sandy bay with a surface area of about 8 km^2. Fifteen different artificial structures were already present in the bay, anchored in water 15–50 m deep (Fig. 1). Some were small shallow-moored FADs specifically deployed for enhancing commercial fish capture; others were marker buoys delimiting a private aquaculture facility, a submerged shipwreck and two aquaculture cages, one with fishes fed daily (Fig. 1), without any increased attractive effect on bigeye scad (results not shown). The distance between adjacent structures ranged between 120 and 1020 m.

Stationary Acoustic Array

Acoustic receivers were deployed at FADs and at random points away from the FADs, called control stations or CSs (Fig. 1). To monitor the behaviour of fish around FADs, we used coded acoustic tags and acoustic receivers (VR2) from Vemco (Vemco, Halifax, Canada). In situ range tests indicated that 80% of signals emitted during 1 h were detected at a range of 150 m. We therefore defined this distance as the maximum range of reliability of the acoustic receivers.

To monitor all FADs, we deployed nine VR2s in total (seven covering individual FADs and two covering groups, containing two and five FADs, respectively). From here on, the term FAD is used to refer to the floating structure(s) equipped with an acoustic receiver. We also deployed seven VR2s on CSs (Fig. 1). Receivers were fixed either to mooring ropes or on the bottom, mounted on anchored bases consisting of tyres filled with concrete (Taquet et al. 2006). Receivers on the bottom were installed 1 m above the seabed with no surface structure to avoid creating new attraction devices. The distance between adjacent FADs ranged from 310 to 1140 m. For

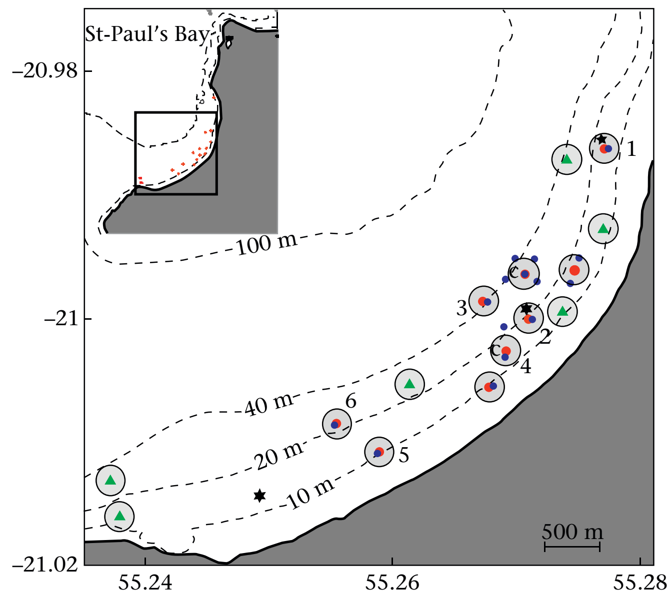

Figure 1. Map of Saint-Paul's Bay with location of FADs (blue dots). The nine FADs equipped with VR2 Vemco receivers are identified (red disks) with their area of detection (outlined circles). The positions of the seven VR2 used as control listening stations (CSs) are indicated (green triangles) and fish release points are also shown (★). The seventh CS was located far to the north and appears only in the upper box. The letter C indicates the position of aquaculture cages. The broken line represents isobaths (m). Numbers adjacent to some of these FADs identify those used in Fig. 2.

FADs located at a distance lower than the range of reliability, we deployed only one VR2 to monitor these neighbouring FADs. In this case, to compensate for VR2s covering multiple FADs, we applied a weighted index to calculate the estimated residence time per FAD. This index took into account the number of FADs involved and the theoretical detection areas which would have been covered by the VR2s, had they been deployed on each FAD. The estimated continuous residence time CRT_{esti} was of the general following form:

$$CRT_{esti} = \frac{\sum_{i=1}^{n}\left(\frac{CRT_{obs}}{n} \times Anci\right) + \sum_{i=1}^{n}\left(CRT_{obs} \times Aci\right)}{n} \qquad (1)$$

where n is the number of multiple FADs, CRT_{obs} is measured by the VR2, Anc_i is the percentage of the area around the FAD_i not covered by the range of detection of the VR2 and Ac_i the percentage of the area around the FAD_i covered by the range of detection of the VR2.

The residence time means of FADs and CSs were compared using a Student's t test.

Capture, Tag Implantation and Releasing Strategy

One hundred and five fish were captured on 19 May 2006 by fishers around the aquaculture facility of Saint-Paul's Bay using hand lines. Immediately after capture fish were transferred into oxygenated 60-litre buckets. Eighteen fish not big enough to be tagged were released. A total of 87 fish were finally conveyed to the Aquarium of Reunion Island and housed in three holding tanks of 2.5 m^3 each. A preventive treatment with methylene blue (3 mg/litre) and copper sulphate (3×10^{-3} ml/litre) was applied. Fish were fed daily with a mixture of pieces of crustacean and fish flesh. On the 30 and 31 May 2006, 46 fish were tagged with coded Vemco V7 transmitters (V7-2L-R04K, 69 kHz, random rate of transmission every 70–140 s, rated battery life 130–150 days, length 18.5 mm, diameter 7 mm, mass in water 0.75 g). The mean fish size ± SD,