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Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design

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ABSTRACT: The fisheries benefits of marine reserves are hard to achieve for highly vagile fish species. An alternative is to protect essential habitats, such as spawning grounds, especially if these are stable over time. We studied the movements and habitat use patterns of white trevally *Pseudocaranx dentex* (Carangidae), a commercially important species, to assist in the design of marine reserves. Diel, seasonal and inter-annual movements of trevally were studied using active acoustic tracking, passive acoustic monitoring and standard tag-release in the Faial Channel, Azores Islands. White trevally were captured at inshore and offshore reefs. Inshore trevally moved daily alongshore, using large activity spaces, while the short-term movements of offshore trevally were restricted to the reef summits. During the summer spawning season, both groups displayed frequent migrations of up to several kilometres, but inshore fish remained inshore, whereas offshore reef fish expanded their range to include visits to inshore sites. This behaviour eventually resulted in low long-term residence within the study area, especially that of inshore fish. During the spawning season, one inshore site was visited by most of the fish. However, instead of gathering in large aggregations at a single location, it appears that the trevally adopted a multiple-site visiting behaviour, which may increase mating opportunities through mixing between inshore and offshore fish that are otherwise segregated for most of the year. Protection of spawning biomass and sites for this species seems potentially feasible, but this would require protecting a suite of sites per island. Furthermore, because fish would not be fully protected under this scenario, we argue that such spatial management measures need to be accompanied by conventional fishing-effort control measures applied to all local populations.

KEY WORDS: Trevally · Acoustic telemetry · Home range · Residency · Spawning aggregation · Marine reserves

INTRODUCTION

The theory of marine reserves (no-take areas) predicts that fisheries can benefit from the establishment of the reserves if these act as sources of emigrant larvae (the 'larval subsidy effect') or post-recruitment fish (the 'spillover effect'). These benefits can occur due to the combined effect of: (1) the increase in number and individual size in populations of exploited fish, which is typically observed within reserve boundaries after protection (the 'reserve effect'), and (2) the allometric increase in fecundity with size of most fish with indeterminate growth, which raises their overall potential fecundity, as well as promoting density-dependent competition for resources (Plan Development Team 1990, Russ 2002). Thus, the effectiveness of

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reserves ultimately depends on the propensity of at least some portion of the fish to reside within the reserve boundaries, i.e. having temporally stable movements and 'home ranges' limited enough compared to the size of the reserve (Kramer & Chapman 1999).

Typically, the benefits of marine reserves have been predicted to best serve benthic species that comply with the small home range and residency requirements, such as some goatfish (e.g. Meyer et al. 2000), parrotfish (Afonso et al. 2008a), or kelp bass (Lowe et al. 2003). In contrast, these benefits will not often be realized in the case of migratory or highly mobile fishes because, unless reserves are large enough to encompass all their habitat and migration corridors (an unrealistic expectation in most cases), protection within reserves will only be effective on a partial or seasonal basis. Arguably, reserves can still be effective for management of migratory species if those reserves protect migration routes and spawning sites that seasonally concentrate the populations' productivity (Kramer & Chapman 1999, Roberts & Sargant 2002). For example, if fish migrate to and aggregate around specific spawning habitats where they traditionally become highly vulnerable to fishing, the protection of such essential fish habitats (Fogarty 1999) can promote the maintenance of local populations and the associated fishery by ensuring reproductive output.

The white trevally *Pseudocaranx dentex* (Bloch & Schneider, 1801) is a commercially important shallow reef fish that occurs on continental and island shelves across the anti-tropical regions of the Indo-Pacific, the Atlantic and the Mediterranean (Smith-Vaniz 1999). In a previous study undertaken around the Azores Islands, central-north Atlantic, we documented that during the summer spawning season, large mature white trevally (local name enxaréu) increase in numbers on the summits of offshore reefs. In contrast, smaller individuals prefer shallower, inshore habitats year-round (Afonso et al. 2008b). Similar size-segregated patterns of white trevally distribution have also been documented in fisheries studies from other regions (Rowling & Raines 2000, Farmer et al. 2005). We hypothesized that offshore reefs are prime spawning habitats and that both offshore and inshore reefs are therefore essential habitats for white trevally in the Azores (and probably in other regions). We concluded that there was a need to study the movements and habitat use by the trevally to test this hypothesis and to assist in the design of proposed marine reserves. Such habitat use information has not been published for any population of this species across its worldwide range.

In the current study, we present data on the short-term, seasonal and inter-annual movement patterns of Azorean white trevally obtained through a combination of acoustic telemetry and standard tagging and recapture methods. Specifically, we wanted to know: (1) whether individuals occupy stable daily home ranges (HR) and, if so, what the size of those home ranges is; (2) if their movements are temporally predictable and follow diel and lunar cycles; (3) whether this species is resident in the area year-round; (4) whether adult fish migrate to the offshore reefs (or other particular habitats during the spawning season), and, if so, whether they aggregate during this period; and (5) whether there is spatial segregation between fish inhabiting inshore and offshore habitats, and if this changes throughout the year.

MATERIALS AND METHODS

Study site. This study was undertaken in the Faial Channel, a shallow insular platform 8 km wide between the islands of Faial and Pico (Fig. 1). The channel is composed of very heterogeneous habitats and represents about 40% of the total coastal habitat (down to 200 m) available around Faial and Pico. It includes 3 offshore reefs ('Barca Reef', 'North Reef', and 'South Reef'), separated from the islands' coastlines by 2.5 to 3.5 km. These reefs are known to aggregate spawning biomass of pelagic predators, including white trevally *Pseudocaranx dentex*, during the spawning season (Afonso et al. 2008b). Inshore habitats include the 'Monte da Guia' promontory at the southeast tip of Faial. This area is a marine reserve with some fishing restrictions around its immediate perimeter and full-protection, no-take status only inside the small (8 ha) sunken crater (Caldeirinhas) (Santos et al. 1995). Monte da Guia and the South Reef were also designated as European Union Sites for Conservation Interest, and a management plan for a marine protected area encompassing the whole channel is in the process of being designed. The channel, especially the offshore reefs, is an area of intense artisanal fishing targeting pelagic predators, of which white trevally is second in importance. This fishery only operates during warm-water months (June to October), roughly coinciding with the reproduction period of those species, including the white trevally (Afonso et al. 2008b). By conducting our studies in the Faial Channel, we ensured that our data would have direct implications for the marine reserve design at this specific site, although the results can probably be extrapolated to give insight into the biology of this species throughout its range.

Capture and tagging methods. We obtained white trevally for tagging and tracking by fishing with a hand-line or pole-and-line. We selected 4 tagging sites in the channel, corresponding to the 2 main general habitat types where the species is known to be distributed (Smith-Vaniz 1999, Afonso 2002, Afonso et al.

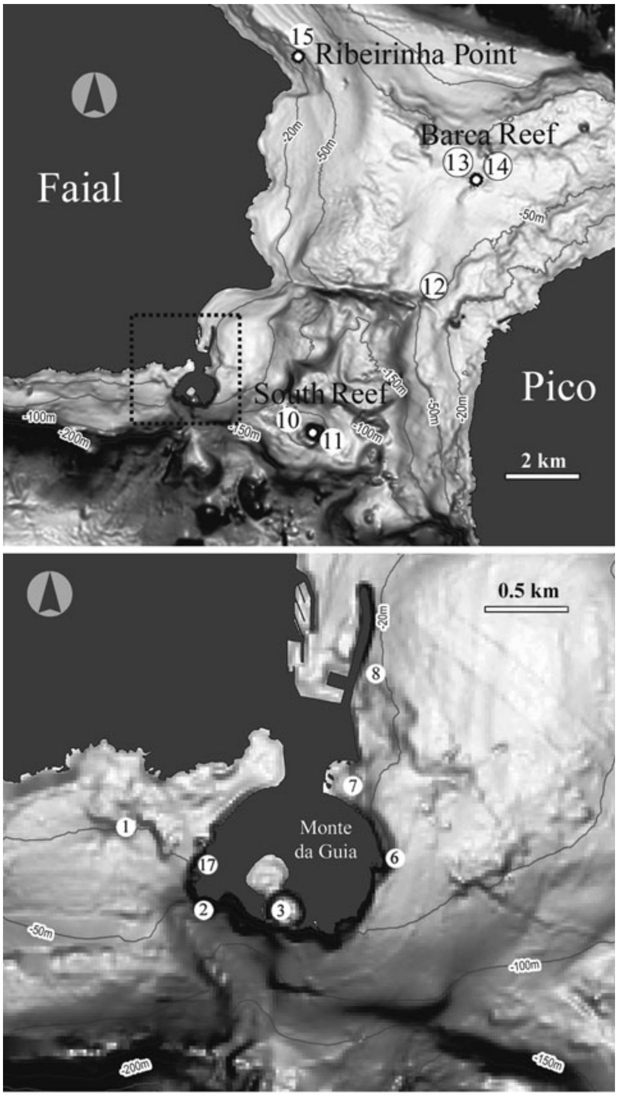

Fig. 1. Location of the study sites in the Faial Channel (upper panel) and around the Monte da Guia Protected Area (lower panel). Stn 3 is located in the no-take reserve area. Encircled numbers: fixed acoustic receivers

2008b): the offshore rocky reef habitat, represented by the Barca and South Reefs, and the inshore reef habitat, represented by Monte da Guia and Ribeirinha Point (Fig. 1). We caught and tagged fish between May and September, the spawning period of white trevally (Afonso et al. 2008b). This protocol was designed to increase the chances of capturing differences in behaviour between offshore and inshore fish, especially in relation to reproduction. Captured trevally did not present signs of gas bladder overinflation or decompression sickness. We measured all fish (fork length, L_F) to the nearest millimetre and double tagged them with T-type external 'spaghetti' tags (Hallprint) printed with a serial number and a reward notice.

Fish selected for acoustic telemetry had an acoustic transmitter surgically implanted while on board the vessel. In order to not bias the analysis of size-dependent movements, we randomly selected fish for telemetry which were in good condition and of a minimum size that would allow transmitter implantation (L_F = 35 cm). We inverted the fish on a foam-padded, v-shaped measuring board, inserted a running saltwater hose inside the mouth and implanted the ultrasonic transmitter (V8, Vemco Ltd.) intra-peritoneally (details of the general procedure given in Afonso et al. 2008a). Fish were released at or near the point of capture after a 15 to 30 min recovery period in 150 l running saltwater tanks.

Active tracking. In the summer of 2004, we used real-time acoustic tracking to study the short-term movements and habitat use of 7 white trevally, ranging in size from 41.3 to 56.0 cm L_F (Table 1). Five fish were implanted with V8SC-2H simple acoustic pingers. Two others were implanted with depth sensitive V9P-2H coded transmitters that measured depth every 5 s; one of these (Fish A6) was also double-implanted with a long-lasting coded transmitter for longer-term passive monitoring (see below). We tracked the fish using an 11 m launch or an inflatable skiff equipped with a multi-frequency acoustic receiver (Vemco VR60) and a directional hydrophone (VH10) and logged their approximate positions every 15 min (for details see Afonso et al. 2008b). All but 1 fish were tracked twice: an initial 48 h track immediately after release plus a 24 h track 8 to 10 d later. Fish A6 was not tracked for a second period.

Passive monitoring. We used VEMCO passive acoustic telemetry components to quantify the long-term presence, total HR and seasonal migrations of 32 white trevally ranging in size from 35 to 71 cm L_F (Table 2). Seven fish were initially tagged at South Reef (offshore) during the summer of 2003, and the remaining 25 fish were tagged in the summer of 2004 at the 4 fishing sites: South Reef (offshore, 6 fish), Barca Reef (offshore, 5 fish), Ribeirinha Point (coastal, 5 fish) and Monte da Guia (coastal, 9 fish). Fish were implanted with V8SC-2L or V8SC-2H long-lasting coded transmitters emitting at 69 kHz and with expected battery lives of 87 to 585 d. We deployed a network of 15 anchored underwater listening stations (VR2 single-frequency receivers) to cover various parts of the channel and neighbouring areas (Fig. 1; Electronic Appendix 1, Table A1, available at www.int-res.com/articles/suppl/m381p273_app.pdf). These stations detected coded tags coming within range and logged the exact time, date and code of a given emission; they were periodically inspected to retrieve the stored information. Range tests revealed that, at all locations, these stations could detect and log

Table 1. *Pseudocaranx dentex*. Characteristics of individual and daily activity areas (see Fig. 2) of 7 trevally actively tracked in the Faial Channel. Home range calculated as kernel utilization distribution areas, KUD_{50}: 50% (core) area; KUD_{95}: 95% (large) area; Length: maximum length of KUD_{95}; Day *x*: 24 h sub-period of tracking *x* days after tagging; MCP: activity area calculated as minimum convex polygon area; L_F: fork length

Fish ID	L_F (cm)	Transmitter type	Period of tracking (2004)	Total period					Day 1	Day 2	Day *x*
				KUD_{50} (ha)	No. of core areas	KUD_{95} (ha)	Length (m)	MCP (ha)	KUD_{95} (ha)	KUD_{95} (ha)	KUD_{95} (ha)
A1	49.0	V8 pinger	25 May–3 Jun	0.5	1	6.5	576	10.6	4.1	4.3	6.4 (10)
A2	49.3	V8 pinger	13–27 Jul	1.9	1	12.4	603	25.6	7.9	4.7	13.2 (15)
A6	56.0	V9 depth	16–24 Sep	2.8	1	14.1	515	11.6	10.4	16.2	8.5 (8)
A7	41.8	V8 pinger	16–24 Sep	2.1	1	12.3	654	18.2	14.7	8.9	5.4 (8)
A3	50.8	V8 pinger	18–26 Aug	2.0	1	22.5	869	33.6	23.4	14.9	16.3 (9)
A4	45.0	V9 depth	24–26 Aug	91.4	3	370.6	4389	172.9	415.0	271.9	–
A5	41.3	V8 pinger	24 Aug–5 Sep	45.7	2	274.1	7740	370.5	40.6	–	403.5 (11)
Median	49.0			2.1	1	14.1	654	25.6	14.7	11.9	10.9

coded tags up to a distance of about 200 m. Receivers were deployed in areas representing the diversity of habitats within the channel (i.e. inshore versus offshore reefs) and based on previous knowledge about the usage of specific habitats by this species (Afonso et al. 2008b). Obviously, the number of sites was limited by the number of receivers available. The total study period (10 July 2003 to 19 September 2006) allowed us to potentially monitor the presence of tagged white trevally for >3 yr. The duty period of individual monitors was somewhat variable due to differences in initial deployment dates (Table A1) or to occasional malfunction: the South Reef (summit) station was inactive for 210 d between 3 October 2004 and 3 March 2005, and one of the Barca Reef stations was inactive for 84 d between 14 April 2005 and 7 July 2005. Stations located in the Caldeirinhas no-take reserve (Stn 3), inside a cave in Monte da Guia (Stn 17) and on the northwest shore of Faial (Stn 16; Fig. 1) were deployed for periods shorter than 1 yr (Table A1) and are not included in the analysis.

Tagging and release. During the fishing surveys, we tagged and released a total of 58 white trevally with 'spaghetti' tags at the 4 sites, including the 39 trevally used in the telemetry studies. Although very limited in sample size, we used this dataset to evaluate the long-term retention of transmitters and to provide further evidence regarding the dispersal of white trevally. Reward announcements were posted to encourage recapture reports.

Data analysis. Daily activity area (i.e. HR) sizes were calculated from the short-term active tracking positions. Activity areas were calculated as kernel utilization distribution (KUD) and minimum convex polygon (MCP) areas (Kernohan et al. 2001). KUD is a probabilistic method that calculates the areas of probability of finding a fish based on position data. We considered the 50 and 95% KUD areas as representative of an animal's core activity area and its total activity area, respectively, and calculated these KUDs for each individual based on the total number of tracking positions (all days combined), as well as on each of the three 24 h sub-periods of tracking. Activity areas were calculated with the animal movement software (Hooge & Eichenlaub 1997) in Arcview 3.02 GIS.

Long-term monitoring data were initially screened for spurious detections. Spurious detection can occur whenever signals from different coded transmitters are emitted simultaneously within the same detection range, resulting in 'false' signals (Heupel et al. 2006). We considered any detection spurious that occurred isolated within a 24 h period in the whole network or in any of the sub-groups of adjacent stations (Stns 2 to 8, 10 to 11, or 13 to 14). This protocol assumes that a fish would be detected at least twice at a given station or once at each of 2 adjacent stations in 24 h if the fish was actually present in that area for that period.

To evaluate levels of site attachment of fish from long-term monitoring data, we used a simple presence index, which consisted of the total number of days a fish was detected divided by the maximum possible number of days that the fish could be detected, i.e. the period between the first and last day that fish was detected. The index could take values between 0 (complete absence) and 1 (complete residency). We calculated a network presence index for the total array, I_T (I_T = total no. of days of fish detection in the network /

([last day detected – first day detected + 1]), and local presence indices for each of the stations, including the station where the fish had been originally tagged, I_L (I_L = total no. of days of fish detection at the site/[last day detected at the site – first day detected at the site + 1]). We corrected these local indices by using only the effective duty period of each station. We used Spearman rank correlations (Zar 1999) to test whether there was any relationship between fish size, fish maximum range (measured as the maximum linear reef distance between stations where a given fish was detected), and presence indices. We used Mann-Whitney *U*-tests to check for differences in presence as a function of habitat type. Fish detected for <15 d were excluded from these analyses.

To look for seasonal migrations and inter-annual patterns in habitat use, we first visually inspected plots for daily presence of each fish at different stations. Additionally, we used the Wilcoxon matched-pair test (Zar 1999) to test for differences in presence at the site of tagging (I_L) between spawning (1 June to 30 September) and non-spawning periods. To test whether fish aggregated in particular habitats during the spawning season, we plotted the proportion of fish tagged at each of the 4 tagging stations present daily at those stations.

We searched for short-term, rhythmic patterns using spectral analysis by fast Fourier transforms (Chatfield 2004). Fast Fourier transforms indicate cyclic patterns in data series measured in constant time units. For example, cyclic tidal patterns in the presence of tagged

Table 2. *Pseudocaranx dentex*. Summary data for 32 trevally monitored with receivers in the Faial Channel. L_F: fork length; I_T: total presence index; I_L: local presence index relative to the original station of tagging and release; Distance: maximum linear reef distance between stations where a fish was detected; L_F: fork length; n.d.: not determined

Site, fish ID	L_F (cm)	Date of release	Period detected (d)	I_T	I_L	Distance (m)
South Reef						
P13	67.5	10 Jul 2003	382	0.12	0.09	9130
P1	47.4	2 Aug 203	6	n.d.	n.d.	0
P9	42.0	2 Aug 2003	4	n.d.	n.d.	0
P15	70.5	14 Aug 2003	1	n.d.	n.d.	0
P22	68.5	18 Aug 2003	411	0.89	0.87	8351
P23	53.0	4 Aug 2003	213	0.04	0.03	3311
P14	37.0	28 Sep 2003	337	0.72	0.69	5357
P8	64.0	17 May 2004	855	0.92	0.73	11745
P10	62.0	17 May 2004	410	0.72	0.57	9130
P31	37.6	18 May 2004	719	0.75	0.59	10526
P32	49.4	18 May 2004	422	0.54	0.27	3311
P33	47.7	18 May 2004	138	0.95	0.89	11745
P48	56.0	16 Sep 2004	296	0.78	0.48	9130
Ribeirinha Point						
P34	63.0	9 Jul 2004	758	0.02	0.01	0
P36	50.0	9 Jul 2004	802	0.62	0.60	10538
P37	60.3	9 Jul 2004	171	0.37	0.06	9794
P38	47.5	9 Jul 2004	802	0.08	0.06	11745
P39	49.5	26 Jun 2004	810	0.29	0.28	9920
Barca Reef						
P41	46.5	11 Aug 2004	522	0.94	0.91	7637
P43	45.0	7 Aug 2004	80	0.62	0.62	0
P44	45.5	13 Aug 2004	767	0.94	0.94	11745
P45	43.0	7 Sep 2004	554	0.34	0.23	8220
P46	40.6	7 Sep 2004	307	0.54	0.54	5889
Monte da Guia						
P40	34.5	24 Aug 2004	213	0.03	0.02	29977
P42	35.2	24 Aug 2004	46	0.39	0.31	1389
P47	43.2	18 Sep 2004	416	0.80	0.50	8076
P49	53.5	18 Sep 2004	699	0.08	0.07	8076
P50	44.0	19 Sep 2004	730	0.88	0.29	8076
P51	52.0	19 Sep 2004	730	0.80	0.62	11745
P52	48.0	19 Sep 2004	18	–	–	4320
P53	39.0	19 Sep 2004	64	0.93	0.74	1389
P54	46.8	18 Sep 2004	731	0.29	0.14	11745
Median	48.0		411	0.67	0.52	8148

trevally at a given station can be expected to produce peaks in the spectral analysis at ca. 6 h and/or 12 h, and diel patterns at ca. 24 h, regardless of the relative magnitude of such peaks. Whenever detections were numerically sufficient for analyses, we searched for tidal (6 and 12 h) and diel (24 h) cyclic patterns of habitat use by binning the number of fish per hour detected at a given station, and for lunar patterns (14 and 28 d) by binning the number of fish per day at a given station.

RESULTS

Active tracking

The main result from active tracking was the difference in short-term movements and resulting activity area estimates between 'offshore' trevally *Pseudocaranx dentex* at South Reef and 'coastal' trevally at Monte da Guia. Offshore fish never left the reef, whereas coastal fish moved extensively along the coastline (Table 1), although the sample sizes are too small to allow statistical comparison of the 2 groups. Offshore fish always remained close to the reef summit where they were captured, never venturing farther than 400 m away (Fig. 2). This behaviour was consistent for all 4 fish throughout consecutive tracking periods and resulted in similar, small and rounded total activity areas around a core activity area located at the reef summit. In contrast, coastal fish (A4 and A5) moved daily along the coastline and ranged up to 4 and 7 km in distance, respectively (Fig. 2). Fish A5 was recaptured by a fisherman 2 wk later, 9 km away from the tagging site (Monte da Guia) in the opposite direction from its tracked movement, totalling a minimum of 14 km of coastline used during this period. These 2 fish used very large areas (an order of magnitude larger than the areas used by the South Reef fish) and multiple core areas within their overall ranges. A third fish (A3) stayed closer to the tagging area at Monte da Guia, but still ranged over an area (23 ha) about twice the size of those used by South Reef fish.

Coastal fish also showed some diel rhythm in inshore habitat use. For example, Fish A4 stayed at Monte da Guia during nighttimes and spent a couple of hours during the afternoon at the western point of its activity area on 2 consecutive days, with the remaining positions corresponding to incidences of commuting back and forth. The depth-sensitive transmitter implanted in this fish revealed that it remained mostly at about 10 m depth in the water column, occasionally moving close to the substrate, especially at night and during crepuscular periods (Fig. 3). During 2 tracking periods several days apart, fish A5 also departed from its Monte da Guia core area at midnight, ventured into the Caldeirinhas no-take reserve for about 2 h, and left this area moving north just before sunrise. The only documented daytime activity area was at the northerly point of its range (Fig. 2). In contrast, movements of offshore reef fish were apparently more influenced by the local current, which is tidally dominated: fish typically occupied the down-current areas in relation to the reef summit and moved to the shallowest part of the reef summit during tide slacks or crepuscular periods. Vertical positions of Fish A6 (South Reef) at 20 to 25 m also showed predominantly pelagic behaviour (Fig. 3).

Passive monitoring

The 32 fish tagged with coded transmitters were detected in the passive monitoring network over periods spanning from 1 to 855 d (median = 411 d). Of these fish, 18 were detected over at least 1 yr, whereas only 3 fish were detected for less than 1 wk (Table 2). Excluding these fish with short-duration visits, overall presence within the network was slightly over half the monitoring period (I_R, median = 0.62). Presence at the original site of tagging was lower (I_L, median = 0.48), although typically higher than local presence at any other station. Presence varied considerably among individuals. There was no indication that this variability would be explained by individual size (Spearman's rank correlation: N = 29, R_S = –0.09, p = 0.65), nor by the maximum distance between stations covered by a given fish (N = 29, R_S = 0.08, p = 0.66).

As with active tracking, the most striking result was the difference in long-term habitat use patterns between fish tagged offshore and those tagged inshore. I_L was significantly higher for fish tagged offshore than for those tagged inshore (Mann-Whitney *U*-test, N = 29, Z = 2.12, p = 0.02). The behaviour of offshore fish was dominated by a very strong seasonal migratory pattern. Offshore fish tagged at South Reef resided on the reef summit and on deeper neighbouring grounds during periods of reproductive inactivity, but frequently left the reef to visit other offshore as well as inshore areas across the channel during the summer spawning season (Fig. 4). This was particularly evident for fish with longer periods of detection (spawning season I_L vs. non-spawning season I_L, N = 9, Wilcoxon matched-pairs test, p = 0.05; Electronic Appendix 1, Fig. A1, available at www.int-res.com/articles/suppl/m381p273_app.pdf). Summer absences from the reef lasted from 3 to 98 d, but were typically between 1 and 2 wk. Trevally tagged at Barca Reef were also periodically absent from the 2 local stations (reef summit and surrounding deep grounds) much more frequently in the summer, but rarely showed up elsewhere in the network (Fig. A1).

In contrast, trevally tagged close to Monte da Guia were either never or, in some cases, only sporadically detected at the stations on the 3 offshore reefs (Fig. 4). They moved frequently around Monte da Guia and its surrounding shores, showing similar behaviour to actively tracked fish. These movements covered considerable distances. For example, Fish P40 was detected at Monte da Guia one day, moved 10 km north to Ribeirinha Point the next day, and was detected a day later at North Beach on the opposite side of the island, thereby covering a minimum distance of 30 km of linear coastline in 48 h. The scale and frequency of these trips were also greater in the summer, when they occurred as frequently as once every 5 d for a given fish (Fig. 4).

Like other trevally, those tagged at Ribeirinha Point also seemed to use this area as a visiting site rather than a core area: 4 out of 5 of these trevally were present at the point only during summer periods (summer I_L vs. non-summer I_L, Wilcoxon matched-pairs test, N = 5, p = 0.04). Only 1 of these fish (P37) frequently

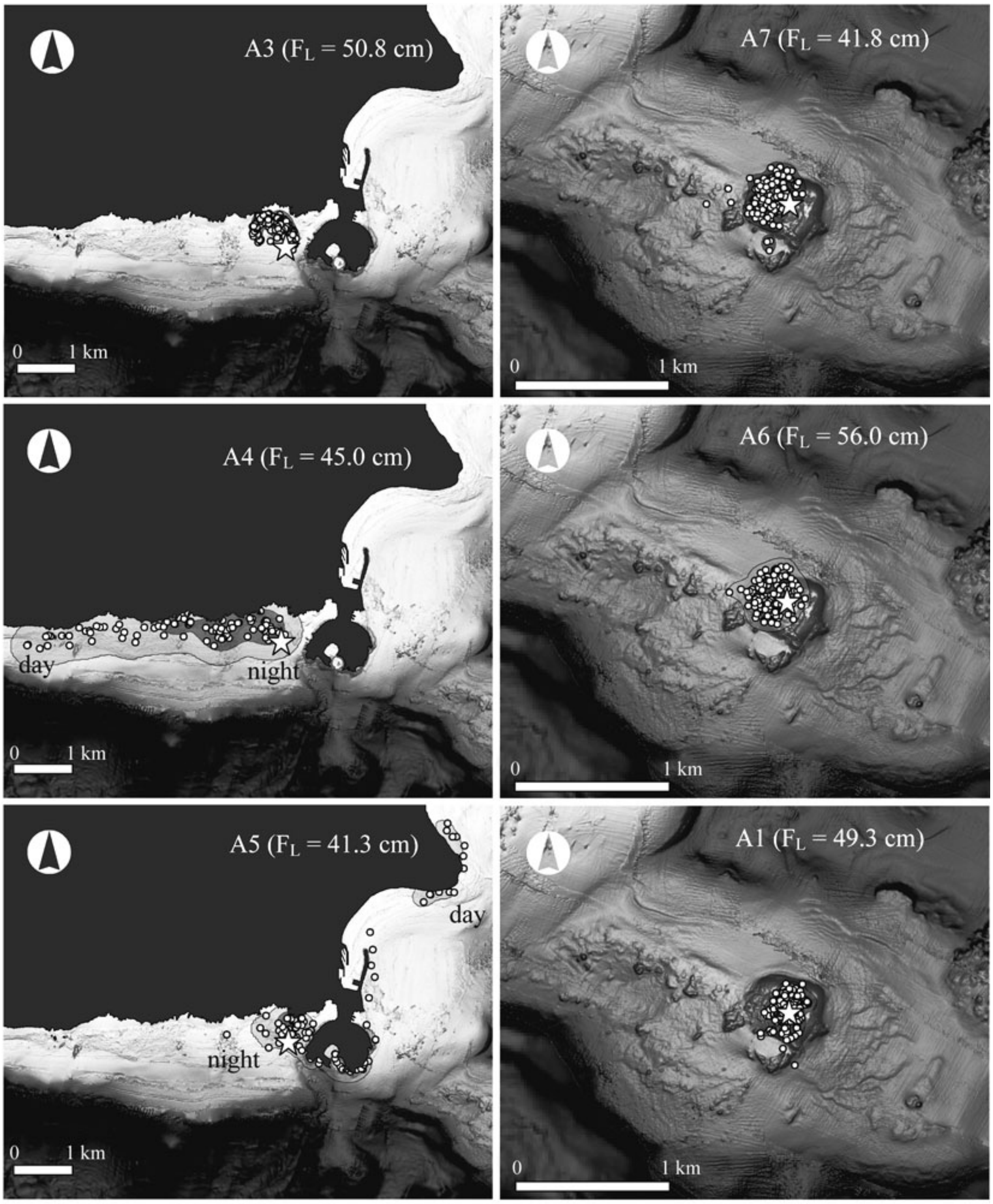

Fig. 2. *Pseudocaranx dentex*. Home ranges (short-term activity areas) for 6 fish (IDs given in Table 1) acoustically tracked (active telemetry) in the Faial Channel. White dots: position fixes; dark shaded and light shaded areas: 50% (core) and 95% (home range) areas, respectively; stars: sites of capture and release

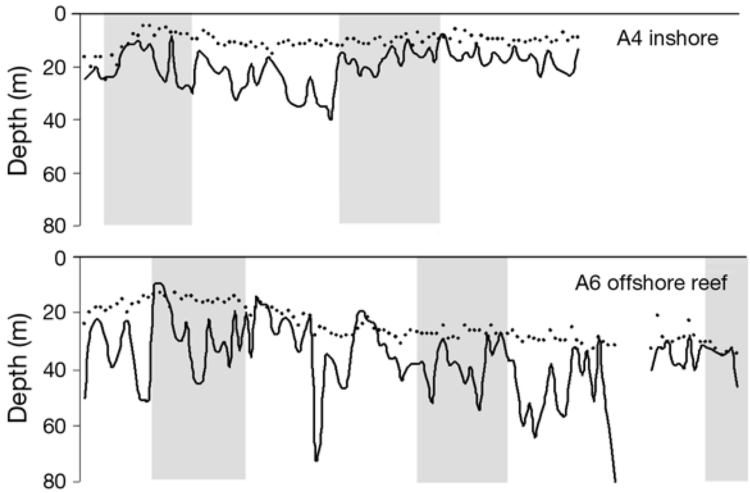

Fig. 3. *Pseudocaranx dentex*. Vertical movement of 2 trevally tracked with depth-sensitive transmitters. Dots: fish depth; line: bottom depth; shaded areas: night periods

Monitored trevally showed strong diel and tidal patterns in their spatial behaviour. Plots according to fast Fourier transforms of the number of trevally present hourly at each station all showed their strongest peaks in 24 h intervals (diel) and smaller, subordinate peaks in 12 h intervals (tidal), except for Almeida Point in Monte da Guia, which showed stronger tidal than diel peaks (Fig. 6). As with actively tracked fish, alongshore migrations of fish tagged at Monte da Guia during summer also showed a clear diel pattern. For example, Fish P47 and P51 usually migrated north during early morning, stayed at the point for about 2 h, and then headed back to Monte da Guia by late night (Fig. 7). We saw no evidence of a lunar cycle in the daily use of the stations.

Four trevally tagged at Monte da Guia visited the small 'Caldeirinhas' no-take area during the 12 mo of monitoring at this site (Stn 3). The period of usage ranged from 3 to 238 d (median = 91 d), but only 2 fish used the area for >20 d. Ten trevally used the sunken cave at the reserve during 7 mo of monitoring at this site (Stn 17), with individual presence inside the cave ranging from 1 to 112 d (median = 23 d). This presence was concentrated

visited other stations. As a result of the combined summer visits of most tagged trevally (regardless of tagging location) to Ribeirinha Point, this area showed a significantly higher number of tagged fish per day during summer months than during the rest of the year (Fig. 5). No other station showed a similar pattern.

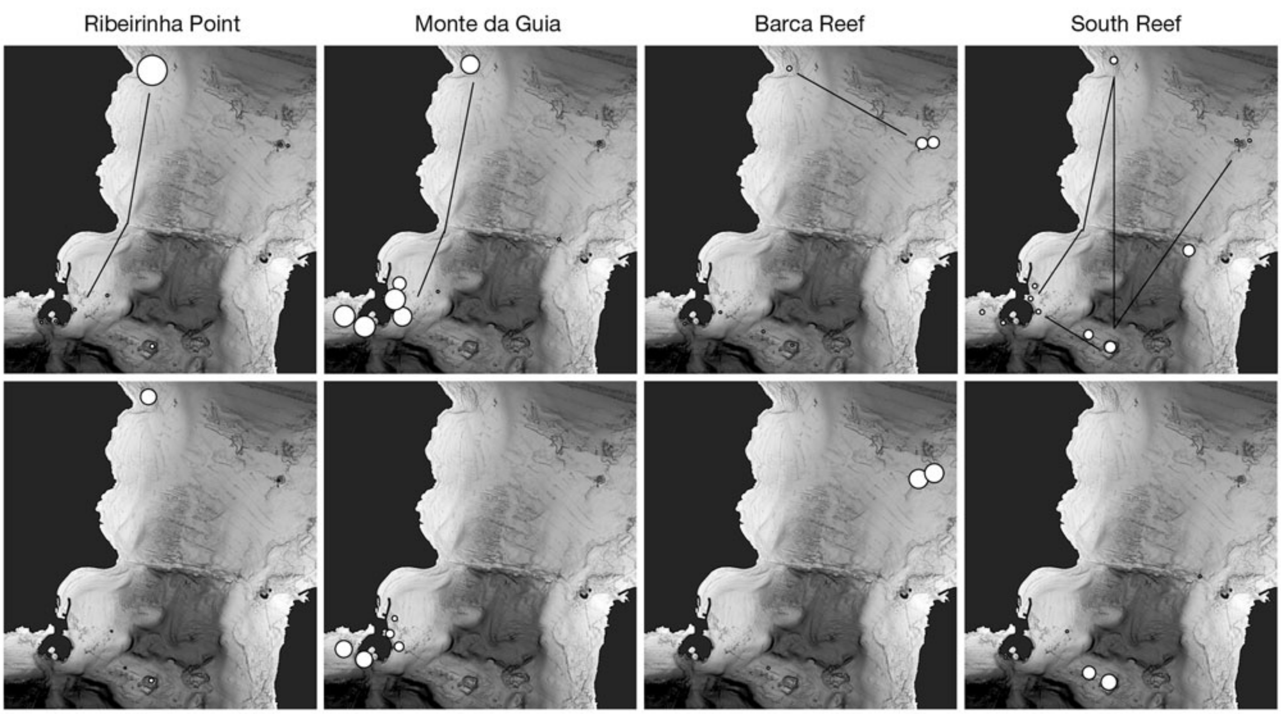

Fig. 4. *Pseudocaranx dentex*. Seasonal variation in detection at the various receivers that composed the acoustic network of trevally tagged at the 4 sites. Upper panels: spawning season (June to September); lower panels: non-spawning season (October to May). Circles: acoustic receivers. The relative size of the circles indicates the average daily presence (I_L) of the fish within a given tagging group, at a given receiver ($0 < I_L < 1$). Lines: main movement pathways as inferred by the minimum distance between receivers where fish were detected sequentially

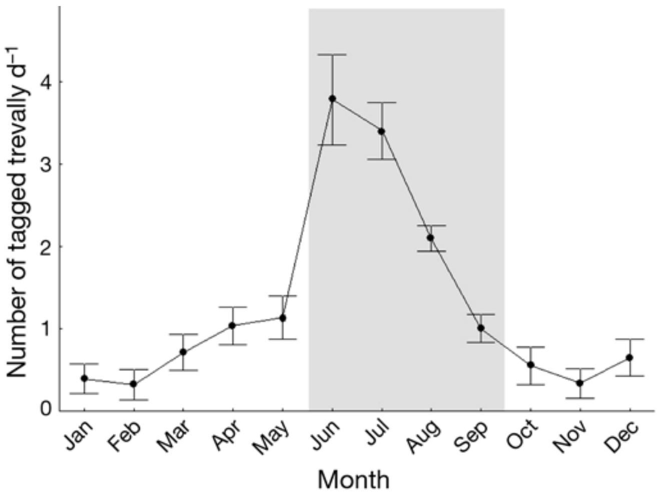

Fig. 5. *Pseudocaranx dentex*. Monthly variation in the number of tagged trevally (means ± SD) present daily at Ribeirinha Point (inshore) over the tracking period

during the day. Nine of these fish had originally been tagged at Monte da Guia, near the cave. We frequently found a school of 20 to 70 different-sized trevally inside the cave during daytime visual inspections by SCUBA diving.

Tagging and recapture

The 7 fish recaptured in the telemetry observations had retained the transmitter, even up to 416 d after tagging. The incision on 1 fish recaptured 11 d after implantation had healed completely. Overall, 8 of the 58 (14%) ID-tagged trevally released in the channel were recaptured. Their time at liberty ranged from 11 to 416 d (median = 77 d). Distances between tagging and recapture locations ranged from 100 m to 52 km (median = 900 m). The largest distance (52 km) was covered by a fairly small fish (L_F = 36 cm) tagged at South Reef in July 2004 and recaptured 88 d later close to the east point of Pico Island.

DISCUSSION

Results of the present study show that, although the short- and long-term spatial behaviours of white trevally *Pseudocaranx dentex* in the Faial Channel are quite variable (both within and among individuals), there appear to be distinct differences in the behavioural patterns of habitat use within the population. This observation has direct implications for the management of trevally in the Azores and, possibly, in similar ecosystems across its range.

Stability and scale of home ranges and residency

White trevally in the Faial Channel utilized daily activity areas (short-term HR) that differed in size depending on location (onshore vs. offshore). Some of these activity areas were of very substantial sizes. Trevally tracked in inshore habitats covered areas of up to 370 ha in only 2 d, whereas trevally tracked on offshore reefs confined their short-term movements to the waters surrounding the reef summit. This is in con-

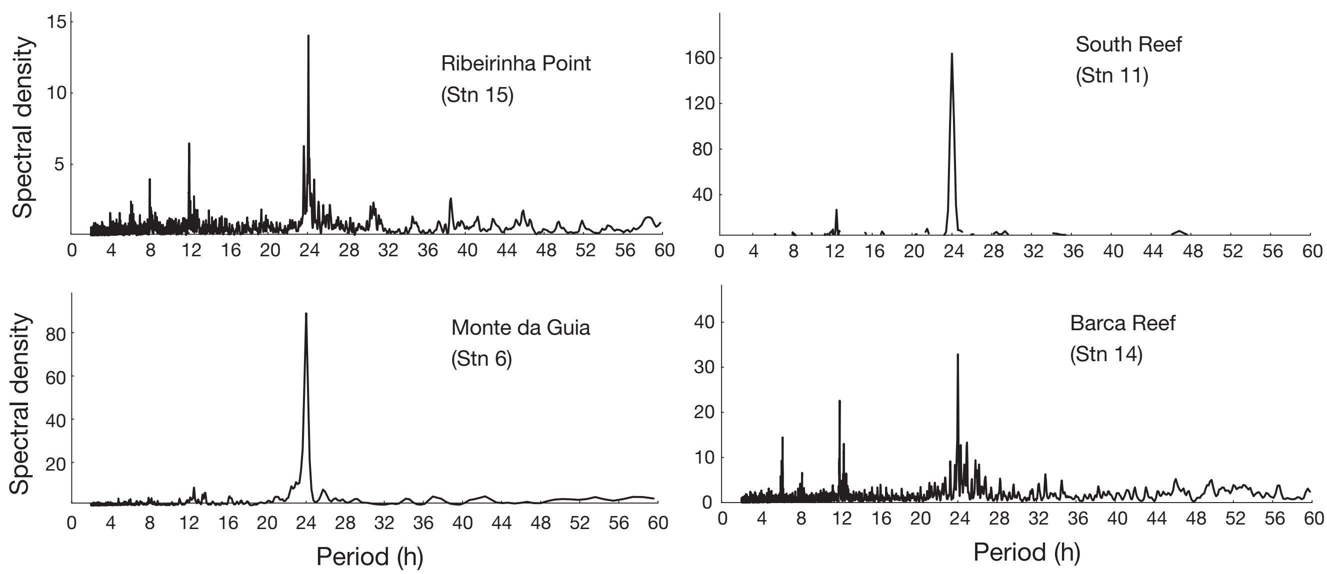

Fig. 6. *Pseudocaranx dentex*. Short-term cyclic habitat usage as revealed by fast Fourier transforms of the number of tagged trevally present hourly at different monitoring receivers across the Faial–Pico Channel. At each of the sites, 24 h peaks indicate diel periodicity and 6 to 12 h peaks indicate tidal periodicity of trevally presence. Note: *y*-scales vary

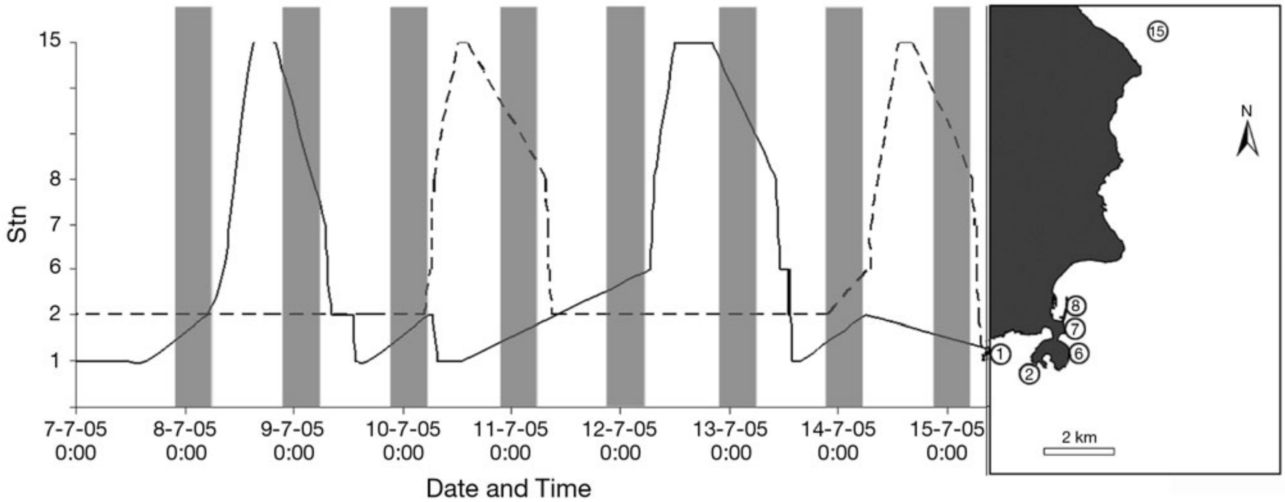

Fig. 7. *Pseudocaranx dentex*. Short-term migrations to Ribeirinha Point during the summer spawning season by 2 trevally (dashed line: P47; solid line: P51) generally resident at Monte da Guia, as revealed by their consecutive presence at monitoring receivers alongshore. The small map to the right shows the locations of the receivers (Stn) displayed on the *y*-axis. Shaded bars: night periods

trast with short-term HRs of many other reef fishes, which have been typically shown to be only a few tens or hundreds of meters in length and 1 to 10 ha in size (e.g. Holland et al. 1996, Samoilys 1997, Lowry & Suthers 1998, Meyer et al. 2000, Meyer & Holland 2005, Lowe et al. 2003, Afonso et al. 2008a). Furthermore, this comparison does not even include HRs of territorial reef fish with demersal eggs, such as blennies and damselfishes, the extents of which are even smaller (e.g. Kramer & Chapman 1999). The scale of short-term HR size of some white trevally is, therefore, among the highest reported for reef fishes. It is only comparable to the HRs of other reef predators with pelagic or bentho-pelagic behaviours that have been inferred or suggested from long-term studies using passive acoustics, such as the HRs for some carangids and lutjanids (e.g. Meyer et al. 2007a,b) or even some coastal sharks (Heupel et al. 2004). Furthermore, passive telemetry also showed that 'offshore' trevally can switch from seasonal attachment to the reef to periods of migratory behaviour, when they move between different areas and habitat types tens of kilometres apart in just a few days or even hours. Therefore, HRs of white trevally can and do change substantially, not only between coastal and offshore individuals, but also in individuals during the course of a year.

Fish were absent from the vicinity of the listening stations for about 40% of the total monitoring time. Absences from the network could result either from the fish being in the channel, but not close to a station, or the fish being outside of the channel study site. That fish moved out of the channel is supported by the documented presence of all types of studied fish (actively tracked, passively monitored and ID-tagged) outside the channel. Furthermore, we are confident that the network included the most frequently visited sites for local populations of white trevally, because they were selected based on extensive previous observations (Afonso et al. 2008b) and the knowledge of local fishermen. Consequently, the low residency of white trevally when compared with other temperate reef fish, such as parrotfish (Afonso et al. 2008a), kelp bass (Lowe et al. 2003), or California sheaphead (Topping et al. 2006), indicates that its short-term, vagile behaviour is maintained and amplified over long-term periods.

In spite of such vagile behaviour, nearly all tagged fish spent more time at the site of tagging than at any other station. Whenever the period of detection was long enough, fish primarily maintained their core areas located at the sites of tagging for consecutive years, although they moved to other (core) areas during certain periods (Fig. 4). This result indicates that trevally are primarily attached to core activity spaces, although their short-term HRs are variable in size and location over the course of a year. In this regard, one should ask: What are the potential limits of an animal's total range, that is, what are the barriers to larger scale movements? Tagged trevally were recaptured at the most distant parts (in relation to the channel) of the Faial and Pico Islands, but the design of the present study did not allow us to test whether trevally migrate between islands or between islands and shallow banks separated by open ocean. Inter-island movements have not typically been reported for other carangid or pelagic reef teleosts (e.g. Holland et al. 1996, Meyer & Holland 2005, 2007a); however, this possibility should not be excluded, especially considering the pelagic behaviour and swimming capacities of these fishes.

Our findings, while demonstrating the advantages of combining short- and long-term tracking techniques in these types of studies, also raise the question as to whether the activity spaces that were observed (and those that are reported in similar studies) constitute 'home ranges' as defined in the ecological literature. Kernohan et al. (2001) suggested that HR be defined as the extent of area with a predefined probability of occurrence of an animal during a specified time period. Active telemetry, which has been widely used to calculate HRs, provides detailed mapping of such areas, but only covering short periods of time (days) and, therefore, resulting in the measurement of daily activity spaces instead of real HRs. Our results show that an accurate (i.e. biologically representative) representation of a HR requires the permanent monitoring of an animal's movements over months or, ideally, over a year, especially in the case of highly mobile reef fishes. Passive monitoring can provide such information if the network coverage is sufficient to construct a probability distribution of the long-term activity, but cases in which this has been feasible are very rare (e.g. Heupel et al. 2004). Whenever network coverage is concentrated on specific habitats, such as in the current study, the presence index is straightforward and a useful measure of site attachment, allowing hypothesis testing based on raw data and without being affected by assumptions, in contrast to HR estimators. It does not, however, allow mapping of long-term HR if full coverage of the activity areas is not possible, such as in the present work and many previous studies. This is an aspect of major importance, because it has direct implications for management decisions, namely for the design of marine reserves (e.g. Kramer & Chapman 1999), and highlights the need for a better operational definition of HR as a parameter.

Predictability of short-term activity patterns

Short-term activity patterns were dominated by strong diel cycles and subordinate tidal cycles. The back-and-forth migrations alongshore of both actively tracked and passively monitored coastal fish reflected the most striking example of diel rhythm. Visits to Ribeirinha Point were always undertaken during daytime, with north- and southbound legs always undertaken in the first and second 12 h of the day, respectively (Fig. 7).

Diel patterns of habitat use have been described for many reef fishes, including other carangids, and usually involve distinct activity spaces for diurnal and nocturnal periods (e.g. Holland et al. 1996, Meyer & Honebrink 2005). Alongshore movements, rather than inshore–offshore movements, have also been found to be common in several reef fishes, particularly in island ecosystems where there is no littoral platform (Holland et al. 1996, Meyer 2003, Meyer & Holland 2005, Meyer et al. 2007b, Garla et al. 2006).

In the current study, the diel behaviour of white trevally seems to reflect the influence of both local habitat conditions and the species' life history. White trevally feed on a variety of items on the seafloor as well as in the water column (Sazima 1998). Our observations during extensive diving across the archipelago suggest that pelagic feeding is more often associated with larger offshore individuals, whereas bottom feeding was always observed in fish of $L_F < 45$ cm, which are the sizes that are typically found inshore (Afonso et al. 2008b). Movements alongshore might, therefore, be associated with feeding excursions from a central refuge area to prime feeding areas. For example, diurnal core areas of Fish A4 and A5 were both located in areas of mixed substrates, where opportunities for feeding might be increased. In contrast, offshore fish would tend to stay within the vicinity of the reef summits, where small pelagic fish are known to aggregate. Inshore–offshore movements were also observed in offshore trevally, but they were not associated with a diel pattern.

Migrations, spawning habitat and (sub) population mixing

We saw a striking seasonal pattern in the use of core areas and migrations associated with the period of trevally reproductive activity, which, in the Azores, occurs from June to September (Afonso et al. 2008b). The monitoring data showed that, during this period, tagged fish were less attached to their core areas, migrated more often, and ranged more widely inside the network than during the remainder of the year. This was particularly evident in South Reef fishes, which adopted a 'visiting' behaviour during the spawning season, frequently leaving the reef to visit other areas and returning after a few days or weeks. Barca Reef fish also left the reef more frequently in the summer, and Monte da Guia fish ranged wider and more frequently alongshore during the spawning season. All fish were above the size at first maturity (L_F = 30 cm).

We did not see clear evidence for large spawning aggregations of tagged trevally at offshore reefs. There was strong evidence that Ribeirinha Point is used mostly for reproduction-related purposes (whether spawning per se or social interaction), because it was visited by nearly all tagged fish (from inshore and offshore tagging locations), but only during the spawning season. However, these visits occurred at different times and with different periodicities within a given spawning season, so we cannot confirm that it serves as a spawning aggregation. Based on our results, we believe that white trevally in the Faial Channel switch between a relatively site-attached behaviour to a 'visiting', wide-ranging, migratory behaviour associated with reproductive activity. This results in increased mixing between inshore and offshore fish that are otherwise segregated for most of the year.

Reproduction-related migrations and changes in habitat use have been reported or inferred from spawning aggregations for a variety of reef fish families, including carangids (Sala et al. 2003, Meyer et al. 2007a), serranids (Zeller 1998, Bolden 2000, Marino et al. 2001) and scarids (e.g. Afonso et al. 2008a). Migrations vary widely in scale among species, from hundreds of meters to hundreds of kilometres, but also within species, even at a particular site. Migration to and aggregation at specific sites are adaptive if they increase the reproductive success of adults (e.g. by augmented mating opportunities, better mate choice, or higher early survival and growth of the offspring), but can also involve increased energy cost or predation risk (Dodson 1997). Therefore, behavioural plasticity in reproduction-related patterns of space use can be expected because the cost–benefit balance should vary individually. For example, some *Caranx ignobilis* (Carangidae) migrate >30 km to a specific reef at a large Hawaiian atoll to spawn during certain lunar phases, while others reside permanently at that same reef (Meyer et al. 2007a). Individuals of *Plectropomus leopardus* (Serranidae) use multiple reef aggregation sites at a small island on the Great Barrier Reef (Zeller 1998).

Based on anecdotal information and current population levels, we hypothesized that larger aggregations traditionally associated with offshore reefs may have been substantially reduced as a result of intense exploitation in recent decades (Afonso et al. 2008b). If this is true, it is possible that the fishery not only reduced numbers, but also promoted the selection (survival) of those offshore fish that display 'migratory' behaviour rather than those that stay and spawn at the offshore reefs. In any case, because white trevally are multiple spawners, the multiple-site visiting behaviour most probably increases their mating and mate-choice opportunities throughout the spawning season (Rowling & Raines 2000, Farmer et al. 2005, Afonso et al. 2008b). This behaviour could reinforce the maintenance of traditional gathering sites within the population and the visiting behaviour of offshore reef fish. It has not previously been described for mobile reef fishes and deserves further research.

Implications for the design and functioning of marine reserves

The data from the present study stress the challenge and limitations of using marine reserves as a spatial management tool for highly mobile reef fishes. Clearly, the large size and variety of shapes among HRs, the variable degrees of site attachment and the migratory behaviour of white trevally make it hard for this species to benefit from permanent protection inside existing marine reserves, which are typically of small to medium size (1 to 10 km^2) (Halpern & Warner 2003). For example, most of the fish tagged around the Monte da Guia Reserve had their core activity spaces close to or partially inside the partial protection perimeter, but they went outside its limits on a daily basis, and some fish even left the area for extended periods of time. The even smaller Caldeirinhas no-take area was used by a few fish, but only for a few hours on each occasion. Two actively tracked fish alone used short-term HRs of 3 to 4 km^2 (200 times larger than the no-take area) within 3 d. Consequently, small to medium reserves will not be effective and, even if well enforced, encourage unrealistic expectations as to the reserve effect and subsequent potential benefits to adjacent fishing grounds for this species (e.g. Fogarty 1999). White trevally would require large reserves (probably at the island scale) to fully protect a portion of the population in the long term and promote the 'reserve effect', but this scenario is unrealistic and would be of little benefit for local fisheries.

Instead, reproductive activity and potential offspring of local populations could be largely ensured if fishing were banned from at least some of the traditional visiting sites. Such a design may also promote interaction between fish of different behavioural patterns and habitats, thereby increasing overall reproductive success. This design would, however, still require the protection of significant numbers of offshore and inshore sites. Given the increased mobility during the spawning season, the adoption of temporal closures during the summer spawning season would achieve the goal of protecting the spawning activity while enabling general fishing benefits during the remainder of the year. For example, for the Faial Channel, the permanent protection of South Reef and Barca Reef, where larger individuals tend to reside, and seasonal protection during the spawning season of the visiting sites at Ribeirinha Point and Monte da Guia could effectively protect the spawning biomass and spawning activity in the channel. This could contribute actively to the maintenance of (meta) population segments (Lipcius et al. 2008), such as those around the islands of Faial and Pico. If other visiting sites of importance for reproduction are identified, a network of appropriate reserves could be established on different islands to promote the sustainable exploitation of white trevally in the Azores and other similar environments, such as the archipelagos of the Canaries or Hawaii. However, the high mobility displayed by this species will make it vulnerable when it leaves the protected areas. Thus, conservation of white trevally stocks will also require conventional management measures to control fishing effort over entire island populations. This might also be the case for many other reef fishes with the potential for such vagile behaviour, such as many carangids and lutjanids. Given their importance for reef fisheries worldwide, it is highly recommendable that knowledge of their movement patterns be gathered to support well-informed spatial management plans.

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