Multi-scale recruitment patterns and effects on local population size of a temperate reef fish

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Recruitment of the temperate reef fish *Coris julis* was studied across the Azores Archipelago (central North Atlantic), over four consecutive recruitment seasons and at three spatial scales: between islands (separated by 100s of km), sites within islands (separated by 10s of km) and transects within sites (separated by 10s of m). At the largest scale (*i.e.* between islands) spatial recruitment patterns were highly variable, suggesting the influence of stochastic processes. Recruitment was spatially consistent within islands, even though magnitude was unpredictable between years, indicating that processes at meso-scales are probably more deterministic. Recruits settled randomly at the transect scale, probably reflecting habitat homogeneity. It was proposed that large and island-scale patterns reflect larval availability, driven by physical and biological processes occurring in the plankton. No evidence was found for a density-dependent relationship between newly settled and 2 week settled *C. julis* nor between cumulative recruitment and young-of-the-year. It appears that adult density is limited by larval supply (pre-settlement regulation) at low recruitment sites, and determined by post-settlement, density-dependent processes at high recruitment sites. This work is one of few to investigate multiple spatial and temporal scales of recruitment for a coastal fish species inhabiting isolated, temperate oceanic islands and hence, provides a novel comparison to the many studies of recruitment on coral reefs and other, more connected systems.   © 2009 The Authors

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INTRODUCTION

Most reef fishes have complex life cycles, involving the broadcast of eggs or larvae into the water column. The transition from the plankton to adult habitat, usually termed settlement (time when an individual takes up permanent residence in the demersal habitat) can have a critical and lasting influence on the demography of a population (Doherty & Fowler, 1994; Carr & Syms, 2006). Although usually variable and difficult to predict, recruitment is vital to sustain marine populations and determining its dynamics (Doherty & Fowler, 1994; Forrester *et al.*, 2002).

The number of settlers available to enter a reef-based population may be influenced by a variety of factors affecting larval production, dispersal, mortality and

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condition of eggs and larvae in the plankton (Sponaugle *et al.*, 2002), as well as larval behaviour and habitat choice at settlement (Schmitt & Holbrook, 2002). Physical processes that advect larvae far offshore, precluding their return to reef habitat, are thought to be a major source of larval mortality and likely to decouple production from recruitment (Cowen *et al.*, 2006). Other environmental factors such as food availability, temperature and predation, all of which may, in turn, be related to oceanography, are also known to affect larval mortality (Hjort 1914; Bergenius *et al.*, 2002). For these reasons, oceanography has frequently been identified as a major determinant of larval delivery patterns (directly or indirectly) over a wide range of spatial scales (Fowler *et al.*, 1992; Caselle & Warner, 1996; Booth *et al.*, 2000). With careful interpretation of correlates of spatial and temporal variation at a range of scales, the causes of that variability can be understood and, ultimately, the understanding of the role of recruitment in population dynamics be improved (Fowler *et al.*, 1992).

A major question for most widespread species with a pelagic larval phase is the degree of connectivity between local populations (Warner & Cowen, 2002). Understanding about connectivity is essential to the development of spatially explicit models used in spatial management of marine fish populations, such as marine protected areas (MPA) (Sale *et al.*, 2005). Despite the increasing number of studies attempting to directly measure larval dispersal, this remains a very difficult task in practice (the exceptions include Jones *et al.*, 1999; Swearer *et al.*, 1999; Almany *et al.*, 2007). The simple combination of settlement patterns with basic geography and oceanographic flow patterns, however, allows hypothesese to be made to test connectivity (Sponaugle *et al.*, 2002; Cowen *et al.*, 2006). Thus, until direct estimates of connectivity become widely available, it is necessary to gather indirect evidence of the degree to which populations are connected or isolated (Sponaugle *et al.*, 2002).

In addition, multi-scale analysis of recruitment may allow inferences to be made about the processes that are likely to influence recruitment rates (Fowler *et al.*, 1992). Recruitment patterns may be preserved, entirely masked or altered by processes that take place after settlement to the benthic habitat (Schmitt *et al.*, 1999; Forrester *et al.*, 2002; White & Caselle, 2008). Gaines & Roughgarden (1985) established that population structure and dynamics vary with density of recruits, and in particular that populations are limited by recruitment when and where larval supply is low, but limited by density-dependent resource competition (for food or space) when larval supply is greater. This idea was later termed the recruit–adult hypothesis, which suggests that the density of recruits is a good predictor of adult density when low but not when high (Menge, 2000). Recent work by White & Warner (2007), however, suggested that the effects of density dependence can be inconsistent, depending on the scale of observation. It is clear that, for marine organisms, a complete understanding of the factors that influence population dynamics requires a thorough consideration of recruitment and subsequent mortality patterns at multiple spatial and temporal scales (Forrester, 1990; Caley *et al.*, 1996; Schmitt *et al.*, 1999). In the past, few papers have addressed spatial and temporal recruitment variability of temperate species over a range of geographical and temporal scales, and such information is non-existent for isolated temperate island systems. By using a widely distributed coastal fish, it was expected that these results could provide useful and general insights on the effect of variable replenishment and post-settlement demographic processes on local

population dynamics, which would contribute to the present debate about optimal MPA design.

The specific aims of this paper were: (1) to document recruitment patterns of *Coris julis* (L.) at three spatial scales over the Azores Archipelago, Portugal and to evaluate spatial consistency over time, and (2) to investigate the relationship between recruitment and subsequent juvenile and adult density. Given the spatial and temporal patterns of recruitment, mechanisms most likely to have accounted for the observed patterns are hypothesized and probable population connectivity scenarios suggested for this isolated archipelago.

MATERIALS AND METHODS

STUDY AREA AND SPECIES

The Azores Archipelago is a chain of nine volcanic islands (37°−40° N; 25°−32° W), arranged in three groups (Eastern, Central and Western) (Fig. 1). Oceanography is influenced by the Gulf Stream, and its south-eastern branch generates the eastward-flowing Azores Current. Although the currents that sweep the Azores islands are, in general, poorly described, at many specific locations currents may be swift, constant and predictable, largely as a result of tidal forces and local topography. Productivity is generally low, but exceptions occur due to localized upwelling at seamounts, island shelf breaks and thermal fronts (Santos *et al.*, 1995; Monteiro *et al.*, 1996; Morato *et al.*, 2008).

Coris julis is a small reef fish that lives for 2−4 years, and is very abundant throughout the Azores (Patzner & Santos, 1993; Afonso, 2002). It has a wide geographic range (from Sweden to Gabon) (Aurelle *et al.*, 2003). In the Azores, spawning is seasonal, lasting *c*. 3 months and peaking in mid-July (P. Afonso, unpubl. data). After a pelagic larval stage of up to 46 days (Raventos & Macpherson, 2001; J. Fontes, pers. obs.), *C. julis* recruit to shallow rocky areas, and may be found singly or in schools of one or multiple size classes. In this
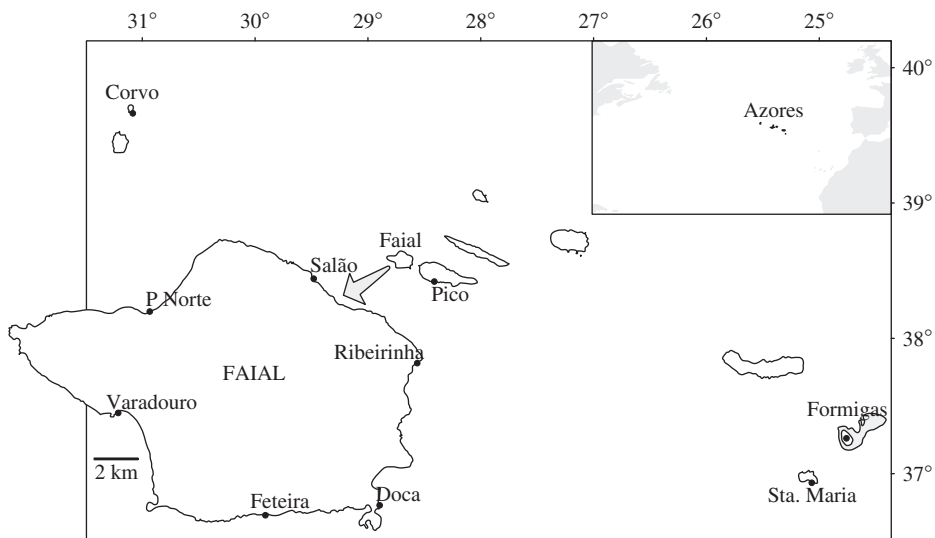

Fig. 1. Map of Azores Archipelago (north-east Atlantic ocean) and detail of Faial Island, showing the locations of the 10 study sites. Transects are located within sites.

study, all *C. julis* <50 mm total length (L_T) were assigned to a size or age class, based on L_T and age relationships derived from previous otolith microstructure analysis (J. Fontes, unpubl. data). Fish <20 mm were assigned to class I (recruits), and recruit density was the number of class I *C. julis* per transect. Fish ranging from 20 to 30 mm were assigned to class II, whereas fish ranging between 30 and 50 mm were assigned to class III. In addition to L_T, body transparency, colour pattern and behaviour were used to assign fish to classes. Young-of-the-year (YOY) included all *C. julis* <50 mm, observed at the time of survey.

SURVEYS

Large-scale (Archipelago wide)

For the large-scale analysis, YOY were counted, once a year from 2004 to 2006, at Corvo, Pico, St Maria and Formigas Islets and Faial (YOY density for Faial was averaged from two sites on the south shore) (Fig. 1). In 2004, due to inclement weather conditions and limited vessel time, recruits were collected but no fish counts were possible at Formigas and Corvo. Instead, recruit density was estimated from the relationship between catch per unit of effort (CPUE; number of recruits collected per dive time; *y*) and YOY density (*x*) measured at the remaining four sites ($r^2 = 0.72$, $P < 0.01$, $y = 11.08x - 1.82$). Because the linear nature of this relationship could not be verified for higher densities than those used in the model (*c*. 30 recruits per transect), it was assumed that the estimated density at Formigas should be no less than the highest density in the model, thus the estimated densities were conservative and likely to be underestimated.

Researchers returned to the same sites every year using GPS and familiar topographic features and surveyed recruits on five or six 20 m × 1 m transects, *c*. 30 m apart. Surveys occurred in late August or early September, within no more than 12 days.

Because it was not possible to sample Pico during the 2004 cruise, recruit counts performed a month later were used to compare recruitment dynamics between these islands.

Island-scale (Faial Island)

In 2003, five sites were established around Faial (Fig. 1) to survey recruitment of *C. julis* and other common reef fish species. Sites were separated by 7–14 km of coastline. At each site, four fixed linear transects (20 m × 1 m) in depths of 10–13 m were surveyed. Transects were roughly parallel to the shoreline and no less than 25 m apart. All transects were placed over the same and most abundant habitat, boulders covered in coralline and turf algae (Tempera, 2008).

Surveys around Faial were conducted every 2 weeks during summer and early autumn, and all sites were visited within a maximum period of 5 days for each survey. In 2003, due to logistical and weather constraints, surveys started in early September and ended in late October.

In 2006 and 2007, only YOY were counted, at the end of the recruitment season, except in Varadouro, which was sampled biweekly in 2006.

Adult *C. julis* were surveyed in late summer 2006 at all sites on Faial. Adults were counted by a diver on four to six, 50 × 5 m reeled transects (20 m line, fish counted within 0·5 m on each side), adjacent to the recruit fixed transects.

STATISTICAL ANALYSIS

The YOY count data from the large-scale surveys were $\log_{10} (x + 1)$ transformed to meet the assumptions of normality and equal variances, and a full factorial two-way ANOVA with site and year as factors, compared YOY densities among sites and years (large-scale and Faial–Pico analysis).

Recruitment variability among sites and transects (Faial Island) was compared using two-way ANOVA, with year and site as factors and transects nested within sites. In order to not lose d.f., the year 2003 was not included in this model because Ribeirinha (the sixth site) was not surveyed until 2004. Non-parametric Kendall's coefficient of concordance *W* (Siegel

& Castellan, 1988) was used to test for spatial consistency in recruitment to transects within seasons and among years. Kendall's W was also used to compare the concordance in rank order of Faial Island sites for end of season YOY density.

ANCOVA analysis was performed using transect identity and recruit density as factors, to test the effects of recruitment (*i.e.* class I fish) at time t and transect on variation of class II recruit density at time $t + 2$ weeks.

Regression methods were used to explore the relationships between (1) density of class I and density of class II recruits counted 2 weeks later (3 years pooled together, all 2006 data measured at Varadouro), (2) between each recruitment season's cumulative recruitment and YOY density at the end of the season and (3) between YOY (averaged from 2003 to 2005) and adult density (observed in 2006). Linear regression slopes were compared using ANCOVA analysis.

RESULTS

LARGE-SCALE PATTERNS

Spatial patterns of YOY density across the Archipelago were highly unpredictable among years (two-way ANOVA, site × year interaction; $F_{2,4}$ $P < 0.001$) (Fig. 2). In 2004 and 2005, clear longitudinal gradients across the Archipelago were observed, but in opposite directions. The maximum YOY density was observed at a different site each year. For example, Corvo had the highest overall density in 2005 and the lowest densities in 2004 and 2006. The high density at Formigas and Sta. Maria in 2004 was not observed in the following years. The only exception to the overall low recruitment in 2006 was Faial.

Even the two closest islands (Pico and Faial, 30 km apart) showed striking interannual relative differences (two-way ANOVA, site × year interaction; $F_{1,2}$ $P < 0.05$). The magnitude of recruitment was variable between years, as well as the site relative YOY densities (Fig. 2).

ISLAND-SCALE (FAIAL ISLAND)

At the island-scale, the spatial recruitment patterns were quite consistent over five consecutive seasons (Figs 3 and 4). The highest recruit densities were always recorded at Varadouro (western shore) except for the initial survey of 2003, during which an abnormally high recruitment event at P Norte and Salão (northern shore) was recorded. Doca and Ribeirinha (east shore sites) always had the lowest recruit densities. Intermediate recruit densities were usually observed at Salão and Feteira (north and south shore, respectively). The consistency of the pattern was reflected in the high concordance in YOY site ranking between years (Kendall concordance, $W = 0.84$, $n = 6$, $P < 0.01$).

Despite the consistency in spatial patterns (site ranks), the magnitude of recruitment was highly variable between years, with approximately five times higher recruitment in 2005 than in 2004 (Fig. 3). A significant interaction was found between year and site, reflecting the disproportional increase in recruitment magnitude observed in some sites (*e.g.* Varadouro) during relatively good recruitment years [two-way ANOVA with site and year as factors and transects nested within sites; site × year interaction; $F_{2,4}$, $P < 0.01$; transect (sites) $F_{3,5} = 6$, $P > 0.05$).
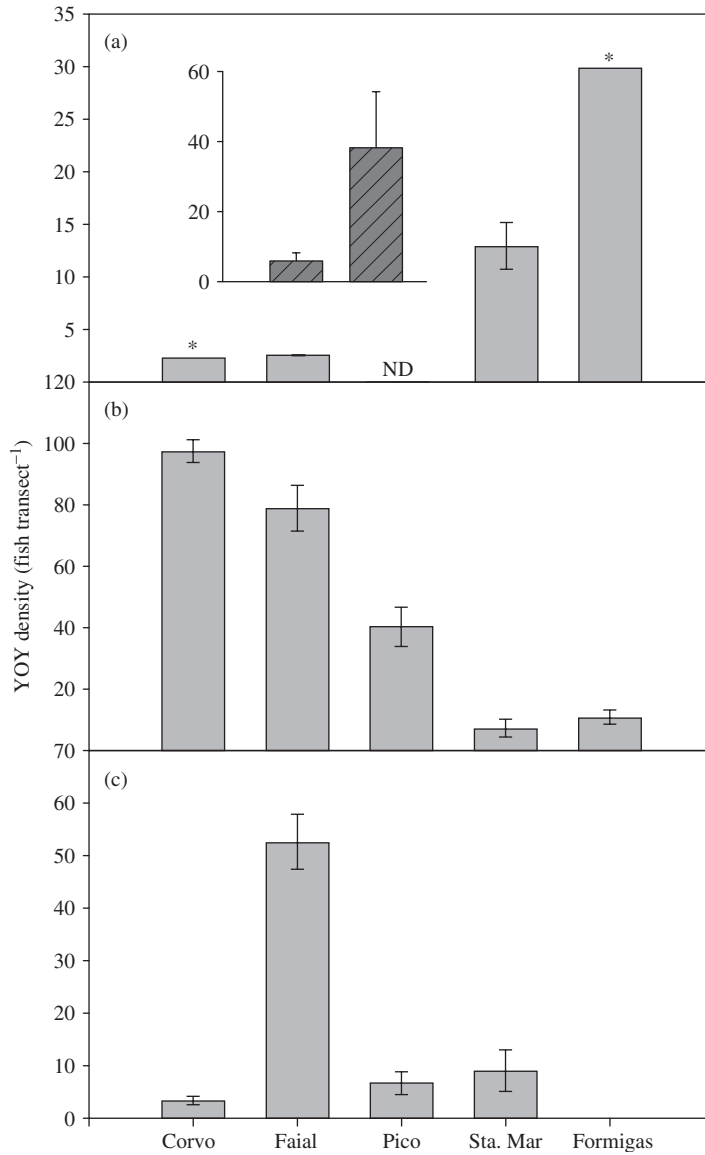
FIG. 2. *Coris julis* young-of-the-year (YOY) density from visual surveys at sites throughout the Azores Archipelago in (a) 2004, (b) 2005 and (c) 2006. Values are means ± S.E. *, estimated densities. Because YOY counts at Pico in 2004 were conducted 20 days after the large-scale cruise, data are shown in the 2004 sub-plot (▨) with Faial counts from the same survey. Note *y*-axis scale differs between plots.

Within sites, there was no concordance in the rankings of transects with respect to class I density between surveys, except for Feteira in 2005 (Table I). The small-scale spatial patterns established at recruitment, however, were preserved during the following 2 weeks, that is, the relative density of class I recruits within a transect at time *t* was usually correlated with density of class II 2 weeks later (Table II).
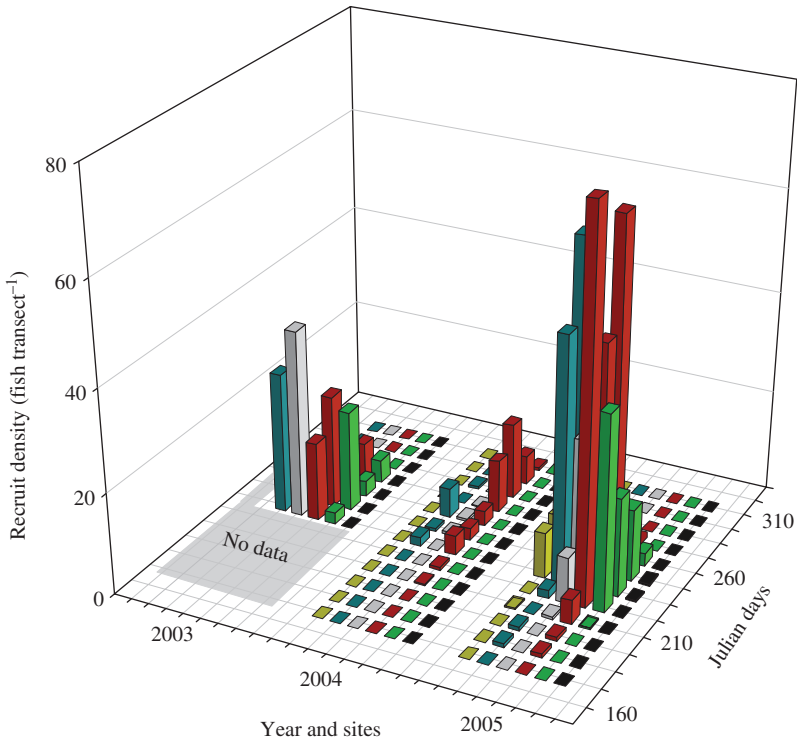
FIG. 3. *Coris julis* mean recruit density at sites on Faial Island. Sites are Doca (■), Feteira (■), Varadouro (■), PNorte (■), Salão (■) and Ribeirinha (■). Shaded areas represent no data (Ribeirinha was not surveyed in 2003).
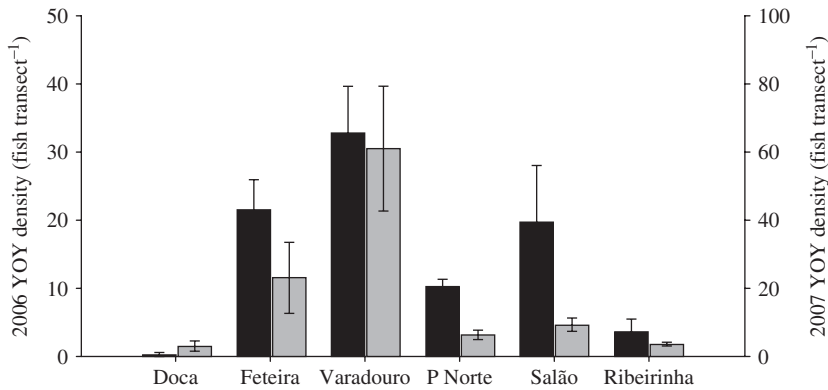

FIG. 4. *Coris julis* mean ± S.E. young-of-the-year (YOY) density in 2006 and 2007 at sites on Faial Island.

POPULATION DYNAMICS

Recruitment at survey time t was positively and linearly correlated with class II recruits (*c.* 2 weeks old) at survey time $t + 2$ weeks (Fig. 5; $r^2 = 0.45$, $n = 49$,

TABLE I. Concordance (Kendall's coefficient of concordance, W) of the ranking of transects (within sites) in recruitment of *Coris julis* over recruitment season within each year

		Kendall W		
Site	2003	2004	2005	2006
Doca	+	+	+	*
Feteira	0·43	+	0·62**	0·03
Varadouro	0·01	0·01	0·01	0·03
P Norte	0·16	+	0·11	*
Salão	0·10	0·02	0·13	*
Ribeirinha	*	+	0·23	*

+, most transects had the same score = zero density;

*, none or only one survey was performed that year;

**, concordance, $P < 0.05$.

TABLE II. Summary of ANCOVA analysis results for comparison of class II recruit density of *Coris julis* at time $t + 2$ weeks *v.* class I at time t (Rec) and transect identity in Faial. Correlation results between the density of recruits (class I) at time t and density of class II fish at time $t + 2$ weeks for all surveys and all years are also given

		ANCOVA				Correlation	
	Source	d.f.	SS	F	P	r	P
Feteira	Rec	1	707·25	12·03	<0·01	0·76	<0·001
	Transect	3	104·85	0·59	>0·05		
	Rec × transect	3	112·35	0·63	>0·05		
Varadouro	Rec	1	5667·50	29·92	<0·001	0·52	<0·001
	Transect	3	377·29	0·66	>0·05		
	Rec × transect	3	255·21	0·44	>0·05		
Pnorte	Rec	1	395·65	12·38	<0·01	0·48	<0·01
	Transect	3	3·16	0·03	>0·05		
	Rec × transect	3	364·95	3·80	<0·05		
Salão	Rec	1	3571·10	43·93	<0·001	0·7	<0·001
	Transect	3	36·75	0·15	>0·05		
	Rec × transect	3	532·54	2·18	>0·05		
Ribeirinha	—	—	—	—	—	0·7	<0·05
	—	—	—	—	—		
	—	—	—	—	—		
All sites	Rec	1	12786	106·37	<0·001	0·58	<0·001
	Transect	3	57·22	0·15	>0·05		
	Rec × transect	3	203·42	0·56	>0·05		

–, too few data to perform ANCOVA analysis. Doca was not included because of insufficient counts different from zero.

$P < 0.001$). In 2004 and 2005, a linear relationship was found between cumulative (each season) recruitment and YOY density at the end of the season by site. The same trend was documented in 2003, although the relationship was less robust (marginally
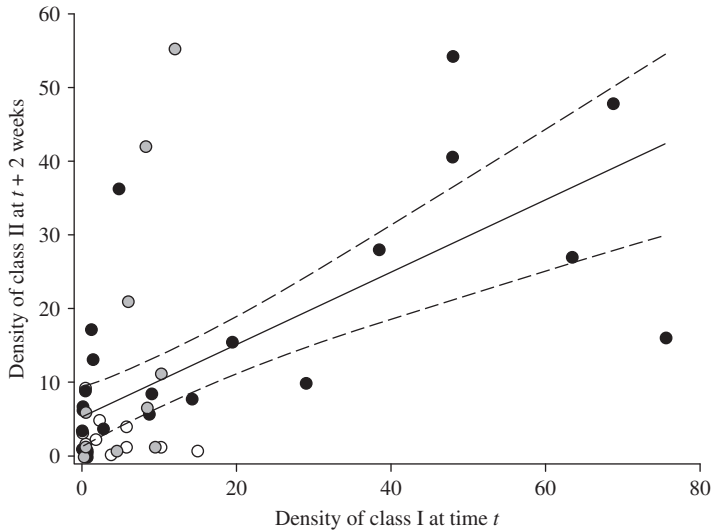
FIG. 5. Relationship between recruitment (density of class I) of *Coris julis* and the density of class II recruits counted 2 weeks later in 2004 (○), 2005 (●) and 2006 (◐). The 2003 season was not included because too few data points were available and in 2006 only Varadouro was surveyed biweekly. Fish density is in number of fish transect^{-1}. ---, 95% CL for the regression. The curve was fitted by: $y = 5.54 + 0.48x$.
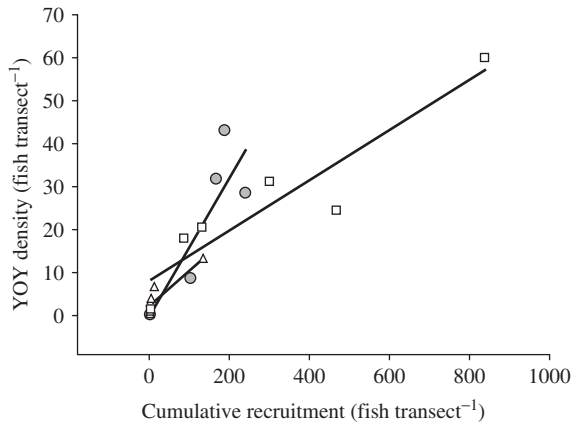

FIG. 6. Relationship between cumulative recruitment of *Coris julis* over all surveys per year and young-of-the-year (YOY) density at the end of the recruitment season for 2003 (◐), 2004 (△) and 2005 (□). The curves were fitted by: 2003, $y = 0.0024 + 0.1613x$, 2004, $y = 2.3949 + 0.08120x$ and 2005, $y = 8.2454 + 0.0583x$.

non-significant) (Fig. 6; 2003: $r^2 = 0.71$, $n = 5$, $P > 0.05$; 2004: $r^2 = 0.82$, $n = 6$, $P < 0.05$; 2005: $r^2 = 0.86$, $n = 6$, $P < 0.01$). Despite the interannual differences in magnitude of cumulative recruitment, the form of the relationship did not differ significantly among years (*i.e.* slopes were not significantly different among years, ANCOVA, $F_{1,2}$, $P > 0.05$).
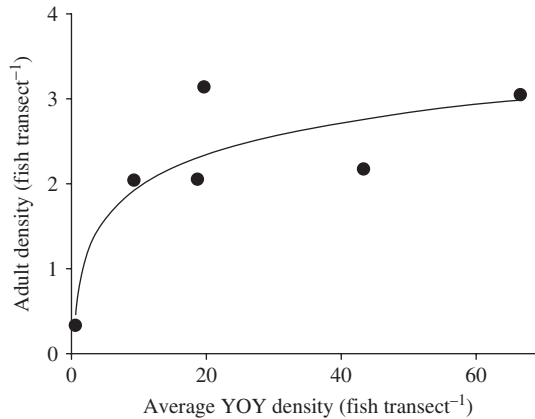
Fig. 7. Relationship between average young-of-the-year (YOY) density over 3 years (2003–2005) and adult density (number of fish 1 year of age or older per transect) observed in 2006. The curve was fitted by: $y = 9 \cdot 0081 + 6 \cdot 7724 \, (\log_{10} x)$.

Finally, density of adults and YOY at the Faial sites, as measured at the end of the 2006 recruitment season, showed a decelerating curvilinear relationship with average recruitment from the previous 3 years, clearly tending toward an asymptote (Fig. 7; $r^2 = 0 \cdot 78$, $n = 6$, $P < 0 \cdot 05$).

DISCUSSION

RECRUITMENT PATTERNS

Large-scale

In this study, as in others dealing with very large spatial scales (Masterson *et al.*, 1997; Vigliola *et al.*, 1998), sampling possibilities are limited, thus it is essential that the selected sites adequately represent the region of interest. While the sampling design used in this study covered a significant portion of the recruitment habitat available on small islands and reefs (Formigas and Corvo), opportunistic surveys performed on different areas around the larger islands showed similar trends to the selected sites (especially when local recruitment was very high or very low, *e.g.* Corvo 2004 and 2005). In addition, the recruitment patterns observed in two consecutive years (2005 and 2006) were positively correlated with regional patterns of chlorophyll-*a* concentration (J. Fontes, pers. obs.), further supporting this assumption.

The large (100s of km) and intermediate (10s of km) scale recruitment patterns were highly unpredictable between years, in terms of both the relative densities among sites and the absolute magnitude within sites. These results agree with the generally accepted view that replenishment of marine populations is highly variable and unpredictable over space and time (Carr & Syms, 2006). At large scales, where populations may be effectively closed, recruitment variability may arise from regional differences in production, either related to variability in individual output or the number of producers (Sponaugle *et al.*, 2005). Large fluctuations in production, however, are unlikely to occur when local community structure is stable (Carr *et al.*, 2002). This should be the case in Corvo and Formigas (Afonso, 2002),

but interannual recruitment variability was extreme at these islands. Alternatively, extreme variation in the local reproductive output may imply short-term dramatic changes in adult abundance or individual fecundity, usually attributed to regional scale climatic events, such as El Niño (Davis & Levin, 2002). As far as is known, no events of an extreme magnitude occurred during this study.

Some reef fish larvae may have sufficient swimming ability to control their pattern of oceanic dispersal and then return to adult habitat (Leis & McCormick, 2002). Yet, swimming abilities will be useful only if larvae can detect cues that may guide them to appropriate settlement habitats (Doherty, 2006). Detection of visual, chemical and acoustic cues are thought to be limited to relatively small spatial scales (Leis, 2006). Although the swimming ability of late stage larval *C. julis* is unknown, it seems unlikely that recruitment patterns at these large spatial scales are determined by oriented swimming behaviour. More likely are the effects of stochastic processes associated with the Azores current system, source of considerable mesoscale variability (Santos *et al.*, 1995) and spatial variability in chlorophyll-*a* and water temperature (Bashmatchnikov *et al.*, 2004; Amorim *et al.*, 2009), which may ultimately produce spatial differences in larval availability through differential delivery patterns and larval mortality. This view, which puts greater emphasis on the physical processes and larval availability to explain the spatial recruitment patterns, has been suggested in previous multi-scale analyses of recruitment patterns (Fowler *et al.*, 1992; Vigliola *et al.*, 1998). While Fowler *et al.* (1992) also acknowledged the potential contribution of habitat selection, Vigliola *et al.* (1998), suggested that spatial recruitment variability observed for two coastal sparids was related to variable coastal circulation during the recruitment season.

The results of this study also suggest that factors determining larval availability and delivery may differ at scales of only 10s of km. Recruitment variability among adjacent reefs or islands is not uncommon (Eckert, 1984; Masterson *et al.*, 1997). Although the shortest distance between Pico and Faial Island is only 9 km, the channel between them is characterized by strong alongshore tidal currents (Duarte, 1997), which may potentially limit larval exchange and mixing between the two islands, increasing the potential for differences in larval availability and recruitment dynamics.

Island-scale (Faial Island)

Unlike the larger scale, the consistency of island-wide recruitment patterns at Faial suggests the influence of strong deterministic processes operating over the range of only a few km. Persistent island patterns have been documented from small atolls (Booth *et al.*, 2000) to 10s of km long tropical islands (Caselle & Warner, 1996; Schmitt & Holbrook, 1999; Hamilton *et al.*, 2006). Most authors reporting persistent recruitment patterns, even at larger spatial scales (Fowler *et al.*, 1992), speculated that these patterns reflect differential availability of pre-settlement fishes, habitat selection or a combination of both (Caselle & Warner, 1996; Hamer & Jenkins, 1997; Vigliola *et al.*, 1998; Holbrook & Schmitt, 2003). Microhabitat selection is more likely to influence fish populations when preferred habitat is limited (Wilson *et al.*, 2008), which was not the case in this study, which was designed to control as much as possible for variation in microhabitat across sites. Specifically, microhabitat (*e.g.* per cent cover of sand, bare rock, coraline algae and fleshy algae) did not differ between some of the 'poor' (*i.e.* P Norte) and 'good' (*i.e.* Feteira and Varadouro) recruitment sites. Sporadic but strong recruitment pulses at consistently

poor recruitment sites, such as P Norte, were also recorded, indicating that suitable habitat is available at those sites. If habitat is not strongly influencing the small scale, island-wide patterns, then what is?

Small-scale physical features (*e.g.* those acting at 1 to 10s of km), such as wind stress, localized upwelling and relaxation events, offshore jets, eddies, internal waves, tides, tidal bores and others, all may contribute to spatial and temporal variation in larval delivery (Carr & Syms, 2006). Many of these features can be spatially consistent, and as such, establish persistent spatial patterns of larval delivery (Cowen, 2002). Additionally, larvae may actively concentrate at particular depths and migrate vertically between stratified currents to remain nearshore (Paris & Cowen, 2004). Although present knowledge about coastal circulation around Faial is limited, alongshore currents in the channel are known to be fast (Duarte, 1997). This may cause the persistently low recruitment observed in the east shore sites (Doca and Ribeirinha), either by flushing larvae offshore or by limiting their ability to swim to nearshore settlement habitat. Moreover, the highest recruitment site (Varadouro) is located in the largest embayment on the island (Fig. 1), where surface water temperature (SST) is cooler and chlorophyll-*a* concentration is relatively higher than other locations (Tempera, 2008). In addition, the preliminary results of a hydrodynamic model forced by wind, tides, surface atmospheric flux and drifter data suggest that Varadouro Bay is on the island lee with relatively slower currents (M. Juliano, pers. comm.). Regions of weak currents as well as wake eddies along the leeward coast of other islands (Harlan *et al.*, 2002) have been suggested to facilitate larval retention (Boehlert *et al.*, 1992; Cowen & Castro, 1994; Swearer *et al.*, 1999; Hamilton *et al.*, 2006). The data presented here suggest that this may be the case for *C. julis*.

POPULATION DYNAMICS

No evidence was found for density-dependent regulation during early post-settlement stages, either over the first 2 weeks after recruits were first seen on the reef, or when cumulative recruitment was compared with YOY density. Although the relationship between recruitment and 2 week old fish was statistically less robust in 2003 (lower *n* as Ribeirinha was not monitored and fewer surveys were possible), it showed the same trend. This is in contrast with other studies that showed high density-dependent initial post-settlement mortality (McCormick & Makey, 1997; Caselle, 1999; Schmitt & Holbrook, 1999; Steele & Forrester, 2002). Given the 2 week interval between surveys, it is possible that some early post-settlement mortality was missed. While possible, if such early regulation did occur, it was moderate and not completely compensatory, because recruitment gradients were obvious at the time of the survey. Moreover, it has been recently demonstrated (White & Warner, 2007) that *per capita* mortality of *Thalassoma bifasciatum* (Bloch) settlers (a relative from the tropics with similar behaviour) decreased locally with group size, even though mortality was density dependent over larger scales. *Coris julis* recruits tend to aggregate during the first 2 weeks on the reef and group size is typically proportional to local abundance (J. Fontes, pers. obs.). Thus, it is possible that, as shown for *T. bifasciatum*, the negative effect of high density of *C. julis* at 'good' recruitment sites was balanced by the survival advantage of early post-settlement schooling behaviour. Finally, while initial high mortality is generally expected, not all species respond to density in the same way (Steele & Forrester, 2002).

Although there was no evidence for density dependence during early post-settlement stages, the decelerating curvilinear relationship found between average YOY density and adult population size suggests that the size of some adult populations (at relatively low recruitment sites) is limited by recruitment, whereas populations that typically experience high recruitment rates are likely to be limited by other demographic processes, *i.e.* density-dependent regulation. These results are consistent with a growing number of studies (Doherty & Fowler, 1994; Carr *et al*., 2002; Caselle *et al*., 2003; Minto *et al*., 2008). According to Forrester *et al*. (2002), it is not unusual for direct density dependence in one stage to be balanced by inverse density dependence in a previous life stage.

Density-dependent regulation is often attributed to predation and migration (Forrester *et al*., 2002). For example White (2007) found that *T. bifasciatum* mortality at sites with few grouper *Cephalopholis fulva* (L.) predators was inversely density dependent, whereas mortality was positively density dependent where this predator was most abundant. *Serranus atricauda* Günther, one of the most abundant carnivores in the Azores (Morato *et al*., 2000), were most abundant at high *C. julis* recruitment sites (P. Afonso, unpubl. data), potentially contributing to the observed density-dependent mortality effect. On the other hand, most reef fishes are known to undergo post-settlement ontogenic changes in feeding, exposure to predators and conspecifics, home range and mobility, all of which are likely to produce changes in competition and survival (McCormick & Makey, 1997). In particular, changes in mobility and home ranges may allow YOY to emigrate from high density sites, potentially modifying recruitment patterns (Forrester *et al*., 2002). Thus, the exact mechanisms causing density-dependent mortality for *C. Julis* remain to be studied in the Azores.

In summary, this multi-scale recruitment study demonstrates the difficulty with dichotomizing recruitment patterns as consistent or variable. The present study also showed consistent spatial recruitment patterns that indicate the importance of deterministic processes on *C. julis* recruitment at the island-scale, whereas interannual differences in magnitude and the spatial variability at the regional scale suggest that stochastic processes are important. Consistent spatial recruitment patterns, in particular the identification of potential recruitment hotspots, will have important implications for the effectiveness of future spatial management schemes including the design of networks of MPA.

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