Reproduction and spawning habitat of white trevally, *Pseudocaranx dentex*, in the Azores, central north Atlantic

PEDRO AFONSO [1,2], JORGE FONTES [1], TELMO MORATO [1], KIM N. HOLLAND [2] and RICARDO S. SANTOS [1]

[1] IMAR / Department of Oceanography and Fisheries, University of the Azores, PT 9901-862 Horta, Portugal.
E-mail: afonso@uac.pt
[2] Deparment of Zoology, Hawai'i Institute of Marine Biology, University of Hawai'i at Manoa, 46-007, Lilipuna Road, Kane'ohe, HI 96744, USA.

SUMMARY: Reproductive biology and habitat preferences of the white trevally, *Pseudocaranx dentex* (Carangidae), were studied in the Azores islands, central north Atlantic, to determine the spatial and seasonal dynamics of habitat use of immature and mature fish. The sex ratio was close to 1:1 and fish matured at about 30 cm fork length. There were no differences in the maturation or length-weight relationships between sexes. The spawning season lasts from June to September. Underwater visual censuses showed that schools of mature individuals preferentially aggregate around the summits of offshore reefs during the spawning season. In contrast, schools of smaller, immature fish use inshore habitats all year round. Our data support the hypothesis that offshore reefs are a preferential spawning habitat of larger white trevally, and most possibly for a number of visitor pelagic predators as well. Inverse relationships between exploitation levels, abundance and size composition at the two different islands suggest that the summer fishery targeting trevally schools around offshore reefs has negatively impacted the population. These findings bring additional ecological and management relevance to offshore reefs.

Keywords: trevally, reproduction, spawning, habitat, offshore reefs, marine reserves.

RESUMEN: REPRODUCCIÓN Y HÁBITAT DE DESOVE DEL JUREL DENTÓN, *PSEUDOCARANX DENTEX*, EN LAS AZORES, ATLÁNTICO NORTE CENTRAL. – Se realizó un estudio de la biología reproductiva y las preferencias de hábitat del jurel dentón, *Pseudocaranx dentex* (Carangidae),en las islas Azores, Atlántico norte central, con el objetivo de comprender la dinámica espacial y estacional de individuos inmaduros y maduros en el uso del hábitat. Se observó un sex ratio próximo a 1:1 y una talla de primera madurez de 30 cm longitud de furca, sin diferencias entre sexos respecto a la talla de madurez, ni tampoco en la relación talla-peso. La época de reproducción se prolongó de junio a septiembre. Los muestreos visuales revelaron que durante la época de reproducción los individuos maduros se agregan preferentemente en torno de las coronas de arrecifes en mar abierto, mientras que los cardúmes de individuos inmaduros utilizan los hábitats costeros durante todo el año. Nuestros datos apoyan la hipótesis de que los arrecifes en mar abierto constituyen el hábitat preferente para el desove del jurel dentón y, muy probablemente, de otros predadores pelágicos. Una relación inversa entre los niveles de explotación y la abundancia y talla del jurel dentón en dos islas distintas sugiere que la pesquería de verano del jurel dentón ha afectado negativamente la población. Estos resultados ponen de manifiesto la relevancia, tanto ecológica como para la gestión, de los arrecifes en mar abierto

Palabras clave: jurel, reproducción, desove, hábitat, arrecifes offshore, reservas marinas.

INTRODUCTION

Jacks are fish of the family Carangidae that play a major ecological role in the piscivore niche of tropical and subtropical reefs worldwide. They are also a major component of catches in tropical reef fisheries (e.g. Jennings and Lock, 1996; Dalzell, 1996). It is therefore surprising how little information is

available from the literature on their spawning behaviour, mating systems or even the type of habitat selected for reproduction in the wild. The sparse information, available mostly for tropical habitats, points to a trend of offshore spawning aggregations, usually around some kind of topographic feature or close to the surface (Johannes, 1981; Sala *et al.*, 2003). This is also supported by indirect evidence of marked habitat segregation within populations, such as younger, immature fish typically selecting inshore habitats like river estuaries or shallow bays (Meyer *et al.*, 2001; Smith and Parrish, 2002). It is therefore quite plausible that the offshore realm, whether pelagic or benthic, is a prime habitat for the reproduction of jack species, but this generalisation still lacks empirical evidence.

The white trevally, *Pseudocaranx dentex* (Bloch and Schneider, 1801), is a widely distributed antitropical reef fish, occurring on continental and island shelves across the Atlantic, the Mediterranean and the Indo-Pacific (Smith-Vaniz, 1999). It is an important food species throughout its distribution range (Smith-Vaniz, 1999; Rowling and Raines, 2000). In spite of its importance, there is very little information on the habitat preferences of white trevally, and data on its reproductive biology in the wild is restricted to continental populations from Australia and New Zealand (e.g. Rowling and Raines, 2000; Farmer *et al.,* 2005). In the Azores islands, central-north Atlantic, fishermen use the acquired knowledge that fish aggregate in the offshore reefs during the summer to orient artisanal fisheries targeting this species and other pelagic predators.

These facts indicate that white trevally could also show ontogenetically-driven shifts in habitat use and, most importantly, that they could form spawning aggregations around offshore reefs. In this case, given the characteristics of the fisheries in the Azores, offshore reefs could become a fishing bottleneck, i.e., local populations become highly vulnerable to fishing during their spawning season (Sadovy, 1996; Colin *et al.*, 2003). This is also probably true for other Atlantic islands with similar fisheries, such as Madeira and the Canary islands. In addition to the implications for fisheries management, this hypothesis would have a direct impact on the conservation of marine habitats.

In this study, data is presented on the reproductive biology as well as population structure of the white trevally in the Azores. This information is used to verify the importance of offshore reefs for the reproduction of non-resident fish predators and discuss the implications of this relationship for spatial management schemes.

MATERIALS AND METHODS

Reproductive biology

The reproductive biology of white trevally in the Azores was studied using a sample of 360 individuals purchased in the local fish auction between August 2003 and November 2004. All the fish had been obtained from the waters around the island of Faial (Fig. 1). From June to November white trevally is specifically targeted by a pole-and-line fishery using live bait. During the cold water months fishermen switch to a bottom handline or fixed gillnet and it becomes an accessory catch. As a consequence some of the winter months were underrepresented in the sample. Total length (L_T, cm), fork length (L_F, cm), total weight (W_T, g) and eviscerated weight (W_E, g) were recorded for each fish and their gonads removed and weighted (W_G, g). Individuals were sexed and staged as immature (stage 0), resting (1), early development (2), late development (3), ripe (4) or spent (5), based on macroscopic examination of the gonads (adapted from Rowling and Raines, 2000). 18 fish were not staged. Water temperature was continuously measured using underwater dataloggers (StowAway TidbiT) moored at 28 m depth off the southeast point of Faial Island.

Sex ratio, expressed as the male:female ratio, was analyzed in the different maturation seasons: spawning (June-September), resting (October-January) and developing (February-May). Deviations from the 1:1 sex ratio null hypothesis were statistically tested with the Chi-square test. Differences in mean length of females and males were tested by single-factor Analysis of Variance, ANOVA (Zar, 1999). Weight-length relationships were obtained for males and females. W_T and L_F were log-transformed and the linear relationship fitted by the least squares regression (Zar, 1999). The total length-fork length relationship was obtained by linear regression. The slopes of the weight-length equations were tested for differences ($P<0.05$) between males and females with the Student's-t test for comparing two slopes (Zar, 1999). Length at first maturity (L_{50}) was estimated for separate and pooled sexes by fitting the relative frequency of mature individuals over 1 cm L_F classes to a logis-
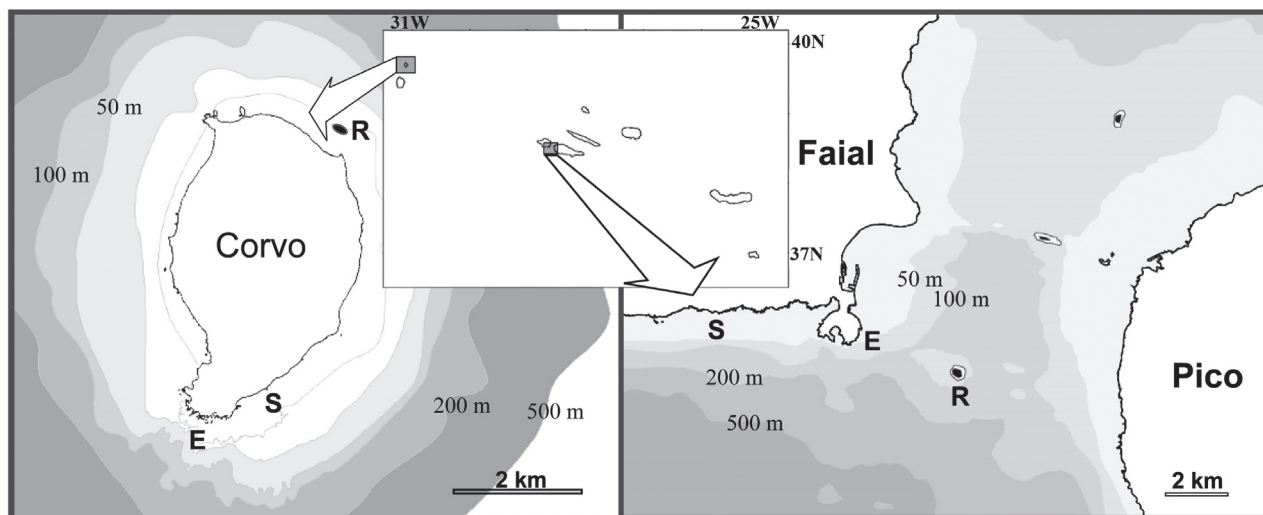
FIG. 1. – The Azores archipelago and study sites at the islands of Corvo and Faial: S, inshore sheltered site; E, inshore exposed site; R, offshore reef site.

tic curve using the Levenberg-Marquardt algorithm for solving non-linear least squares regression (Zar, 1999). Spawning season was determined according to the monthly variation of macroscopic gonad maturity stages and the gonadosomatic index (I_G), the ratio of W_G and W_E for mature individuals.

Habitat preferences

Habitat preferences of white trevally were characterized using fishery-independent data from underwater visual censuses (UVC) undertaken around the islands of Faial and Corvo between 1997 and 2002 (Fig. 1). The two islands are separated by 200 km of deep ocean and subjected to different levels of fishery exploitation. Faial supports a pole-and-line commercial fishery that targets pelagic predators in the summer, including white trevally, as well as a growing recreational fishery and spearfishing. White trevally catches are incidental in Corvo's small fishery.

Strip transects of 50 x 5 meters were used to count all mobile fish and the data on white trevally was later extracted from that assemblage. Individual trevally were assigned to one of five predefined size classes, as follows: juvenile (<10 cm L_T), small (10-30 cm), medium (31-50 cm), large (51-70 cm) and very large (>70 cm). To look for possible habitat preferences, we surveyed the abundance and size composition in three different types of reef habitats at both of the two islands: inshore sheltered, exposed shoreline and offshore reef. Early work showed that

the variability within habitat types is smaller than between different habitats (Afonso, 2002), therefore the selected sites for each type can be considered as replicates. The offshore reefs selected for surveying were Baixa do Sul in Faial and Moldinho in Corvo. Baixa do Sul is a large sunken volcano reaching 7 m depth at its summit and located 4 km from the nearest shore, halfway between the islands of Pico and Faial. Moldinho is a small basaltic reef that nearly breaks the surface and is located 1 km from the northeast tip of Corvo Island (Fig. 1). Each site was sampled from the surface down to 40 meters at 10 meter depth intervals, depending on the existence of rocky substrate, with a minimum of three randomly assigned replicates per plot (depth strata within site). All six sites were surveyed during the summer breeding season (June-September) for inter-island comparisons. This design resulted in 173 transects in Faial and 128 in Corvo. The sites in Faial were also sampled during non-breeding periods (October-May) to look for possible seasonal differences in habitat use (n = 114 transects).

The hypothesis of overall habitat preference was assessed with a two-way crossed ANOVA on total abundance using island and habitat types within each island as fixed factors. To investigate the occurrence of size segregation according to habitat type and differences in size composition between islands a two-way crossed ANOVA on mean fish size in the different habitats and islands was applied, using centre size class values and pooling all fish sighted per site. Only comparable summer data were used in these tests.

To look further at preferred spawning habitats, the hypothesis that mature fish converge to offshore reefs during the spawning season was only tested in Faial Island by assessing seasonal differences in total abundance of mature fish (>30 cm L_T) in each of the three habitats with a two-way crossed ANOVA with sites and season as fixed factors. For analysis purposes, we considered fish as immature if they pertained to the juvenile or small size classes, and mature for the remaining classes, given that the limit between small and medium classes roughly coincided with the size at first maturity.

All data were verified for normality (K-S tests) and homogeneity of variance, and a square root transformation (n + 1) was applied whenever needed to meet parametric assumptions. Pair-wise unequal N Tukey HSD tests for unequal sample sizes (Zar 1999) were conducted between levels whenever the models were significant.

White trevally was sighted in 91 out of 276 dives (33.0 %) but only counted in 47 out of 425 transects (11.1 %). Therefore, we complemented the analyses of total abundance with an analysis of the frequency of occurrence in dives.

RESULTS

Reproductive biology

Three hundred and sixty sampled white trevally ranged in size from 11.1 to 78.3 cm L_T (Fig. 2). We could not identify the sex for three small fish. Males (n=175) and females (n=182) showed similar length frequency distributions with no significant difference in mean sizes (Fig. 2; mean ± SD, 51.6 ± 8.4 vs. 53.0 ± 8.0 cm L_T, ANOVA; $F_{1.356}$ = 2.43; P=0.12). Large size fish were fairly well represented in the sample: 44 fish (12%) were above 60 cm L_T and ten fish were above 70 cm L_T. The total length-fork length relationship was L_T=0.83+1.12L_F (n=370, r^2=0.99). The weight-length relationship was W_T=0.02$L_F^{3.006}$ (n=360, r^2=0.98) and there was no difference between sexes in the slopes of the two regression equations (Student-t test, df=174.181, P>0.05).

Overall sex ratio in the sample was 1 male to 1.04 females (χ^2, df=1; P>0.05). Seasonal sex-ratio was, however, biased to males during the resting and developing periods and to females in spawning periods, although this difference was only significant during the 2003 spawning period (Table 1). There was no
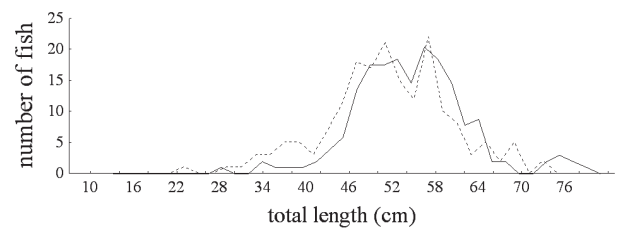

FIG. 2. – Size frequency of white trevally sampled in the fish auction at Faial island, Azores. Solid line, males; dashed line, females.

TABLE 1. – Variation in sex ratio in white trevally in relation to maturity season in the Azores.

	Males	Females	Sex ratio	p
Jul-Set 03 (spawning)	17	39	1:2.3	<0.01
Out 03-Jan 04 (spent/resting)	36	22	1:0.6	0.07
Fev-Jun 04 (developing)	70	54	1:0.8	0.15
Jul-Set 04 (spawning)	42	53	1:1.3	0.26
Nov 04 (resting)	10	14	1:1.4	0.41
Total	175	182	1:1.0	0.71

significant difference between sexes in size at first maturity (L_{50}) (male L_{50} = 27.8 cm, female L_{50} = 30.0 cm). L_{50} was 28.3 cm L_F for pooled sexes, which corresponds to 32.5 L_T (Fig. 3). All males and females were mature at 33 cm and 36 cm L_F respectively.

Macroscopic examination of gonad development and the gonadossomatic index showed a clear pattern of annual summer spawning for white trevally in the Azores. Gonads developed from February to July (stages 2 and 3), were ripe from June to September (stage 4), spent from September to October (stage 5) and in resting condition (stage 1) from October to February, before initiating a new maturation process (Table 2). This pattern was very closely matched by the evolution of I_G, which increased steadily from February to June, decreased from July to September and remained low until February (Fig. 4). Reproduc-
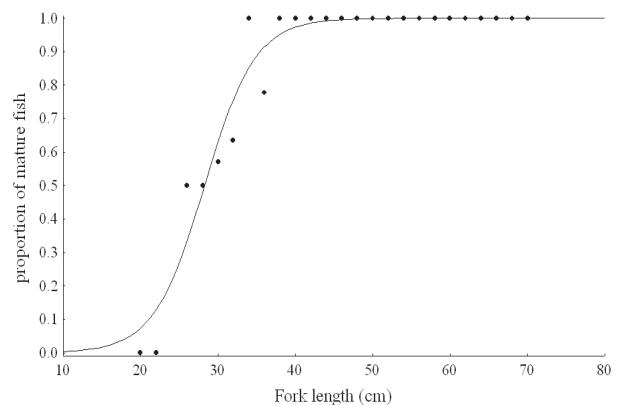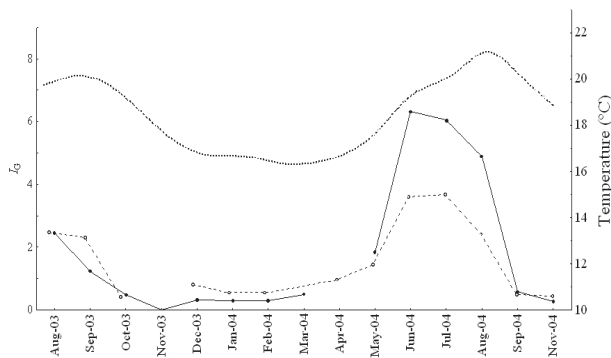

FIG. 3. – Length at first maturity of white trevally in the Azores.

TABLE 2. – Monthly proportion (%) of maturity stages per sex in white trevally: 0=immature; 1=resting; 2=early development; 3=late development; 4=spawning (ripe); 5=spent.

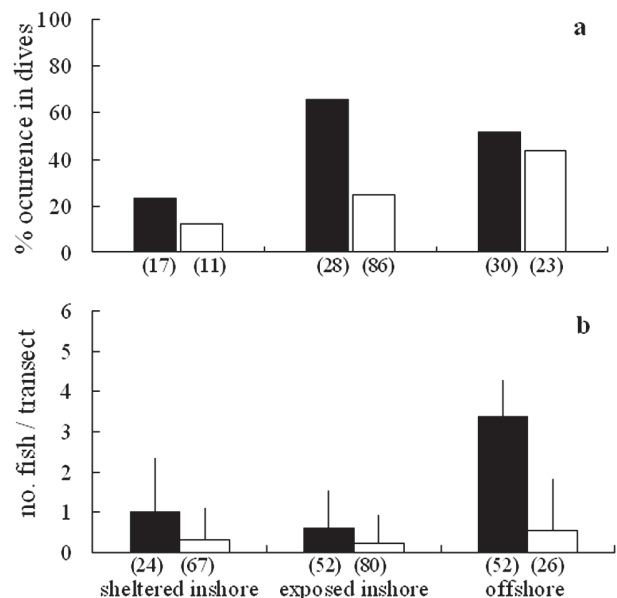| | Males | | | | | | Females | | | | | |
	1	2	3	4	5	N	1	2	3	4	5	N
January	100					6	80	20				5
February	36.4	63.6				11	35.7	64.3				14
March		100				4		100				1
April						0		100				2
May		21.7	78.3			23		20	80			15
June		7.4	44.4	48.1		27		14.3	42.9	42.9		14
July			78.6	21.4		14			66.7	33.3		12
August		6.3	9.4	84.4		32			12.9	83.9	3.2	31
September				53.8	46.2	13		8.7		47.8	43.5	46
October	55.6				44.4	9	78.6				21.4	14
November	100					11	28.6	71.4				14
December	100					18	100					3

FIG. 4. – Monthly evolution (mean ± SD) of the gonadossomatic maturity index (I_G) for mature male (solid line) and female (dashed line) white trevally caught in the Azores; variation of mean monthly temperature (at 28 m depth) is also shown (dotted line).
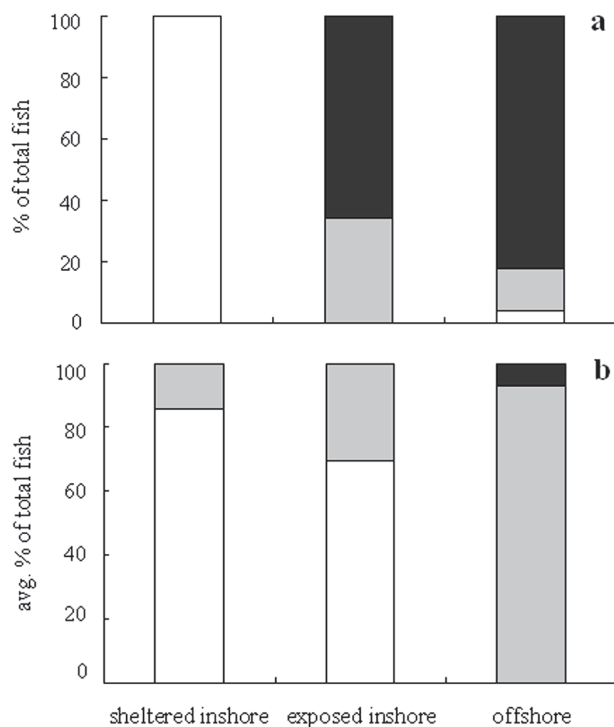

FIG. 5. – Differences between islands in the occurrence of white trevally in summer according to the type of reef habitat surveyed, measured by: a) relative frequency of occurrence in dives; b) total abundance per transect (x ± SE); black bars = Corvo island, white bars = Faial island. Sample sizes (number of dives and transects, respectively) are given in brackets.

tion also followed mean water temperature: maturation started with the spring temperature increase, and spawning began at around 19ºC and finished when the water temperature reached its peak.

Habitat prefferences

White trevally was substantially more abundant in Corvo than in Faial during the summer transects (mean ± SE, 1.8 ± 0.6 vs. 0.3 ±0.5 fish/transect, t-student test, df=1, P =0.03), and also occurred more frequently during the dives (45.7% out of 105 dives vs. 26.9% out of 120 dives, χ^2 test, df=1, P<0.01).

Relative frequency was always higher in Corvo than in Faial when comparing habitats of equivalent exposure, although this difference was only significant between the two exposed inshore habitats (χ^2 test, df=1, P<0.05; Fig. 5a). Relative frequency was lower in sheltered inshore reefs when compared to the other two habitats at both islands. Abundance in summer transects showed a similar trend to that of relative frequency (Fig. 5b), but neither island

nor site significantly explained total abundance in a crossed ANOVA (Table 3). Mean abundance was much higher in the offshore reef in Corvo but its relative frequency was not higher when compared to that of the inshore reef (Fig. 5). This reflects the predominance of larger schools in the offshore reef, whereas individuals were generally seen alone or in smaller numbers on inshore habitats (Fig. 5).

In contrast, size structure varied significantly across islands and among habitats at both islands (Table 3). Small, immature individuals occurred almost exclusively in the sheltered inshore habitats, whereas large sized individuals (51-70 cm L_T) occurred on the two offshore reefs and Corvo's inshore

TABLE 3. – Results of two-way crossed ANOVA of total abundance and size of white trevally in relation to island and reef habitat type.

	SS	d.f.	MS	F	P
Number					
Island	1.7	1	1.7	2.96	0.09
Habitat	1.2	2	0.6	1.02	0.36
Island x Habitat	0.3	2	0.2	0.29	0.75
Error	171.6	295	0.6		
Size					
Island	7053.7	1	7053.7	92.3	<0.01
Habitat	25614.7	2	12807.4	167.6	<0.01
Island x Habitat	4809.1	2	2404.6	31.8	<0.01
Error	24220.8	317	76.4		

FIG. 6. – Relative abundance of large (51-70 cm L_T, black bars), medium (31-50 cm, grey bars) and small (10-30 cm, white bars) white trevally according to reef habitat type in underwater visual censuses at a) Corvo island and b) Faial island.

exposed reef (Fig. 6). Mean fish size was significantly higher in Corvo than in Faial (51.8 ± 13.9 cm L_T vs. 29.0 ± 10.9 cm L_T). Pair-wise comparisons were significantly different between all three habitats in Faial, whereas in Corvo L_T was substantially lower in the inshore sheltered reef when compared with the other two habitats (unequal N Tukey HSD test, $P<0.01$, Fig. 7). Very large fish (>70 cm L_T) were never counted during transects, but a school of six was eventually sighted in three dives on Corvo's offshore reef.

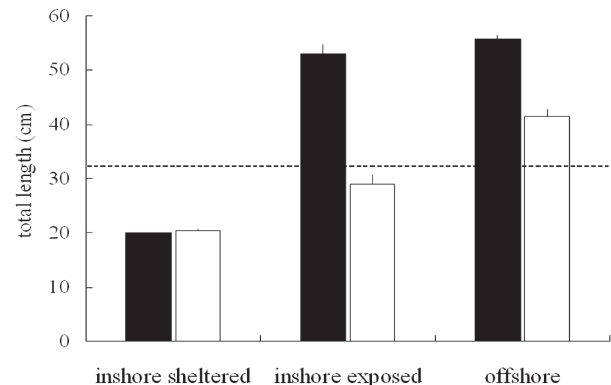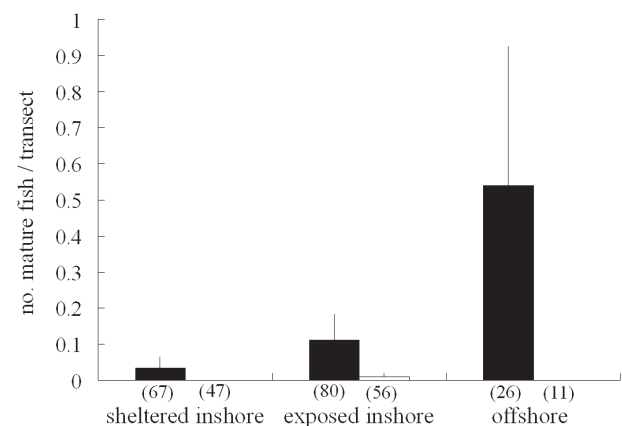A comparison of transects between seasons in Faial in order to determine the seasonal differ-

FIG. 7. – Total size (x ± SE) of white trevally in transects according to reef habitat type in Corvo (black bars) and Faial (white bars). Dashed line represents size at first maturity.

TABLE 4. – Results of two-way crossed ANOVA of the abundance of mature white trevally in relation to season (spawning vs. non-spawning) and reef habitat type at Faial island.

	SS	d.f.	MS	F	P
Season	0.2	1	0.2	5.0	0.03
Habitat	0.1	2	0.1	1.6	0.20
Season x Habitat	0.1	2	0.1	1.6	0.21
Error	11.1	281	0.0		

ences in the occurrence of white trevally showed that season significantly explained the abundance of mature fish (Table 4). The offshore reef gave the highest abundance of mature fish in the summer whereas in the winter transects only one mature fish was counted on the inshore exposed reef (Fig. 8). Mature fish were also absent in an additional eight transects undertaken on Corvo's inshore exposed reef in the winter of 1998. Immature fish, however, were counted in 13% of the inshore winter transects in Faial.

FIG. 8. – Abundance in transects (x ± SE) of mature white trevally (fish >30 cm L_T) at Faial island according to reef habitat type during the summer spawning season (black bars) and the non-spawning season (white bars). Sample sizes are given in brackets.

DISCUSSION

White trevally is a summer spawner in the Azores. Fish undergo the maturation process throughout late winter and spring, and become reproductively active in June. Spawning peaks in August and recedes in September. This conclusion is clearly supported by the evolution of macroscopic maturation of the gonads and the gonadossomatic index. Therefore, white trevally is an annual spawner that most probably releases gametes in multiple events during the summer, given that it has been previously shown to be a partial spawner (Rowling and Raines, 2000; Farmer *et al.*, 2005). The sex-ratio of the white trevally population is most likely 1:1 throughout the year. It remains possible, however, that the white trevally displays some sex-related segregation that was difficult to access due to the small number of individuals sampled in some seasons.

Results from this study strongly indicate that key environmental factors, including temperature and habitat type, determine where and when such reproductive events take place. Maturation accompanied the spring increase in temperature and dropped just when the temperature reached its peak in September for two consecutive years. Reproduction of many fish is known to be highly influenced by water temperature, and local thermal regimes can limit a species' ability to reproduce in good conditions or in any conditions at all (e.g. Van Der Kraak and Pankhurst, 1996). This also seems to be the case for white trevally.

The Azores constitute the northern distribution limit for viable populations of white trevally in the Atlantic, which is consistent with its short spawning season limited to the warmer months in the region. The same short reproductive period is shown by populations in SW Australia, which are subjected to very similar temperature values and reproductive schedule as the Azorean population (Farmer *et al.*, 2005). However, the reproductive period of subtropical populations of west and east Australia, which are subjected to higher temperatures, is protracted to an extended period of about six months (Rowling and Raines, 2000; Farmer *et al.*, 2005). One other possibility would be that solar irradiance is the key physical factor determining the reproductive schedule, rather than temperature. In the Hawaiian archipelago, adult white trevally is rarer and lives deeper in the warmer waters of the main Hawaiian islands. They become more abundant and live closer to the surface across the SE-NW geographic gradient towards cooler waters in the northwestern Hawaiian islands (Randall, 1996). These regional trends, and the overall anti-tropical geographic distribution of white trevally, support the notion that this species is very limited by temperature.

At a local scale, specific habitats also seem to be important for reproduction. Ontogenetic size segregation in relation to habitat type was evident from the UVC data. Fish larger than size at first maturity selected offshore reefs and deeper inshore reefs swept by faster currents. Immature individuals preferred reefs located in sheltered, inshore areas. Furthermore, the presence of mature individuals in the summits of shallow offshore reefs was limited mainly to the summer months, when spawning takes place. Additional underwater observations made by the authors confirmed this trend. It was common to see large schools of 20 to 70 mature individuals during the summer in other offshore reefs in the Faial-Pico Channel. This was very uncommon in shore habitats, where schools are typically composed of less than 10 immature fish, regardless of the season.

We did not see any direct evidence of spawning in offshore reef aggregations: spawning behaviour, the presence of hydrated eggs or post-ovulatory folicules in the females from reef aggregations (Colin *et al.*, 2003). We did, however, observed intensive social interaction between schooling individuals in the offshore reefs on various occasions. The fact that trevally have an epipelagic behaviour during the summer but not in winter, when they are thought to be at greater depths (personal observation), might also indicate surface spawning behaviour. In southeast Australia, mature white trevally is also thought to aggregate and spawn in offshore epipelagic waters (Rowling and Raines, 2000). Spawning aggregations and behaviours of *Seriola lalandi* and *Caranx sexfasciatus* were also observed at offshore islands and seamounts in the Gulf of California (Sala *et al.*, 2003). This behaviour may occur widely among carangids. In summary, although it is possible that fish aggregate around the reefs for purposes other than spawning, our data strongly support the hypothesis that offshore reefs are important spawning habitats for white trevally in the Azores and, possibly, elsewhere.

As to the important question of the whereabouts of larger mature fish after spawning, it appears that they migrate locally to deeper habitats rather than migrating off-islands. Our observations matched the

perception of local fishermen who only target this species over reef summits from June to November. The fish then become an accessory and rare catch and are caught with bottom handlines at greater depths during cold water months. In addition, white trevally is not caught in the surrounding offshore seamounts. Movement studies using acoustic telemetry are being carried out to clarify this behaviour.

Juveniles, in contrast, seem to select inshore habitats after settlement. Very small juveniles (ca. 5-7 cm L_T) are frequently seen at the end of summer and autumn, seeking protection under moored buoys and floating devices close to reefs (Castro *et al.*, 1999; personal observation). This indicates that larvae settle at this point and probably select suitable inshore habitats in doing so. Furthermore, data from this study show that immature fish prefer sheltered reef habitats to other high energy or offshore reefs. The use of inshore, shallower habitats by juveniles has been reported for white trevally (Rowling and Raines, 2000) and for other carangids (Meyer *et al.*, 2001; Smith and Parrish, 2002) and mostly regarded as the result of feeding preferences. Younger white trevally uses suction feeding to prey mainly on invertebrates and small fish that live in the sand and algae (Sazima, 1998; personal observation). Protection from predators might also play a role in this habitat choice, as indicated by frequent observations of juvenile white trevally hiding very close to large bottom reef predators, such as groupers (Debelius, 1997, personal observation). A very similar pattern was found in a study that compared populations fished over shallower sandy bottoms and deeper reef bottoms in Western Australia, which concluded that the latter are dominated by mature individuals and the former by immature fish (Farmer *et al.*, 2005). Therefore, this pattern might be consistent for populations of white trevally across its distribution range, even in different ecosystems.

Finally, our data give some evidence that the Azorean artisanal fishery impacts local populations of reef predators, even if this evidence should be interpreted cautiously as the sampling was restricted to shallow waters and was limited in size. White trevally was more abundant and larger at Corvo, where catches are incidental, than at Faial, which sustains a traditional fishery that targets white trevally. Anecdotal information from local fishermen supports this hypothesis, as it cites frequent catches of large schools (up to one metric ton) and very large individuals before fishing intensity increased locally in the 1980s

(Santos *et al.*, 1995). In the Azores, and probably in other oceanic islands, it appears that the major threat to local populations is when aggregations of larger mature fish are targeted. This bottleneck fishing effect is amplified by the fact that fecundity increases with size (Rowling and Raines, 2000), exponentially increasing the proportion of offshore reef individuals in the total reproduction of the population.

The same reasoning can be extended to other pelagic predator fish that are targeted by coastal fisheries in the region. Yellowmouth barracuda (*Sphyraena viridensis*), almaco jack (*Seriola rivoliana*), greater amberjack (*S. dumerilli*) and atlantic bonito (*Sarda sarda*) constitute, together with white trevally and other species, the pelagic predator guild of the reef fish fauna in the Macaronesian archipelagos (Falcón *et al.*, 1996; Afonso, 2002). There is good evidence that they all spawn during the summer in the Azores region (unpublished data), and that during this period they aggregate at the offshore reefs (Afonso, 2002; Barreiros *et al.*, 2002). Therefore, offshore reefs and shallow water seamounts should be considered as prime targets for protection in spatial management plans (Morato *et al.*, 2008). This hypothesis deserves further study.

In conclusion, the present paper provides the first information on the reproductive biology and habitat use of wild Atlantic populations of an important, wide-ranging reef fish. Furthermore, it supports the hypothesis that offshore reefs are a preferential spawning habitat for larger, mature white trevally, and most possibly for a number of other visitor pelagic predators as well. This conclusion brings additional ecological relevance to specific habitats that are of priority for conservation within EU environmental policies, and points to the usefulness of this information for defining the Essential Fish Habitat (Fogarty, 1999) for these species. These habitats should be explicitly taken into consideration in precautionary approaches to fishery management of pelagic predator fish.

ACKNOWLEDGEMENTS

REFERENCES

Afonso, P. – 2002. *Spatial patterns in the littoral fish community of the Azores*. MSc. thesis, University of Coimbra.

Barreiros, J.P., R.S Santos and A.E. Borba. – 2002. Food habits, schooling and predatory behaviour of the yellowmouth barracuda, *Sphyraena viridensis* (Perciformes: Sphyraenidae) in the Azores. *Cybium* 26(2): 83-88.

Castro, J.J., J.A. Santiago and V. Hernández-García. – 1999. Fish associated with fish aggregation devices off the Canary Islands (Central-East Atlantic). *Sci. Mar.* 63(3-4): 191-198.

Colin, P.L., Y.J. Sadovy and M.L. Domeier. – 2003. Manual for the Study and Conservation of Reef Fish Spawning Aggregations. Society for the Conservation of Reef Fish Aggregations, Special Publication 1 (Version 1.0), pp. 1-98+iii.

Dalzell, P. – 1996. Catch rates, selectivity and yields of reef fishing. In: N.C. Polunin and C.M. Roberts (eds.), *Reef Fisheries*, pp. 161-192. Chapman and Hall, London.

Debelius, H. – 1997. *Mediterranean and Atlantic fish guide*. Ikan, Frankfurt.

Falcón, J.M., S.A. Bortone, A. Brito and C.M. Bundrick. – 1996. Structure and relationships within and between the littoral rock-substrate fish communities off four islands in the Canarian Archipelago. *Mar. Biol.*, 125: 215-231.

Farmer, B.M., D.J.W. French, I.C. Potter, S.A. Hesp and N.G. Hall. – 2005. Determination of biological parameters for managing the fisheries for Mulloway and Silver Trevally in Western Australia. Fisheries Research and Development Corporation Report. Murdoch Univ., Murdoch.

Fogarty, M.J. – 1999. Essential habitat, marine reserves and fishery management. *Trends Eco. Evol.*, 14(4): 133-134.

Jennings, S. and J.M. Lock. – 1996. Population and ecosystem effects of reef fishing. In: N.C. Polunin and C.M. Roberts (eds.), *Reef Fisheries*, pp. 193-218. Chapman and Hall, London.

Johannes, R.E. – 1981. *Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia*. University of California Press, Berkeley.

Meyer, C.G., K.N. Holland, B,M. Wetherbee and C.G. Lowe. – 2001. Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. *Fish. Res.*, 53: 105-113.

Morato, T., D.A. Varkey, C. Damaso, M. Machete, M. Santos, R. Prieto, R.S. Santos and T.J. Pitcher. – 2008. Testing a seamount effect on aggregating visitors. *Mar. Ecol. Prog, Ser.*, 357: 23-32.

Randall, J.E. – 1996. *Shore fishes of Hawai'i*. University of Hawai'i Press, Honolulu.

Rowling, K.R. and L.P. Raines. – 2000. *Description of the biology and an assessment of the fishery for Silver Trevally Pseudocaranx dentex off New South Wales*. Sydney: NSW Fisheries, Report to Fisheries Research and Development Corporation.

Sadovy, Y. – 1996. Reproduction of reef fishery species. In: N.C. Polunin and C.M. Roberts (eds.), *Reef Fisheries*, pp. 15-60. Chapman and Hall, London.

Sala, E., O. Aburto-Oropeza, G. Paredes and G. Thompson. – 2003. Spawning aggregations and reproductive behaviour of reef fishes in the Gulf of California. *Bull. Mar. Sci.*, 72(1): 103-121.

Santos, R.S., S. Hawkins, L.R. Monteiro, M. Alves and E.J. Isidro. – 1995. Marine research, resources and conservation in the Azores. *Aq. Cons. Mar. Fresh. Ecos.*, 5(4): 311-354.

Sazima, I. – 1998. Field evidence for suspension feeding in *Pseudocaranx dentex* with comments on ram filtering in other jacks (Carangidae). *Env. Biol. Fishes*, 53(2): 225-229.

Smith, G.C. and J.D. Parrish. – 2002. Estuaries as nurseries for the Jacks *Caranx ignobilis* and *Caranx melampygus* (Carangidae) in Hawaii. *Est. Coast. Shelf Sci.*, 55: 347-359.

Smith-Vaniz, W.F. – 1999. Carangidae. Jacks and scads (also trevallies, queenfishes, runners, amberjacks, pilotfishes, pampanos, etc.). In: K.E. Carpenter and V.H. Niem (eds), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 4. Bony fishes part 2 (Mugilidae to Carangidae)*, pp. 2659-2756. FAO, Rome.

Van Der Kraak, G. and N.V. Pankhurst. – 1996. Temperature effects on the reproductive performance of fish. In: G. McDonald and C.M. Wood (eds.), *Global Warming: Implications for Freshwater and Marine Fish*, pp. 159-176. Cambridge University Press, Cambridge.

Zar, J.H. – 1999. *Biostatistical analysis* (4rd edition). Prentice Hall, New Jersey.