Behaviour and trophic ecology of oceanic triggerfish (*Canthidermis maculata*) and rainbow runner (*Elagatis bipinnulata*) associated with floating objects in the open ocean

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Abstract

The oceanic triggerfish (*Canthidermis maculata*) and rainbow runner (*Elagatis bipinnulata*) are epipelagic species that commonly associate with floating objects throughout the world's tropical oceans. Besides tunas, these two species often form the bulk of the aggregation and are major non-target species (bycatch) incidentally captured at fish aggregation devices (FADs) by tropical tuna purse seiners. Despite being abundant, little is known about their basic biology, ecology and associative behavior with floating objects. This thesis aims to address knowledge gaps in their associative behavior and ecology at floating objects and attempts to explore potential bycatch mitigation methods. Acoustic telemetry was used to characterise several aspects of the two species' behavior at floating objects. Fish were captured and tagged at drifting FADs in the core of the western Indian Ocean tuna fishing grounds. Prolonged remote observations were obtained through satellite linked receivers which provided fine-scale data on the behavior of oceanic triggerfish (n= 46 919 cumulated observation days) and rainbow runner (n= 24 538 cumulated observation days). The two species remained associated with the same floating object for periods extending up to several months. The mean residence time estimated using a survival analysis was 65 days for oceanic triggerfish and 94 days for rainbow runner. A distinct diel pattern in association was observed; the two species were closely associated to the FAD during the night and increased their home range during the day while performing short excursions (oceanic triggerfish mean: 2.0 hours ±1.6 SD; rainbow runner mean: 2.4 hours ±2.2 SD) away from the FAD. Similarly, distinct patterns in the vertical movements and locomotory activity (measured using accelerometer tags) were observed as the two species increased their vertical movements and activity levels during the day. Generally, their vertical movements were largely restricted to the mixed layer (< 60 m). At night, the two species remained close to the surface (0-5 m) where they appear to be in a resting state. An interesting behavioural switch in activity levels and vertical distribution was observed for oceanic triggerfish which coincided with a change in the environment as the FAD drifted close to a cold-core cyclonic eddy. Ambient light appears to be the key stimulus triggering the observed diel behavioural patterns. species-specific vulnerability for target species, skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*) and non-target species, including silky shark (*Carcharhinus falciformis*), oceanic triggerfish, and rainbow runner, to the purse seine fishing gear were investigated. Hourly presence rates at FADs over 24 hours were examined to assess whether the capture rate of non-target species could be reduced at specific times during the day. Silky sharks displayed a similar associative pattern to that of targeted tunas. Moreover, the vulnerability of both target and non-target species were close to the maximum during the period of behavioural transitions at sunrise when the majority of the fishing sets are made. As such, a change in set time in the western Indian Ocean does not appear to be a feasible method to reduce capture rates of non-target species. Stomach content and stable isotope analysis were conducted on oceanic triggerfish (stomach n = 152, isotope n = 65) and rainbow runner (stomach n = 156, isotope n = 71) incidentally captured individuals at FADs by purse seiners. Typical FAD-associated prey items represented a minor component of their diet as they predominantly foraged on zooplankton and micronekton in the water column, suggesting that oceanic triggerfish and rainbow runner do not associate to floating objects for direct trophic advantages. Overlap in their dietary and isotopic niches indicates an intermediate level of competition. Overall, the spatial and trophic ecology of both species are remarkably similar and prolonged associations with FADs indicates that floating objects play a significant ecological role in the pelagic environment for the two species.

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Chapter 1

General Introduction

1.1 Introduction

Large multi-species aggregations under floating objects are a striking and unique feature of the world's tropical oceans. A total of 333 species have been reported at floating objects (Castro *et al.*, 2002), however, it appears that far fewer, approximately 20 species, regularly associate at floating objects in tropical oceans (Kingsford, 1993; Taquet *et al.*, 2007b). These aggregations are diverse in terms of species richness but also in terms of life history traits, ontogenetic stages and trophic levels (Castro *et al.*, 2002). Species commonly found at floating objects include tropical tunas, including skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*), but also include dorado (*Coryphaena hippurus*), rainbow runner (*Elagatis bipinnulata*), oceanic triggerfish (*Canthidermis maculata*), wahoo (*Ancanthocybium solandri*) and sharks such as silky sharks (*Carcharhinus falciformis*) and oceanic whitetip sharks (*Carcharhinus longimanus*). Numerous hypothesis have been proposed to explain the causes of this associative behaviour with floating objects (see reviews: Castro *et al.*, 2002; Fréon and Dagorn, 2000). Popular motives that have been hypothesised include: refuge from predators, availability of food, spatial reference point for fish, Indicators of rich water masses and a meeting point to form larger schools (Castro *et al.*, 2002; Gooding and Magnuson, 1967; Fréon and Dagorn, 2000)

Floating objects have long been used by fisherman to locate and facilitate the capture of pelagic species and the first records of this activity date back to 200 AD in the Mediterranean to target dorado (Dempster and Taquet, 2004). In more recent history, fisherman started to construct and deploy anchored floating structures, known as Fish Aggregating Devices (FADs), to concentrate and target pelagic fish, and since the 1970's, this practice rapidly spread across the globe (Dempster and Taquet, 2004). In the open ocean, tropical tunas can form large aggregations under floating objects that can exceed 200 t (Dagorn *et al.*, 2012; Hallier, 1985). Large commercial purse seiners started to use floating objects to locate and capture schools of tuna, and rapidly became an important fishing mode. The alternative fishing strategies are to target free swimming schools of tuna that are visibly feeding on the surface or associated with marine mammals (Hall, 1992b). In the early 1980's, tuna purse seiners deployed FADs equipped with electronic buoys to facilitate their relocation (Fonteneau *et al.*, 2000). This strategy proved to be highly effective, as it yielded a higher set success rate when compared to other fishing modes, and rapidly lead to a massive increase in FAD deployments (Fonteneau *et al.*, 2000; Miyake *et al.*, 2010). Moreover, since the mid 2000's, FADs were equipped with echosounders buoys which provide fishermen with biomass estimates of tunas, allowing them to localise tuna schools and considerably increased their fishing efficiency (Fonteneau *et al.*, 2013; Lopez *et al.*, 2014). Currently, about 60% of the world tropical tuna catch originates from fishing on floating objects (Dagorn *et al.*, 2013) and in the Indian Ocean FAD sets contributed up to 75% of the yearly catch (Dagorn *et al.*, 2013).

The efficiency and magnitude of the FAD-based fishery generated concern in the scientific community and the capture rates of juvenile yellowfin and bigeye tuna has raised managerial concerns for these two target species (Harley *et al.*, 2010; Gilman, 2011). Additionally, due to the multispecies nature of FAD aggregations, this practice generates 2.8–6.7 times more bycatch (ocean dependant) than when fishing on free-swimming tuna schools (Dagorn *et al.*, 2013). Major incidentally captured non-target species include dorado, rainbow runner, oceanic triggerfish, wahoo, silky shark as well as some billfishes (Amandè *et al.*, 2011; Amande *et al.*, 2011; Romanov, 2002). With increased emphasis placed on an ecosystem based approach to management (Pikitch *et al.*, 2004a), impacts of fisheries on the entire ecosystem must be considered; including both target and non-target species. Owing to the higher bycatch rate of the FAD-based fishery, the impacts of this fishing practice on biodiversity and the pelagic ecosystem has been questioned (Hall *et al.*, 2000; Gilman, 2011). Currently, significant knowledge gaps impede a comprehensible risk assessment of this fishing practice, and in the interim, research efforts have been directed towards limiting risk through bycatch mitigation methods (Gilman, 2011). More specifically, one approach involves investigating behavioural interactions of non-target species with fishing gear to come up with best practices that can contribute toward reducing bycatch (e.g. use of circle hooks mitigating turtle bycatch, see Watson *et al.* (2004), 'backdown' manoeuvre and Medina panel for the release of dolphins from purse seine nets, see Hall (1998)). Moreover, some have hypothesised that the change in seascape caused by the massive increase of drifting FADs could act as an 'ecological trap' for associated species (Marsac *et al.*, 2000; Hallier and Gaertner, 2008a). This hypothesis contends that the unnatural amount of floatings could modify the movement patterns of tuna, displacing them to ecologically unsuitable areas that could negatively impact their growth rates, and ultimately increase their natural mortality (Marsac *et al.*, 2000; Hallier and Gaertner, 2008a).

1.2 Biology and ecology of study species

Oceanic triggerfish

Oceanic triggerfish (*Canthidermis maculata,* Bloch, 1786) have a circumglobal distribution (except the Mediterranean sea) and, unlike most members of the Balistidea family, are largely pelagic but are occasionally found close to continental shelf dropoffs. Another distinct characteristic of this species within the Balistidea is that they form large schools under floating objects throughout the world's tropical oceans. Variability and overlap of some morphological characters of species in the *Canthidermis* genus appeared to have caused great confusion to distinguish between the various species of this genus (Sahayak *et al.*, 2014). The oceanic triggerfish has the ability to change its coloration from uniform pale blue, to blue-brown with pale blue/white spots to a uniform dark-brown colouration (Hunter and Mitchell (1967), unpublished personal observations) which has more than likely contributed to misidentifications and the large number of junior synonyms for this species. There is a distinct lack of data available on several aspects of oceanic triggerfish's and fundamental biology including: age growth, size at sexual maturity and reproductive biology. Most of the knowledge on oceanic triggerfish behaviour originates from underwater observation in the 1960's by Gooding and Magnuson (1967) and Hunter and Mitchell (1967) who reported several behaviours, including predator avoidance, courtship and parasite removal. More recently, Dagorn *et al.* (2007b) tagged six oceanic triggerfish at drifting FADs in the western Indian Ocean and provided the first measurements of residency (mean: 12.46 days).

Oceanic triggerfish are amongst the most abundant non-target species incidentally captured at FADs by purse seiners globally. According to data from observer programmes, the incidental capture of this species appears to be higher in the Indian and Atlantic Ocean and to a lesser degree in the western Pacific Ocean followed by eastern Pacific Ocean (Amande *et al.*, 2011; Amandè *et al.*, 2011; Bailey *et al.*, 1996; Chavance *et al.*, 2011; Leroy *et al.*, 2012). It has been recognised that the catch estimations of this species is particularly difficult due to its small size (Hall and Roman, 2013) and that it appears to be one of those rare species, together with rainbow runner, that look lively when discarded from the deck of purse seiners (Bailey *et al.*, 1996). Interestingly, some skippers believe that their presence can enhance the attractiveness of FADs to tunas (Moreno *et al.*, 2007a). As such, some skippers encourage their crew to discard some live individuals after having fished on a FAD in aim to attract tuna faster (unpublished personal observation).

Rainbow runner

The rainbow runner (Quoy & Gaimard, 1824) is a Carangidae with a circumglobal distribution (except the Mediterranean sea). It is the only species of its genus and recent genetic studies have revealed that its closest relatives are from the *Seriola* genus (Ma *et al.*, 2015). The rainbow runner is a common epipelagic species that can be found around offshore reefs, pinnacles and under floating objects in the open ocean where they can form large schools (Yesaki, 1979). The largest known seine catch of this species was made by the FAO pool vessel RV *Lemuru* during a training project in Indonesia where a 6 t school (predominantly rainbow runner) was captured around a submerged log detected on the sonar (cited in Yesaki, 1979). Rodrigues and Lessa (2010) investigated the population structure of rainbow runner in north western Brazil and reported otolith ring counts ranging from 6 to 20, however, the frequency of the ring formation has not yet been validated, which precludes ageing estimations. Some aspects of reproductive biology have been studied. Pinheiro *et al.* (2011) investigated the reproductive biology of rainbow runner at the São Pedro and São Paulo Archipelago and reported a marked seasonality in the reproductive activity and estimated the length at first sexual maturity at 64.6 cm FL. However, samples from the latter study were obtained from the local handline fishery and small individuals were poorly represented. Rainbow runner larvae have been observed close to the continental shelf in Brazil (Souza and Mafalda Júnior, 2008) and can be abundant offshore on the tuna fishing grounds (Okiyama, 1970).

Few details about the behaviour of rainbow runner are known besides that fact they associate with floating objects. They have been observed to swim in small groups in close proximity to silky and oceanic whitetip sharks while occasionally rubbing against the shark's skin (unpublished personal observation).

Yesaki (1979) provided an early review of the available information on rainbow runner in a work entitled "Rainbow runner: a Latent Oceanic Resource?". The author gleaned available data and anecdotal evidence from across the world and suggested that rainbow runner, despite being largely incidentally captured by fishermen, was more abundant in the pelagic environment than it appeared, and could be a "latent resource of appreciable magnitude in the low-latitude ocean". Indeed, despite being abundant, this species is relatively poorly represented in the landings of artisanal and small-scale commercial fisherman and experimental fishing attempts suggest that, unlike other predatory epipelagics, rainbow runner are particular hard to target (Yesaki, 1979; Viana *et al.*, 2015). Rainbow runner is a major bycatch species incidentally captured at FADs by tropical purse seiners throughout the world's tuna grounds (Amande *et al.*, 2011; Amandè *et al.*, 2012; Leroy *et al.*, 2012; Hall and Roman, 2013).

1.3 Aim and objectives

The rainbow runner and oceanic triggerfish are two abundant epipelagic fish with relatively high incidental capture rates amongst non-target species in the tropical purse seine fishery. However, as indicated above, little or no information is available on key biological parameters and their ecology. Considering an ecosystem approach to fisheries management, the growing use of FADs in the tropical tuna fishery poses major questions about the sustainability of this fishing mode for the pelagic ecosystem. The aim of this thesis is to address the knowledge gaps on the behaviour of these species at FADs and aspects of their ecology. The specific objectives of the study were to:

1. characterise their associative behaviour with floating objects and provide an estimation of residency at FADs

2. characterise their fine scale movement behaviour and activity patterns during their association to FADs

3. Use patterns in associative behaviour and vertical distribution of both tunas and non-target species to investigate species-specific vulnerability at FADs to explore potential technical mitigation measures for bycatch reduction

4. Investigate the trophic ecology of oceanic triggerfish and rainbow runner associated with FADs in the western Indian Ocean.

1.4 Thesis layout

The layout of this thesis is as follows:

- Chapter 1 - General Introduction: provides background information to contextualise the rational for conducting this study.

- Chapter 2 - Study site and acoustic telemetry in the open ocean: this chapter provides broad description of the oceanographic patterns in the study area, provides an overview of acoustic telemetry and its applications in the pelagic environment

- Chapter 3 - Associative behaviour of oceanic triggerfish and rainbow runner with floating objects: investigates the residency at floating objects and characterises the fine scale associative patterns of the two species.

- Chapter 4 - Vertical movement behaviour and activity of oceanic triggerfish and rainbow runner associated with floating objects: characterises the fine scale vertical movements and activity patterns of the two species during their association with floating objects.

- Chapter 5 - Behaviour and vulnerability of target and non-target species at drifting FADs in the tropical tuna purse seine fishery: in this chapter information on the associative behaviour and vertical distribution are combined to assess species-specific vulnerability to the purse seine gear and possible technical measures to reduce capture of non-target species are explored. This chapter was published as: Forget, F., Capello, M., Filmalter, J.D., Govinden, R., Soria, M., Cowley, P.D., and Dagorn, L. 2015. Behaviour and vulnerability of target and non-target species at drifting FADs in the tropical tuna purse seine fishery determined by acoustic telemetry. Canadian Journal of Fisheries and Aquatic Science, 72:1398-1405.

- Chapter 6 - Diet and stable isotope analyses of oceanic triggerfish and rainbow runner at floating objects: describes the diet of the two species in attempt to assess potential foraging benefits of association with floating objects. The trophic and isotopic niche widths of the two species were estimated and the overlap in resource utilisation of these co-occurring species was examined.

- Chapter 7 - General discussion: This chapter provides an overview of the results and integrates the new ecological information gained in the study to discuss potential evolutionary benefits in association with floating objects. Additionally, this chapter discusses potential impacts of the increased use of FADs by tropical tuna purse seiners, and possible management options of non-target species in the tropical purse seine fishery.

Chapter 2

Study site and acoustic telemetry in the open ocean

This chapter is divided into two sections. The first provides a broad description of the oceanographic patterns in the western Indian Ocean and the second provides an overview of acoustic telemetry and its applications in the pelagic environment. Additionally, the specifications of the equipment used in the study are outlined.

2.1 Study site

The oceanography of the western Indian Ocean is dynamic and has received special attention from oceanographers. In this region, wind stress forcing on the surface has a large influence on the complete monsoonal reversal between boreal winter (November- March) and boreal summer monsoons (May to September). This is turn drives various current systems (Schott and McCreary, 2001; Schott, 2002). During the summer monsoon (Fig.2.2), the South Equatorial Current (SEC) branches off Madagascar into the Northeaster Madagascar Current and the Southeast Madagascar Current (NEMC and SEMC). The water masses then reach the African continent where it splits into the East African Coast Current (EACC) and is forced southwards into the Mozambique channel. The East African Coast Current (EACC) then flows parallel to the coast and feeds into the cross equatorial current north-ward Somali Current which generates the Southern Gyre (SG) and the Great Whirl (GW) (Schott, 2002).

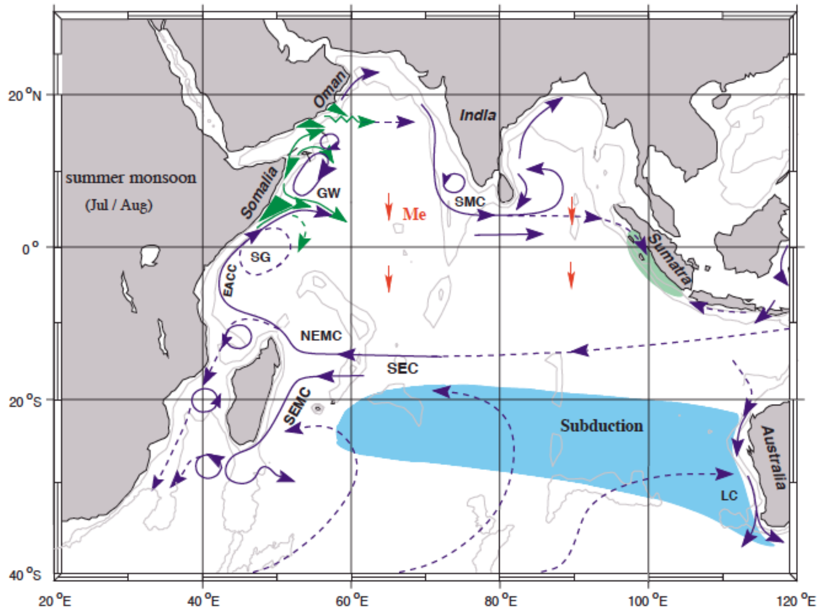


Figure 2.1 A schematic representation major current branches during the Southwest Monsoon. Marked are winter subduction area in southern subtropics (blue), upwelling areas (green) and southward Ekman transport on both sides of the equator (red). Current branches indicated (see also Fig. 2.2) are the South Equatorial Current (SEC), Northeast and Southeast Madagascar Current (NEMC and SEMC), East African Coast Current (EACC), Somali Current (SC), Southern Gyre (SG) and Great Whirl (GW), Southwest Monsoon Current (SMC), and Leeuwin Current (LC). Source: Schott (2002)

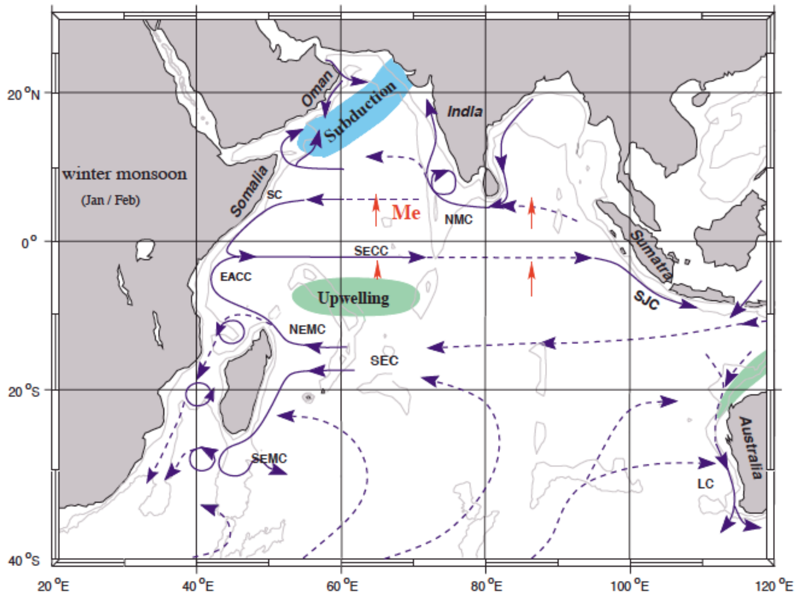


Figure 2.2 A schematic representation of identified current branches during the Northeast Monsoon. Marked are the winter subduction area in the northern Arabian Sea (blue), presumed upwelling area in 5–10°S doming region, and northward Ekman transport on both sides of the equator (red). Current branches indicated are the South Equatorial Countercurrent (SECC), Somali Current (SC), Northeast Monsoon Current (NMC) and South Java Current (SJC). Source: Schott (2002)

These two structures generate intense upwelling off the coast of Somali and colder nutrient rich waters are brought up to the surface, which control the local climate and biological productivity of the area. During the winter monsoon (Fig. 2.1), the current circulation in the north western Indian Ocean changes while it remains unchanged in the Mozambique Channel area. In the north west, the Somali Current flows southwards and meets the EACC and confluences into the South Equatorial Countercurrent (SECC) while the northward undercurrent flows across the equator and feed back towards the coast in a Somali Undercurrent (SM) (Schott, 2002). This northward undercurrent is believed to generate upwelling in the southern equatorial area (Schott, 2002).

These seasonal patterns in circulation described above largely drives the productively of the western Indian Ocean where the core of the European tropical tuna purse seine fishing grounds is situated and both FAD and free-swimming school fishing modes occurs (Fig. 2.3). Figure 2.3 indicates the specific area where the study was conducted in the western Indian Ocean.

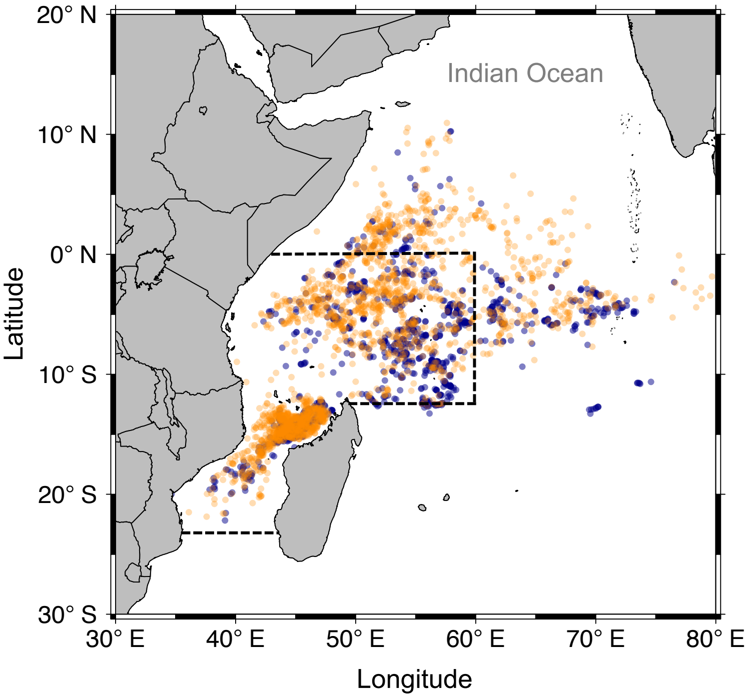


Figure 2.3 Distribution of purse seine fishing sets on FADs (orange) and free swimming school (blue) in the western Indian Ocean. The area delimited by the black doted lines indicates the specific study area. The set position data originates from the french observer programme for periods 2005-2014.

2.2 Tagging cruises

Four tagging cruises were conducted in the western Indian Ocean between 2010 and 2012; two were in the Mozambique Channel and two in the Seychelles area. Different vessels were used during these cruises and included two private chartered vessels (M/V Dugong and M/Y Inventive) and two commercial vessels; a small pelagic longliner (F/V Mtwaro II) and a large tropical tuna purse seine vessel (F/V Torre Giulia).

Table 2.1 Summary information of acoustic tagging cruises conducted in the western Indian Ocean.

Vessel	Area	Start	End	Duration (days)
M/Y Inventive	Mozambique C.	04/03/10	17/3/10	13
F/V Mtwaro II	Mozambique C.	14/4/11	21/4/11	7
M/V Maya's Dugong	Seychelles	16/6/11	27/6/11	11
F/V Torre Giulia	Seychelles	31/3/12	08/5/12	39

2.3 Acoustic telemetry in the open ocean

Acoustic telemetry technique involves placing autonomous electronic transmitters (i.e. "acoustic tags") on animals which then transmits a signal to a listening station that logs the data. These listening stations can either be fixed (i.e. "passive monitoring") to the ocean floor or mobile; by being on the vessel to track a tag equipped animal (i.e. "active tracking"). There are two methods to equip fish with acoustic tags, internally through surgery, or , attached externally to the body or appendages. The transmitter emits a series of acoustic signals ("pings") that code an ID number and sensor data. Each tag has a unique ID code which allows the listening stations (receivers) to discriminate between different tagged individuals and logs a time stamp for each detection and for the sensor data, which is then used to infer the movements of individuals. Acoustic tags can be equipped with various sensors, including pressure sensors to determine swimming depth, temperature sensors, and more recently accelerometers, which allows to gather additional information on the fish's behaviour and environment. Generally, receivers have to be recovered and the detection log manually downloaded. The recovery of the receivers can represent significant logistical constrains in the marine environment due to variations in sea conditions.

Active tracking was initially conducted to study movements of pelagic fish and was successfully used on skipjack tuna (*Kasuwonus pelamis*; Yuen 1970), blue marlin (*Makaria nigricans*; Holland *et al.* 1990a), yellowfin (*Thunnus albacares*) and bigeye tuna (*T. obesus*; Holland *et al.* 1990b; Brill *et al.* 1999; Dagorn *et al.* 2000a). However, this method is extremely labor intensive and requires a considerable amount of time, logistical efforts, and is largely reliant on favourable sea conditions. However, it remains one of the best methods to obtain fine scale and real time movements of fish. The subsequent development of autonomous acoustic receivers allowed for passive monitoring of fish movements (Klimley *et al.*, 1998; McKibben and Nelson, 1986). This method cannot be applied anywhere in the open ocean as the receivers have to be fixed to the ocean floor and its use is largely restricted to coastal reefs and seamounts (Klimley *et al.*, 1998). Anchored FADs offers a unique opportunity to study the associative behaviour of pelagic fish while providing structure onto which the receivers can be fixed. As such, this method was used throughout the world in anchored FADs arrays where prolonged continuous monitoring (several months) could be conducted with minimal logistical constrains (Dagorn *et al.*, 2007a; Govinden *et al.*, 2013; Klimley and Holloway, 1999; Ohta and Kakuma, 2005; Robert *et al.*, 2012). Studies conducted on drifting FADs using such receivers, requires the recovery of the equipment and experiments are thus often interrupted to prevent the equipment to drift out of reach (Taquet, 2004; Taquet *et al.*, 2007a; Matsumoto *et al.*, 2005). The next step in technological development involved acoustic receivers that were linked to the Argos satellite network (VR3-Argos, Vemco, Amirix , Canada) and allowed to monitoring of aggregations at FADs remotely, however, due to satellite transmission limitations, the data had to be aggregated into bins and consequently fine scale data was lost (Dagorn *et al.*, 2007b). More recently, technological improvements have allowed for the receivers to transmit the complete detection time series, including sensor data, and provides position estimates through the Iridium satellite network (VR4-Global, Vemco, Amirix, Canada). The VR4-Global receivers (Fig. 2.4) were used in this study, it allows the monitoring of tagged fish at drifting FADs remotely for up to seven months while providing daily detection logs.

Figure 2.4 VR4-Global acoustic receiver attached to a drifting FAD (left) and a schematic diagram of the receiver unit showing the submerged part with the hydrophone (right).

Tag specifications

Various type of coded acoustic tags were used in this study and Table 2.2 provides their respective specifications. The tags used for oceanic triggerfish and rainbow runner were the V9 family (Vemco, Amirix, Canada), which are 9 mm in diameter but vary in length and weight depending on the presence of sensors; 2.1 mm and 3.3g V9 to 4.5 mm for the V9AP. For tunas and silky sharks the V13 (Vemco, Amirix, Canada) size transmitters were used. All the tags used in this study emitted on the 69 kHz frequency. The nominal delay means that the transmission rates varies randomly ±50% of the nominal delay value, for example, a 90 s nominal delay indicates that the tag transmits randomly every 50 to 120 s. This randomisation is important as it minimises simultaneous emissions from multiple tags which inhibits receivers from discriminating between different ID codes. Simultaneous emissions causing them to overlap is referred to as "acoustic collisions". Acoustic collisions are more important with an increasing number of tags in the reception range of the receiver and exponentially increases with short nominal delays. As such, to limit the effect acoustic collisions in this study, a maximum of 25 fish were tagged at each VR4 Global receiver. Additionally, in Chapter 5, a method was developed to account for acoustic collisions as a function of number of tagged fish present in the listening range of the receiver.

Table 2.2 Specifications of the acoustic tags used in this study. For the tag types, each letter denotes sensor data type: "P" pressure sensitive , "T" temperature, "A" accelerometer.

Tag type	Nominal delay	Depth range (m)	Length (mm)	Weight in water(g)	Estimated tag life (days)
V9	120	-	2.3	1.6	320
V9P	120	100	4.1	2.2	251
V9TP	120	100	4.1	2.9	194
V9AP	140	100	4.5	2.9	81
V13	90	-	36.0	6	879
V13P	90	200	48.0	6.5	214

Detection range

Knowing the detection range of acoustic receivers is important to allow spatial interpretation of the data. The detection range can vary considerably as a function of environmental parameters surrounding the acoustic receiver. For example, these can include sea state, water flow, depth, amount of suspended solids, but also biological noise (in coastal reef environments) and physical noise (driven by ocean energy and wind) (Kessel *et al.*, 2013). These parameters are dynamic and detection range tests are thus recommended, especially in coastal environments, to assess receiver performance and variability (Heupel *et al.*, 2006; Kessel *et al.*, 2013). It is usually recommended to conduct range testing before initiating the study in order to optimise the receiver array configuration. In the open ocean, range tests are usually performed by drifting away from the a receiver (attached to the floating object) using a GPS equipped vessel with a deployed submerged tag, the detection performance is subsequently assessed by using the distances (calculated from GPS) between the tag and the receiver (Dagorn *et al.*, 2007a). Comprehensive range testing could not be performed in the study area due to the threat of piracy in the western Indian Ocean (Sumaila and Bawumia, 2014). The manufacturer theoretical detection range estimations are 550-682 m for V13 tags and 500-627 m for the V9 in calm to moderate sea conditions. Schaefer and Fuller (2013) following the method described above obtained comparable detection ranges during range tests for V13 at drifting FADs in the offshore equatorial eastern Pacific.

Chapter 3

Associative behaviour of oceanic triggerfish and rainbow runner with floating objects

3.1 Introduction

Large multispecies aggregations at floating objects are a common feature of the world's tropical and subtropical oceans. While a total of 333 species have been found at floating objects (Castro *et al.*, 2002), it appears that far fewer, approximately 20 species, regularly associate with floating objects (Kingsford, 1993; Taquet *et al.*, 2007b). Numerous hypothesis have been proposed to explain the causes of this associative behaviour (reviews in: Castro *et al.*, 2002; Fréon and Dagorn, 2000). An initial hypothesis was that fish use floating objects as shelter to reduce predation (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Rountree, 1989). While underwater observations provide some support to this hypothesis for small fish (Gooding and Magnuson, 1967), it does not appear to be valid for larger schooling species such as tunas. Other authors have suggested that association could be driven by a trophic advantages, by predating on associated fish (Gooding and Magnuson, 1967; Kojima, 1956). While predation events have been observed at FADs (Hunter and Mitchell (1967), unpublished personal observation), diet studies of tunas and dorado (*Coryphaena hippurus*) tend to indicate that the associated fauna does not represent a major component of the diet of predators at floating objects (Taquet, 2004; Menard, 2000). The meeting point hypothesis suggests that fish use the floating object as a spatial reference point to gather around floating objects and facilitate schooling behaviour to form larger schools (Dagorn and Fréon, 1999; Fréon and Dagorn, 2000). Another motive that has been suggested is that floating objects act as good indicators of productive environments by accumulating in frontal areas (Bakun, 2006; Hall, 1992a).

A striking characteristic of multispecies aggregations is that the community appears to spatially structured relative to the floating objects. Kojima (1960) was the first to propose a categorisation of the community based on radial distribution relative to the floating objects.Parin and Fedoryako (1992) then proposed three broad categories of spatial distribution: intranatant (< 50 cm from the object), extranatant (50 cm to 2 m from the object) and circumnatant (> 2m from the object) and subsequently, Fréon and Dagorn (2000) proposed some distance modifications for these categories. However, none of these categories were determined empirically (Girard *et al.*, 2007). Acoustic telemetry studies have allow empirical investigations on the distribution range FAD associated species which varied from 300-400 m for dorado (Taquet *et al.*, 2007a) to

5-10 km for tunas (Dagorn *et al.*, 2000b; Holland *et al.*, 1990b; Matsumoto *et al.*, 2014). With similar intent, Moreno *et al.* (2007b) used acoustic surveys to observe the spatial distribution of biomass at FADs and while distinct structures could be identified, species specific details could not be determined. Other than tunas, oceanic triggerfish and rainbow runner often form the bulk of the aggregations at drifting FADs (Romanov, 2002; Lezama-Ochoa *et al.*, 2015; Amande *et al.*, 2011), yet little is known about their associative behaviour, ecology or potential role in multispecies aggregations.

Large schools of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye tuna (*T. obesus*) are found at floating objects and fisherman have used floating objects as a visual cue to locate pelagic fish in the open ocean. In the early 80's, tropical purse seiners started to deploy man-made floating objects (i.e. FADs) which were subsequently equipped with electronic buoys to facilitate their relocation (Fonteneau *et al.*, 2000). This strategy proved to be highly effective and rapidly lead to a massive increase in FAD deployments (Fonteneau *et al.*, 2000). Moreover, since the mid 2000's, FADs were equipped with echosounder buoys which now provided fishermen with biomass estimates of target tuna species, allowing them to localise larger schools and considerably increased their fishing efficiency (Fonteneau *et al.*, 2013; Lopez *et al.*, 2014). To date, about 60% of the world's tropical tuna originates from fishing on floating objects (Dagorn *et al.*, 2013). The multispecies nature of aggregations around floating objects means that this practice generate 2.8–6.7 times (ocean dependant) more bycatch than when fishing on free-swimming tuna schools (Dagorn *et al.*, 2013). Incidentally captured non-target species include dorado, rainbow runner (*Elagatis bipinnulata*), oceanic triggerfish (*Canthidermis maculata*), wahoo (*Acanthocybium solandri*) and silky shark (*Carcharhinus falciformis*)(Amandè *et al.*, 2011; Amande *et al.*, 2011; Romanov, 2002). Owing to higher bycatch rates and the preponderance of the FAD-based fishery, concerns have been raised on its impacts on pelagic ecosystems and the sustainability this fishing practice has been questioned (Hall, 1996; Hall *et al.*, 2000; Gilman, 2011). Moreover, some authors suggested that drifting FADs could act as an ecological trap for associated species by altering the natural movements of populations towards less favourable environment which could lead to increase in natural mortality and population declines (Marsac *et al.*, 2000; Hallier and Gaertner, 2008b).

Currently, little to no data is available on the basic biology, ecology and behaviour of oceanic triggerfish and rainbow runner. Information on their associative behaviour may contribute towards a better understanding of the causes driving this associative behaviour and bring elements to better understand multispecies aggregations at floating objects. Additionally, with an increased emphasis placed towards an ecosystem based management, key ecological parameters of captured species are required to evaluate the impacts of fishing mortality on the ecosystem. This study aims to characterise the associative behaviour of oceanic triggerfish and rainbow runner at floating objects using acoustic telemetry. The objectives were to 1) estimate the residency, 2) examine the fine scale associative patterns and 3) examine the temporal patterns of their associative behaviour at drifting FADs.

3.2 Materials and methods

Acoustic tagging

Four scientific cruises were conducted in the western Indian Ocean between March 2010 and April 2012. These cruises took place in the Mozambique Channel and the Seychelles area. FADs were located through collaboration with European purse seine skippers. Firstly, a VR4-Global (VEMCO, Amarix Ltd., Canada) acoustic receiver was attached to the drifting FAD. These receivers utilise the Iridium satellite system to transmit acoustic detection logs from tagged individuals on a daily basis. Oceanic triggerfish and rainbow runner were caught using rod and reels or hand lines. Coded acoustic transmitters were surgically implanted into the peritoneal cavity following the standard methods implantation technique (Dagorn *et al.*, 2007a; Schaefer and Fuller, 2005). Oceanic triggerfish and rainbow runners and oceanic triggerfish were equipped with V9, V9P, V9TP and V9AP (120 s nominal delay, 69 kHz, 1H; Table **??**). Briefly, captured individuals were brought onboard using a scoop net and placed on V-shaped the tagging table. The individuals were then rapidly examined to verify that no injury was sustained during the capture. Only individuals that appeared to be in good condition were tagged. The eyes of the fish were covered with a wet cloth, a hose pumping seawater was placed by the mouth to irrigate the gills and a small incision (~2 cm) was made on close to the ventral midline into the peritoneal cavity. The tag was implanted into the peritoneal cavity and two independent sutures were made to close the incision, the length of the fish was then measured to the closest 0.5 cm (fork length for rainbow runner and total length for oceanic triggerfish) and the fish was then released in close proximity to the FAD. Once tagging was complete, the FAD and attached VR4-Global receiver were left to drift and the data was relayed remotely. Daily detection logs and position logs from the VR4-Global receiver were then consolidated into a database for subsequent analysis. The FAD drift patterns were constructed using positions obtained by the VR4-Global receiver.

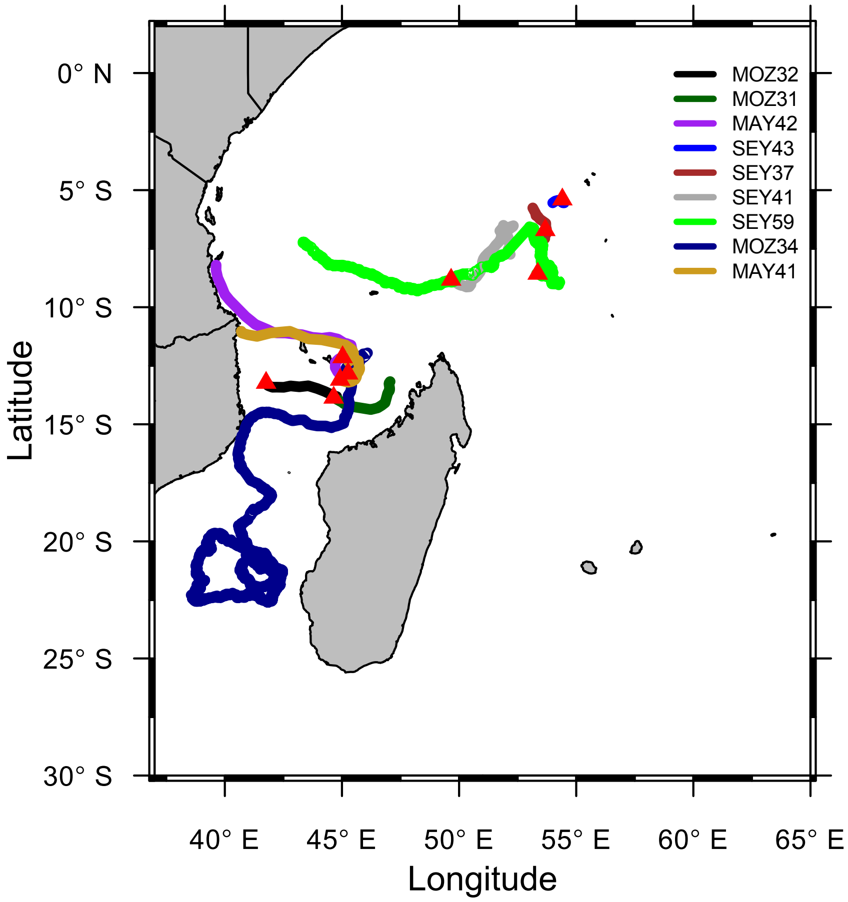


Figure 3.1 Drift trajectories of the 9 experimental FADs monitored in the western Indian Ocean. Red triangles indicate the starting point of the experiments .

Data Analysis

Residency

The total residence time (TRT) provides an indication of the residency of tagged fish at FADs. It is the amount of time between the first detection and last detection before the fish permanently leaves the FAD. The time when an individual first associated with the floating object, prior to the experiment, is unknown. Hence, the real residency of individuals cannot be known. Additionally, some experiments were prematurely interrupted by either commercial fishing operations, resulting in the capture of the entire FAD aggregation, or by equipment failure. TRTs that were not interrupted artificially indicates that the individuals left the FAD and were denoted as "natural departures". In order to standardises the varying experiment durations to allow comparisons, a residency index was calculated for each individual by dividing the TRT by the experiment durations at each FAD (Table3.1). This standardised index ranges from 0 to 1 and is commonly used in acoustic telemetry to provide estimates of the relative residency of tagged individuals within an acoustic telemetry array (Afonso *et al.*, 2012; Lédée *et al.*, 2015). In order to estimate the durations of residency of the two species at FADs, a survival analysis of the TRT was conducted. Survival analysis is used to analyse data where the outcome variable is the time until the occurrence of a particular event (here departure from FAD) with the particularity of being able to handle censoring of observations (truncations). Survival analysis has previously been used in acoustic telemetry experiments with truncated data (Ohta and Kakuma, 2005; Robert *et al.*, 2012; Stehfest *et al.*, 2013). Kaplan-Meier estimate of the survivor function of TRTs was calculated with 95% confidence intervals. For comparative purposes, two Kaplan-Meier survival functions were generated using i) TRTs considering censored data (i.e. stratified into natural departures and censored data) and , ii) all TRTs with no censoring considered (i.e. all TRTs) to provide residence time estimations and assess the effect of censored data on estimates. A longrank test was used to test the differences in survivor function between the two species. An exponential survival regression model was then fitted to each of the censored and uncensored curves to provide an estimation of the residency estimates for the two species at FADs. A constant hazard assumption was made for the regression model, whereby the probability of leaving the FAD was independent of time. Additionally, the mean of the uncensored TRT was calculated to allow comparisons with other studies reporting residency at FADs.

Temporal patterns in association

Detection timelines were constructed for each FAD depicting all detections for individuals of oceanic triggerfish and rainbow runner and were visually inspected to assess the patterns in the detection rates. Additionally, the detection time series was converted into a hourly detection time series and an hourly chronogram was constructed to examine temporal patterns in associative behaviour. A cluster analysis was conducted to determine if individuals displayed a species-specific behaviour. First, the detection time series were converted into hourly presence-absence time series to remove the effect of detection variance and acoustic collisions. Secondly, for each FAD, the hourly presence-absence time series were trimmed synchronously to obtain the same time segments for each individuals. Finally, a hierarchical clustering was computed using the Ward algorithm on euclidean distance matrices based on the presence-absence time series at each FAD using the R software (RCoreTeam, 2014).

Cyclic temporal patterns in the associative behaviour of each individual were examined through a fast Fourier transform (FFT) applied to the hourly detection rates and the resulting spectral density was plotted. FFT indicates whether there are rhythmic patterns in the presence of tagged individuals at FADs (Barnett *et al.*, 2012). Distinct peaks in the spectral density indicates the presence of cyclic rhythms and the time scale at which they occur , denoting the periodicity. The spectral analysis was performed on individuals that had $\geq$5 days of data to ensure sufficient sample size for the analysis. Additionally, a continuous wavelet transformation (CWT) was computed to examine the stability of the cyclic rhythms, such as diel pattern, over time. The CWT decomposes a time series into time-frequency space (Percival and Walden, 2000) and has previously been used in acoustic telemetry to examine cyclic rhythms in fish behaviour (Alós *et al.*, 2012b; March *et al.*, 2010). Morlet wavelets, using the "dplR" package in R, was used to construct a 2-dimensional wavelet spectrum and calculate a point wise test with 95% significance level. Spectrograms were then inspected to determine how persistent the cyclic rhythms were over time according to the significance of the signal.

Gaps in the detection time series are indicative of periods when individuals ventured outside the range of the receiver. An excursion was defined by a detection gap of > 1 hour and were used as temporal units to describe excursions (movements away) from the FAD . To assess the level of variability in the excursion behaviour amongst individuals an excursion index was calculated by dividing the total number of excursions by the TRT. This time standardised index reflects on the excursion activity of individuals and provided the excursions per unit time. A high index value indicates more frequent excursions per unit time. The distribution and durations of excursions were then examined on a 24 h cycle.

3.3 Results

A total of 24 rainbow runners and 46 oceanic triggerfish were tagged at nine drifting FADs (Fig. 3.1). Details of the tagging information are provided in Table3.1. All 70 individuals were detected at the FAD where they were released. The cumulated number of observation days at FADs was 919.5 days for oceanic triggerfish and 538.1 days for rainbow runner, which yielded a total of 273 866 and 114 397 detections, respectively.

Table 3.1 Metadata of oceanic triggerfish and rainbow runner tagged at FADs. TRT is the total residence time. * Denotes TRT with natural departures from FAD.‡ Rainbow runner lengths are given in FL and and oceanic triggerfish lengths by TL.

Tagging		Species	Size	FAD ID	Acoustic tag		Experiment		Excursion	
Date	Time		(TL/FL cm)‡		Type	ID	Duration	TRT	Num.	Index
15/04/11	11:56	TRI	31.0	MAY41	V9TP	3601	21.4	20.7	1	0.0
15/04/11	11:42	TRI	30.0	MAY41	V9TP	3603	21.4	21.3	1	0.0
15/04/11	16:27	TRI	32.0	MAY41	V9P	64826	21.4	20.7	11	0.5
15/04/11	16:04	TRI	30.0	MAY41	V9P	64827	21.4	20.7	58	2.8
15/04/11	22:01	TRI	33.0	MAY41	V9P	64828	21.4	20.5	14	0.7
16/04/11	07:15	TRI	33.0	MAY41	V9P	64829	21.4	20.7	16	0.8
16/04/11	23:48	TRI	34.0	MAY41	V9P	64830	21.4	21.1	9	0.4
16/04/11	21:46	TRI	30.0	MAY41	V9P	64831	21.4	21.12	20	0.9
16/04/11	22:25	TRI	36.0	MAY41	V9P	64832	21.4	21.12	38	1.8
16/04/11	-	TRI	30.0	MAY41	V9P	64834	21.4	1.6*	0	0.0
20/04/11	11:59	ELA	24.0	MAY42	V9TP	3599	26.9	16.8*	1	0.1
20/04/11	12:16	ELA	23.0	MAY42	V9P	30112	26.9	24.3	70	2.9
20/04/11	18:45	ELA	23.0	MAY42	V9P	30114	26.9	24.6	81	3.3
20/04/11	08:02	ELA	23.5	MAY42	V9P	64819	26.9	24.7	56	2.3
21/04/11	-	ELA	23.5	MAY42	V9P	64835	26.9	24.7	66	2.7
20/04/11	11:46	TRI	32.5	MAY42	V9P	3605	26.9	24.3	16	0.7
20/04/11	11:05	TRI	32.5	MAY42	V9P	30113	26.9	10.5*	4	0.4
20/04/11	07:43	TRI	36.5	MAY42	V9P	64820	26.9	10.1*	2	0.2
20/04/11	07:10	TRI	34.0	MAY42	V9P	64821	26.9	8.0*	13	1.6
20/04/11	07:01	TRI	31.0	MAY42	V9P	64822	26.9	8.0*	6	0.7
21/04/11	16:50	TRI	32.0	MAY42	V9P	64823	26.9	9.1*	8	0.9
21/04/11	16:35	TRI	35.0	MAY42	V9P	64824	26.9	9.0*	9	1.0
15/03/10	18:21	TRI	33.0	MOZ31	V9P	64810	11.6	11.5	2	0.2
15/03/10	18:13	TRI	33.0	MOZ31	V9P	64811	11.6	7.3*	1	0.1
16/03/10	18:06	TRI	31.0	MOZ31	V9P	64813	11.6	10.8	28	2.6
16/03/10	17:58	TRI	32.0	MOZ31	V9P	64814	11.6	10.8	3	0.3
16/03/10	17:45	TRI	33.0	MOZ31	V9P	64815	11.6	9.3	2	0.2
16/03/10	07:37	TRI	33.0	MOZ31	V9P	64816	11.6	10.8	0	0.0

16/03/10	16:17	TRI	33.0	MOZ31	V9P	64817	11.6	10.8	1	0.1
21/04/11	07:04	TRI	32.0	MOZ32	V9P	64809	10.8	11.0	0	0.0
08/03/10	11:25	ELA	45.0	MOZ34	V9P	64804	67.0	67.0	172	2.6
08/03/10	11:39	ELA	43.0	MOZ34	V9P	64805	67.0	67.0	172	2.6
09/03/10	18:53	TRI	28.0	MOZ34	V9	54304	67.0	26.8*	18	0.7
09/03/10	11:13	TRI	31.0	MOZ34	V9	54305	67.0	66.2	171	2.6
09/03/10	11:59	TRI	39.0	MOZ34	V9P	64806	67.0	66.2	80	1.2
09/03/10	12:05	TRI	34.0	MOZ34	V9P	64807	67.0	12.5*	9	0.7
09/03/10	07:19	TRI	30.0	MOZ34	V9P	64808	67.0	26.4*	34	1.3
22/06/11	17:40	ELA	65.0	SEY37	V9TP	3593	16.6	13.5	5	0.4
23/06/11	17:00	ELA	62.0	SEY37	V9TP	3595	16.6	15.4	1	0.1
24/06/11	14:05	ELA	79.5	SEY37	V9TP	3597	16.6	7.8*	3	0.4
24/06/11	14:30	ELA	77.0	SEY37	V9P	3621	16.6	11.4	1	0.1
23/06/11	17:45	TRI	30.5	SEY37	V9P	3617	16.6	10.8	0	0.0
23/06/11	18:00	TRI	28.0	SEY37	V9P	3618	16.6	10.8	0	0.0
24/06/11	13:52	TRI	30.0	SEY37	V9P	3619	16.6	10.1	1	0.1
24/06/11	14:15	TRI	30.5	SEY37	V9P	3620	16.6	13.5	3	0.2
13/04/12	14:48	ELA	63.5	SEY41	V9AP	4668	21.4	27.7*	36	1.3
14/04/12	08:56	ELA	28.5	SEY41	V9P	7072	21.4	29.8	75	2.5
14/04/12	11:30	ELA	30.0	SEY41	V9P	7073	21.4	29.8	77	2.6
14/04/12	18:32	TRI	29.0	SEY41	V9AP	4672	21.4	29.5	17	0.6
13/04/12	16:55	TRI	33.5	SEY41	V9P	7069	21.4	27.6*	93	3.4
14/04/12	07:40	TRI	30.5	SEY41	V9P	7070	21.4	29.9	50	1.7
14/04/12	08:02	TRI	30.0	SEY41	V9P	7071	21.4	29.9	30	1.0
18/06/11	14:00	ELA	30.5	SEY43	V9P	3586	4.4	3.4	1	0.3
19/06/11	10:59	ELA	57.0	SEY43	V9P	3588	4.4	3.3	2	0.6
19/06/11	11:20	ELA	32.0	SEY43	V9TP	3590	4.4	3.3	1	0.3
19/06/11	11:45	ELA	34.0	SEY43	V9P	3606	4.4	1.9	1	0.5
19/06/11	13:15	ELA	61.5	SEY43	V9TP	3607	4.4	2.3	1	0.4
19/06/11	13:45	ELA	79.0	SEY43	V9TP	3610	4.4	4.3	1	0.2
18/06/11	14:35	TRI	32.0	SEY43	V9P	3611	4.4	4.2	3	0.7
18/06/11	14:45	TRI	30.5	SEY43	V9P	3612	4.4	4.2	2	0.5
18/06/11	14:55	TRI	34.0	SEY43	V9P	3613	4.4	4.2	2	0.5
18/06/11	15:15	TRI	26.5	SEY43	V9P	3614	4.4	2.8	0	0.0
18/06/11	15:30	TRI	30.5	SEY43	V9P	3615	4.4	4.2	3	0.7
26/04/12	11:34	ELA	64.0	SEY59	V9AP	4680	85.2	16.8*	7	0.4
26/04/12	11:57	ELA	61.0	SEY59	V9AP	4682	85.2	17.0*	22	1.3
26/04/12	13:37	ELA	44.5	SEY59	V9AP	4684	85.2	16.7*	17	1.0
26/04/12	17:50	ELA	35.0	SEY59	V9AP	4686	85.2	84.9	206	2.4
26/04/12	10:15	TRI	30.5	SEY59	V9AP	4674	85.2	57.9*	17	0.3
26/04/12	10:27	TRI	35.0	SEY59	V9AP	4676	85.2	66.4*	23	0.3
26/04/12	10:33	TRI	32.0	SEY59	V9AP	4678	85.2	64.4*	16	0.2

Residency

TRT at FADs for the rainbow runner ranged between 1.9 to 84.9 days and 2.8 and 66.4 days for the oceanic triggerfish. The large range in residency was not always indicative of natural behaviour as observations were often terminated prematurely due to either fishing operations, which resulted in the capture of the FAD-associated fish, or equipment failure (Table 3.1). A high residency index score was obtained for both oceanic triggerfish (0.75 ±0.28, mean ±SD) and rainbow runner (0.75 ±0.25, mean ±SD). Kaplan-Meier survival curves depicts the survival function of TRTs for both species at FADs (Fig. 3.2).

Considerable overlaps in confidence intervals of both curves indicate that they had similar residency (Fig. 3.2). This was confirmed by the log rank test as no significant difference was observed between the survival functions of the two species (censored curve: χ^2= 0.8, df = 1, p = 0.36, uncensored: χ^2= 0.9, df = 1, p = 0.344). Kaplan-Meier survival curves considering the censored TRT did not reach 0 as the longest TRTs were censored due to equipment failure and suggest that the maximum residence time of rainbow runner and oceanic triggerfish was underestimated. The Median values from the Kaplan-Meier survival curves with censoring was 59 days for oceanic triggerfish but could not be determined for rainbow runner as the curve did not decrease below 0.5 due to the censoring of the longest TRTs. Instead, the survivorship at 60% was used for comparisons. The Kaplan-Meier survival curves with censoring estimated that 60% of oceanic triggerfish remained associated with FADs for approximately 30 days and 25 days for rainbow runner (Fig.3.2(b)) while with the uncensored data, the estimation was reduced to approximately 15 days for oceanic triggerfish and 17 days for rainbow runner (Fig. 3.2 (a)). Mean residence time estimation using the survival regression model on censored data was 65 days for oceanic triggerfish and 94 days for rainbow runner. The overall TRT mean (no regression model) was of 21.01 days (±17.59 SD) for oceanic triggerfish and 23.5 days (± 21.80 SD) for rainbow runner.

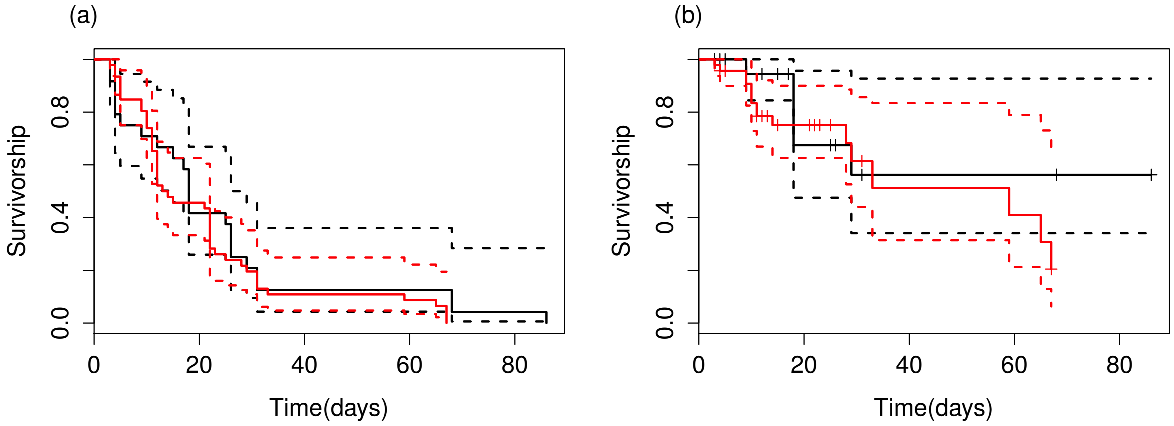
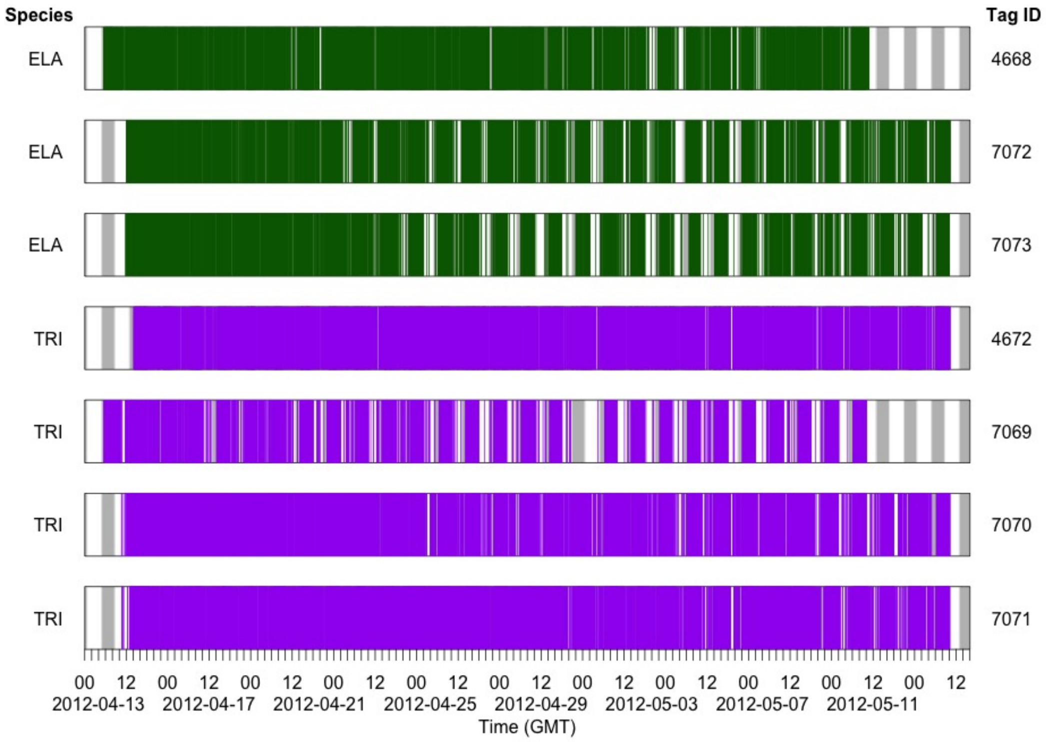


Figure 3.2 Kaplan-Meier survival functions based for oceanic triggerfish (red line) and rainbow runner (black line) for (a) all TRTs and (b) natural departure TRTs and censored TRTs. Horizontal ticks indicate censored data points. Dotted lines represent 95% confidence interval.

Fine-scale behaviour

Fig 3.33.43.5 shows that the two species generally remained within the reception range of the FAD during most of the day. Gaps in the detections indicate when individuals were out of the reception range, away from the FADs (Fig. 3.3). The variability in the associative behaviour amongst individuals of the two species as well as temporal variability of individuals during their association is depicted on Figs. 3.3,3.4,3.5. While some detection gaps appear to be synchronised, they do not appear to be systematic for the two species (Fig.3.3). The clustering analysis revealed that there was no clear species-specific grouping; some triggerfish had displayed more similar associative behaviours to rainbow runner than their conspecifics (Fig.3.6).



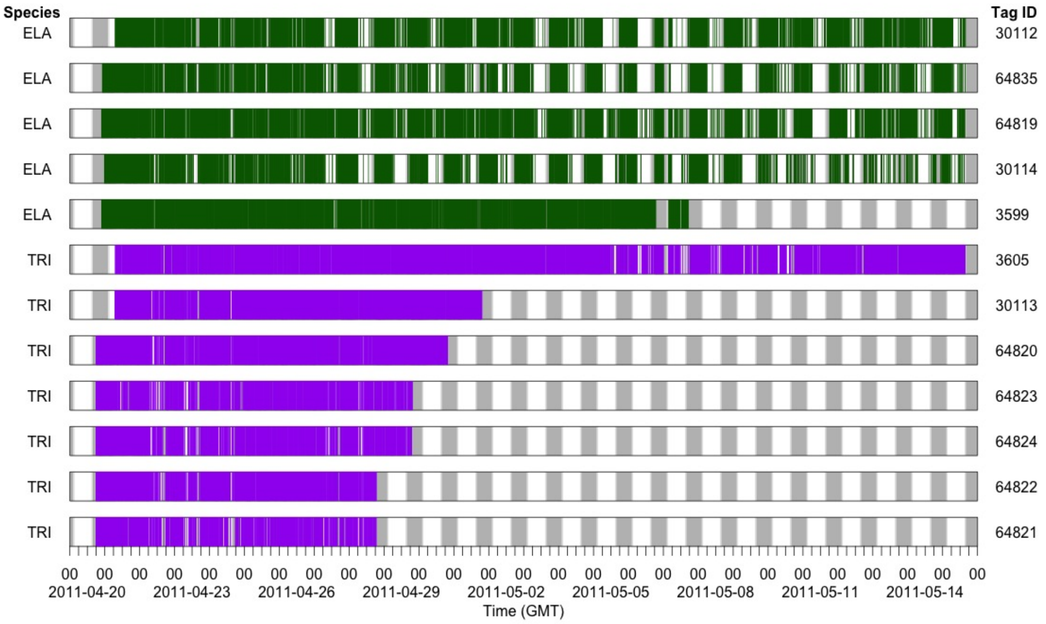


Figure 3.3 Examples of fine scale detections timelines for oceanic triggerfish and rainbow runner at FAD SEY41 (top) and FAD MAY42 (bottom). Each row illustrates the detections from an individual (ID on the right). The coloured vertical bars represents single detections with spaces indicating gaps in the detections. ELA is rainbow runner (green) and TRI is oceanic triggerfish (purple). The grey areas indicate nighttime

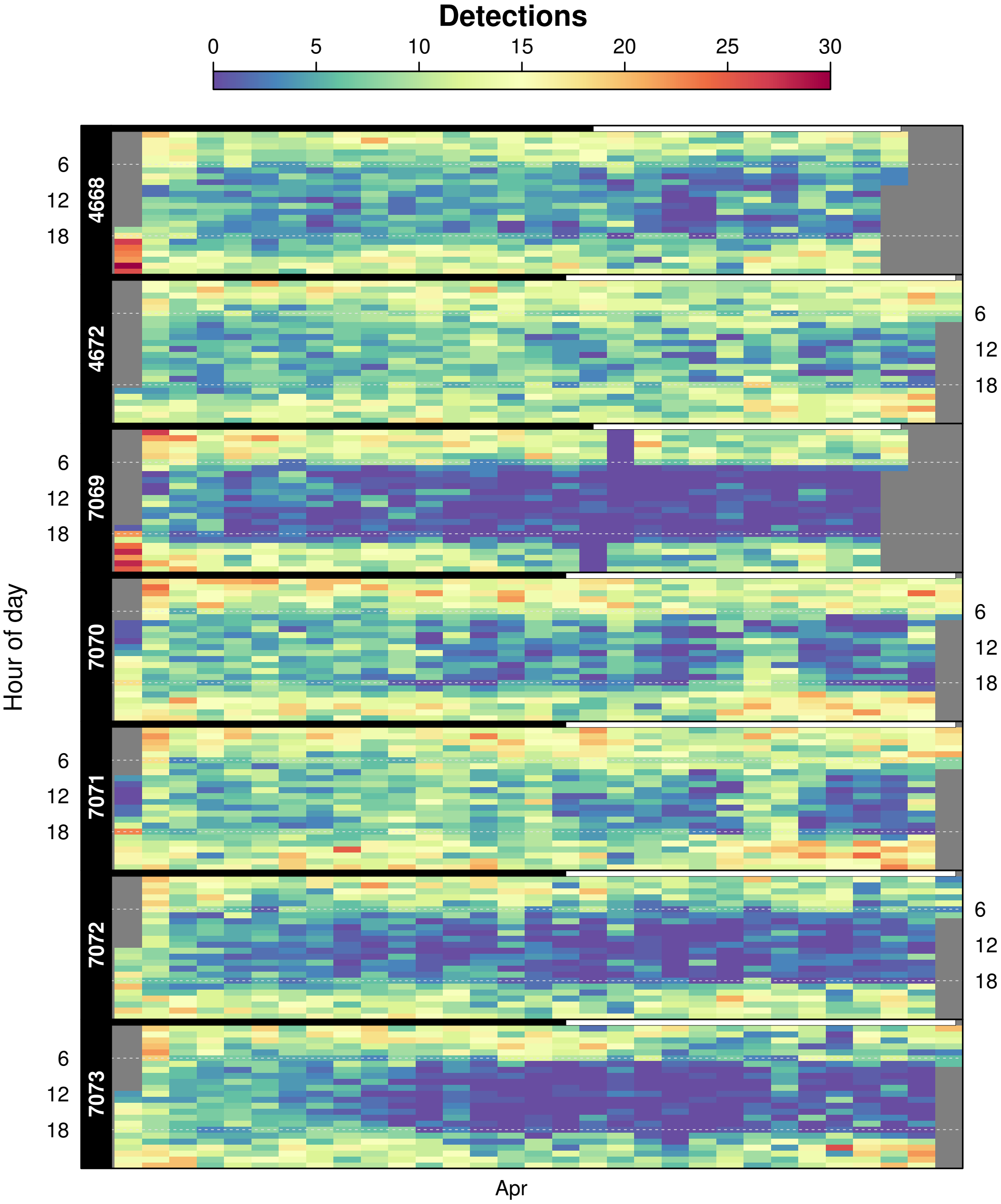


Figure 3.4 Examples of hourly detection chronograph for oceanic triggerfish (ID# 4672, 7069, 7070, 7071) and rainbow runner (ID# 4668, 7072, 7073) at FAD SEY41. Each strip illustrates the hourly detections of an individual (ID# on the right). Hour of the day is on the y-axis and time (days) on the x-axis. The scales denotes the corresponding number of detections.

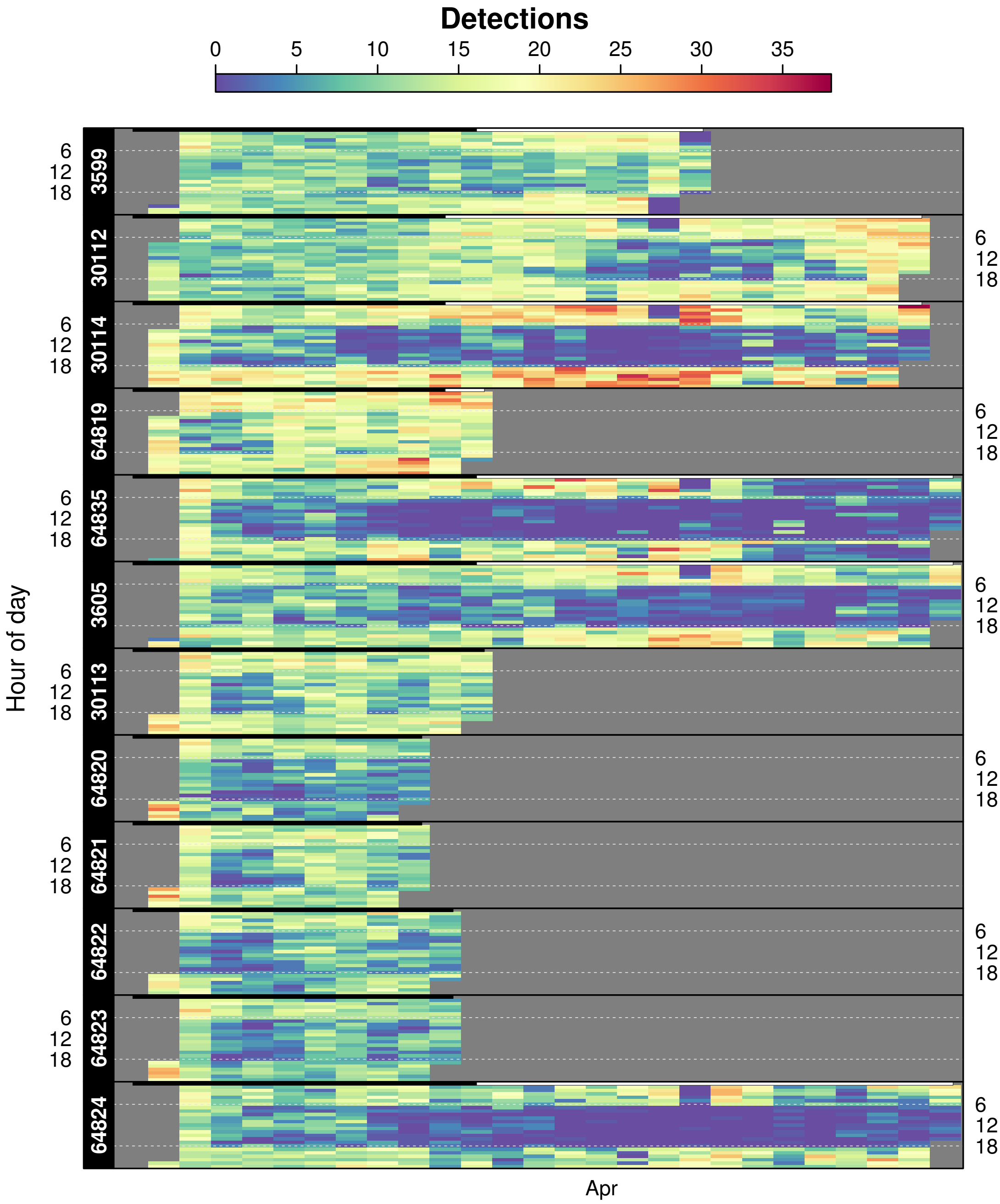


Figure 3.5 Examples of hourly detection chronograph for oceanic triggerfish (ID# 3605, 30113, 64820, 64823, 64824, 64822, 64821) and rainbow runner (ID# 30112, 64835, 64819, 30114, 3599) at FAD MAY42. Each strip illustrates the hourly detections of an individual (ID# on the right). Hour of the day is on the y-axis and time (days) on the x-axis. The scales denotes the corresponding number of detections.

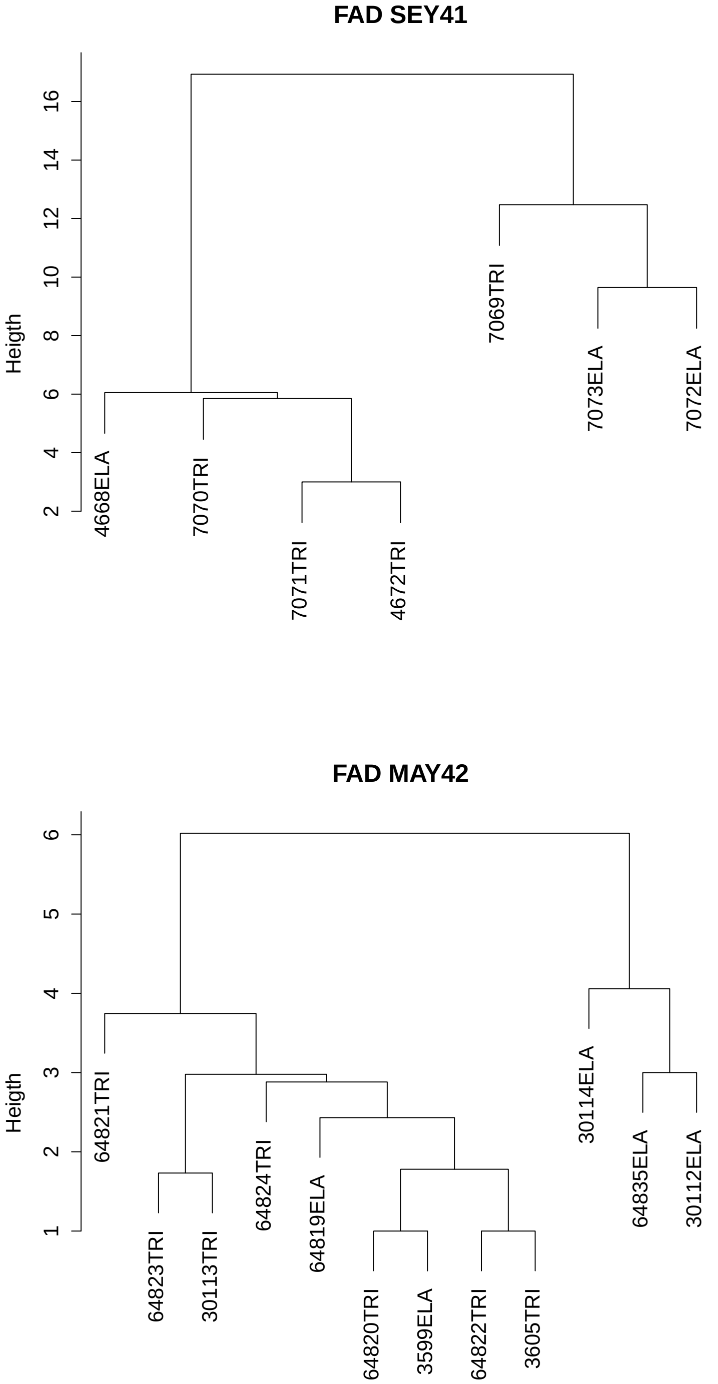


Figure 3.6 Examples of cluster dendrogram of hourly presence-absence segments for FAD SEY41 and MAY42. End nodes are denoted by ID number and species code (TRI = oceanic triggerfish, ELA = rainbow runner).

Overall, 82% of tagged oceanic triggerfish performed excursions while all tagged rainbow runner performed at least one excursion (Table**??**). The distributions of the excursion index was not unimodal (Fig.3.7). A second mode was observed in the excursion index distributions of rainbow runner and to a lesser extent for oceanic triggerfish. This indicates a different modality in the associative behaviour were some individuals performed ~2-3 times more excursions per unit time than their conspecifics (Fig.3.7). The mean duration of excursions was of 2.0 hours (±1.6 SD) for oceanic triggerfish and 2.4 hours (±2.2 SD) for rainbow runner (Fig.3.8). Rainbow runner performed more excursions per unit time than oceanic triggerfish; the mean excursion index was of 0.86 (±0.8 SD) for oceanic triggerfish and 1.31 (±1.1 SD) for rainbow runner.

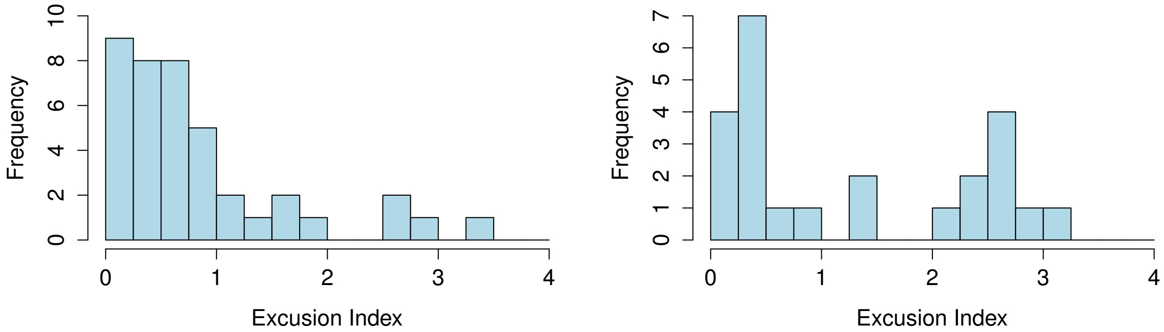


Figure 3.7 Distributions of excursion index for oceanic triggerfish (left) and rainbow runner (right)

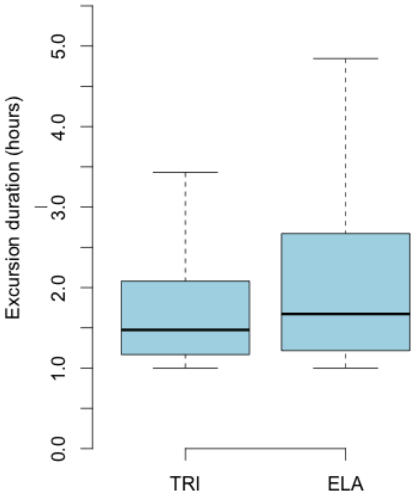


Figure 3.8 Excursion durations of oceanic triggerfish (TRI) and rainbow runner (ELA)

Temporal patterns in association

Temporal patterns in association using FFT spectral analysis revealed a strong periodicity in the association of both species at FADs with a distinct peak at 24 h (Fig. 3.9). This pattern was observed for all analysed individuals of the two species (rainbow runner n = 18, oceanic triggerfish n = 40) with sufficient data (> 5 days of data) which suggests the presence of a distinct diel pattern in their associative behaviour.

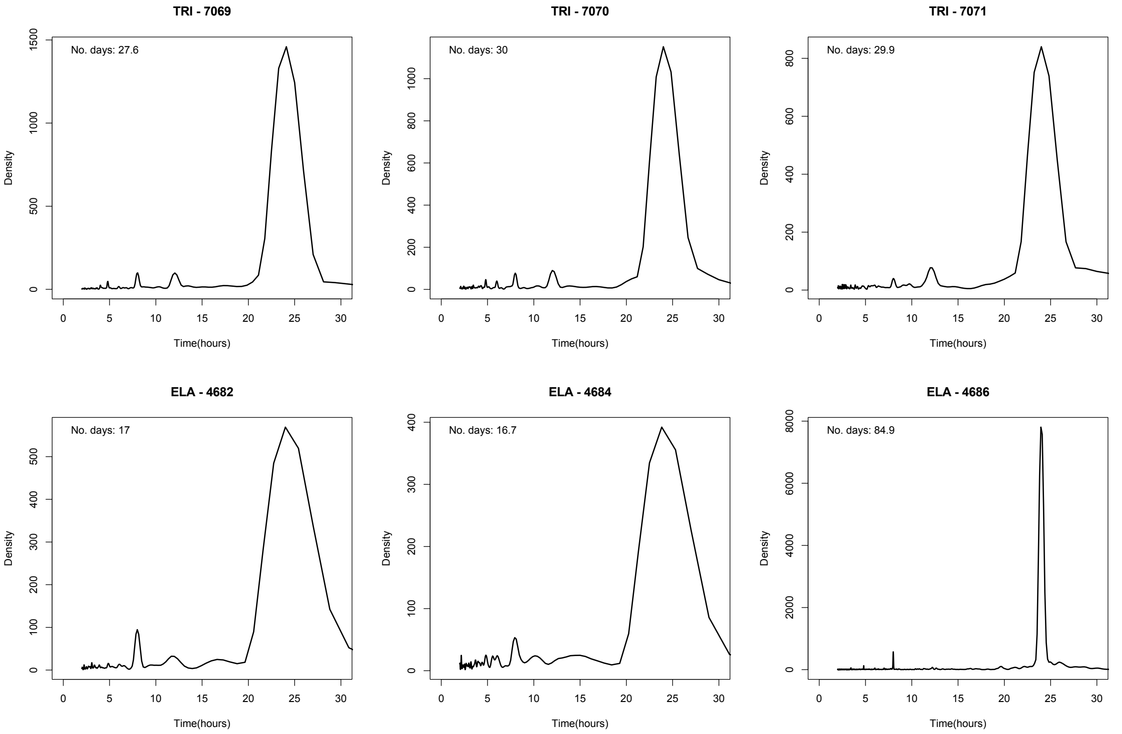


Figure 3.9 Examples of FFT spectral densities for three oceanic triggerfish (top) and three rainbow runner (bottom) at drifting FADs.

Moreover, the 24 h periodicity was clear on the wavelet spectrograms with a significant signal (Fig.3.10). However, intraspecific variability in the persistence of the 24 h periodicity was apparent (Fig. 3.10). Examples in Fig. 3.10 illustrates different patterns in the persistence of periodicity; some individuals exhibited continuous periodicity (oceanic triggerfish: ID# 7079, 7070, 7071; rainbow runner: ID# 7072, 7073, 4668) throughout their residency at FADs while others displayed intermittent periods of periodicity (oceanic triggerfish: ID# 3605, 64824, 64827; rainbow runner: ID# 4686, 30114, 3588). These observed differences in pattern were not FAD specific.

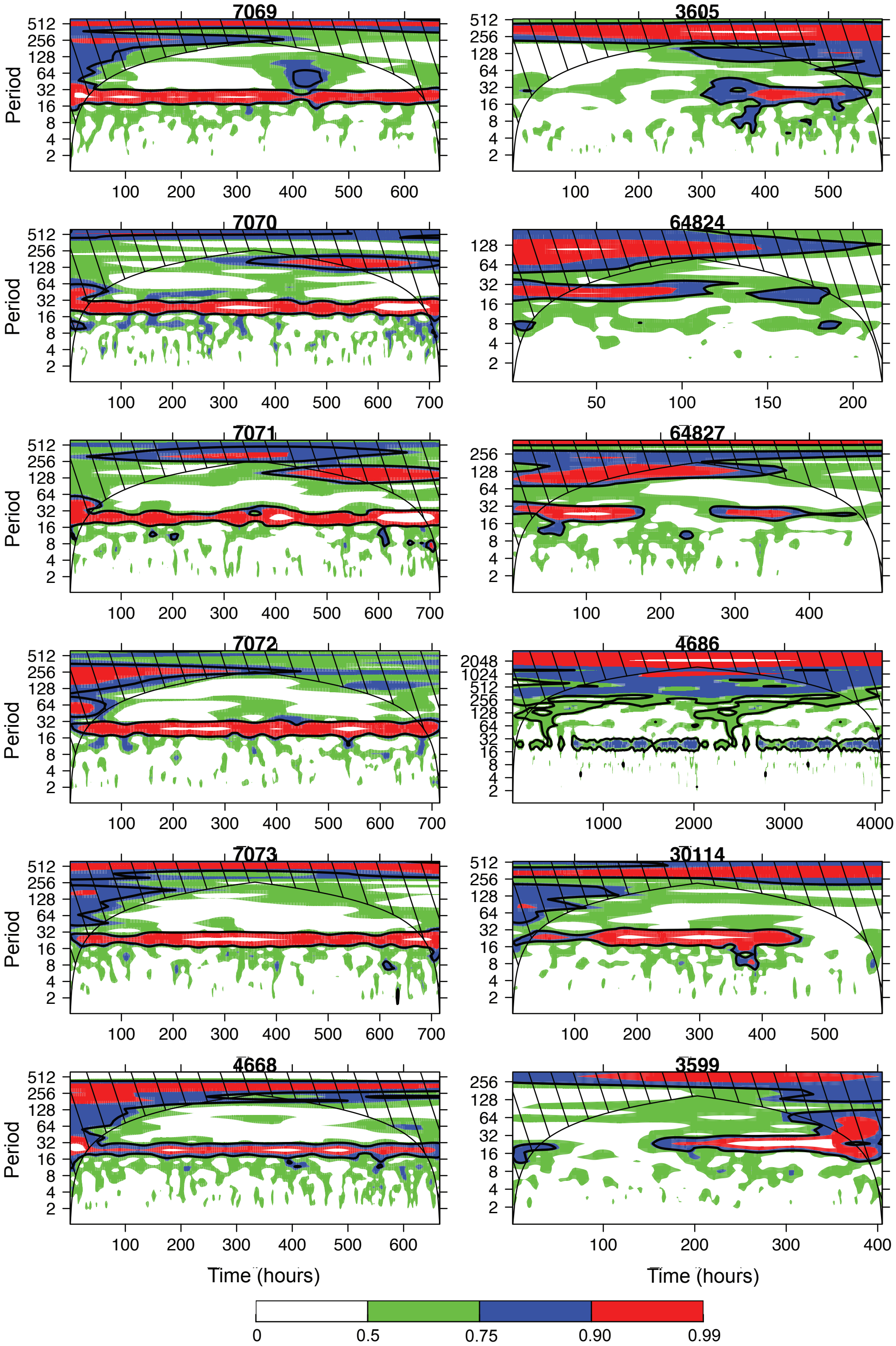


Figure 3.10 Wavelet spectrum examples of oceanic triggerfish (Top; ID# 7069, 7070, 7071, 3605, 64824, 64827) and rainbow runner (bottom; ID# 7072, 7073, 4668, 4686, 30114, 3599) using Morlet wavelet of hourly detections showing persistent diel behaviour (left) and intermittent diel behaviour (right). Barred area represents the cone of influence (COI). Values inside the COI cannot be interpreted due to edge effects. The thick black contour lines represent 95% confidence level and the scale bar represents the intensity of the time-frequency space over time.

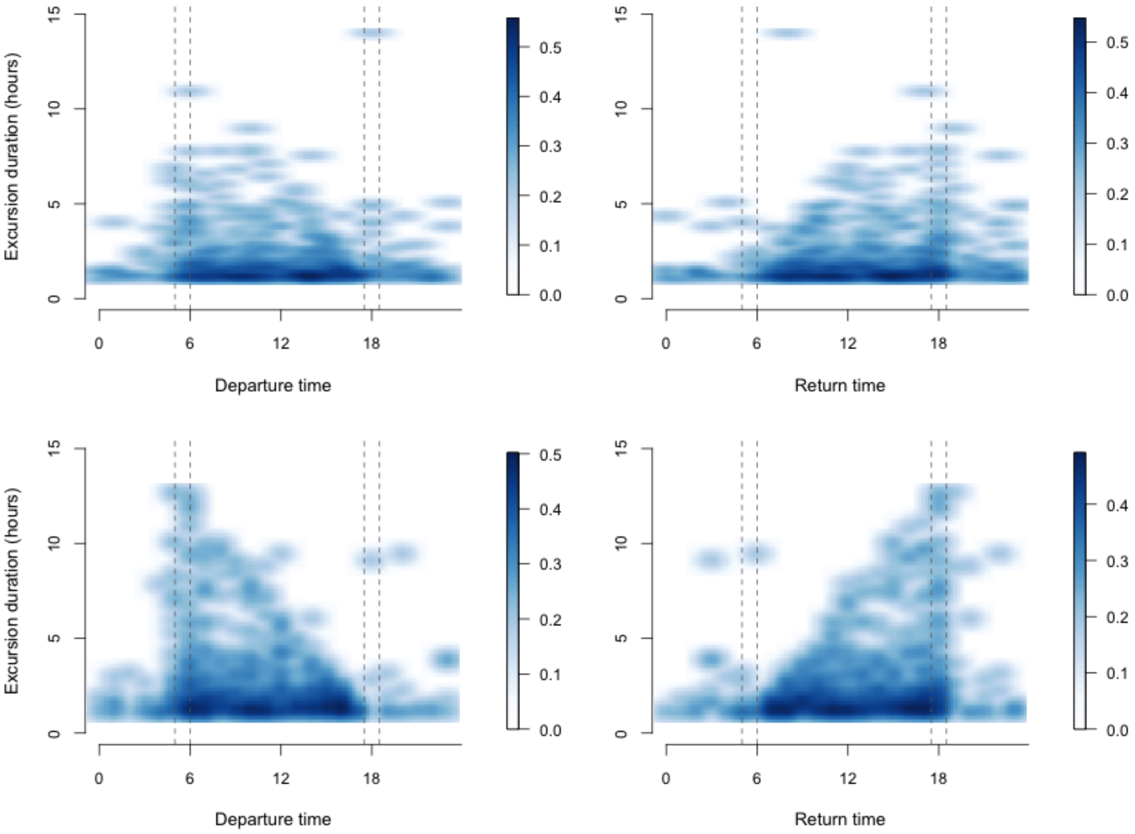


Figure 3.11 Heatmap of departure and return time (local time) of excursions with corresponding durations for oceanic triggerfish (top) and rainbow runner (bottom) at FADs. Densities are represented on the scalebars. Areas between doted lines represent sunrise and sunset hours.

The distribution and durations of excursions were then examined at a 24 h scale. The heatmap indicates that most of the excursion activity (departures and returns) occurred mostly during the daytime for both species (rainbow runner; 72.5 %, oceanic triggerfish: 81.2%). A sharp increase in excursion departure occurred with sunrise and a decrease at sunset irrespective of the excursion duration. While excursion durations were typically short (Fig.3.7,3.11), the pattern observed for longer excursions was distinct; for both species, there was a linear decrease in longest excursion returning at the FAD before sunset.

3.4 Discussion

Residency at FADs

Both rainbow runner and oceanic triggerfish remained associated to the same floating object for an extended period of time. The two species have the longest measured residence time (rainbow runner 84.6 days and oceanic triggerfish 66.4 days) at the same drifting FAD that has been reported. Dagorn *et al.* (2007b) were the first study to tag both tuna and non-target species (121 fish of 7 different species) at drifting FADs. The study provided a general mean residence time for yellowfin tuna (mean: 1.04 days, ±2.23 SD), skipjack tuna (mean: 0.91 days, ±2.17 SD), bigeye tuna (mean: 1.43 days, ±1.46 SD) silky sharks (mean: 5.33 days, ±3.16 SD), wahoo (mean: 1.57 days, ±2.73 SD), dolphinfish (mean: 3.96 days, ±3.86 SD), silky sharks (mean: 5.33 days, ±3.16 SD) and oceanic triggerfish (mean: 12.49 days, ±6.08 SD). Filmalter *et al.* (2015) reported a mean residence time of 14.03 days at drifting FADs for silky sharks. Taquet *et al.* (2007a) reported that the mean residence time of dorado at drifting FADs was of 6.25 days (median of 5.09 days). The overall mean residence time in this study was 21.03 days for oceanic triggerfish and 23.5 days for rainbow runner which is considerably longer than what was reported above. No previous investigations were done on the residency of rainbow runners at drifting FADs. While the 'raw' mean residence time provides some general indication of residency, it is biased by observation lengths and truncations. Indeed, the mean residence time estimation from the regression model of censored data was considerably higher with 65 days for oceanic triggerfish and 94 days for rainbow runner. Using mean values as a descriptor of the survivorship can be misleading due to the skewed nature of the survival functions. It is therefore recommended that median values from Kaplan-Meier survival curves (with censoring) are jointly reported in order to allow appropriate comparisons of residency between studies. The residency index also indicated highly resident with scores above 0.75 which is comparable to scores obtained for resident reef species (Alós *et al.*, 2012b; Mason and Lowe, 2010; O'Toole *et al.*, 2011). The ecological trap hypothesis suggests that massive seeding of drifting FADs could have a negative impact on the populations of associated species (Hallier and Gaertner, 2008a; Marsac *et al.*, 2000). To date, there no clear evidence in favour of this hypothesis and the few studies that have investigated this topic have focused on tunas (Hallier and Gaertner, 2008a; Menard, 2000; Robert *et al.*, 2014). In a hypothetical ecological trap scenario, the impacts on populations of oceanic triggerfish and rainbow runner, due to their long residency, should be more prominent. However, as highlighted by Robert *et al.* (2014), demonstrating the presence of an ecological trap scenario is not trivial and requires baseline information on the biological parameters (e.g. body condition, reproductive success). While the two studied species could be good candidates to study the ecological trap hypothesis, the difficulty remains in finding a control to test this hypothesis.

Temporal patterns in association

Diel pattern in association with FADs have been reported for yellowfin, bigeye and skipjack tuna at anchored FADs (Holland *et al.*, 1990b; Marsac and Cayré, 1998; Ohta and Kakuma, 2005; Yuen, 1970) and drifting FADs (Forget *et al.*, 2015; Schaefer and Fuller, 2013; Matsumoto *et al.*, 2014) with a closer association during the day. Similarly, silky sharks displayed a stronger association during the day (Filmalter *et al.*, 2015; Forget *et al.*, 2015) while no clear pattern was found for dorado at FADs (Taquet *et al.*, 2007a). A distinct diel pattern in the associative behaviour with FADs was observed here for oceanic triggerfish and rainbow runner. Contrastingly, the diel pattern observed for these two species was opposite to that of other pelagic species described above. During daytime, the two species increased their home range as they performed excursions away from the FAD, out of the hydrophone's reception range. This diel pattern at FADs is more commonly observed in reef associated species (Koeck *et al.*, 2014; Alós *et al.*, 2011). The studies mentioned above have suggested that nocturnal feeding behaviour drives the switch in the associative mode of tunas and silky shark as they move away from the FAD and feed on the deep scattering layer. An opposing diel pattern in the pelagic realm observed for oceanic triggerfish and rainbow runner is intriguing and may reflect differences in foraging strategy or predator avoidance mechanisms. Information on their vertical movement behaviour to investigate the depth strata usage and feeding ecology may help elucidate this different diel associative pattern.

Ambient light intensity appears to be the stimulus triggering the onset and end of the associative modes. After sunrise, the two species typically increase their home range and perform excursions away from the FAD. The average excursion duration of oceanic triggerfish (2.05 h) and rainbow runner (2.45 h) suggests that individuals, generally, do not venture far from the FAD. Considering a swimming speed of 1 body length per sec, the maximum home range size of the two species (assuming constant speed and a linear movement away from FAD) during a typical excursion could range between 1.1 and 2.2 km. During an active tacking experiment conducted on FAD SEY41, the maximum measured distance of oceanic triggerfish away from the FAD (during an excursion), while tracking a silky shark, was 800 m (Filmalter *et al.*, 2015). The homing abilities and mechanisms used by fish to return and relocate FADs has intrigued scientists. Tunas perform extended nocturnal excursions away from FADs and active tracking studies have reviled that, during that time, they can be found within a radius of 5-10 km from FAD (Dagorn *et al.*, 2000b; Holland *et al.*, 1990b; Matsumoto *et al.*, 2014). The ability of tuna to relocate FADs from such large distances demonstrates their navigational and homing abilities (Holland *et al.*, 1990b). Girard *et al.* (2007) investigated the homing abilities of dorado through displacement experiments and acoustic telemetry and reported successful homing up to 1.6 km from the FAD. Filmalter *et al.* (2015) actively tracked a silky shark at a drifting FAD during one day and reported a maximum straight line distance of 1.2 km away from the FAD. Ibrahim *et al.* (1990) investigated the homing ability of various small ($<$ 40 cm TL) FAD-associated species to locate FADs by displacing fish tagged with floats at various distances from the FAD and reported that a maximum homing distance of 180 m. In their pioneer study, Hunter and Mitchell (1967) looked into the homing ability of oceanic triggerfish by tagging and releasing 10 individuals at 7.5, 15 and 30.5 m from their original drifting log. None of the fish released at 30.5 m returned to the original log. The authors concluded that the greatest distance was outside the visual range of the fish and thus the fish could not orientate towards it. The results from this study, however, indicate that both oceanic triggerfish and rainbow runner are capable of returning to the FAD after several hours out of its visual range (several hundred meters) and as highlighted by previous studies (Dempster and Kingsford, 2003; Ibrahim *et al.*, 1990) vision cannot be of aid from such large distances. It is conceivable that other sensory cues, such as sounds generated by the floating object, is used by FAD associated species for homing, however, the hearing capabilities of pelagic fish and its use for navigation remains unclear (Dempster and Kingsford, 2003).

The motive of excursions away from FADs displayed by tunas, dorado and silky shark has largely been attributed to foraging activities (Filmalter *et al.*, 2015; Holland *et al.*, 1990b; Taquet *et al.*, 2007a). Foraging could also be the primordial motive causing the increase in home range of the two studied species. If so, the fact that excursion occur during the day suggest that the two species have a different foraging strategy to that of tunas and silky sharks; which tend to be more active nocturnally. Klima and Wickham (1971) proposed that floating objects act as a spatial reference point that fish use to orientate in an otherwise unstructured environment. The two species may temporarily increase their home range for feeding while using the FAD as a reference point.

The clustering revealed that there was no species-specific grouping of the associative behaviour at FADs. Variability was observed in the associative behaviour amongst individuals of the two species and the fact there was no systematic synchronisation in absences from FAD amongst individuals suggests that oceanic triggerfish and rainbow runner do not form unique monospecific schools at FADs and are more likely to form smaller sub schools. Some individuals of the two species performed 2 to 3 times more excursions per unit time than their conspecifics. This intraspecific difference in behaviour was more apparent for rainbow runner and suggests the presence of a different behavioural mode. The fact that individuals at the same FAD experiencing the same abiotic and biotic environmental conditions display different behaviours indicates behavioural polymorphism. Behavioural variability in fishes has been observed at fine scales under controlled laboratory conditions (Raimondi and Keough, 1990) and has also been used to explain differences in large scale movements, such as migration (see partial migration: Kerr *et al.*, 2009). Explaining behavioural variability is challenging as the interplay between genetic variability, historical shifts in selection pressures and adaptive behaviour is hard to disentangle. Nevertheless, it is conceivable that foraging competition amongst numerous aggregated individuals (several hundreds at a single FAD; personal observation), within a restricted spatial sphere could favour this different behavioural mode.

Temporal variability in associative behaviour was apparent for both species. The wavelet analysis was found to provide additional information on the persistence of diel patterns. Periods (days) when diel behaviour were less distinct were apparent as gaps in the periodicity signal were observed. Interestingly, periods with altered associative behaviour were sometimes synchronised amongst individuals suggesting a change in behaviour that could be a response to a particular stimulus of biotic or abiotic nature. In order to resolve which factors can influence the associative behaviour, biotic and abiotic factors should be collected simultaneously during experiments. More specifically, biotic factors, such as prey and predator density and details on the species assemblage, and abiotic factors, such as thermal structure of water column, would aid understand the factors that can influence associative behaviour.

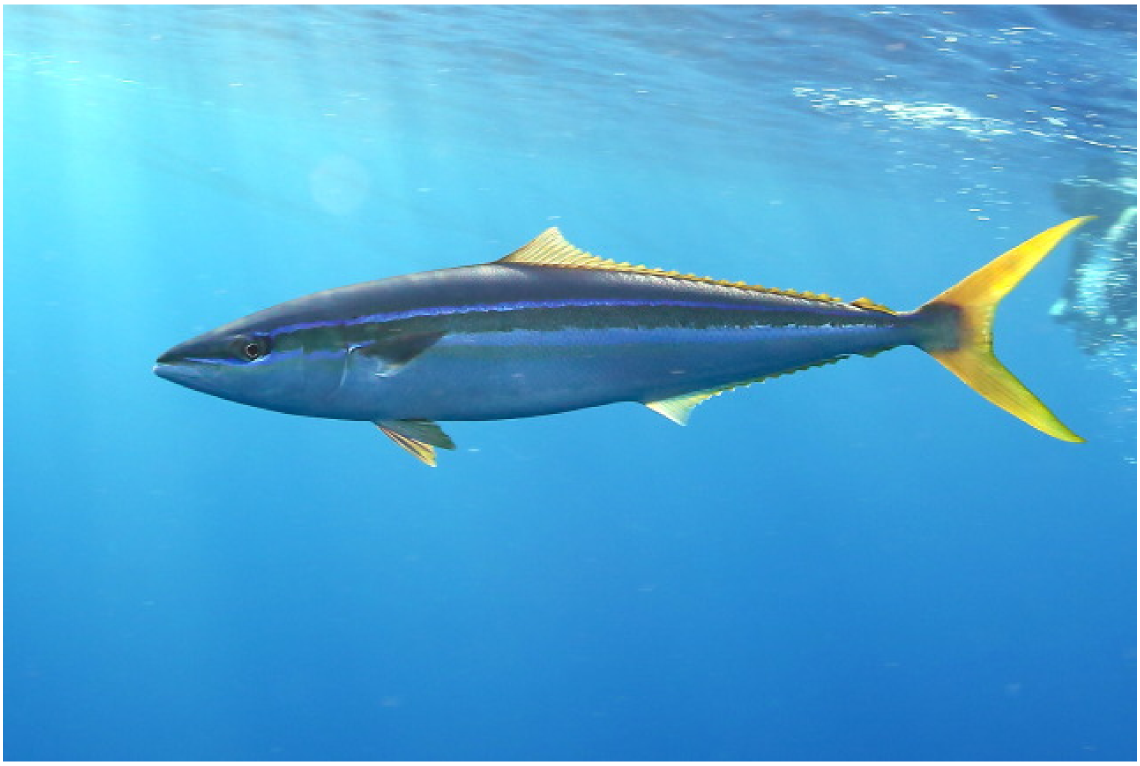
Conclusion

Oceanic triggerfish and rainbow runner and triggerfish have remarkably similar behavioural patterns in their association with FADs. This suggests that the convergence of their behaviour has risen from similar selective pressures and, hence, the two species are likely to have similar motives in associating with floating objects. More data on the ecology of the two species are required to pinpoint the exact motives of their behaviour. The long residence times observed for the two species implies that they are susceptible to high fishing effort on FADs. As such, key biological parameters and data to determine their ecological role in the pelagic ecosystem are need to model increased fishing mortality linked to the FAD based fishery.

It must however be noted that the obtaining natural departure from FADs metric is challenging as it requires large efforts, but, nevertheless, it remains a key parameter for modelling approaches to estimate direct and indirect impacts of FADs on the pelagic ecosystem .

Chapter 4

Vertical movement behaviour and activity of oceanic trigger fish and rainbow runner associated with floating objects.



4.1 Introduction

Large multispecies aggregations at floating objects are a common feature of the world's tropical and subtropical oceans, yet , the motives driving fish to associate with floating objects remains unclear. Species assemblages at floating objects are diverse and several explanations have been proposed in attempt to explain the possible evolutionary benefits for different species (see reviews: Castro *et al.*, 2002; Fréon and Dagorn, 2000). Oceanic triggerfish and rainbow runner are the two most abundant non-tuna fin-fish found at floating objects (Lezama-Ochoa *et al.*, 2015; Romanov *et al.*, 2009) but little is known about their ecology and associative behaviour at FADs. This may be due to the fact that these species are not targeted by fisherman and have a relatively little economic value. Oceanic triggerfish and rainbow runner are known to associate with floating objects for prolonged periods of time during which they occasionally perform short excursions (1-2 hrs) away from the FAD (Chapter 3). These extended associations suggests that floating objects play an important role in the life of the two species in the pelagic environment. Consequently, additional information on their fine-scale behaviour could provide some key insights in their behavioural ecology and help to better explain why fish associate with floating objects. Acoustic telemetry has enabled the study of vertical movement behaviour of pelagic fish at fine-scales (Brill *et al.*, 1993; Cayré and Chabanne, 1986; Cayré, 1991; Holland *et al.*, 1990a; Schaefer and Fuller, 2013; Yuen, 1970; Dagorn *et al.*, 2007b). Diel patterns in the vertical movement and general depth preferences have been used to infer habitat use, characterise different life strategies and to identify species-specific niches (Block *et al.*, 2003; Sims *et al.*, 2005; Young *et al.*, 2010). Moreover, the recent development of accelerometer tags now provides new insights into animal behaviour (Whitney *et al.*, 2007; Wilson *et al.*, 2008). In previous studies, activity level of pelagic fish was inferred from vertical movements, however, recent studies have shown that vertical movements does not necessarily reflect locomotory activity patterns or foraging (Gleiss *et al.*, 2013). Rhythmic patterns in animal behaviour can inform about the specific traits which have evolved in response to biotic factors, including predation and prey availability (Berger and Gotthard, 2008), and abiotic factors such as temperature and light intensity (Elliott and Gaston, 2015; Taylor *et al.*, 2013). Furthermore, an improved understanding of habitat utilisation and spatial niche partitioning of pelagic species will contribute towards a better understanding of the pelagic ecosystem and, as such provide valuable information for an ecosystem-based management. This study investigates the vertical movement behaviour and activity patterns of oceanic triggerfish and rainbow runners at FADs using acoustic telemetry. The specific objectives were to 1) characterise the vertical and thermal habitat and 2) to assess the temporal patterns in vertical movements and activity.

4.2 Materials and Methods

Study site and tagging

The study site and tagging methods are described in the Materials and Methods section of Chapter 3.

Data Analysis

Vertical movement

The vertical movements of the two studied species was inferred from depth measurements obtained from pressure sensitive transmitters (V9P, V9TP, V9AP; 120 s nominal delay, 69 kHz, 1H, Vemco, Amirix, Canada). Depth measurements that exceeded the 100 m limit of the sensor were excluded from the analysis (n = 4). Daily position estimates obtained from the VR4Global allowed the tracking of FADs' drifts. For each FAD, the local daily sunrise and sunset as well as the astronomical dusk and dawn were calculated from daily positions using the “maptools” R Package (Bivand and Lewin-Koh, 2015). Cyclic temporal patterns in the vertical movement behaviour for each individual were examined, a fast Fourier transform (FFT) was applied to the hourly mean depths and the resulting spectral density was then plotted. FFT indicates whether there are rhythmic patterns in the vertical movements. Distinct peaks in the spectral density indicates the presence of cyclic rhythms and indicates its periodicity. The spectral analysis was performed on individuals that had $\geq$ 5 days of data to ensure sufficient sample size for the analysis.

Temperature distributions

Temperature data at the FAD MAY41 was fortuitously obtained for a period of 30 days from a recovered MK9 archival tag (Wildlife Computers, Redmond, USA) that was deployed on a silky shark also tagged with an acoustic transmitter. This temperature data from the archival tag was linearly interpolated to produce continuous daily temperature profiles with a 0.5 m grid resolution (method described in Bauer *et al.*, 2015). The thermocline depth was estimated using the "maximum slope by difference" method (Fiedler, 2010). This method defines the thermocline as the depth segment with the maximum negative temperature gradient (-dT/dz) between all temperature pairs spaced by dz $\geq$ 20 m. Additionally the shallow mixed layer depth (MLD), defined here by a gradient > 0.8 °C was calculated (Kara *et al.*, 2000, 2003).

Activity

Data from tri-axial accelerometer transmitters (V9AP, 69kHz, 120 s nominal delay, Vemco, Amirix, Canada) were used to analyse activity patterns. The transmitters measured acceleration in the X, Y, and Z axes over a period of 20 s at a sampling rate of five times per second. Acceleration in m s^{-2} was then calculated by the transmitter as the root mean squared value from each axis and transmitted. Tri-axial accelerometers represent a general locomotive activity index of the fish including surges, dorso-venteral and lateral movements and are analogous to overall dynamic body acceleration (Taylor *et al.*, 2013). The sensor range limits of the transmitters acceleration sensor were between 0 and 5 m s^{-2}. As for vertical movement, the rhythmicity of activity was examined for each individual using FFT on the hourly mean acceleration. The spectral analysis was performed on individuals that had $\geq$5 days of data to ensure sufficient sample size for the analysis

Vertical movement versus locomotory activity

The relationship between acceleration and vertical movement was examined in order to determine whether vertical movement was analogous to locomotive activity. As depth and acceleration data are transmitted sequentially, the data was binned hourly to allow comparison. Only hourly bins with both acceleration and depth values were used for this analysis. The total vertical distance was calculated by summing the vertical movement in hourly bins. For example, when a fish ascended 10 m in the water column followed by a descent to 40 m the total vertical movement was 50 m. Similarly, the sum of acceleration measurements for each hourly bin was calculated. A linear model and a non parametric loess model (Jacoby, 2000) were used to examine the relationship between vertical movement and activity levels during the same hours.

Environmental data

Daily SST were obtained from the Moderate Resolution Imaging Spectroradioeter (MODIS) of the Aqua platform between 2010 and 2012 at a 4.5 km spatial resolution (http://oceancolor.gsfc.nasa.gov/). The SST daily fields were estimated using a 3 day moving average. Daily global altimeter products -sea level anomalies (SLA)- at a resolution of 0.25° were used. This data are produced by Ssalto/Duacs and distributed by Archiving Validation and Interpretation of Satellite Oceanographic data AVISO, with support from CNES (http://www.aviso.altimetry.fr/duacs/).

4.3 Results

A total of 148 783 and 64 494 depth measurements and 40 422 and 16 967 acceleration measurements were obtained for oceanic triggerfish and rainbow runner respectively. Details of the tagging information are provided in Table 4.1.

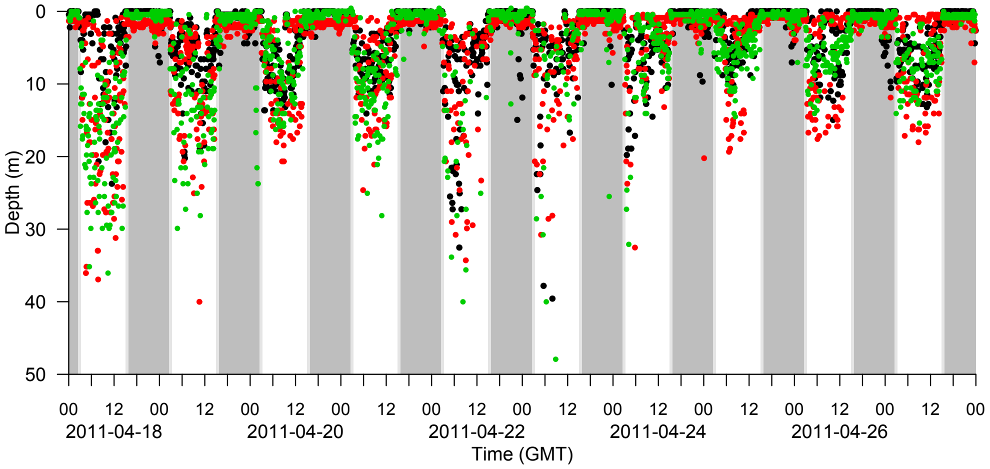
Table 4.1 Metadata for oceanic triggerfish and rainbow runner tagged with pressure sensitive and accelerometer tags. TRT is the total residence time. * denotes TRT with natural departures from FAD.‡ rainbow runner lengths are given in FL and and oceanic triggerfish lengths in TL.

Tagging		Species	Size	FAD ID	Acoustic tag		Experiment	
Date	Time		(TL/FL cm)‡		Type	ID	Duration	TRT
15/04/11	11:56	TRI	31.0	MAY41	V9TP	3601	21.4	20.7
15/04/11	11:42	TRI	30.0	MAY41	V9TP	3603	21.4	21.3
15/04/11	16:27	TRI	32.0	MAY41	V9P	64826	21.4	20.7
15/04/11	16:04	TRI	30.0	MAY41	V9P	64827	21.4	20.7
15/04/11	22:01	TRI	33.0	MAY41	V9P	64828	21.4	20.5
16/04/11	07:15	TRI	33.0	MAY41	V9P	64829	21.4	20.7
16/04/11	23:48	TRI	34.0	MAY41	V9P	64830	21.4	21.1
16/04/11	21:46	TRI	30.0	MAY41	V9P	64831	21.4	21.12
16/04/11	22:25	TRI	36.0	MAY41	V9P	64832	21.4	21.12
16/04/11	-	TRI	30.0	MAY41	V9P	64834	21.4	1.6*
20/04/11	11:59	ELA	24.0	MAY42	V9TP	3599	26.9	16.8*
20/04/11	12:16	ELA	23.0	MAY42	V9P	30112	26.9	24.3
20/04/11	18:45	ELA	23.0	MAY42	V9P	30114	26.9	24.6
20/04/11	08:02	ELA	23.5	MAY42	V9P	64819	26.9	24.7
21/04/11	-	ELA	23.5	MAY42	V9P	64835	26.9	24.7
20/04/11	11:46	TRI	32.5	MAY42	V9P	3605	26.9	24.3
20/04/11	11:05	TRI	32.5	MAY42	V9P	30113	26.9	10.5*
20/04/11	07:43	TRI	36.5	MAY42	V9P	64820	26.9	10.1*
20/04/11	07:10	TRI	34.0	MAY42	V9P	64821	26.9	8.0*
20/04/11	07:01	TRI	31.0	MAY42	V9P	64822	26.9	8.0*
21/04/11	16:50	TRI	32.0	MAY42	V9P	64823	26.9	9.1*
21/04/11	16:35	TRI	35.0	MAY42	V9P	64824	26.9	9.0*
15/03/10	18:21	TRI	33.0	MOZ31	V9P	64810	11.6	11.5
15/03/10	18:13	TRI	33.0	MOZ31	V9P	64811	11.6	7.3*
16/03/10	18:06	TRI	31.0	MOZ31	V9P	64813	11.6	10.8
16/03/10	17:58	TRI	32.0	MOZ31	V9P	64814	11.6	10.8
16/03/10	17:45	TRI	33.0	MOZ31	V9P	64815	11.6	9.3
16/03/10	07:37	TRI	33.0	MOZ31	V9P	64816	11.6	10.8
16/03/10	16:17	TRI	33.0	MOZ31	V9P	64817	11.6	10.8
21/04/11	07:04	TRI	32.0	MOZ32	V9P	64809	10.8	11.0
08/03/10	11:25	ELA	45.0	MOZ34	V9P	64804	67.0	67.0
08/03/10	11:39	ELA	43.0	MOZ34	V9P	64805	67.0	67.0
09/03/10	11:59	TRI	39.0	MOZ34	V9P	64806	67.0	66.2
09/03/10	12:05	TRI	34.0	MOZ34	V9P	64807	67.0	12.5*
09/03/10	07:19	TRI	30.0	MOZ34	V9P	64808	67.0	26.4*
22/06/11	17:40	ELA	65.0	SEY37	V9TP	3593	16.6	13.5
23/06/11	17:00	ELA	62.0	SEY37	V9TP	3595	16.6	15.4
24/06/11	14:05	ELA	79.5	SEY37	V9TP	3597	16.6	7.8*
24/06/11	14:30	ELA	77.0	SEY37	V9P	3621	16.6	11.4
23/06/11	17:45	TRI	30.5	SEY37	V9P	3617	16.6	10.8
23/06/11	18:00	TRI	28.0	SEY37	V9P	3618	16.6	10.8
24/06/11	13:52	TRI	30.0	SEY37	V9P	3619	16.6	10.1
24/06/11	14:15	TRI	30.5	SEY37	V9P	3620	16.6	13.5
13/04/12	14:48	ELA	63.5	SEY41	V9AP	4668	21.4	27.7*
14/04/12	08:56	ELA	28.5	SEY41	V9P	7072	21.4	29.8
14/04/12	11:30	ELA	30.0	SEY41	V9P	7073	21.4	29.8
14/04/12	18:32	TRI	28.9	SEY41	V9AP	4672	21.4	29.5
13/04/12	16:55	TRI	33.5	SEY41	V9P	7069	21.4	27.6*
14/04/12	07:40	TRI	31.0	SEY41	V9P	7070	21.4	29.9
14/04/12	08:02	TRI	30.0	SEY41	V9P	7071	21.4	29.9
18/06/11	14:00	ELA	30.5	SEY43	V9P	3586	4.4	3.4

19/06/11	10:59	ELA	57.0	SEY43	V9P	3588	4.4	3.3
19/06/11	11:20	ELA	32.0	SEY43	V9TP	3590	4.4	3.3
19/06/11	11:45	ELA	34.0	SEY43	V9P	3606	4.4	1.9
19/06/11	13:15	ELA	61.5	SEY43	V9TP	3607	4.4	2.3
19/06/11	13:45	ELA	79.0	SEY43	V9TP	3610	4.4	4.3
18/06/11	14:35	TRI	32.0	SEY43	V9P	3611	4.4	4.2
18/06/11	14:45	TRI	30.5	SEY43	V9P	3612	4.4	4.2
18/06/11	14:55	TRI	34.0	SEY43	V9P	3613	4.4	4.2
18/06/11	15:15	TRI	26.5	SEY43	V9P	3614	4.4	2.8
18/06/11	15:30	TRI	30.5	SEY43	V9P	3615	4.4	4.2
26/04/12	11:34	ELA	64.0	SEY59	V9AP	4680	85.2	16.8*
26/04/12	11:57	ELA	60.9	SEY59	V9AP	4682	85.2	17.0*
26/04/12	13:37	ELA	44.6	SEY59	V9AP	4684	85.2	16.7*
26/04/12	17:50	ELA	35.0	SEY59	V9AP	4686	85.2	84.9
26/04/12	10:15	TRI	30.5	SEY59	V9AP	4674	85.2	57.9*
26/04/12	10:27	TRI	35.0	SEY59	V9AP	4676	85.2	66.4*
26/04/12	10:33	TRI	32.0	SEY59	V9AP	4678	85.2	64.4*

Vertical movement

Both species exhibited a distinct diel pattern in their vertical movements at FADs. The presence of distinct peaks in spectral density around 24 h revealed strong rhythmicity in their vertical behaviour (Fig.4.3). During the night, both species remained close to the surface (0-5 m) (Fig.4.1,4.2). The change in vertical movement behaviour was apparent at dawn when individuals increased their vertical movements in the water column to depths generally ranging from 40 to 70 m (Fig.4.1,4.2). At dusk, they rapidly returned to surface waters. The deepest dives generally occurred around midday. The maximum depth recorded was 91.5 m for oceanic triggerfish and 95.8 m for rainbow runner. Temporal variations in depth amplitudes were observed amongst individuals (Fig.4.5; ID: 7071, 4672). A distinct change from the normal diel pattern, termed 'type I' behaviour, was observed for three oceanic triggerfish at FAD SEY59 (ID: 4674, 4676, 4678) in June. This change in behaviour, termed 'type II' behaviour, was characterised by an absence from surface waters (0-5 m), a higher amplitude in nocturnal vertical movement and an increase in overall depth distribution (Fig.4.4). However, one rainbow runner (ID 4686) present at the same FAD did not display such behavioural switch in vertical movements and only exhibited type I behaviour and a slight decrease in daytime activity (Fig.4.4). The occurrence of type II behaviour for oceanic triggerfish during the last part of the monitoring coincides with a decline in both the SLA and SST which indicates changes in the environmental conditions driven by a cyclonic eddy (cold-core eddy) (Fig. 4.4, Appendix A)



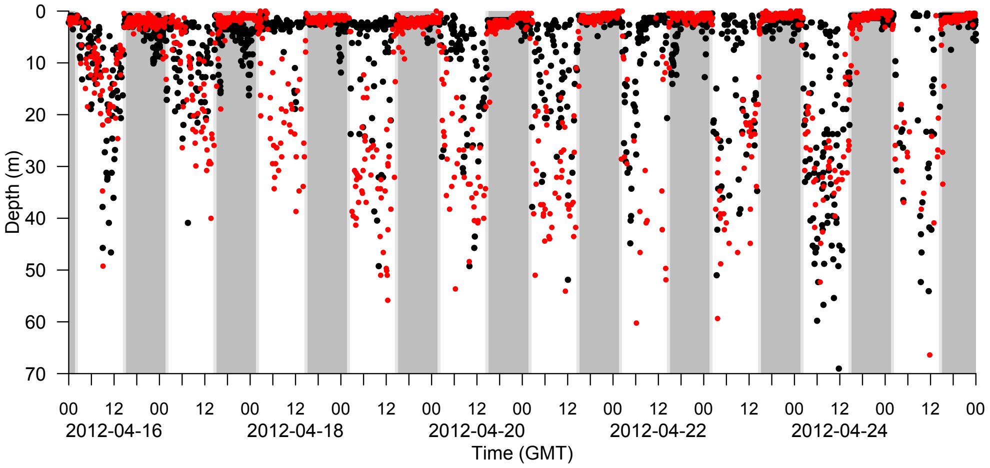


Figure 4.1 Example of vertical movement of (a) oceanic triggerfish (ID# 3601, 3603, 64826) (b) rainbow runner (ID# 7072, 7073) during a 10 day period at drifting FADs. Each colour represents the depth measurement of an individual. The lightgrey areas indicate time of twilight periods and the darkgrey areas indicate nighttime.

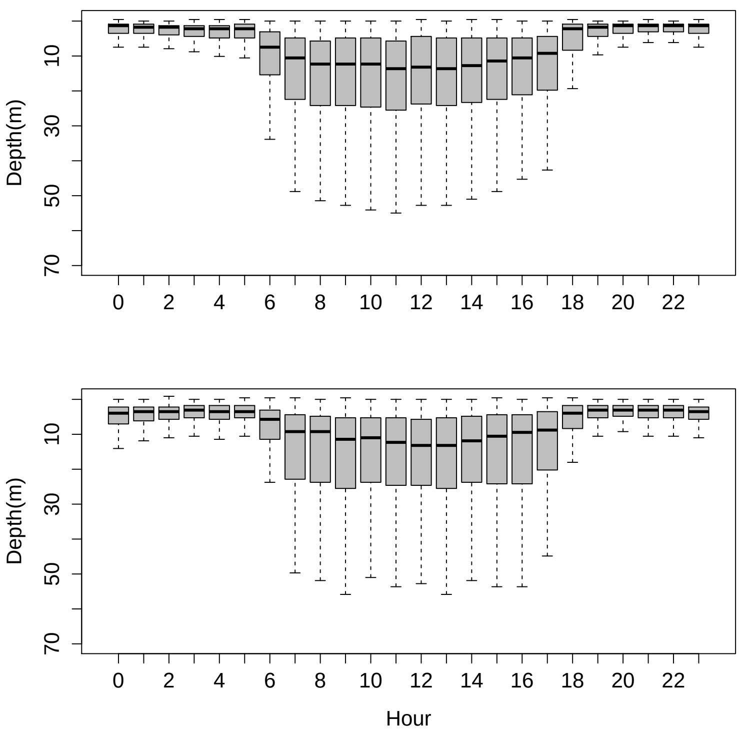


Figure 4.2 Depth distributions per hour in local time of oceanic triggerfish (top) and rainbow runner (bottom) at drifting FADs.

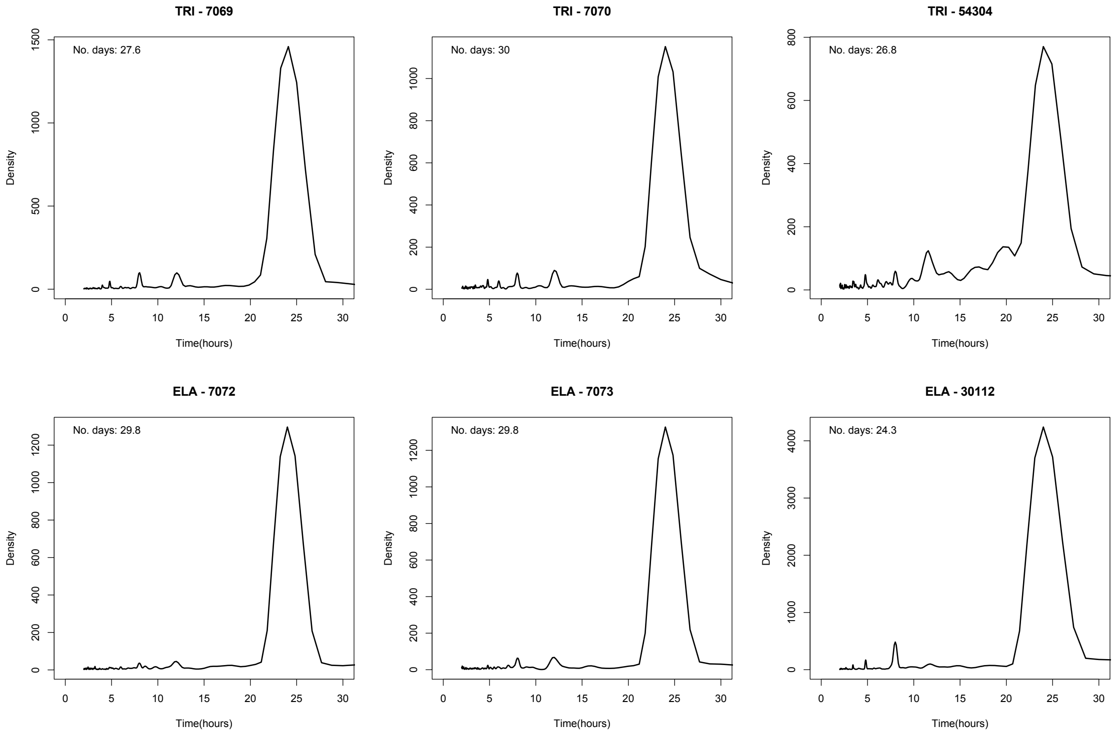


Figure 4.3 Examples of FFT spectral densities on depth of three oceanic triggerfish (ID# 7069, 7070, 54304) and three rainbow runner (ID# 7072, 7073, 30112) at drifting FADs.

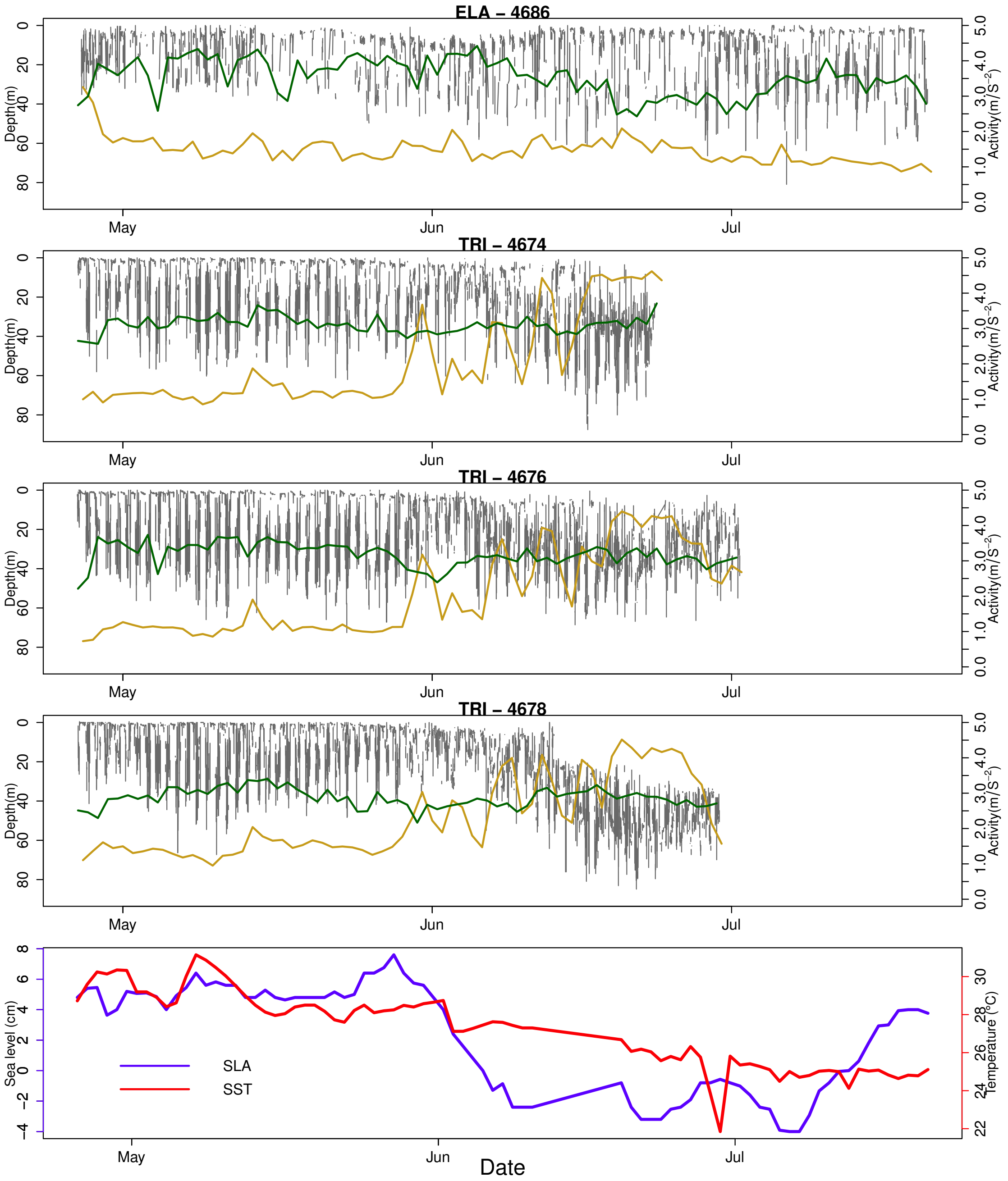


Figure 4.4 Depth time series of three oceanic triggerfish and one rainbow runner at FAD SEY 59. Grey lines represent depths (y axis), yellow line represents daily mean acceleration during the night, the green line represents daily mean acceleration during the day. Bottom graphs show sea level anomaly (SLA) and sea surface temperature (SST).

Temperature distributions

The vertical movements of oceanic triggerfish and rainbow runner in relation to thermal properties of the water column were examined at FAD MAY41, where a recovered MK9 archival tag deployed on a FAD associated silky shark, provided high resolution temperature data. The observations at this FAD lasted 30 days after which the aggregation was fished by a purse seiner, and both the shark and the archival tag were recovered. During this period the thermal structure of the water column was fairly stable with a persistent thermocline between 60 and 80 m (Fig. 4.5). Individuals of the two species occurred predominantly in warmer surface waters as they were mostly detected between the surface and the MLD (Percentage detection: oceanic triggerfish = 96.9%, rainbow runner = 91.7%) while performing dives closer to the thermocline during the day (Fig. 4.5). Both species generally remained above the thermocline (Percentage detection: oceanic triggerfish = 99.9 %, rainbow runner = 99.4 %). The temperature histograms confirm that both species have a tendency to remain in warmer surface waters; mean of 29.7 °C (± 0.7 SD) and 29.6 °C (± 0.4) for oceanic triggerfish and rainbow runner respectively (Fig.4.6).

Temperature data obtained from temperature and pressure sensitive transmitters (V9TP) deployed at other FADs (Table 4.1) were not as informative as external temperature data was not available. Additionally, since sensor data transmission is alternated the lag between a temperature record and a depth record was too long to infer ambient water temperature. However, these temperature data provided an indication of the internal body temperature range, which was 29.4 °C (± 0.4 SD, min 26.4°C, max 30.4°C, n = 15 062) for oceanic triggerfish and 27.8 °C (± 0.9 SD, min 24.7°C, max 30.2°C, n = 9 515) for rainbow runner.

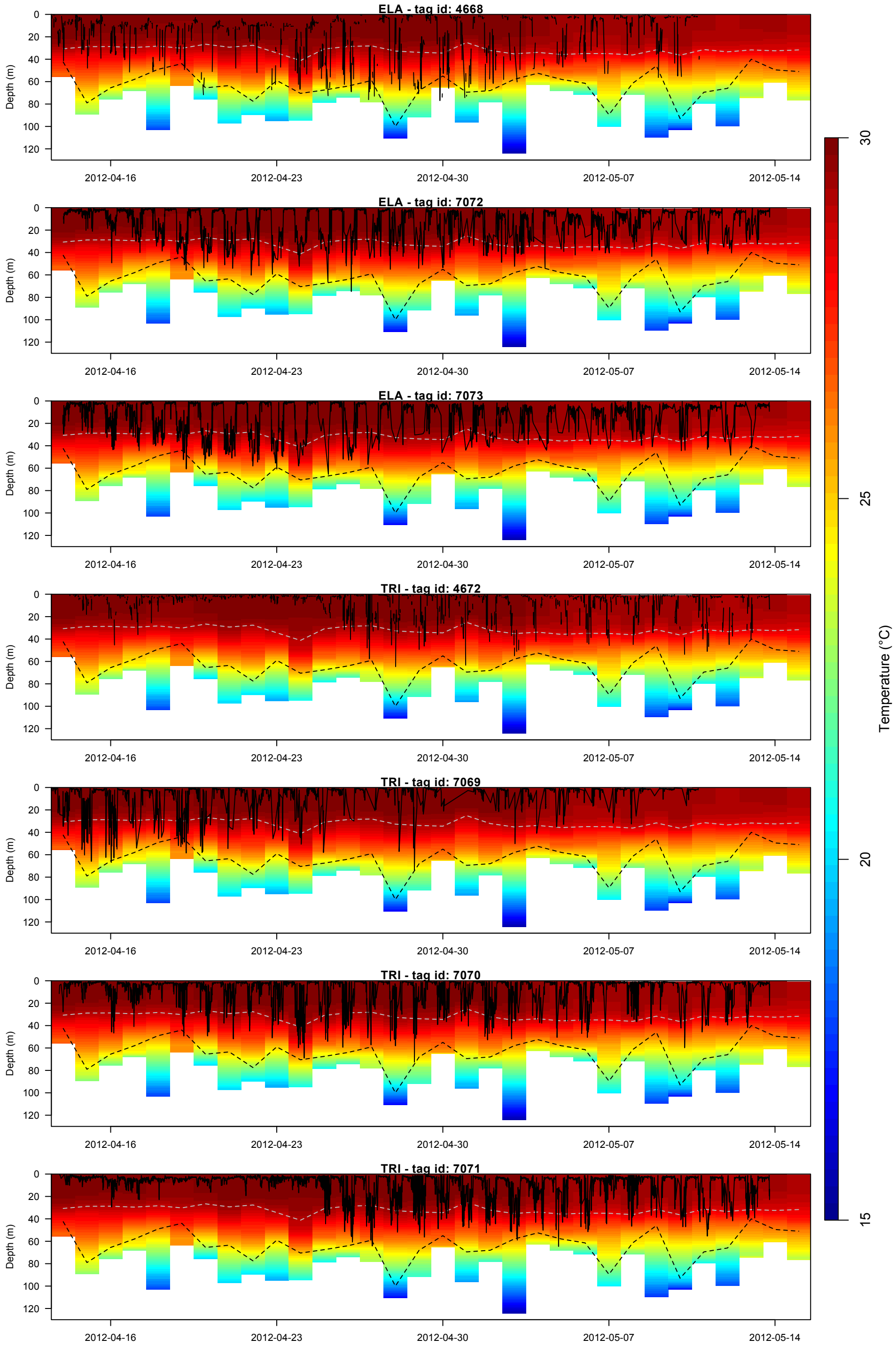


Figure 4.5 Vertical movements of three rainbow runner (ID# 4668, 7072, 7073) and four oceanic triggerfish (ID# 4672, 7069, 7070) at FAD MAY41 overlaid onto interpolated high resolution temperature data obtained from the archival tag (MK 9) deployed on a silky shark. Black dotted line indicates the thermocline and grey dotted line indicates the shallow MLD.

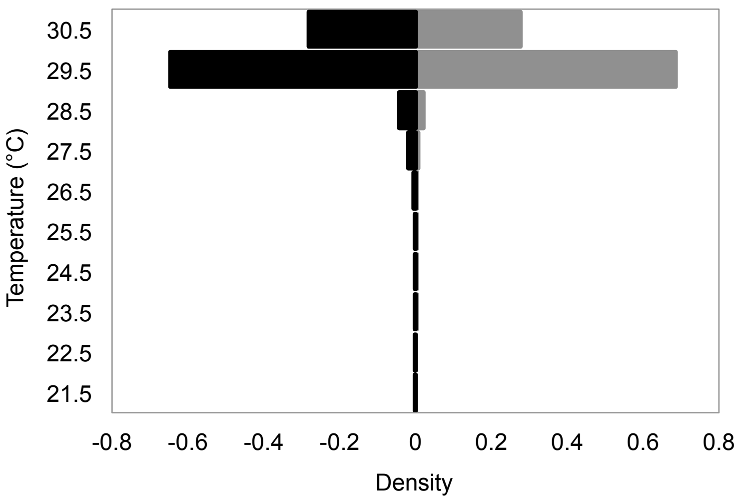


Figure 4.6 Histograms showing temperature distributions estimated for oceanic triggerfish (grey) and rainbow runner (black) at FAD MAY41.

Activity

Activity patterns of tagged oceanic triggerfish and rainbow runner recorded at two FADs (MAY41 and SEY59) were similar, with low activity levels at night and higher levels during the day (Fig.4.7,4.9). A distinct change in activity level was apparent during twilight periods (Fig.4.7). This distinct diel pattern was confirmed by dominant peaks in the spectral densities, which occurred around 24 h (Fig. 4.8). Minor peaks were observed around 8 and 12 hour for some individuals. Acceleration values ranged from 0.3 to 5 ms^{-2}for both species. Mean daytime and night-time (type I behaviour) activity values for oceanic triggerfish were 3.1 ms^{-2}(± 0.8 SD) and 1.3 ms^{-2}(± 0.9 SD), respectively. Similarly, rainbow runner activity values 2.8 ms^{-2}(±1.1 SD) and 1.3 ms^{-2} (± 0.8 SD) during the day and night, respectively. However, at FAD SEY59, three oceanic triggerfish changed their behaviour (type II) and exhibited higher nocturnal activity levels (Fig.4.9). Differences in the nocturnal activity between type I and type II behaviours were apparent on the acceleration histograms with the presence of a second mode for the type II behaviour (Fig. 4.4). The mean daytime activity was 3 ms^{-2}(± 0.8 SD) and 3.1 ms^{-2}(± 1.6 SD) during the night for type II behaviour. The behavioural switch to type II occurs synchronously amongst the three individuals as depicted by the simultaneous peaks in mean nocturnal activity (Fig.4.4). The onset of the type II behaviour coincided with a drop in the SLA and SST, indicating a change in the environmental conditions during that time (Fig.4.4). The rainbow runner

(ID 4686) present at the FAD during this time did not display a behavioural switch and only a slight decrease in mean daytime activity could be observed (Fig.4.4).

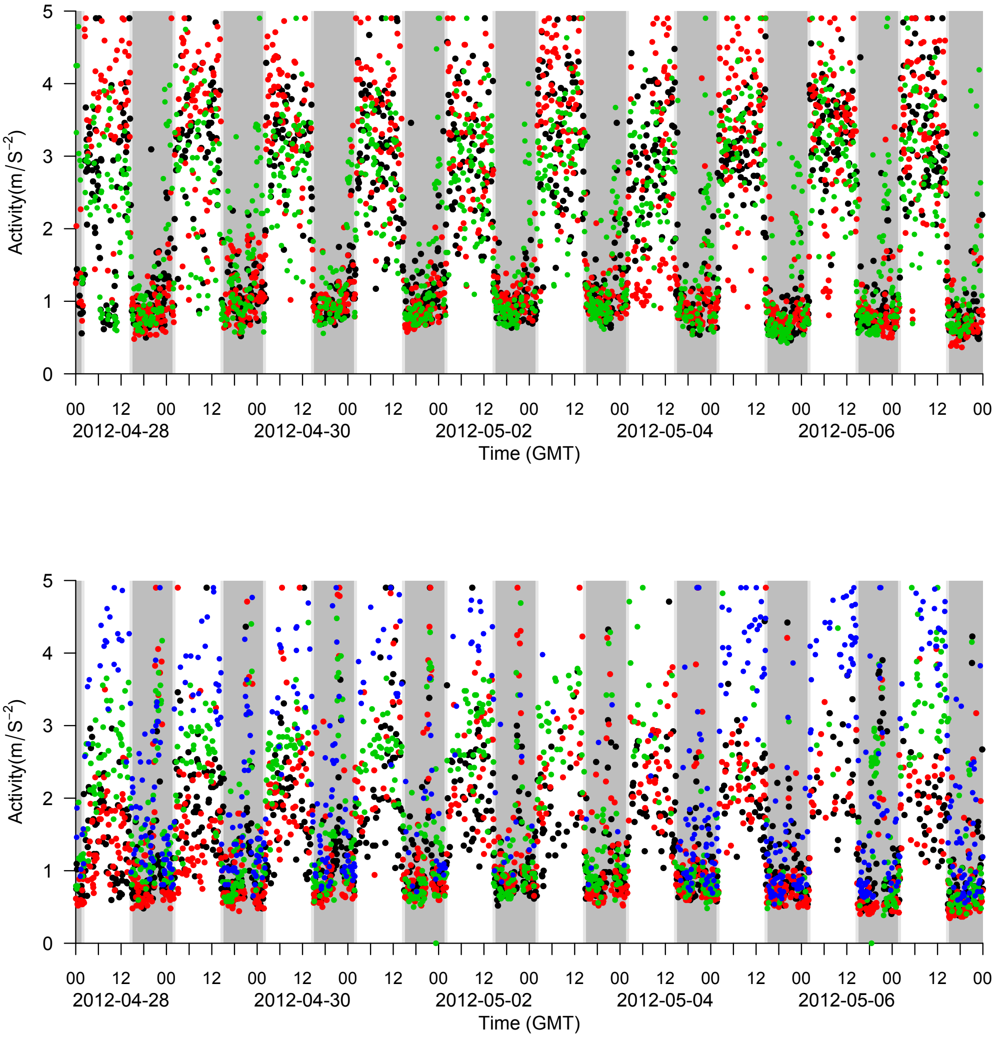


Figure 4.7 Example of activity time series for (a) oceanic triggerfish (ID# 4674 4676 4678) (b) rainbow runner (ID# 4680, 4682, 4684, 4686) during a 10 day period at drifting FADs. Each colour represents the acceleration measurement from an individual. The lightgrey areas indicate time of twilight periods and the darkgrey areas indicate nighttime.

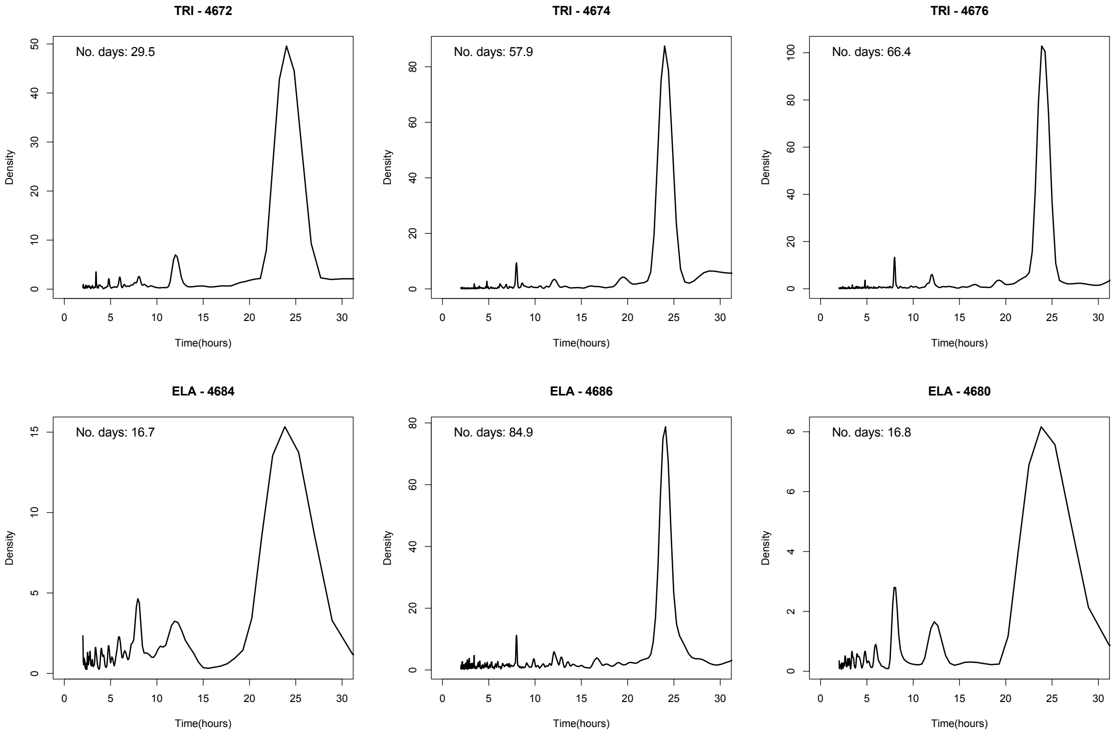


Figure 4.8 Examples of FFT spectral densities on hourly acceleration for 3 oceanic triggerfish and 3 rainbow runner at drifting FADs.

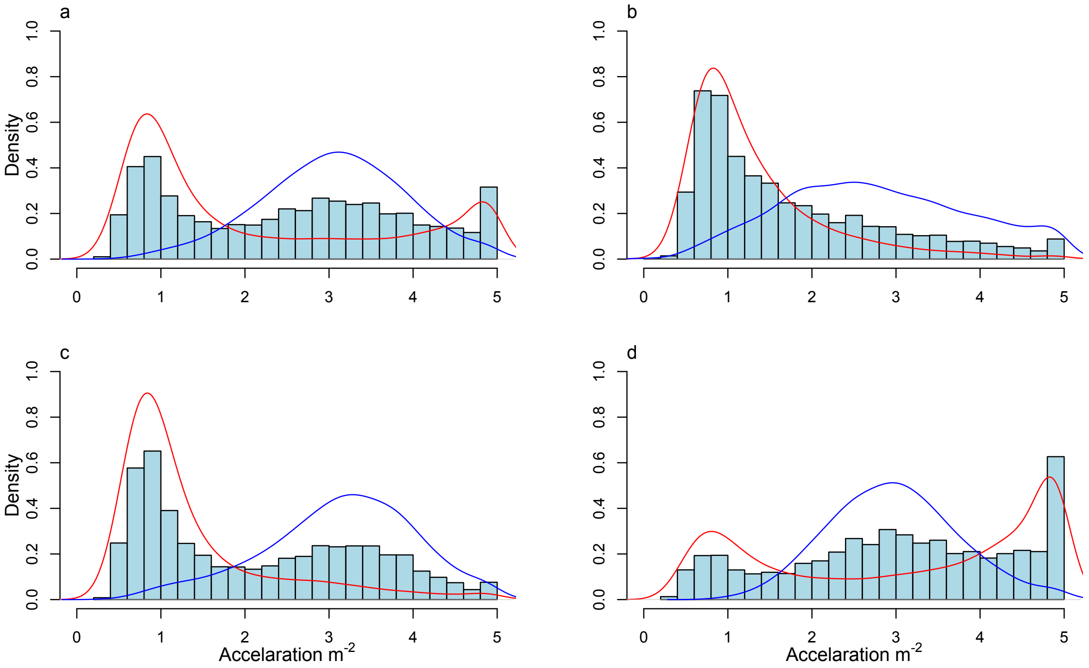


Figure 4.9 Density histogram of acceleration measurements of all oceanic (a) triggerfish, (b) rainbow runner, (c) type I oceanic triggerfish, (d) type II oceanic triggerfish. Blue lines represent densities during the day and red lines densities during the night.

Vertical movement versus locomotive activity

Overall, hourly vertical movement and activity showed a weak positive correlation (oceanic triggerfish; $p < 0.05$, $R^2 = 0.2$, rainbow runner; $p < 0.05$, $R^2 = 0.1$). For oceanic triggerfish, however, day and night appears to have an affect the relationship between the two variables. The relationship observed for oceanic triggerfish for type II at night appears to be bell shaped with highest activity levels occurring when limited vertical movement occurred (Fig. 4.10d). No distinct relationship were observed for rainbow runner including day and night differences (Fig. 4.10b).

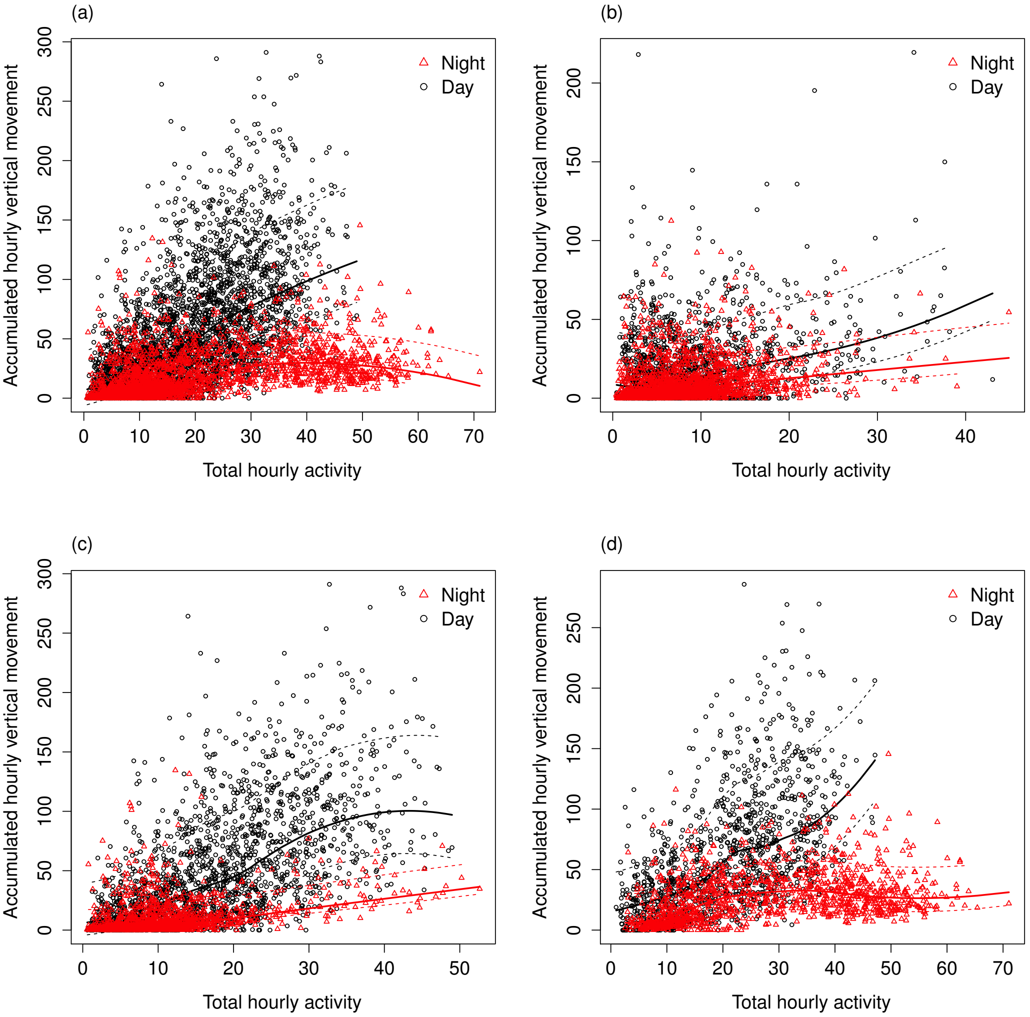


Figure 4.10 Relationship between hourly vertical movement and acceleration for (a) all oceanic triggerfish, (b) all rainbow runner, (c) oceanic triggerfish type I, (d) oceanic triggerfish type II. The curves represent a loess model with 95% confidence intervals (dotted lines) for day (red triangles) and night (black dots).

4.4 Discussion

The study of pelagic fish behaviour is challenging due to the vastness of this environment and difficulty to observe or record fish distribution. The development and application of new technologies (e.g. PATs and archival tags) has improved our understanding of many open ocean animals (Block *et al.*, 2003; Hussey *et al.*, 2015) and in some cases led to profound discoveries (e.g. transoceanic migration: Bonfil *et al.* (2005), behavioural thermoregulation: Holland *et al.* (1992)) but considerable miniaturisation of data-logging or transmitting devices is still required to yield equivalent information on smaller bodied fish. Acoustic telemetry applications provide limited opportunities to study small to medium-sized animals however with the ability to attach acoustic receivers to floating devices such as FADs substantially improves our ability to document their behaviour in the open ocean. This is the first study to describe the vertical movement and activity patterns of oceanic triggerfish and rainbow runner at FADs drifting in the pelagic environment.

Vertical movements and temporal patterns

Oceanic triggerfish and rainbow runners both exhibit a clear diel pattern in their vertical movements. Generally, during the night they remain close to the surface (0-5 m) and occur deeper during the day (5-50 m). Ambient light appears to be the stimulus, or "zeitgeber", driving the change in vertical behaviour as a strong response in depth can be observed during twilight periods. Ambient light is a salient stimulus in regulating exogenous circadian rhythm throughout the animal kingdom. The two species spend most of their time in the mixed layer while performing dives close to the thermocline during the day. Investigations on the vertical behaviour of other epipelagic fish have reported similar diel vertical movement behaviour. Studies on the vertical movements of yellowfin, bigeye and skipjack tuna indicated that depth distributions were shallower at nighttime (Cayré and Chabanne, 1986; Cayré, 1991; Holland *et al.*, 1990b; Schaefer and Fuller, 2005; Yuen, 1970). Few studies investigated the vertical movement behaviour of fish associated to drifting FADs; Matsumoto *et al.* (2006) and Schaefer and Fuller (2013) conducted acoustic telemetry experiments on yellowfin, bigeye and skipjack tuna at drifting FADs and found a similar diel pattern with a shallower depth distribution for the three species at the night. Investigations of depth distributions of istiophorids showed mixed results. Blue marlin appeared to occur deeper during the day (Holland *et al.*, 1990a), while other studies did not find such clear cut patterns for blue marlin (Block *et al.*, 1992), black marlin (Pepperell and Davis, 1999), striped marlin (Brill *et al.*, 1993). In contrast, Merten *et al.* (2014) reported that dorado occurred deeper at night. It must be noted that diel pattern observed in the depth distribution of pelagic fish reported above were not as distinct as observed here for oceanic triggerfish and rainbow runner.

The thermal habitat of oceanic triggerfish and rainbow runner appears to be restricted to the mixed layer. It is generally agreed that the energetics required to remain in colder waters below the thermocline are costly and avoided if it does not offer additional benefits, such as feeding or thermoregulation. Some epipelagic species benefit from thermal inertia due to their larger size and/or physiological thermoregulatory adaptations (endothermia) that enables them to temporarily extend their vertical habitat by performing excursions below the thermocline for foraging (e.g. bigeye tuna; see Holland *et al.* (1992)). Oceanic triggerfish and rainbow runner are ectothermic and do not have sufficient thermal inertia, like large fish, to retain metabolic heat. As such, the extent of their vertical habitat appears to be limited by the thermocline which acts as a physical (or physiological) barrier for the two species. The restricted vertical movements in relation to the thermocline has been reported for several epipelagic fish including dorado (Furukawa *et al.*, 2011), oceanic whitetip shark (Musyl *et al.*, 2011; Tolotti *et al.*, 2015), silky shark (Musyl *et al.*, 2011), skipjack tuna (Matsumoto *et al.*, 2013) and blue marlin (Block *et al.*, 1992; Holland *et al.*, 1990a).

The vertical movement behaviour of a marine organism is often explained by the distribution of its prey (Hays, 2003). An important part of the oceanic triggerfish and rainbow runner diet is zooplankton (Chapter 6) which are known to occur in higher concentrations in the water layer close to the thermocline (Huggett, 2014; Saltzman and Wishner, 1997). During the day, the two species appear to perform a series of dives close to the thermocline for foraging. Additionally, zooplankton are known to perform diurnal vertical migration (DVM). The DVM of zooplankton is thought to drive daily shifts in vertical habitat of large filter-feeding planktivores such as whale sharks (*Rhincodon typus*) and basking sharks (*Cetorhinus maximus*) as a response to their prey movement (Sims *et al.*, 2005). The decrease in light levels during the night is thought to reduce visual predation by zooplankon feeders and is believed to explain the DVM of zooplankton (Folt and Burns, 1999). If vertical movements patterns of pelagic planktivores mirrors that of their prey, then the diel vertical pattern observed in oceanic triggerfish and rainbow runner could be a reflection of their prey distribution. Alternatively, the two species could be resting in the warmer surface waters close to the FAD. Activity data is key to distinguish between these two hypothesis.

Activity

The recent development of miniaturised accelerometers has allowed scientists to access a new dimension of behaviour and can provide valuable insights into the cryptic behaviour of marine species. Activity levels inferred from tri-axial accelerometers is particularly powerful metric as activity is correlated with metabolic rates and energy expenditure of animals (Wilson *et al.*, 2006, 2008).

Similarly to vertical movement, a strong diel rhythmicity was observed in the activity levels of oceanic triggerfish and rainbow runner with more elevated activity levels during the day than at night time (except for oceanic triggerfish type II behaviour). This suggests that the two species are actively feeding during the day while low nocturnal activity levels suggests that the two species are in a resting state and not feeding extensively in low light conditions. This results corroborates with nighttime observations where tight schools of rainbow runner and triggerfish were observed close to FAD on the surface while appearing to have limited movements (unpublished personal observation). This diel pattern is similar to that of visual zooplanktivorous reef fish, where feeding activity increases from nearly nil to maximum levels after morning twilight and decreases again with evening twilight (Rickel and Genin, 2005). Hence, the diel change in vertical distribution as a response to prey movement during the DVM is here not supported. Indeed, the two species are visual predators and, unlike ram filter-feeding zooplanktivores (Taylor, 2007), have to target individuals prey particles. The low light levels is a considerable disadvantage for visual predators and, in accordance with the optimal foraging theory which postulates that an animal display a foraging pattern that maximises its caloric intake per unit time (Pyke, 1984), foraging during such time would not be energetically efficient. Considering that the two species remain in close proximity of the FAD (Chapter 3) with limited vertical movement a low activity levels suggests that they are in a resting state close to the FAD at night.

The type II behaviour displayed by oceanic triggerfish coincided with a change in the environment, depicted by a negative SLA and a decline in SST, when the FAD drifted inside a cyclonic eddy. Cyclonic mesoscale eddies are know to drive upwelling through their interior and is also referred to as cold-core eddies (see Appendix B). An optimal foraging mode should minimise the ratio of energy expenditure (and risk of mortality) and net food intakes (Metcalfe *et al.*, 1999). Diel activity patterns of animals is usually shaped by the diel fluctuations in food availability and/or predation risks and the pattern reflects the most optimal time to feed. However, in some instances, changes in the environment can cause a switch in the activity patterns. Switches in activity patterns have been previous be reported in mammals (Fenn and Macdonald, 1995), insects (Bloch and Robinson, 2001) and fish (Payne *et al.*, 2012) where predation risk reduction, sociality, prey availability and environmental conditions have been identified as drivers of the switch. Such a mechanism might explain the type II behaviour displayed by oceanic triggerfish, where changes in environment may impact their metabolic requirements or prey availability during the day causing this switch in the foraging strategy. The higher level of nocturnal activity observed during type II, as well as its synchronicity amongst individuals, is intriguing; if the oceanic triggerfish had shifted their foraging strategy to a nocturnal one, what causes the activity levels to be higher than "normal" feeding activity levels during the day? Two hypothesis stand out to explain this activity pattern change. 1) Activity levels could reflect an escape ('fleeing') behaviour caused by nocturnal predation; that could also explain such high acceleration values. Higher predator densities may be attracted to higher productivity of the cyclonic eddy for foraging. Potential predators of oceanic triggerfish and rainbow runner could include silky shark, oceanic white tip and large tunas. However, tuna and sharks are typically away from the FADs at night (Chapter 6). 2) The cooler waters (due to eddy driven upwelling) may impact on prey type availability and, for instance, larger more mobile prey would require additional investments in locomotion to ensure foraging success. Oceanic triggerfish, like other Balistidea, primarily use undulations of the dorsal and anal fins for locomotion (balistiform swimming) while maintaining a rigid body. This primary swimming mode, known as 'gait' (Webb, 1998), is known to be energy efficient at low swimming speeds and enhances manoeuvrability (Korsmeyer *et al.*, 2002). However, this gait can only be used at slow speeds after which the caudal fin has to be used which, as an evolutionary trade off, is far less energy efficient for members of the Balistidea (Korsmeyer *et al.*, 2002). This "burst" swimming using the caudal fin is likely to explain such high acceleration values obtained for this species. Additionally, this suggests that the energetic requirements of the type II behaviour is considerably higher due to the increase of overall activity and change in swimming mode. Thus, the change to type II behaviour might be essential to compensate for increased metabolic requirements imposed by the change in habitat and/or intensified predatory pressure. Vertical movement was generally poorly correlated to activity and shows the complementarity of acceleration data to that of depth data. This is particularly evident at night when levels of activity are high and vertical movement is limited. The activity during that time thus reflects movements in the horizontal plane. This result has important implications for the interpretation of vertical movement data from telemetry studies of pelagic fish. While vertical movement can be linked to activity (e.g. feeding or predator avoidance), the lack of vertical movements cannot be assumed to reflect limited activity as individuals can be dynamic in the horizontal plane. This result supports the finding of Gleiss *et al.* (2013) where vertical activity did not necessarily reflect on locomotary activity levels. However it must be noted that depth and acceleration data had to binned by hour to ensure sufficient data to allow for a meaningful comparison. This is due to the transmission-reception limitations of acoustic telemetry whereby only one metric (either depth or acceleration) can be transmitted at a time. Simultaneous high resolution (sub-minute) acceleration and depth data from data loggers would help to further resolve the vertical movement and activity relationship. This technical limitation further limits the possibilities of performing fine-scale investigations in the syncronicity of vertical movement and activity amongst individuals as the update time of sensor measurements is often too variable.

Conclusion

This study provided some valuable insights into the behavioural patterns of oceanic triggerfish and rainbow runner at FADs. The two species were more active during the day and appear to be feeding between in the mixed layer while being restricted by the thermocline. Combining depth and accelerometer data proved to be highly informative and provided insights into the foraging strategy and energetics of pelagic fish during their associations to FADs. How does changes in habitat type, or quality, influences behavioural strategies of fish at FADs remains a key question. To address this question, in-situ estimations of biotic factors such as resource densities, predatory pressure, species assemblages and presence of conspecifics, and abiotic factors (some of which can be obtained by remote sensing) such thermal structure of water column and productivity. Additionally, a combined ethogram and respiratory study of captive fish (Murchie *et al.*, 2011; Brownscombe *et al.*, 2014) would help to catalogue distinct behaviours with their corresponding acceleration values provide estimation baseline metabolism and metabolic scope for the species. Data gathered by such studies could then be used to develop a bioenergetic model which could inform on the energetics of specific behavioural patterns at FADs. Such data would also be useful in a theoretical modelling approach to investigate possible energetic advantages of associating to floating objects by testing a range of different biotic and abiotic factors including resource density, predator densities, competition and school size.

Chapter 5

Behaviour and vulnerability of target and non-target species at drifting FADs in the tropical tuna purse seine fishery

5.1 Introduction

Commercial fisheries typically capture several species including those that are specifically targeted and others that are incidentally taken. Historically, fisheries management strategies focused primarily on the fishery impact on the target species and paid little attention to the impacts on the ecosystem as a whole. More recently, the emergence of the ecosystem-based approach to fisheries management (Pikitch *et al.*, 2004a), has lead to both managers and scientists focusing on the broader impacts of commercial fishing activities. Specifically improving methods to reduce bycatch, i.e. the killing of non-target species or undersized individuals of the target species (Hall *et al.*, 2006), have become a priority. A salient challenge in this process is to develop methods of bycatch reduction that are both economically viable and practical to implement (Gilman, 2011). Meeting these criteria vastly improves the chance of any method to being adopted.

In the open ocean, numerous pelagic fish species associate with floating objects and regularly form large multi-species aggregations (Castro *et al.*, 2002). Three species of tropical tunas; skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye tuna (*T. obesus*), regularly aggregate in large numbers around floating objects in tropical and sub-tropical regions. Since the late 1960s, large purse seine vessels have targeted such aggregations to capture the tuna. Historically, vessels would search for natural floating objects (such as logs) to locate aggregations of tuna. However, since the 1990s, man-made floating objects known as Fish Aggregating Devices (FADs) have become a critical fishery enhancement tool for tropical tuna purse seine vessels (Dagorn *et al.*, 2013; Fonteneau *et al.*, 2013). This method represents one of three fishing modes employed by purse seine vessels. The alternatives include finding free-swimming schools of tuna when they are feeding at the surface, or locating schools of dolphins, with which large yellowfin tuna regularly associate (specifically in the eastern Pacific Ocean). However, the use of FADs is highly advantageous for fishers as it not only assists them in locating tunas but also ensures higher success rates than when targeting free-swimming or dolphin associated schools. Furthermore, by attaching tracking buoys, which now typically have integrated echo-sounders (Lopez *et al.*, 2014) to their FADs, vessels are able to locate and even predict their catches with ease. Currently, approximately 60% of the global catch taken by tropical tuna purse seine vessels originates from fishing sets around floating objects (Dagorn *et al.*, 2013). Skipjack tuna dominate FAD catches, however, the capture of juvenile yellowfin and bigeye tuna has raised management concerns (Harley *et al.*, 2010; Gilman, 2011). Additionally, the multispecies aggregations around floating objects means that this practice generate 2.8-6.7 times (ocean dependant) more bycatch than when fishing on free swimming tuna schools (Dagorn *et al.*, 2013). Owing to this higher bycatch rate, there is a clear need to investigate bycatch reduction methods in the FAD based purse seine fishery (Dagorn *et al.*, 2013; Hall *et al.*, 2000; Gilman, 2011).

The European tuna purse seine fleet has been active in the Indian Ocean since the 1980's (Floch *et al.*, 2012). In the early 2000s about 50 vessels were operating in this ocean. Currently, there are 37 vessels (primarily French and Spanish) active in this area (Chassot *et al.*, 2013). The annual total tuna catch has ranged between 200 and 400 thousand tons during the past decade (Floch *et al.*, 2012), with the majority of fishing activity taking place in the western Indian Ocean. The primary fishing mode involves setting around FADs and represents more than 60% of all sets (Dagorn *et al.*, 2013). Bycatch rates generated from FAD fishing in this region equate to 3.5-4.7% of the total tuna catch (Amandè *et al.*, 2012; Dagorn *et al.*, 2013) and is 4.3 times higher than when fishing on free swimming schools (Dagorn *et al.*, 2013). The major FAD bycatch species include rainbow runner (*Elagatis bipinnulata*), dolphin fish (*Corypheana hipurrus*), oceanic triggerfish (*Canthidermis maculata*), silky sharks (*Carcharhinus falciformis*), wahoo (*Acanthocybium solandri*) and small tuna-like species (*Euthynnus affinis*, *Auxis* sp.) (Amandè *et al.*, 2012; Romanov, 2002).

The vulnerability of associative species to being caught during purse seine fishing activities depend upon (i) their temporal pattern of association (are they close to the FAD throughout the day and night?), (ii) their vertical distribution (iii) the time when fishing sets take place (fishing time), and (iv) the vertical range of the gear. Using their empirical knowledge, fishers typically set the seine around FADs at dawn in order to optimise the catch rates of tunas. However, fishing time can vary according to the area and the skipper but also depends on whether they encounter a large fish aggregation during the course of the day (Moreno *et al.*, 2007a).

Making use of passive acoustic telemetry, we investigated the vulnerability to capture of both target and non-target species captured by the FAD-dominated purse seine fishery in the Indian Ocean. Through this investigation we aim to assess whether any theoretical change in fishing times could alter the bycatch to target catch ratio in this fishery.

5.2 Materials and Methods

Acoustic telemetry experiments

Four scientific cruises were conducted in the western Indian Ocean between March 2010 and April 2012. These cruises took place in two areas: the Mozambique Channel and the Seychelles (Fig. 5.1). FADs were located through collaboration with European purse seine skippers. Once the FADs were found, an underwater visual census, following Taquet *et al.* (2007b), was performed to assess the species composition of the aggregation. When an appropriate multispecies aggregation, comprising both tuna and bycatch species, was found, the acoustic telemetry experiment was initiated. Firstly, a Vemco VR4-Global (VEMCO, a division of Amarix Ltd., Canada) acoustic receiver was attached to the drifting FAD. These receivers utilise the Iridium satellite system to transmit logs of acoustic detection from tagged individuals on a daily basis. Tuna and bycatch species were caught using rod and reels or hand lines. All three tuna species targeted in this fishery (skipjack, yellowfin and bigeye tuna) were caught and tagged with acoustic transmitters. Bycatch species selected for acoustic tagging included rainbow runners, oceanic triggerfish and silky sharks. Coded acoustic transmitters were surgically implanted into the peritoneal cavity following the methods described in Dagorn *et al.* (2007a). The three tuna species and silky sharks were equipped with V13, V13P (pressure sensitive) and V13TP (temperature and pressure sensitive) tags (90 s nominal delay, 69 kHz, 1H) (see Table 5.1). Rainbow runners and oceanic triggerfish were equipped with smaller V9, V9P, V9TP (120 s nominal delay, 69 kHz, 1H) and V9AP (140 s nominal delay, 69 kHz, 1H), details are provided in Table 5.1. Once tagging was complete, the FAD and attached VR4-Global receiver were left to drift and the data was relayed remotely.

A tagged fish was considered present at a FAD when it was detected by the acoustic receiver. Its presence was thus dependant on the detection range of the tag. Comprehensive range testing could not be performed in the study area due to the threat of piracy (Sumaila and Bawumia, 2014). However, the manufacturer provides theoretical range estimations of 550-682 m for V13 tags and 500-627 m for the V9. Schaefer and Fuller (2013) obtained comparable detection ranges during range tests at drifting FADs for V13 tags in the offshore equatorial eastern Pacific. As the theoretical detection ranges for both tag types are greater than the typical radius of a tropical tuna purse seine net (200-300 m wide and 140-240 m deep; Hall and Roman (2013)), we assumed that a non-detected fish was beyond the reach of the purse seine gear.

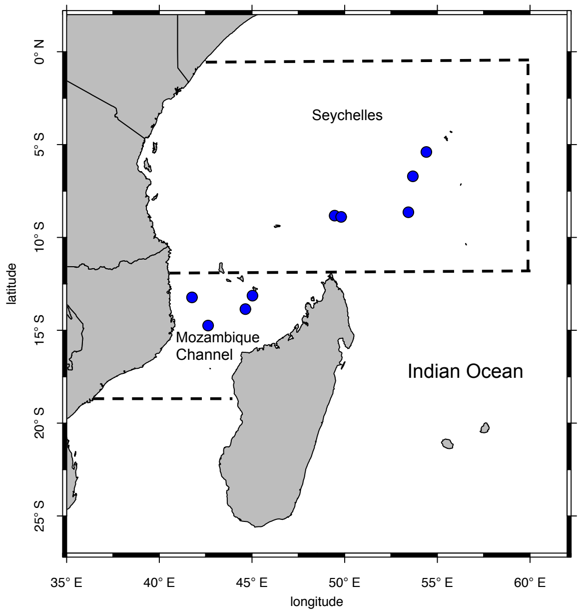


Figure 5.1 Map of western Indian Ocean indicating the two study areas (demarcated by dashed lines). Blue circle indicate locations of the acoustic telemetry experiments conducted on drifting FADs.

Data analysis

Collision-corrected presence rate

For each tagged fish, the hourly total number of acoustic detections was calculated at each FAD. When all of the individuals of a species were observed for less than 24 hours at a FAD, this species was not included in the analysis as the diel presence rate and depth distributions over 24 hours could not be calculated. For each individual, only the hours subsequent to the tagging hour where taken into account. Similarly, only the hours prior to the last detection were considered for the analysis to avoid truncation in the middle of an hour.

As the time of sunrise and sunset varied by less than one hour throughout the study period, in both areas, patterns of hourly presence were referenced to the hour of the day rather than the time of sunrise or sunset. Sunrise and sunset occurred at approximately 06:00 and 18:00 respectively.

For each species, the hourly detection rate around the FAD was estimated by considering the number of acoustic detections recorded for each tagged individual at the acoustic receivers. When emissions from two or more tags overlap in time, the receiver is unable to record the identification number (and depth data) encoded in the emission. This is generally referred to as an acoustic collision. The rate of acoustic collisions depends upon i) the number of tagged fish within the reception range of the acoustic receiver, ii) the emission rate of the tags and iii) the coding scheme, i.e., the time required for signal transmission (Heupel *et al.*, 2006; Simpfendorfer *et al.*, 2008). Hence, using the number of detections as an indicator of fish presence could be biased by the occurrence of such collisions, particularly when several tagged individuals are present simultaneously within the range of the receiver. In order to overcome this bias, we derived a correction factor based on the number of fish present at each experimental FAD.

The theoretical relation between the total number of recorded detections (F) per unit of time in the presence of acoustic collisions and the number of tagged fish F follows an exponential law (collision calculator tool, www.vemco.com):

$$D\left(F\right)=D_0\left(F\right)e^{\beta F} \qquad \text{(Equation 1)}$$

where $D_0\left(F\right)=\alpha F$ represents the total number of detections recorded for F fish in the absence of acoustic collisions with the tag's emission rate equal to α and β is the detection depletion factor related to acoustic collisions. The values of α and β depend on the tag characteristics. Different tag types with different nominal delays were used in our study, which makes it difficult to determine which values of α and β should be used. Moreover, environmental and behavioural factors could affect the theoretical detections rates α even for a single fish (i.e. no collisions). For example, background noise in the vicinity of the receiver and the movements of the tagged fish in and out of the receiver's range will negatively impact the α. As such, using the theoretical values of α and β is generally not appropriate. We thus empirically estimatedα and β, fitting the experimental total number of hourly detections through the analytic form given in Equation 1 using the R software (RCoreTeam, 2014). For both study areas the factor $\hat{\beta}$ was estimated for each FAD independently and the estimated collision-corrected total number of detections was obtained for each species by reverting (Equation 1):

$$(\hat{DO}) = D(F)exp(\hat{\beta}F) \qquad \text{(Equation 2)}$$

Details can be found in the Supplementary Information (Appendix B). For each study area, the collision-corrected presence rate for each species S and hour of the day h was estimated following:

$$\hat{P}^h_s = \frac{\sum_{k=1}^{Z}\sum_{i=1}^{Ns}\sum_{d=1}^{Ti} \hat{DO}^{d,h}_{S,k,i}}{Q^S} \qquad \text{(Equation 3)}$$

where $\hat{DO}^{d,h}_{S,k,i}$represents the estimated collision-corrected hourly detections recorded for individual i of species S at day d, hour h and FAD k, Ns is the total number of individuals of species S, Ti is the total number of days per individual (from the day of tagging to the day when the last detection was recorded), Z is the total number of FADs in the study area and Q^S is a normalisation factor such that, for each species. We used Rao's spacing test on to determine whether its temporal distribution over 24 hours was non-uniform (Batschelet, 1981). We then used a Mann-Whitney U test (Zar, 2010) to determine if there were day/night differences in the presence rate for each species.

Vertical behaviour

Depth data emitted from the pressure sensitive tags was used to calculate the hourly mean depth and standard error and the vertical distribution of all the species when associated to the FAD for both study areas. For the vertical distribution the density was calculated using kernel density estimates using the package 'stats' in R software (RCoreTeam, 2014). Unlike the number of detections, the acoustic collisions did not bias the vertical distributions, as the depth measured by the tags are independent from the number of tagged fish. The only possible effect of acoustic collisions is on the total number of depth measurements. However, the relatively large depth dataset (n = 1 108 – 56 047 measurements per species; Table 5.1) provided for a statistically robust estimate of the vertical distribution for each species. A Rao's spacing test was performed to determine if the temporal distribution of the depth during 24 hours was non-uniform. We then used the Mann-Whitney U test to determine if there were day/night differences in vertical distribution.

Purse seine set times

A total of 1152 FAD set times were obtained from the French DRC observer program database during the 2005-2013 period covering both study areas (Fig. 1). All set times were converted to local time. The time when the set started was used to calculate the hourly distribution of setting times in the two study areas.

Table 5.1 Summary data for the acoustic telemetry studies conducted on six FAD-associated species in two regions of the western Indian Ocean between 2009 and 2012.

Area	**Species**	**Number of FAD experiments**	**Total number of tagged fish**	**Tagged fish analysed (>24 hrs)**	**cumulated observation days**	**Vertical data points**	**Mean fork length (SD)**
Mozambique Channel	Yellowfin	3	17	8	178	22 3089	55.5 (7.8)
	Bigeye	1	3	2	12	1 108	55 (1)
	Skipjack	2	13	10	93	6 871	49.5 (2.7)
	Silky shark	2	9	6	53	8 090	72 (10)
	Triggerfish	4	30	23	496	56 047	32.6 (2.4)
	Rainbow runner	1	7	2	136	12 419	29.3 (10)
Seychelles	Yellowfin	4	17	10	108	4 441	57.4 (9.4)
	Bigeye	1	5	4	40	6 399	48.9 (8.4)
	Skipjack	2	7	0	< 1	52	52.1 (6.8)
	Silky shark	3	19	15	265	11 434	63.1 (5.8)
	Triggerfish	4	17	16	387	77 538	30.5 (2.5)
	Rainbow runner	4	17	17	307	39 094	53.9 (17.6)

5.3 Results

A total of 161 fish from six different species were tagged at 9 drifting FADs (Table 5.1). The duration of the acoustic telemetry experiments varied for each FAD and ranged between 2 and 86 days. This large variability was due to the premature interruption of some experiments, either due to fishing sets, which resulted in the capture of the aggregation, or through equipment failure. In the Seychelles, all tagged skipjack tuna spent less than 24 hours at the FAD and were thus excluded from the analysis for this study area.

The estimated depletion factors caused by acoustic collisions ($\hat{\beta}$ in Equation 2) differed for each FAD (Table 5.2) and were consistently higher in the Seychelles area than in the Mozambique Channel. In two cases the exponential model used in the calculation of the collision correction factor did not converge, as only a few tagged fish remained associated to the FAD, minimising the rate of collisions occurring. In these cases, where the effects of collisions were negligible due to the small number of fish present at the FAD, the collision correction was not performed.

Table 5.2 Experimental FADs and their estimated collision correction factors ($\hat{\beta}$) with their corresponding standard error (SE).

FAD ID	Area	$\hat{\beta}$	SE
MOZ34	Mozambique Channel	0.031	0.002
MOZ31	Mozambique Channel	0.044	0.002
MOZ32	Mozambique Channel	*	-
MAY41	Mozambique Channel	*	-
MAY42	Mozambique Channel	0.035	0.003
SEY37	Seychelles	0.050	0.003
SEY41	Seychelles	0.060	0.002
SEY43	Seychelles	0.053	0.006
SEY59	Seychelles	0.062	0.001

The corrected presence rate (Equation 3) was not uniform over 24 hours (Rao's spacing test; $p < 0.05$) for all six species in both study areas (Fig. 5.2). Two distinct diel patterns were apparent and consistent in both areas. The three tuna species and silky sharks were more regularly present at FADs during the daytime than during the night (Mann-Whitney U; $p < 0.05$). Oceanic triggerfish and rainbow runner displayed an inverse pattern and were detected more frequently at FADs during the night (Mann-Whitney U; $p < 0.05$) than during the day. In general, overall patterns of presence were similar in both areas. Typically, each species alternated between a high and a low plateau in presence rate, highlighting that all species consistently alternated their associative behavioural mode (Fig. 5.2). In the Mozambique Channel (Fig. 5.2a) the presence rate of skipjack tuna and yellowfin tuna peaked at dawn (6:00) followed closely by bigeye tuna (07:00). Similarly, silky sharks presence peaked at dawn (05:00). The overall highest presence rate for bigeye tuna was observed at 17:00 but with a large standard error. All four species switched to low presence rates towards the end of the day, with a sharp decrease after dusk (18:00). Skipjack were the first to decrease their presence rate (at 15:00), followed by silky sharks and yellowfin tuna (18:00) and finally bigeye tuna (19:00). Rainbow runner and oceanic triggerfish displayed opposite trends. After sunrise (07:00), a rapid decrease in presence rate was observed with a low level maintained throughout the day for both species. Around the time of dusk their presence rates increased and quickly reached a maximum level (19:00), which was steadily maintained throughout the night.

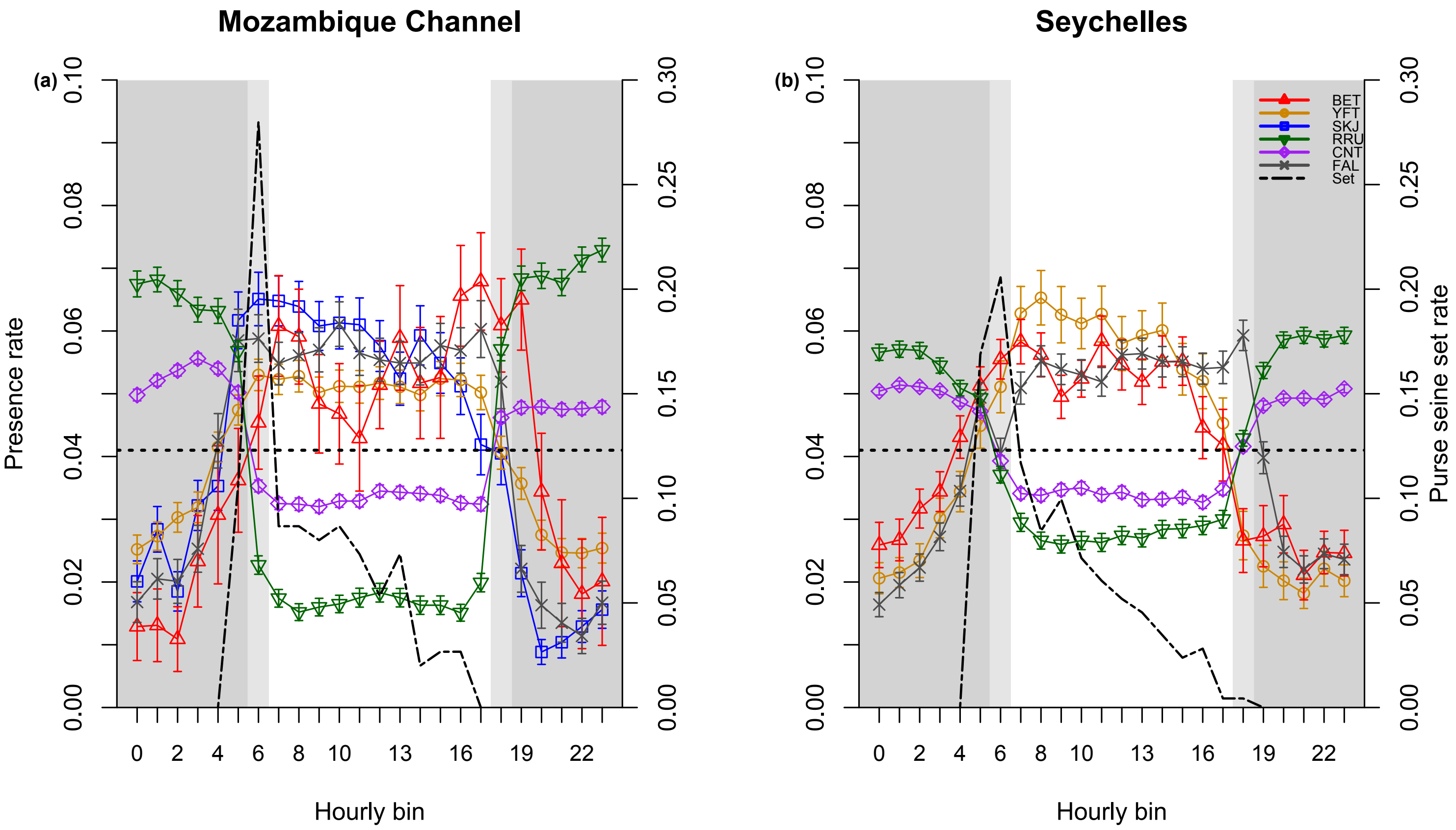


Figure 5.2 Collision-corrected presence rate (left axes) by species per hour in the Mozambique Channel (a) and the Seychelles (b). The error bars represent standard errors of the mean. The horizontal dotted line indicates the reference for a hypothetical constant presence rate over 24 h. The dashed line indicates the frequency rate of set times of purse seiners (right axes). The light grey areas indicate time of sunrise and sunset, and the dark grey areas indicate nighttime. FAO species codes are used in the legend: bigeye tuna (BET), yellowfin tuna (YFT), skipjack tuna (SKJ), rainbow runner (RRU), oceanic triggerfish (CNT), silky sharks (FAL), and purse seine set rate (Set).

In the Seychelles area (Fig. 5.2b), the rapid departure (i.e. < 24 hours) of tagged skipjack tuna prevented their inclusion in the analysis. The rise in the presence of yellowfin and bigeye tuna was both attained at 07:00. The decrease in presence for both tuna species occurred after 16:00. Again silky sharks displayed a similar pattern to the tuna species, however, they maintained a high presence rate until 18:00. Rainbow runner and oceanic triggerfish displayed the same trend as observed in the Mozambique Channel, with their presence decreasing in the morning prior to sunrise (05:00) and increasing again in the evening at sunset (18:00).

Analysis of fishing times revealed that sets were more often initiated between 05:00 and 06:00. In the Mozambique Channel the peak in fishing effort corresponded to the peak in presence of skipjack and yellowfin tuna, whereas in the Seychelles area it occurred one hour prior to the maximum presence rate of yellowfin tuna.

The overall vertical behavioural patterns were similar for all species in the two study areas. Bycatch species were consistently shallower than target species in both areas (Fig. 5.3). A diel pattern in the vertical distribution was observed (Rao's spacing test; $p < 0.05$) in both regions for all species (Fig. 5.3c, 5.3d) . The vertical distribution of tuna species appeared to be slightly deeper in the Mozambique Channel than in the Seychelles area. This was particularly evident for bigeye tuna (Fig. 5.33b). Daytime depths were significantly deeper in both areas for all the tuna species than those observed during the night (Mann-Whitney U; $p < 0.001$). Silky sharks were only significantly deeper during the day in the Seychelles area (Mann-Whitney U; $p < 0.001$) with no apparent trend observed in the Mozambique Channel (Mann-Whitney U; $p = 0.378$). Oceanic triggerfish and rainbow runners were consistently deeper during the day than during the night in both study areas (Mann-Whitney U; $p < 0.001$).

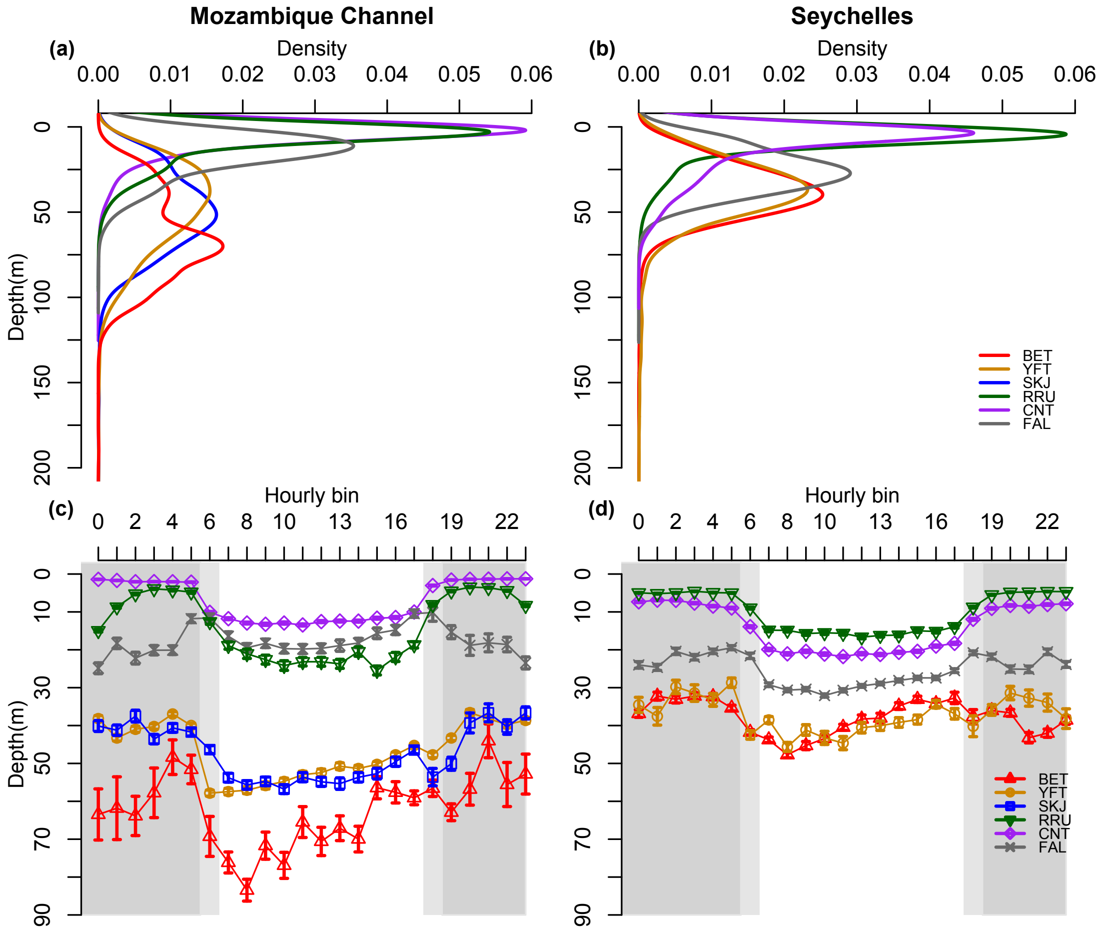


Figure 5.3 Fig. 3. Vertical distribution by species in the Mozambique Channel (a) and the Seychelles (b), as well as mean depth and standard error (bars) per hourly bin by species in the Mozambique Channel (c) and the Seychelles (d). The light grey areas indicate time of sunrise and sunset, and the dark grey areas indicate nightime. FAO species codes are used in the legend: bigeye tuna (BET), yellowfin tuna (YFT), skipjack tuna (SKJ), rainbow runner (RRU), oceanic triggerfish (CNT), silky sharks (FAL).

5.4 Discussion

Accounting for acoustic collisions

The occurrence of acoustic collisions requires specific consideration when using acoustic telemetry methods to study the behaviour of aquatic organisms. This is especially important when multiple tagged individuals are likely to be present around a receiver at the same time. Ultimately a compromise has to be reached between the acceptable resolution of data (sampling rate) and sample size (number of tags). In this study, numerous individuals were tagged around a single receiver and it was important to consider the effects of acoustic collisions on our estimates of absence and presence of tagged fish. Our approach led to estimating the number of acoustic detections that were missed due to collision effects and to take them into account for quantifying the presence rates of each species. For example, we could assess that between 27% (for a FAD with a lower value of $\hat{\beta} = 0.031$) and 46% (for the highest value of $\hat{\beta} = 0.062$) of the emissions were not detected when 10 tagged fish were within range of the receiver. The simultaneous presence of numerous fish was a common situation during our experiments and the nominal number of detections could be corrected through equation 2 (see Fig.B2, Appendix B). Previously, numerous studies have used the number of detection or detection rates to express site fidelity or space use preferences of simultaneously tagged individuals and species. However, changes in detectability can lead to the inferred behavioural patterns being inaccurate (Payne *et al.*, 2010) and have to be accounted for. More recently, several authors have promoted the use of control tags to assess changes in detection probability (Alós *et al.*, 2012a; Payne *et al.*, 2010). However, the addition of a control tag was not appropriate in the current study as this would have further limited the potential number of tags that could be deployed, as the control tag would itself increase the acoustic collision rates. Owing to the high cost and logistical difficulties involved with conducting experiments of this nature, data from every fish is highly valuable. As such, developing a method to simultaneously account for different tag specifications and variable numbers of fish around a receiver was preferable to the use rather than a control tag. Not only does the method developed here allow for the empirical measurement of acoustic collisions, it also facilitates the comparison of behavioural results from different types of tags configurations and areas.

Associations of species with FADs

Acoustic tagging of both tuna and bycatch species provided valuable insights into the dynamics of multispecies FAD aggregations at the diel scale. For the first time, the simultaneous vertical and horizontal behaviours of both target and non-target species at drifting FADs are described. Interestingly, two different associative modes were very apparent: skipjack, yellowfin, bigeye tunas and silky sharks were more closely associated to the FAD during the daytime and less so during the night. This association pattern has previously been observed for tunas (Schaefer and Fuller, 2013) and silky sharks (Filmalter *et al.*, 2011). Oceanic triggerfish and rainbow runner displayed the opposite behaviour and were more closely associated to the FAD during the night than during the day. Diel patterns were consistent in both study sites with tunas and silky sharks maintaining a higher presence rate for most of the day in the Mozambique Channel and in the Seychelles area. The peak in presence of bigeye tuna at 17:00 and the larger standard error bars in the Mozambique Channel was likely to be due to a lower sample size obtained for this species (Table 5.1). The shifts in associative modes for the two categories of behaviour consistently took place around the time of dusk and dawn.

Changing fishing time and gear modifications

In both areas, fishing sets mainly occurred at dawn, which corresponds to the time when the shift in behavioural patterns took place. The occurrence of regular diel patterns in associative behaviour for both target and non-target species is an essential prerequisite to facilitating a change in bycatch to catch ratio through the modification of fishing time. Following these results it is apparent that fishing earlier would likely reduce the catch of tunas and increase the catch of oceanic triggerfish and rainbow runner. Reducing the bycatch of silky sharks is currently a major priority in this fishery, with much work being focused towards this objective (Filmalter *et al.*, 2013; Hutchinson *et al.*, 2015; Poisson *et al.*, 2014a,b). Here, silky sharks were found to display similar associative patterns to the tuna species and, as such, there is no apparent benefit from a modification in fishing time for this species. A shift in fishing time beyond 06:00 could potentially decrease the bycatch rates of oceanic triggerfish and rainbow runner. More than 60% of the fishing sets were done after the mode (06:00) in both areas. This corroborates the findings of our study, which suggest that tunas are often present at FADs after sunrise. As such it is peculiar that fishers do not set more often throughout the day. This may reflect the variability in probability of successfully capturing the target tunas, which is not explicitly apparent in the acoustic telemetry data. Alternatively, it may reflect strategic decisions by the skipper related to other activities onboard, such as locating free swimming schools or other FADs during the daylight hours.

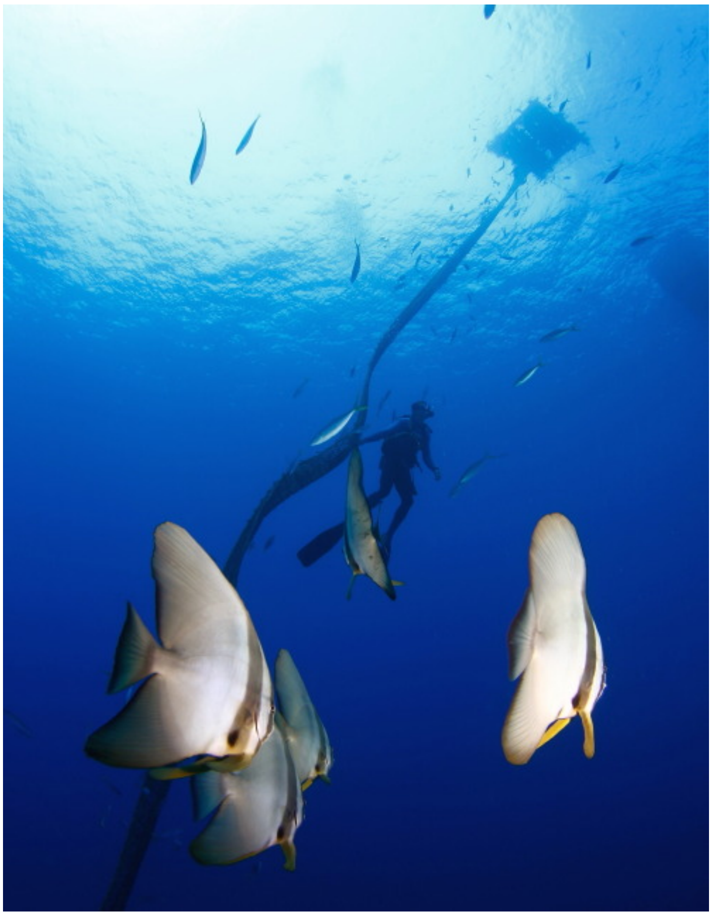
The vertical distributions of the various species studied here were generally similar in both study areas. Tunas were consistently deeper than bycatch species. Generally, all species tended to be deeper during the day and shallower during the night. Schaefer and Fuller (2013) observed similar diel patterns in the vertical distribution of yellowfin, bigeye and skipjack tuna in the eastern Pacific Ocean. Bigeye tuna in the Mozambique Channel occurred deeper than the other tuna species (Fig.5.3a). This vertical difference was greatest between 07:00 and 15:00 (Fig.5.3b). Despite this clear difference, the small magnitude is unlikely to be sufficient to avoid the capture of juvenile bigeye tuna through a modification in the gear depth. In the Seychelles area, yellowfin and bigeye tuna occupied similar depths. As bycatch species were always shallower than the tunas, reduction in net depth cannot lead to a reduction of non-tuna bycatch. Nonetheless, the consistent pattern strongly supports the development of methods to i) separate the bycatch using a different gear, without encircling the tunas, keeping them away from the large purse seine net, or ii) use a particular stimulus that could further enhance this vertical separation.

Other methods have been proposed to reduce the bycatch to catch ratio in the tropical tuna purse seine fishery. The use of best handling and release practices (Poisson *et al.*, 2014b) onboard purse seine vessels could reduce by about 20% the mortality of silky sharks (Poisson *et al.*, 2014a). The highest mortality rates were observed for sharks that were sacked up and brailed with the tunas (Poisson *et al.*, 2014a). These results tend to indicate that technical measures to reduce bycatch mortality should thus take place before the end of the set. Hence, methods to avoid encircling sharks and other non-targets, or release them from the net (Itano *et al.*, 2012), should be developed. For example, Watson *et al.* (2009) showed that an area closure in the eastern Pacific

Ocean could reduce the silky shark bycatch by 33% while compromising the tuna catch by only 12%. Another method was proposed by Dagorn *et al.* (2012) where a reduction in sets of 10 tons or less would globally reduce bycatch rates by 25-45 % while only reducing tuna catch by 4-10%. Considering that the vulnerability of target and non-target species at FADs depend on their associative behaviour, we believe that it is important to keep investigating the fine-scale behaviour of tunas and non-target species, with experiments in various oceanic regions. Both the associative patterns and the swimming depth behaviours could vary between areas. Consequently, different region specific behavioural patterns could have potential in terms of bycatch mitigation. It is likely that a combination of several mitigation measures is likely to be more efficient in the reduction of the bycatch to catch ratio, especially in the short term for sensitive species such as silky sharks (Filmalter *et al.*, 2013), and it is essential to investigate various potential solutions.

Chapter 6

Diet and stable isotope analyses of oceanic triggerfish and rainbow runner at floating objects



6.1 Introduction

Multispecies aggregations at floating object are ubiquitous in the world's tropical and subtropical pelagic environment. These aggregations are diverse regrouping fishes at different ontogenic stages, several families and with a broad range of trophic levels; herbivores, omnivores, planktivours and piscivorous predators. Several hypothesis have been proposed in attempt to explain the evolutionary benefits of this associative behaviour across a broad range of taxa (see reviews: Castro *et al.*, 2002; Fréon and Dagorn, 2000), which, to date, remains unclear.

Data on trophic ecology is key to understand basic mechanisms such as growth, reproduction, survival and behaviour of a species. Some authors have suggested that associated species could gain direct foraging benefit from fauna concentrated at floating objects. This "concentration of food supply" hypothesis has been proposed by Kojima (1956) for small groups of predators such as dolphinfish and has subsequently been suggested for large tuna (Ménard *et al.*, 2000) and silky sharks (Duffy *et al.*, 2015) at FADs. Studies that have investigated the diet of tuna and dorado associated to floating objects concluded that tuna do not feed extensively on associated fauna (Taquet, 2004; Ménard *et al.*, 2000). Furthermore, as highlighted by Fréon and Dagorn (2000), the biomass of potential prey typically found at floating objects is largely insufficient to meet the metabolic requirements (approximately 5 % of body mass, Olson and Boggs (1986)) for 20-40 tonnes of tuna. Given the fact that most of the biomass at FADs comprises of the economically importance tuna species, most of the research attention has been directed towards this group (Jaquemet *et al.*, 2011; Menard, 2000; Potier *et al.*, 2004; Zudaire *et al.*, 2015; Ménard *et al.*, 2000)). Studies investigating the trophic ecology or non-tuna species at FADs remain scarce. Data on the trophic ecology of oceanic triggerfish and rainbow runner is key to determine if they associate with floating objects for trophic reasons.

With increasing emphasis on ecosystem based management in fisheries, data on trophic ecology and niche segregation are priorities to establish the ecological relationships amongst species in an ecosystem (Young *et al.*, 2010). Understanding trophic relationships of ecosystems is key to predict, thought modelling approaches, the impacts of fisheries on pelagic ecosystems (Dambacher *et al.*, 2010). Additionally, on a finer scale, trophic relationships of associated fauna will also aid to the understanding the interspecific processes (e.g. predation, competition) of multi-species pelagic aggregation at floating objects (Deudero, 2001). Stomach content analysis is the most widely used method to study the feeding ecology and resource niche of fish (Hyslop, 1980). It can provide detailed information on the diet composition and foraging habitats by providing a 'snapshot' in time of individuals' feeding habits (Chipps and Garvey, 2007). However, stomach content analysis can be easily biased by opportunistic feeding, variations in digestion rates of prey, sampling design and does not adequately consider spatial and temporal variations when inferring a species's diet (Cortés, 1997). Conversely, stable isotope analysis provides a more integrated measure of foraging habitats and dietary preferences over longer timescales (Araújo *et al.*, 2007). The temporal inference of stable isotopic data is dependant on tissue turnover and, in fish, muscle isotopic turnover typically reflects foraging over a few months. The utility of stable isotope analysis is that the sources of carbon and nitrogen can be distinguished and the predator's diet and trophic position can be inferred (Araújo *et al.*, 2007). Oceanic triggerfish and rainbow runner are abundant co-occurring species at FADs that share similar associative patterns (Chapter 3), vertical distribution and temporal pattern in activity (Chapter 4) which poses interesting questions on the trophic interaction between the two species.

This study combines stomach content and stable isotope analyses to investigate the general trophic ecology and potential trophic interactions of oceanic triggerfish and rainbow runner based on individuals opportunistically caught at FAD as bycatch by purse seiners. The objectives of this study are to provide i) general descriptions of the feeding habits of oceanic triggerfish and rainbow runner, ii) quantify incidence of foraging on FAD associated fauna, iii) determine the niche width of each species, iv) estimate the degree of dietary and isotopic niche overlap.

6.2 Materials and Methods

Study area and sample collection

Oceanic triggerfish and rainbow runner were captured and sampled opportunistically from sets made on floating objects (mostly FADs) by European purse seiners in the western Indian Ocean (Fig.6.1) during 2011 and 2012. Whole individuals were stored onboard either in the blast freezer or in the brine wells (-17 °C) along with the tuna catch. Samples stored in brine were only used for stomach content analysis as the brine might alter the tissue and affect isotopic readings. The frozen samples were then transferred to holding freezers in the lab (-20 °C). Samples were thawed and measured (lower jaw fork length for rainbow runner and total length for oceanic triggerfish to the nearest 0.5 cm), weighed (nearest g) and the stomach were removed for the diet stomach content analysis. A piece of white muscle of ~2 cm^3 was then sampled from the dorsal musculature above the pectoral fin for each individual and stored in the freezer (-20°C).

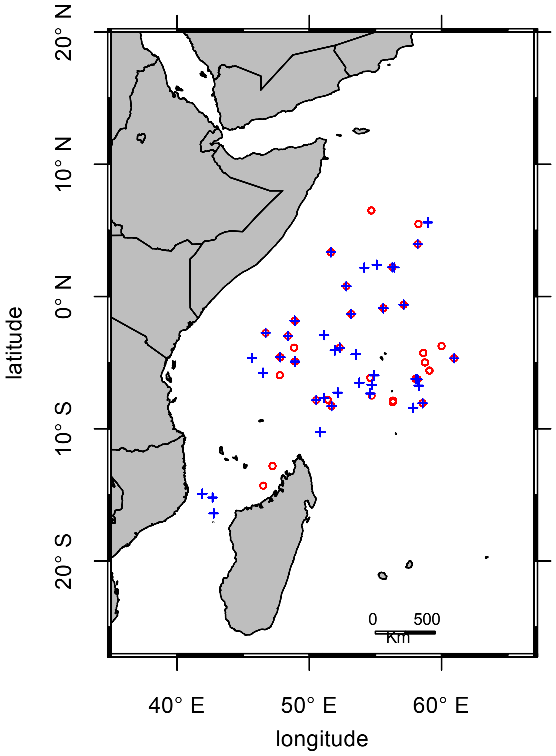


Figure 6.1 Spatial distribution of oceanic triggerfish and rainbow runner samples obtained from FAD sets by purse seiners in the western Indian Ocean. The red dots indicate positions for oceanic triggerfish samples and the blue crosses indicate positions for rainbow runner samples.

Stomach content analysis

Once thawed, samples were measured, weighed, the stomachs were removed and treated following the steps below following the methods from Potier *et al.* (2007):

1. The total weight of each stomach was measured. For oceanic triggerfish no distinct muscular stomach, the anterior part of the intestine, an elongated sac-like structure, was used. Accumulated items, i.e. indigestible parts of prey (eg. chephalopod beaks, eroded fish otoliths, eroded pteropod shells) were sorted and excluded from the analysis to prevent overemphasis of some prey items in the diet.

2. Prey items and identifiable remains were sorted and grouped according to prey categories (e.g. fish, cephalopod, crustacean, molluscs, other) and were weighted to obtain the wet weight proportion of each category.

3. Prey items were then identified using a dissecting microscope to the lowest possible taxon using several keys and descriptors found in Conway *et al.* (2003); Rampal (2002); Smith *et al.* (2003) and by comparison with personal reference collection.

4. Prey items were then individually measured using precision callipers and weighed using a electronic balance (d = 0.002) . For each prey item type specific measurements were made. For fishes, standard length (SL in mm). For cephalopods, the total length mantle length and lower rostral length (LRL in mm, when measurable). For pelagic crabs the carapace width and propods (in mm).

Owing to the small size of most prey items (< 10 mm), the reconstituted weight method was not applied as done for large predatory fish (Potier *et al.*, 2007) and the wet weight was used. Prey items were then categorised by their general vertical habitat usage of the pelagic environment into: epipelagic prey, that are found day and night within the first 200 m, and mesopelagic prey which remain between 200 and 1000 m during day time and migrate to the surface layers during nighttime. Additionally, prey items were also categorised by their known associative behaviour with floating objects ('associative') or mostly found free swimming ('non-associative') following Taquet *et al.* (2007b) and underwater personal observations at FADs. Randomised species accumulation curves of prey was calculated with 1000 permutation to compute the 95 % confidence intervals for each curve.

Three trophic indices were used to describe the importance of diet categories of the two studied species:

1. Percentage by weight (%W)
2. Percentage by number (%N)
3. Frequency of occurrence in stomachs (%F) defined as the percentage over total on non empty stomachs.
4. Index of relative importance (%IRI, Cortés (1997))

$$\%IRI = \frac{IRI}{\sum_{a=1}^{n}} \times 100$$

Where $IRI = \%F \times (\%N + \%W)$ and n in the number of prey item (Cortés, 1997). %IRI allows to represent the most important prey items as a percentage relative to the diet in a way that allows comparison between dietary items of a same species (Cortés, 1997; Hyslop, 1980). The diet niche width and dietary overlap between the two species based on prey abundances was calculated using the "indices" R package (De Cáceres *et al.*, 2011). The niche width for each of the two species were calculated with bootstrapping to provide 95% CI for the estimates. The minimum niche width is 0 and is obtained when all prey are equal or when a single prey is consumed. The dietary overlap between the two species was then assessed using the equation below:

$$O = \frac{\sum_{j=1}^{r} f_{1j} f_{2j}}{\sqrt{\sum_{j=1}^{r} f_{1j}^2 \sum_{j=1}^{r} f_{2j}^2}}$$

O is bounded between 0 (no overlap) to 1 (complete overlap) and 95% CI was computed with bootstrapping. If two predators do not share the same resource and have distinct preferences in prey, then O will yield zero. A value ≥ 0.6 is considered to represent a significant overlap of the resource. No distance value was assigned to prey taxa and thus each prey taxa was weighted equally.

Stable isotope analysis

A subsample of individuals was used for stable isotope analysis. The white muscle samples were freeze-dried during 48h and ground into fine powder before being encapsulated in tin cup and sent for stable isotope analysis in the LIENS laboratory (La Rochelle, France). A continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific) coupled to an elemental analyser (Flash EA1112, Thermo Scientific) were used to perform stable isotope measurements. $\delta^{13}C$ and $\delta^{15}N$ were expressed parts per thousand (‰) according to the formula: relative to the Vienna PeeDee Belemnite and atmospheric N_2 for

$$\delta X = (R_{sample}/R_{standard}) - 1) \times 10^3$$

Where X is ^{15}N or ^{13}C and R_{sample} is the isotopic ratio sample and $R_{standard}$ is the corresponding ratio of standard (atmospheric nitrogen for $\delta^{15}N$ and Pee Dee Belemnite for $\delta^{13}C$). In order to further reduce the possible bias of varying lipid content amongst fish samples, the procedure of Post *et al.* (2007) was applied whereby samples with $C : N$ ratio > than 3.5 were removed.

First, the effect of fish size, latitude and longitude on $\delta^{13}C$ and $\delta^{15}N$ were tested with linear regression models. Samples were grouped per year to ensure sufficient sample size for subsequent analysis. The $\delta^{13}C$ and $\delta^{15}N$ ratios were examined using a biplot to determine differences in the isotopic position of the two species. The range of $\delta^{13}C$ and $\delta^{15}N$ values of population can be used to quantify the isotopic niche dimension and express how generalist a species is in terms of feeding habits and is thus closely correlated to the trophic and spatial niche of a population (Newsome *et al.*, 2007). There are several metrics that can be used to represent isotopic niches. A common metric is the total area of the convex hull (TA) which encompasses all of the data points and gives the "maximum" niche width (Layman *et al.*, 2007). However, some authors have recently argued that the inference of niche widths using this approach may be subject to sample size bias and does not incorporate variability (Jackson *et al.*, 2011). The two metrics were used here to calculate niche isotopic niche overlap between the two species. First, the isotopic niche widths were calculated using the SIAR function "SIBER" R package (Jackson *et al.*, 2011) that uses a Bayesian approach which takes into account uncertainty in the sampled data and naturally incorporates error arising from the sampling process. Standard Ellipses Areas (SEA) represent the isotopic niche width of 40% of typical individuals within the two species based on a bivariate normal distribution (Jackson *et al.*, 2011). Secondly, a Bayesian estimate of the standard ellipse area (SEA_B) was used to compare niche widths of the two species with 10 000 iterations (Jackson *et al.*, 2011). Differences in niche widths were then compared based on the size of simulated ellipse areas and their estimated posterior distributions. Finally, the isotopic niche overlap was investigated by calculating the area of overlap between the 1) standard ellipses areas (SEA) and 2) convex hulls area (TA) of the two species.

6.3 Results

Stomach sampling

A total of 308 individuals were sampled from the western Indian Ocean (Fig.6.1) for dietary analysis (152 for oceanic triggerfish and 156 for rainbow runner). Size of individuals ranged from 20.5 to 42 cm TL (31.8±3.5, mean±SD) for oceanic triggerfish and from 29.4 to 86.4 cm FL (54.8±11.4, mean±SD) for rainbow runner. The proportion of empty stomachs was 34.9 % for oceanic triggerfish and 18.6 % for rainbow runner. The randomised species accumulation curve of prey of the two species did not have a similar slope as that of triggerfish had a reduced curve after ∼40 samples after which it tended towards a plateau whereas the curve for rainbow runner started to reduce only after ∼50 samples while trending towards an asymptote more gradually and with a higher total species richness. The stomach wet weight that contained prey varied from 0.001 and 24.5 g (7.7±6.9, mean±SD) for oceanic triggerfish 0.001 and 357.7 g (18.4± 47.4, mean±SD) for rainbow runner.

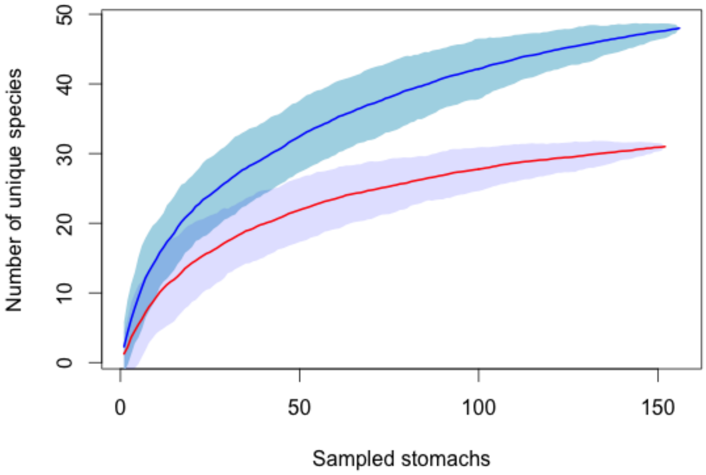


Figure 6.2 Randomised species accumulation curves of prey in found in the diet of oceanic triggerfish (red line) and rainbow runner (blue line). Envelopes indicate confidence intervals with 1000 permutations.

Diet composition

The stomachs contained a range of epipelagic and mesopelagic organisms with pelagic crustaceans and pteropods representing a major component in the diet of the two species (Table 6.1). The diet of rainbow runner were largely dominated by crustaceans (%IRI = 53.6, %F = 52.6) followed by fish (%IRI = 36.6, %F = 23.4) and pteropods (%IRI = 9.7,%F = 21.2). In terms of bulk weight, fishes largely dominated the diet (%W = 80), followed by crustaceans (%W = 19) with pteropods and cephalopods having almost no contribution (< 1%). While *Decapterus macarellus* was the most important prey by bulk weight (%W = 64.5), it was rarely consumed (%F = 3.67) but had a strong influence on the %IRI (23.5%). Crustaceans and pteropods were the dominant groups in the diet of oceanic triggerfish (%IRI = 52.0, %F = 46.2 and %IRI = 45.8, %F = 41.1%, respectively), while fishes (%IRI = 0.9, %F = 11.2) and cephalopods (%IRI > 0.1 %F = 1.5) were a minor part of the diet. In terms of bulk weight crustaceans were largely dominant (%W = 73%), followed by "other" (mostly invertebrates, %W = 12) and pteropods (%W = 10). Detailed information on the frequency of prey occurrence in the stomachs and item are given in Table 6.1 and by broad category in Fig. 6.3.

Most prey consumed by oceanic triggerfish (%IRI ∼ 99) and rainbow runner (%IRI ∼ 75) do not typically associate with floating objects. Prey items of both species mostly consisted of zooplankton and micronekton belonged to the epipelagic category (%IRI ∼ 95%).

Table 6.1 Prey taxonomic composition items form oceanic triggerfish and rainbow runner stomach associated with floating objects in the western Indian Ocean.*indicates trace amounts < 0.001

			Rainbow runner				Oceanic triggerfish					
Category	Family	Species	%N	%F	%W	%IRI	%N	%F	%W	%IRI	Associated	Habitat
Teleosts	Diodontidae	*Diodon histrix*	-	-	-	-	0,10	0,48	0,08	-	Yes	Epipelagic-reef
	Monacanthidea	*Pseudalutarius nasicornis*	5,44	0,82	2,67	0,63	-	-	-	-	No	Epipelagic
	Monacanthidea	Monacanthidea sp	0,60	0,82	0,19	0,06	-	-	-	-	Yes	Epipelagic-reef
	Monacanthidea	*Aluterus sp*	0,08	0,27	0,09	-	-	-	-	-	Yes	Epipelagic-reef
	Monacanthidea	Pervagator sp	0,15	0,55	0,60	0,04	-	-	-	-	Yes	Epipelagic-reef
	Ostraciidae	*Ostracion cubicus*	0,15	0,55	0,05	0,01	-	-	-	-	No	Epipelagic-reef
	Ostraciidae	Ostraciidae sp	0,15	0,27	0,03	*	-	-	-	-	No	Epipelagic-reef
	Mullidea	unkown sp	0,38	0,27	0,41	0,02	0,10	0,48	0,08	*	No	Epipelagic
	Clupeidea	unkown sp	0,08	0,27	0,15	0,01	-	-	-	-	No	Epipelagic
	Carangidea	*Decapterus macarellus*	5,74	3,56	64,54	23,55	-	-	-	-	Yes	Epipelagic
	Carangidea	Carangidea sp	0,30	0,82	0,44	0,06	-	-	-	-	Yes	Epipelagic-reef
	Clupeidea	unkown sp	0,08	0,27	0,15	0,01	-	-	-	-	No	Epipelagic
	Engrulidea	unkown sp	0,23	0,27	1,50	0,04	-	-	-	-	No	Epipelagic
	Pomacentridea	*Abudeduf vaigensis*	0,30	0,82	0,10	0,03	-	-	-	-	Yes	Epipelagic-reef
	Pomacentridea	Pomacentridea sp	0,30	0,82	0,10	0,03	0,10	0,48	0,05	*	Yes	Epipelagic-reef
	Acanthuridae	Acanthuridea sp	0,30	0,27	0,12	0,01	-	-	-	-	No	Epipelagic-reef
	Scombridea	Scombridea sp	0,30	0,55	0,90	0,06	-	-	-	-	No	Epipelagic
	Kyphosidea	*Kyphosus vagiensis*	0,08	0,27	1,37	0,04	-	-	-	-	Yes	Epipelagic-reef
	Ogcocephalidae	*Ogcocephalus sp*	0,68	1,10	0,04	0,07	-	-	-	-	No	Epipelagic-reef
	Teleostei	Fsh unkown	6,27	10,41	6,56	12,56	2,31	9,09	3,58	2,23		
Cephalopods	Ommastrephidae	*Ommastrephidea spp*	-	-	-	-	-	-	-	-	No	Mesopelagic
		Sthenoteuthis oualaniensis	-	-	-	-	0,10	0,48	1,27	0,03	No	Mesopelagic
		Squid unkown	1,06	2,74	0,36	0,37	0,20	0,96	0,51	0,03	No	
Crustaceans	Platyscelidae	*Platyscelus ovoides*	4,38	4,66	0,01	1,92	0,80	1,91	*	0,06	No	Epipelagic
		lembos sp	0,30	*	*	*	0,40	0,96	*	0,02	No	Epipelagic
		Unknown Sp	2,49	3,84	0,01	0,90	4,23	6,70	0,10	1,20	No	
	Stomatopoda	hooded shrimp	4,38	7,40	0,57	3,45	-	-	-	-	No	Epipelagic-reef
	Stomatopoda	Unknown Sp	5,74	5,21	0,96	3,28	0,80	3,83	1,37	0,35	No	Epipelagic-reef
	Copepoda	*Calanopia spp*	0,08	0,27	*	*	-	-	-	-	No	Epipelagic
		Crab larvea	16,39	12,88	1,57	21,75	3,12	5,74	1,48	1,10	No	Epipelagic
		Crab sp	0,08	0,27	0,79	0,02	-	-	-	-	No	Epipelagic
	Portunidae	*Charybdis smithii*	2,72	6,58	11,40	8,73	4,73	18,18	69,31	55,91	No	Epipelagic
	Lepasdidae	*Lepas sp*	-	-	-	-	0,40	1,44	*	0,02	Yes	Epipelagic-reef
	Decapoda	larvea	8,08	8,22	1,10	7,10	0,70	2,87	0,01	0,09	No	Epipelagic
	Luciferidae	*Lucifer sp*	0,60	0,55	*	0,03	-	-	-	-	No	Epipelagic
		Crustacean unknown	0,01	1,92	2,56	0,46	0,50	1,91	1,19	0,13		Epipelagic
Pteropods	Cavolinidae	*Cavolina spp*	11,03	7,40	*	7,67	42,35	14,35	4,78	28,10	No	Epipelagic
	Cavolinidae	*Cavolina globulosa*	0,53	0,55	0,04	0,03	1,91	1,44	0,25	0,13	No	Epipelagic
	Cavolinidae	*Diacavolina longirostrum*	13,29	4,11	0,40	5,29	13,98	8,61	2,72	5,97	No	Epipelagic
	Cavolinidae	*Diacria sp*	0,30	1,10	0,01	0,03	0,10	0,48	*	*	No	Epipelagic
	Creseidae	*Creseis sp*	-	-	-	-	11,77	4,31	0,04	2,11	No	Epipelagic
	Atlantidae	*Atlanta sp*	2,57	5,75	0,09	1,44	3,92	4,31	0,17	0,73	No	Epipelagic
		Limacina sp	0,15	0,55	*	0,01	1,01	3,83	0,01	0,16	No	Epipelagic
		Pteropod spp	-	-	-	-	1,01	0,96	0,70	0,07	No	Epipelagic
	Janthinidae	*Janthinidae sp*	0,45	1,37	0,07	0,07	-	-	-	-	No	Epipelagic
		Unkown	-	-	-	-	0,20	0,48	*	*	No	Epipelagic
Invertebrates	Porpitidea	Jellyfish	-	-	-	-	4,23	2,87	5,33	1,14	No	Epipelagic
		Nematod	0,68	1,10	*	0,07	-	-	-	-		
		Anelid	-	-	-	-	0,20	0,96	0,84	0,04		
		flat worm	2,19	0,55	0,01	0,11	-	-	-	-		
		Macro algea	-	-	-	-	0,10	0,48	0,84	0,02		
		Unknown	0,38	0,55	0,01	0,02	0,60	1,44	5,28	0,35		

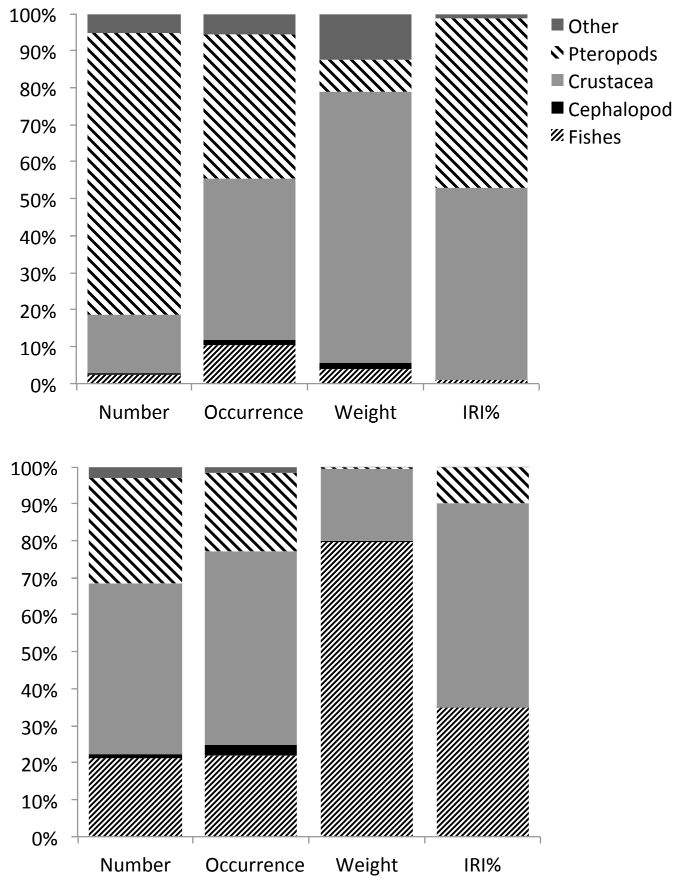


Figure 6.3 Relative proportions of main prey categories of oceanic triggerfish (top) and rainbow runner (bottom) at FADs.

Dietary niche width and overlap

The dietary niche width for oceanic triggerfish was 0.38 (95% CI: 0.32, 0.42) and significantly narrower than that of rainbow runner with 0.46 (95% CI: 0.45, 0.46). The dietary overlap O between the two species was considerable and close of being significant with 0.58 (95% CI: 0.37, 0.82).

Stable isotope analysis

A subsample of the 71 rainbow runner and 65 triggerfish were used for stable isotope analysis. Size of individuals ranged from 20.5 to 37.8 TL cm (31.7±3.8, mean±SD) for oceanic triggerfish and from 37.0 to 83.7 FL cm (54.8±11.4, mean±SD) for rainbow runner. The results from the linear regression model indicate that the latitude and longitude did not have a significant effect on $\delta^{13}C$ and $\delta^{15}N$ for the two species ($p < 0.05$). The data was pooled by species. $\delta^{15}N$ values ranged from 10.25 to 13.17 ‰(11.78 ± 0.61 ‰, mean ±SD) for oceanic triggerfish and 10.26 to 13.13 ‰(11.87 ± 0.58 ‰, mean ±SD) for rainbow runner. $\delta^{13}C$ values ranged from -18.23 to -16.50 ‰(-17.50 ± 0.31, mean ±SD) for oceanic triggerfish and -17.67 to -16.53 for ‰$\delta^{13}C$ (-17.13 ± 0.24 mean ±SD) for rainbow runner (Fig.6.4). No significant difference in $\delta^{15}N$ was observed between the two species (Kruskal–Wallis: χ^2= 0.20, p = 0.65) whereas rainbow runner were significantly more enriched in $\delta^{13}C$ than oceanic triggerfish (Kruskal–Wallis: χ^2 = 57.64, p < 0.001). For oceanic triggerfish, fish size did not affect levels of $\delta^{13}C$ or $\delta^{15}N$ significantly. For rainbow runner, fish size effect was not significant for $\delta^{13}C$ but had marginally significant positive effect for $\delta^{15}N$ (p = 0.04; R^2= 0.51) with larger fish having larger $\delta^{15}N$.

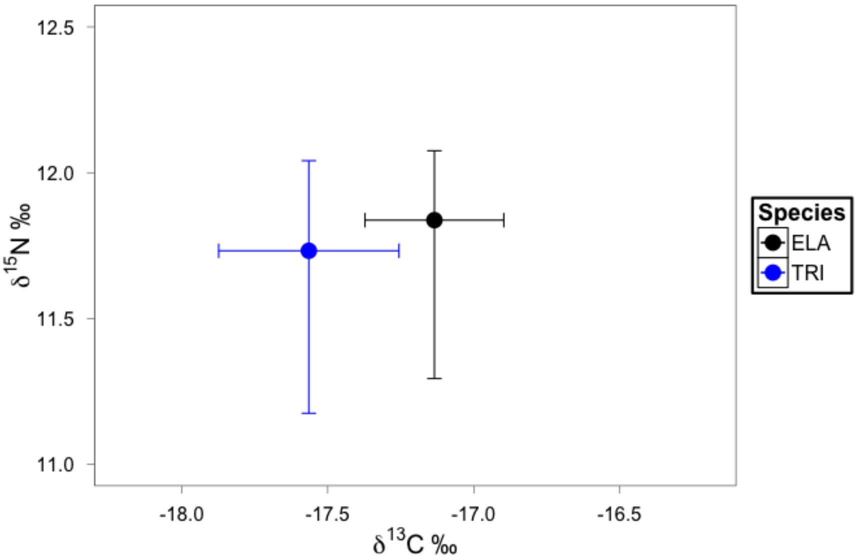


Figure 6.4 Biplot of $\delta^{13}C$ and $\delta^{15}N$ values (mean ‰± SD) from of oceanic triggerfish and rainbow runner in the western Indian Ocean.

Isotopic niche width and overlap

The raw isotopic data for the two species are depicted in Fig. 6.5 with their respective convex hulls and their standard ellipses based on maximum likelihood estimates (SEA). Testing for differences in ellipse size (Fig.6.5(b)) indicate that ellipse of oceanic triggerfish were generally larger than those of rainbow runner (with a probability = 0.67). The overlap of the SEA and the convex hull were 5.8% and 30.7% respectively between the two species.

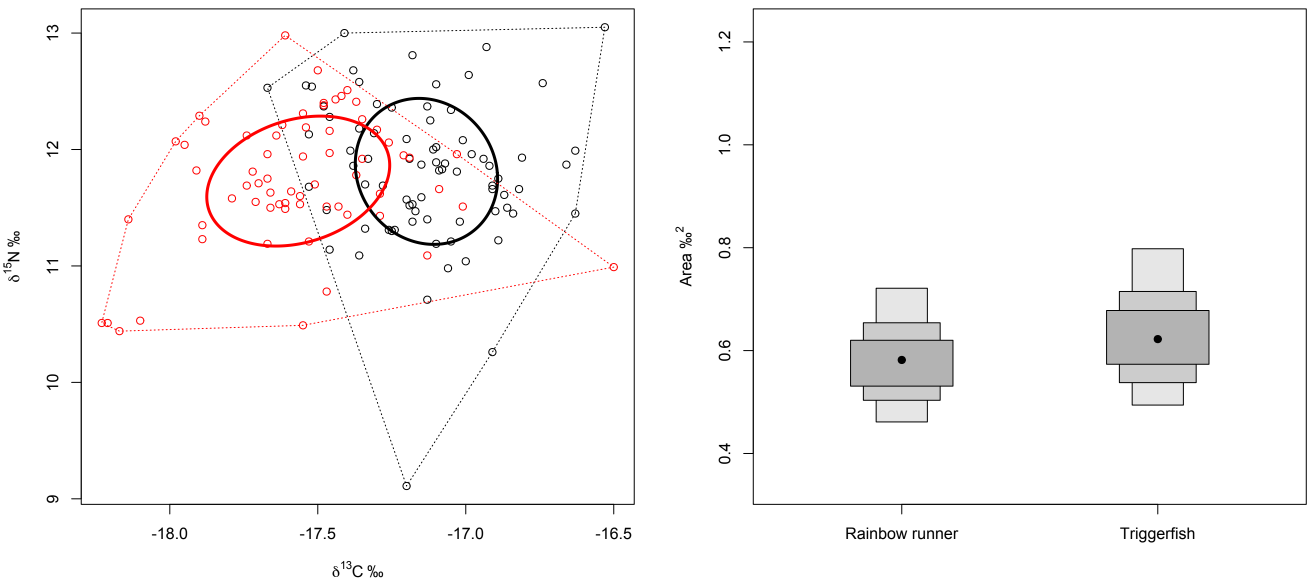


Figure 6.5 (a) Isotopic values of oceanic triggerfish (red) and rainbow runner (black) with corresponding standard ellipse representing their niche area and corresponding the convex hull (dotted polygons). (b) The posterior estimates of the standard ellipse areas (SEAb) for the two species. The boxes represent the 95, 75 and 50% credible intervals in ascending order of size, with the mode indicated by the black circles.

6.4 Discussion

Diet composition

This study provides the first combined dietary and stable isotope analysis for oceanic triggerfish and rainbow runner and provide valuable insights in their trophic ecology and trophic position in the pelagic ecosystem. Despite being common epipelagic species in the tropical oceans, data on the trophic ecology of the two species are scarce. There are few reports and studies describing diet of rainbow runner (Bocanegra Castillo, 2007; Hiatt and Strasburg, 1960; Senta *et al.*, 1993; Vaske *et al.*, 2006). Vaske *et al.* (2006) carried out a more comprehensive study focusing on the diet of rainbow runner in the western equatorial Atlantic Ocean, at Saint Peter and Saint Paul archipelago, where this species is incidentally captured the local hand-line fishery (Viana *et al.*, 2015). The authors reported a total of 27 species in the diet of rainbow runner (n = 309) around the archipelago which was dominated (according to %IRI) by crustaceans (mostly euphausiids and carb larvae), fish (mostly flying fish component: *Cheilopogon cyanopterus, Exocoetus volitans* and *Oxyporhamphus* *micropterus*) and some pelagic pteropods (*Cavolina* sp.). García Ramírez and Posada (2014) investigated the diet of rainbow runners in the coastal waters of Columbian Caribbean (n = 42) and found a total of 25 prey species with the diet being largely dominated (%W = 75%) by dwarf herring (*Jenkinisia lamprotaenia*) followed by crustaceans and molluscs. Senta *et al.* (1993), during investigations of sea skaters (*Halobates* spp.) predation by pelagic fish, examined the stomach content of rainbow runner (n = 65) associated to FADs in the western Pacific Ocean and reported that crustaceans and gastropods were the most occurrent in the stomachs followed by fish. Romanov *et al.* (2009) looked at importance of *C. smithii* in the diet of pelagic predators in the western Indian Ocean and reported high occurrence of this prey *(%F* = 12-25%, n = 36) of rainbow runner caught by purse seiners. More recently, a report by Wang *et al.* (2013) providing preliminary results (no quantitative analysis) on the diet of rainbow runner indicated that fish (including *Decapterus* sp.) were most frequent prey items at drifting FADs followed by cephalopods and crustaceans. It thus appears that the diet of rainbow runner can vary substantially across its distribution range. However, similarly to some of the the reports and studies mentioned above, the diet of rainbow runner in the western Indian Ocean was dominated by crustaceans, fish and pteropods. The prey species richness, with a total of 48 prey taxa identified, was considerably higher than the 27 species reported by Vaske *et al.* (2006) in the Atlantic. It appears that rainbow runner is a generalist epipelagic predator with a diet composed mostly of pelagic zooplankton and micronekton. *Decapterus macarellus* had the highest %IRI score (23.55%) amongst the prey items, however, this prey is not frequently found in the diet (%F = 3.7) and due its considerably larger size relative to other prey, had a strong influence of the %IRI score.

The only diet study providing comprehensive data on the diet of oceanic triggerfish at drifting FADs was by Senta *et al.* (1993). The authors were investigating the predation of sea skaters (*Halobates* spp.) by pelagic fish. The authors, incidentally, reported that the dominant prey items (by occurrence) were molluscs and crustaceans followed by fish but did not provide more comprehensive quantitative indices to describe the diet in manner that could allow comparisons. Romanov *et al.* (2009) reported the presence of *C. smithii* in all five individuals sampled at FAD in the western Indian Ocean. Gooding and Magnuson (1967) observed pelagic aggregations at FADs for several days using a floating observation chamber off the coast of Hawaii and made some interesting observations on the foraging behaviour of associated fish. The authors observed what appeared to be an ectoparasite cleaning behaviour amongst oceanic triggerfish and other species present at the FAD. The authors also provide brief diet description for 10 individuals and reported that they contained mostly pteropods and stomatopods, and lesser numbers of crab larvea, amphipods, and copepods. In this study, at total of 31 prey taxa were identified and a diet being largely dominated by crustaceans and gastropods. *C. smithii* was the most dominant dominant prey (%IRI =55.9, %F = 18.2, %W = 79). This swimming crab species is endemic to the western Indian Ocean and is known to be highly abundant as they can often be observed in large swarms, particularly during the north east and south west monsoons (Romanov *et al.*, 2009; Van Couwelaar *et al.*, 1997). *C. smithii* have been reported to be a major prey species for lancetfish (*Alepisaurus ferox*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*) in the western Indian Ocean (Potier *et al.*, 2004, 2007; Romanov *et al.*, 2009; Zudaire *et al.*, 2015) and thus appears to be an important component of the region's pelagic ecosystem. Gastropods were another import prey group, Cavolinidea were observed frequently in the diets (%IRI = 34, %F= 41.1) but were not as important in the diet of rainbow runner (%IRI = 13.0, %F = 13.3). Despite being reported in the diet of yellowfin tuna and lancetfish, pelagic pteropods appear to be a rare prey item for these larger predators.

Stable isotope

Stable isotopes of nitrogen is a useful tool to examine the relative trophic position of species (Vanderklift and Ponsard, 2003). In this study, both species had similar range of $\delta^{15}N$ (Fig.6.4) which suggest that they occupy a similar trophic level. The lack of baseline isotopic value for the region precluded the calculation of trophic levels value for the two species. Additionally, no detailed isotopic studies on either of the two species are available for comparison. Body size had a significant but weak effect (p = 0.04, R^2= 0.51) on $\delta^{15}N$ for rainbow runners with larger individuals being more enriched in $\delta^{15}N$. Larger $\delta^{15}N$ values generally reflects higher trophic level (Deniro and Epstein, 1981) and is generally known to increase with predatory body size and has been reported in pelagic predators (Ménard *et al.*, 2007; Rabehagasoa *et al.*, 2012; Tsai *et al.*, 2014).

The carbon isotopic composition of fish mainly reflects on ingested preys which is influenced by primary producer at the base of the food web (Graham *et al.*, 2010). $\delta^{13}C$ values can track the productivity at relatively small scales, within oceanic basins, with more enrichment associated with more productive costal waters, such as upwelling zones, compared to less productive pelagic areas (Graham *et al.*, 2010). Values for $\delta^{13}C$ differed between species with rainbow runner being significantly higher in $\delta^{13}C$ than oceanic triggerfish, however, the difference in the mean values was minor ($\sim 0.4\ \delta^{13}C$). The higher $\delta^{13}C$ value suggest that rainbow runner diet have a stronger coastal influence. Indeed, the proportion of epipelagic-reef prey was more important in the diet of rainbow runner than for oceanic triggerfish and, more precisely, with a higher Carangidae (epipelagic-coastal) component. In contrast, the diet of oceanic triggerfish had a strong pteropods component which, as purely pelagic animals, can be expected to have a stronger pelagic signature with a lower $\delta^{13}C$ enrichment. Interestingly, Rabehagasoa *et al.* (2012) observed a similar pattern between silky sharks and blue sharks in the western Indian Ocean with silky sharks having a higher $\delta^{13}C$. The authors suggested that this difference could be due to the fact that silky sharks habitat was not solely restricted to the pelagic habitat as they can occur close to the shelf and over deepwater reefs. Similarly, Graham *et al.* (2010) showed a difference in $\delta^{13}C$ between two seal species with the coastal harbor seals having a higher $\delta^{13}C$ value than offshore foraging northern fur seals, while having the same trophic levels. However, in must be noted that in both of the mentioned studies, the difference in $\delta^{13}C$ was more distinctive than observed in this study. Alternatively, differences in $\delta^{13}C$ can also be explained by differences in growth rates with higher $\delta^{13}C$ associated with higher growth rates (Popp *et al.*, 1998). Currently, no validated age and growth study are available for either species that could allow comparisons in growth rates.

Feeding behaviour

The dietary data from this study suggests that oceanic triggerfish (%IRI $\sim$ 99, %F $\sim$ 97) and rainbow runner (%IRI $\sim$ 75, %F $\sim$ 92) feed primarily on unassociated organisms. The relatively low proportion of empty stomach when compared to tunas (Menard, 2000) suggests that the two species actively feeding when associated to FADs. Most prey items consumed were free swimming epipelagic zooplankton and micronekton which suggest that there is little to no direct dietary advantage by being associated with FADs. Similarly, studies investigating the diet of tunas caught at FADs indicate that this group does not take direct dietary advantage from FAD associated species (Potier *et al.*, 2004; Menard, 2000). However, Duffy *et al.* (2015) recently investigated the feeding habits of silky sharks (*Carcharhinus falciformis*) at FADs and concluded that this species does takes advantage of the associative behaviour of prey to increase their probability of encountering and capturing prey.

The vertical movement and activity data in Chapter 4 suggest that the two species are active during the day when they are likely to feed more intensively. During the day, the two species typically display a series of dives close to the thermocline, where they are likely to be feeing on zooplankton and micronekton. Indeed, this section of the water column, close to the thermocline, is known for its higher primary productivity and zooplankton densities (Huggett, 2014; Saltzman and Wishner, 1997). *C. smithii*, an important prey item, are also known to occur close to the thermocline during the day in the western Indian Ocean (Romanov *et al.*, 2009). The thermocline layer is an important section of the water column for large number of epipelagic organisms in an otherwise oligotrophic environment. Its proximity to cooler, nutrient rich waters and penetration of light are favourable condition for primary productivity, phytoplankton blooms, which, thought a bottom up process, concentrates primary consumers (zooplankton), secondary consumers (micronekton) and ultimately, predators (Potier *et al.*, 2014). As such, the vertical distribution and feeding behaviour of pelagic fish and mammals is strongly influences by the thermocline (Goodyear *et al.*, 2008; Scott and Chivers, 2009).

The absence of mesopelagic prey (%F < 1), which typically undergo vertical migration, supports the findings of Chapter 4 as the two species do appear to feed extensively nocturnally when mesopelagic prey are abundant in the mixed layer. In contrast, the large component of mesopelagic prey in other epipelagic species such as yellowfin tuna caught at FADs suggests that they forage at night Ménard *et al.* (2013).

Niche overlap and resource partitioning

The trophic niche width and isotopic niche width estimation did follow the same pattern for the two species. While trophic niche is often tightly correlated to isotopic niche, the two metrics are not equivalent (Jackson *et al.*, 2011). The trophic niche width calculated from taxon in the stomach content indicate that rainbow runner had a broader trophic niche than oceanic triggerfish. This observed difference is driven by the higher species diversity in the diet of rainbow runners. However, the isotopic data suggest the oceanic triggerfish has a wider isotopic niche than rainbow runner. Isotopic measurements are myopic as they cannot distinguish specific taxonomic identities of prey, but rather reflects their compositions (Newsome *et al.*, 2007). One interpretation of these results is that rainbow runner has a larger prey diversity but with a more similar isotopic composition than oceanic triggerfish.

At FADs, oceanic triggerfish and rainbow runner have similar horizontal and vertical distributions and thus have the same spatial niche. Additionally, the two fish species have similar activity patterns which indicates that there is a strong spatial and temporal overlap in their foraging pattern. Dietary and isotopic niche overlap are useful as they provide a complementary insight into resource partitioning and competition of co-occurring species at different temporal scales. While stomach samples provide a snapshot of the last meal, stable isotope analysis of muscle tissue reflects dietary habits over larger time scale (1-3 months depending on the tissue turnover rates). According to the dietary overlap index O, that the two species was very close of being significant ($O = 0.57$) which suggest some degree of overlap in their diet. At FADs, Potier *et al.* (2004) reported a significant overlap in the diet of yellowfin and bigeye tuna in the western Indian Ocean. The area overlap in the convex hulls (30.7%) suggest that maximum isotopic niche of that the two species share a portion of their foraging resource at FADs. The isotopic niche overlap estimation giving by the statistically more robust SEA also indicated overlap (5.8%) and indicates that two species share a portion of their foraging resource when associated to FADs and have an intermediate level of competition

Potential caveats and improvement for future studies

Samples were collected from FAD fishing sets which are predominantly made at sunrise (see Chapter 5). However results on activity patterns suggest that both species feed more intensively during the day. As such, this affect dietary composition of the two species. Schaefer and Fuller (2005) reported that time of the day did affect the stomach content of FAD associated tuna. An improvement would be to sample individuals from sets thought the entire day to test whether the dietary composition of the species changes through the day.

The examination of oceanic triggerfish stomach content is challenging as this species often bits chunks out of its larger prey making the identification of prey taxon difficult. Furthermore, the examination of frozen samples was not ideal as invertebrates lacking hard structures (ex: jellyfish, shell-less pteropods) were difficult to distinguish due to additional degradation caused by the freezing process. It is thus possible that invertebrate taxa lacking hard structure have been underestimated. For future studies, it is therefore recommended that stomach content is either examined fresh or stored in ethanol for subsequent examination in the laboratory. This was however not possible in the current study as the samples were collected by commercial fisherman which allowed us to have a large spatial coverage.

Stomach samples from individuals that are not associated to FADs would be useful to understand if the feeding habits of free swimming individuals are any different. However, unlike tuna, sharks and other top predator that can be captured by longliners, free swimming rainbow runner and oceanic triggerfish, despite their abundance, are rarely encountered and captured in the open ocean.

Currently, there is no available isotopic baseline (obtained from phytoplankton) for the western Indian Ocean. The isotopic base in an import reference point to estimating of the trophic level value which could then be used to infer the food web dynamics of the pelagic ecosystem in the western Indian Ocean.

Conclusion

Oceanic triggerfish and rainbow runner are opportunistic predators that feed mostly on epipelagic zooplankton and micronekton in the water column and only a minor portion of their diet comprised of fauna directly associated with FADs. The stable isotope analysis revealed that the two species have a similar trophic level. A minor but significant difference in $\delta^{13}C$ was observed which suggests a difference in the foraging habits of the two species. Niche width inferred from both prey diversity and isotopic niche show that rainbow runner is a more generalist predator than oceanic triggerfish. The two species have overlapping niches with suggests that an intermediate level of competition exists between the two species at FADs.

Chapter 7

General discussion

Overview

The oceanic triggerfish and rainbow runner are two abundant epipelagic species with high incidental capture rates in the tropical purse seine fishery and yet little is known about their biology and ecology. This thesis addressed this knowledge gap and key findings of this study were:

- Both species have similar associative behaviour and display high fidelity to FADs while remaining associated to the same object up to several months. During these extended associations they undertake short excursions suggesting that they occupy small home ranges at FADs. Two behaviour modes were observed in the associative behaviour as some individuals tend to be more dynamic in their excursion behaviour (behavioural polymorphism).
- The vertical distributions of the two species were similar and restricted to the mixed layer (< 60 m). A distinct diel pattern was observed in the vertical distribution with a restricted surface orientated behaviour at night and active vertical movements during the day.
- Ambient light is a key exogenous stimulus that drives switches in diel behavioural patterns: associative behaviour (i.e.home range), vertical movement and activity levels.
- Oceanic triggerfish can display behavioural plasticity and change its behavioural patterns with altering environmental conditions which could reflect changes in biotic and abiotic factors.
- Two patterns of diel associative behaviour at FADs was identified. Tunas and silky sharks have a stronger association during the day while oceanic triggerfish and rainbow runner are strongly associated at night. However, the vulnerability of both target and non-target species are close to their maximum during the period of diel behavioural switch that occurs at sunrise when most of the fishing sets are made. A change in set time in the western Indian Ocean does not appear to be a an effective method to reduce capture rates of silky sharks while minor reductions in capture of rainbow runner and oceanic triggerfish could possibly be achieved by fishing after sunrise. Non-target species are generally positioned above target species, as such a modification in net depth cannot be used as a mitigation measure.

- Oceanic triggerfish and rainbow runner are opportunistic predators that feed mostly on epipelagic zooplankton and micronekton in the water column. Only a minor portion of their diet comprised of fauna directly associated with FADs (oceanic triggerfish: %IRI $\sim$ 1, rainbow runner: %IRI $\sim$ 25)

- The two species have overlapping dietary and isotopic niches with suggests that an intermediate level of competition exists between the two species at FADs.

Why do oceanic triggerfish and rainbow runner associate to floating objects?

Several hypothesis have been proposed to explain associative behaviour of epipelagic fish with floating objects (reviews: Castro *et al.*, 2002; Fréon and Dagorn, 2000) and given the diversity of associated species, ontogenetic stages and life history traits it is possible that different motives apply to different species groups. Most behavioural mechanisms can be explained by strategies involving resource acquisition and survival, or the interplay between both. Oceanic triggerfish and rainbow runner exhibit similar behavioural patterns at FADs. This suggests that their resulting convergence in behaviour have been subjected to similar selective pressures, hence they have the same motive for associating with floating objects.

Tropical oceans are vast and considered to be relatively oligotrophic environment where the strong thermocline limits the mixing of deeper nutrient rich water. However, the productivity is not homogenous, in fact, local productivity driven by oceanic structures can be quite heterogeneous, and a glance at ocean colour and chlorophyll-a satellite images depicts this notion. Surface fronts are boundaries between water masses that differ in density and cause convergence zones. Such convergent zones drives productivity which, in turn, can structure habitats and pelagic communities. Generally, strong intensive fronts are associated with the coastal waters whereas weaker fronts are more common in the open ocean (Roa-pascuali *et al.*, 2015). The effect of costal frontal zones on ecosystems are prominent and well document. Weaker oceanic fronts are typically driven by mesoscale features such as eddies and by being spatially and temporally dynamic are more challenging to study. Advances in remote sensing technology has contributed to the study of mesoscale structures in the open ocean and their role in driving local productivity in oligotrophic systems. Cyclonic eddies enhances productivity through the upwelling of nutrients in their core while anticyclonic eddies are characterised by the convergence of the surface layer which promotes the formation of frontal structures (Fig.7.1). Small organisms with limited swimming abilities (e.g. plankton) are swept along horizontally and accumulate at such convergent frontal zones (Bakun, 2006). Similarly, on the surface, floating objects also tend to accumulate at such frontal areas (Bakun, 2006). Several studies have demonstrated the importance of such frontal areas between eddies in structuring the distribution of pelagic communities from zooplankton (Huggett 2014), micronekton (Sabarros *et al.*, 2009) to higher trophic levels such as frigate birds (Tew Kai *et al.*, 2009). The higher concentration of planktonic organisms in such areas would provide considerable trophic advantages to fish, but how do they locate these localised productive areas? Hall (1992b) suggested that epipelagic fish use floating objects as indicators of productive frontal areas and this hypothesis was referred to as the "Indicator-log hypothesis". Indeed, detecting convergent water masses may be difficult for predators to perceive without a noticeable feature such as a prey patch. Floating objects may well be a means for epipelagic fish such as oceanic triggerfish and rainbow runner to locate and remain in such patchy productive areas in the open ocean (Bakun, 2006). As such, by remaining associated with floating objects in the open ocean, the probability of encountering favourable productive area for foraging may be higher than when swimming freely and relying on sensory capacities to detect prey patches. While results from this study indicate that oceanic triggerfish and rainbow runner do forage directly on FAD associated fauna, their motive for association could still be driven by a "medium-term" foraging success. This hypothesis is not easy to validate through field experimentation, however, by demonstrating that drift patterns of floating objects have a higher probability of "finding" productive frontal structures (i.e. zooplankton rich areas) when compared to a randomly swimming particle, would support this hypothesis.

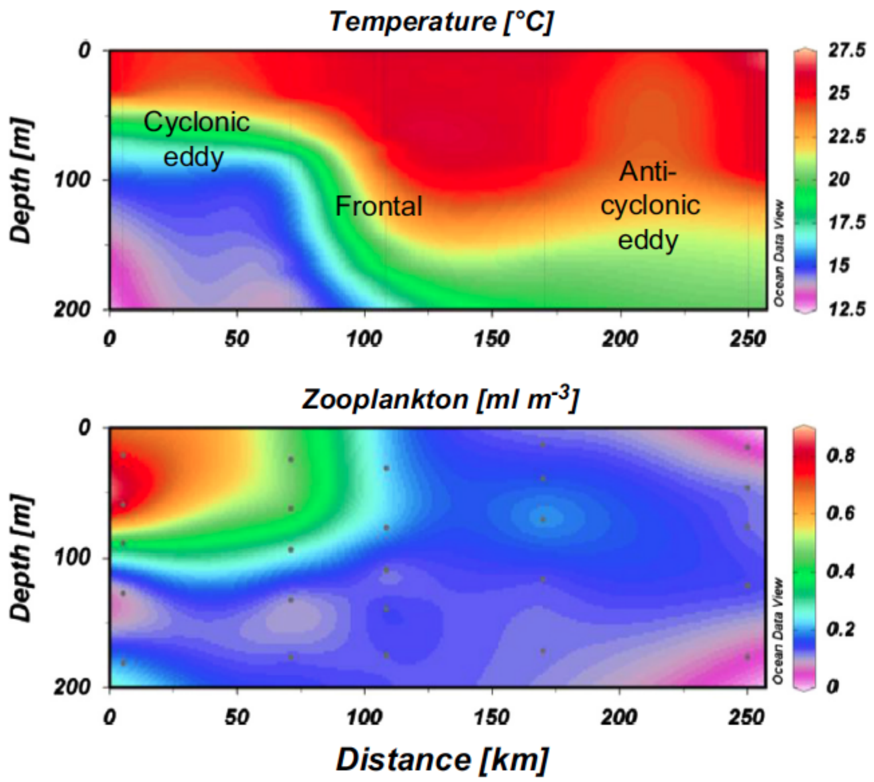


Figure 7.1 Vertical distribution and temperature of mesozooplankton biovolume along a transect through a series of eddies in the Mozambique Channel in the western Indian Ocean illustrating higher concentrations of zooplankton above the thermocline close in a frontal area. Source: Huggett (2014)

Floating objects can provide other benefits to these two species. Variations in presence absence between individuals suggest that oceanic triggerfish and rainbow runner do not form unique monospecific schools but are rather divided into several sub-schools. This was apparent during underwater observations as smaller group of individuals were observed swimming back and forth from the FAD independently (unpublished personal observation). Moreover, On different occasions during underwater observations, the predatory menace of a marlin caused a rapid regroup with their conspecifics close to the FADs (unpublished personal observation). Similar underwater observations were made by Hunter and Mitchell (1967), Gooding and Magnuson (1967) and Wickham and Russell (1974) who reported that individuals from several species (including oceanic triggerfish and rainbow runner) swam towards the floating objects when large predators were present in the vicinity. It appears that while oceanic triggerfish and rainbow runner do not constantly form single monospecific schools, they use the FAD as spatial reference point (Klima and Wickham, 1971) to form larger schools as response to predatory threat.

Similarly, at night, individuals tend to remain close to the FAD while resting close to the surface while probably forming single larger monospecific larger schools.

It thus appears that act as a spatial reference point and can provide benefits to oceanic triggerfish and rainbow runners at two different time scales. The two species may use the floating objects to increase their medium-term trophic advantages, while on the diel scale, the floating object acts as a spatial reference point to regroup and increase the chances of survival as a school.

FADs as fishing traps

The long residency of oceanic triggerfish and rainbow runner (months) observed in this study suggest that FADs are effective at retaining these species. A comparison of residency indices for targeted and non-targeted species at FADs provides an indication of their susceptibility to capture by purse seine fishing vessels (Fig.7.2). The fact that non-target species have yield an index ~3-4 times higher (Fig.7.2) indicates that FADs are better fishing traps for this group than for the targeted tunas. Using behavioural patterns at FADs, the species-specific vulnerability to the purse seine fishing gear was examined at a day scale. While distinct opposing diel associative patterns were observed it appears that only minor changes in bycatch to catch ratio could potentially be achieved by a change in fishing time. While the vertical distribution target and non-target species appears to be stratified, a change in fishing gear design (i.e. shallower nets) does not appear feasible . Given the high vulnerability of non-target species at FADs, efforts to find alternative technical mitigation methods. Additionally, the fact that FADs are effective fishing traps for non-target species is valuable information that should be considered in an ecosystem based management.

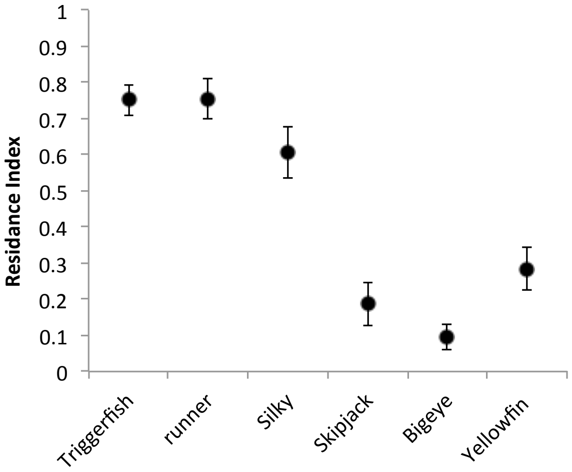


Figure 7.2 Residency Index of targeted tuna species (skipjack, yellowfin and bigeye tuna) and major non-target species (oceanic triggerfish, rainbow runner, silky shark) at FADs. Error bars represent standard errors.

Can FADs represent an ecological trap for oceanic triggerfish and rainbow runner?

Following investigations comparing condition indices (thorax girth) and stomach fullness suggesting that tuna associated with FADs appeared to be in an inferior condition than tuna in free swimming schools, some authors have suggested that the massive deployment of FADs could represent an 'ecological trap' for FAD associated species by displacing the population towards less suitable habitats (Marsac *et al.*, 2000; Hallier and Gaertner, 2008b). Ecological traps are essentially evolutionary traps that are caused by an anthropogenic influence that induces organisms to make maladaptive behavioural decisions on habitat choice based on cues that correlated formally to advantageous habitats resulting in reduced survival and ultimately extinction (Battin, 2004; Schlaepfer *et al.*, 2002). Hence, a prerequisite for an ecological trap scenario is that FADs are cues for advantageous habitats. There is much debate about this hypothesis and most studies that have investigate this topic have focused on tunas (Hallier and Gaertner, 2008b; Robert *et al.*, 2014; Marsac *et al.*, 2000; Menard, 2000).

As discussed above it is feasible that oceanic triggerfish and rainbow runner use floating objects as a cue to find, and remain, in productive frontal areas. Given their long residency at floating objects, FADs can displace aggregations over long distances. However, displacement itself does not imply an ecological trap and the difficulty resides in showing detrimental effects causing population declines or finding an appropriate control treatment to determine causation. First, to determine the presence of an ecological trap, it is important to distinguish between a natural situation, i.e. natural floating objets in the ocean, and the anthropomorphically modified habitat, i.e. addition of man-made FADs to the seascape. FADs and natural floating objects drift with oceanic currents, and investigations by Dagorn *et al.* (2012) in the western Indian Ocean showed that the distributions of natural floating objects (representative of the natural habitat) and that of FADs (modified habitat) are similar and therefore that artificial FADs do not occur in "new" habitats. From an evolutionary perspective, it seems flawed to suggest that associative behaviour of epipelagic fish would have evolved if natural floating objects, given that they occur in the same habitat, could act as an evolutionary trap. Nevertheless, it is clear that the density of floating objects (including debris) has dramatically increased in the last few decades and further investigations are required to determine the potential impacts of this change (Dagorn *et al.*, 2013). It is noteworthy, however, that given high vulnerability of some FAD associated species, the considerable fishing mortality incurred by the FAD based fishery appears to be the most relevant factor with regards to population declines.

Management considerations for bycatch of non-target species

The bycatch management is an urgent issue in FAD-based fisheries (Hall, 1996; Hall and Mainprize, 2005; Gilman, 2011). Moreover, with increasing emphasis placed on ecosystem based management (Pikitch *et al.*, 2004a), impacts of fisheries on the ecosystem must be assessed in order to determine the sustainability of fishing practices. Broadly, this requires 1) adequate monitoring and quantitative assessment of fishery induced mortality of the different component species, 2) data on biological parameters to estimate resilience to fishing mortality and to estimate possible population level effects, 3) an understating of ecosystem structure and relationship of the component species.

Tuna regional fisheries management organisations (t-RFMOs) have active observer programmes which estimate bycatch of the tropical tuna purse seine fishery. Scientific observer coverages varies from 100% in the eastern and western Pacific ocean to < 10% in the Atlantic and Indian Ocean (Dagorn *et al.*, 2013). Data gathered from such programs is key as it allows for the detection of population declines of impacted species (e.g. oceanic whitetip in EPO, Clarke *et al.* (2013)) and has lead to several investigations on bycatch trends and biodiversity (Amande *et al.*, 2011; Amandè *et al.*, 2008, 2012; Clarke *et al.*, 2013; Lezama-Ochoa *et al.*, 2015; Torres-Irineo *et al.*, 2014; Watson *et al.*, 2009). Concerted efforts to increased observer capacity in the Indian and Atlantic ocean should be made as the current observer capacity in these oceans has been shown to be inadequate in monitoring of pelagic communities (Amandè *et al.*, 2012).

Basic biological parameters, such as growth and age at sexual maturity, are poorly known for several non-target species including oceanic triggerfish and rainbow runner. Life history traits determined from such data can provide an approximate estimation on the sensitivity of captured species to fishing mortality. Additionally, these parameters will also allow for stock assessments of these species (Dagorn *et al.*, 2013) which could be used to establish species-specific target levels for fishing mortality aiming towards sustainability.

Fishing can affect ecological processes at a very large scale (Garcia *et al.*, 2003) and sufficient knowledge on ecosystem processes need to be understood to determine if fishing practices are sustainable (Pikitch *et al.*, 2004a). More specifically, the excessive removal of some components of the ecosystem could causes food web shifts (Pikitch *et al.*, 2004a). Food web models of pelagic ecosystems can be used to assess and predict consequences of the removal of different components of the ecosystem (Dambacher *et al.*, 2010) and should be pursued to determine impact the removal of non-target species.

Several t-RFMOs have recently adopted retention requirements for targeted tunas caught by purse seine vessels in order to reduce discards at sea (Chan *et al.*, 2014). This requirement could act as a disincentive to catch undersized tuna by decreasing purse seiners holding capacity of marketable catch and allows for a better estimation of fishing mortality. Recently, some have suggested that this requirement should be considered for non-target species (Lewis, 2014). The retention policy of non-target catch (as opposed to undersize target catch) is unlikely act as a disincentive to reduce the capture of this species group as they only account for 2 % of target catch landings (Lewis, 2014). Whilst a full retention policy and subsequent utilisation of non-target addresses the ethical issue of discards and resource wastage, it is unlikely to contribute positively towards bycatch mitigation or an ecosystem based management.

Changes in fisheries systems are often only slowly reversible and a precautionary approach to fisheries management should be applied if impacts of a fishing practise in not well understood (Pikitch *et al.*, 2004b). In the short term, this implies the limitations on FAD-based fishing effort. For example, a management measure that would limit the total amount of sets made on FAD, this would encourage fisherman to target larger aggregations which should reduce the total amount of bycatch (see Dagorn *et al.*, 2012). In parallel, investigations of technical mitigation measures should be pursued to reduce bycatch rates. The long term goal should be to gather sufficient knowledge on the pelagic ecosystems so that threshold points can be determined for all impacted species, target and non-target, to ensure the sustainability the FAD-based fishery.

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Appendices

A Western Indian Ocean eddies

Fig.A.1 illustrates the position of the FAD SEY59 when the normal type I behaviour for oceanic triggerfish was observed and the position of the FAD as it drifted into into a cyclonic eddy when a switch to type II behaviour was observed.

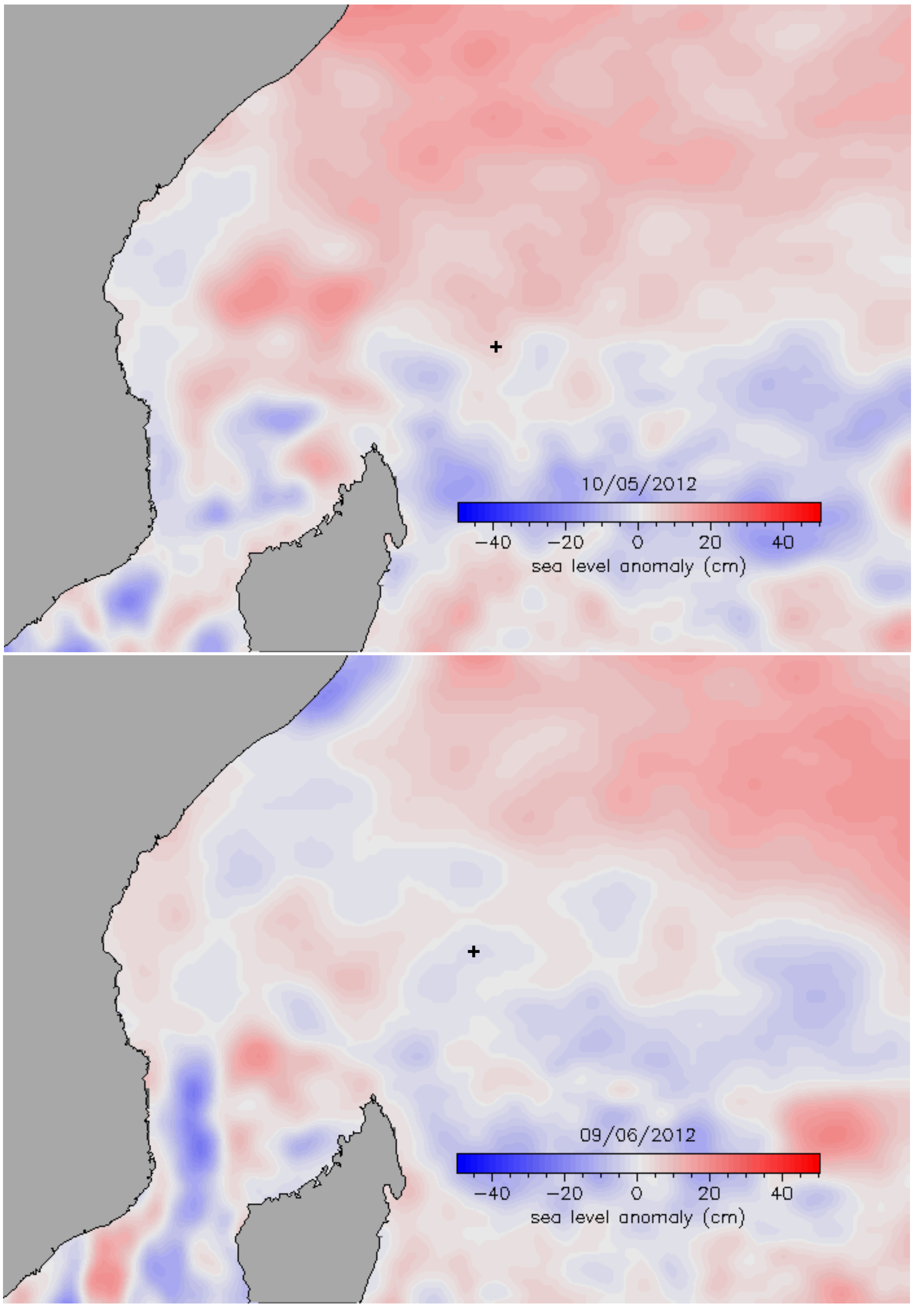

Figure A.1 FAD SEY 59 positions in the western Seychelles area with sea level anomalies. Spherical blue structures indicate cyclonic features and spherical red structures indicate anti-cyclonic features. Position of the FAD is denoted by the black cross.

B Acoustic collision correction

The collision-correction factor $\hat{\beta}$ was estimated by fitting the relation between the total number of hourly detections and the total number of fish (Equation 1). To this purpose, for each FAD, we binned the total number of detections hourly for each tagged individual and recorded the total number of fish present during each corresponding hour. The total number of fish present was estimated by fixing a threshold δ representing the minimum number of hourly detections required for counting a fish as present at the FAD. Indeed, when a tagged fish spent most of its time out of the listening range of the hydrophone, it did not contribute significantly to collisions and was thus not considered in Equation 1. A sensitivity analysis was conducted in order to assess the variability of our results as a function of this detection threshold δ. To this purpose, different curves D(F) were fitted with Equation 1 for increasing δ values. The optimal value of $\delta = 4$ (i.e., a minimum of 4 detections per hour to consider a fish as present) lead to a stable exponent $\hat{\beta}$ (Fig. S1). For each FAD k, given the estimated value of $\hat{\beta}_k$, the collision-corrected total number of detections $\hat{DO}^{d,h}_{S,k,i}$ for individual i of species S at day d, hour h and FAD k was obtained following (Equation 2):

$$\hat{DO}^{d,h}_{S,k,i} = D^{d,h}_{S,h,i} exp(\hat{\beta}_k F^{d,h}_k) \qquad \text{(Equation S1)}$$

where $D^{d,h}_{S,h,i}$ represents the nominal number of detections recorded for individual i of species S at day d, hour h at FAD k and $F^{d,h}_k$ is the total number of fish (independent of the species) present during the same hour h and day d at FAD k.

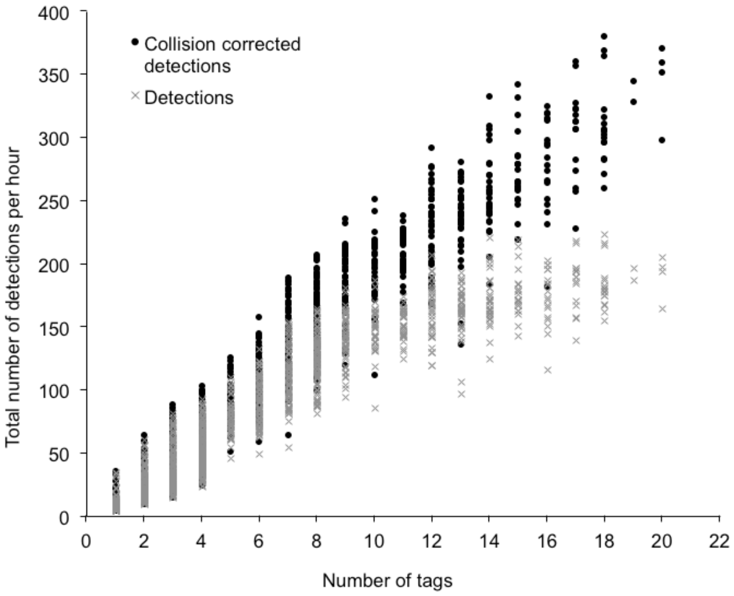

Figure B.2 Effect of collisions on the total number of detections per hour for FAD MOZ34: nominal (grey crosses) and collision corrected detections (black circles) using $\hat{\beta}$ = 0.031 in (Equation 2).

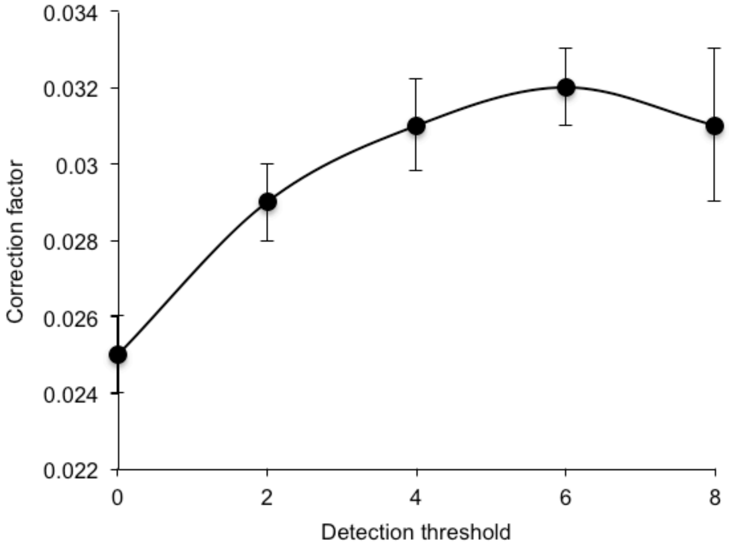

Figure B.1 Sensitivity analysis of the estimated collision correction factor $\hat{\beta}$ when varying the value of the threshold (δ) related to the minimum number of hourly detections.