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Larval growth, size, stage duration and recruitment success of a temperate reef fish

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ABSTRACT

Understanding the causes of variation in recruitment of marine fishes has been a central goal for marine ecologists, fishery scientists and resource managers over the last century. Although the idea that recruitment variability is linked to the pelagic environmental conditions that enhance larval growth, survival, and/or delivery is consensual, such relationship is poorly known for most species. In this study we analyzed patterns of recruitment and early life history of a temperate reef fish, *Coris julis* from the Azores archipelago to test the relationships between early life history and recruitment success over two consecutive years. Growth from hatch to larval age 30 d was the best predictor of recruitment, implying that fast growing larger-at-age larvae have a survival advantage and contribute more to high recruitment, supporting the “bigger-is-better” hypothesis. The “stage-duration” hypothesis and the predictions regarding the relationships between size at age (SAA), size at settlement (SAS) and recruit abundance were also partially supported. The results presented in this study highlight the importance of understanding the early life traits that determine recruitment and larval-survivorship patterns, especially early larval growth, as this may provide a basis for prediction of recruitment and thus management of resources.

1. Introduction

For most of the 20th century, researchers have operated on the belief that year-class strength (and recruitment) in marine fishes is determined during the larval stage (Leggett and Deblois, 1994). This link between recruitment and abundance or survival during early life of marine fishes is sufficiently well documented to justify a continued interest in factors regulating survival and abundance in the egg and larval stages (Leggett and Deblois, 1994). As a result, one of the major quests in fish biology and management has been to understand the mechanisms linked to highly variable larval survival and recruitment rates in fish populations (Pyper and Randall, 1997), which have major biological and economic implications for the management of commercial fisheries.

For marine organisms with complex life cycles, characteristics of larvae including size, growth rate and condition are key factors influencing both individual performance and abundance of older stages (Hamilton et al., 2008; Jenkins and King, 2006; Phillips, 2002; Robert et al., 2007). The relationship between growth rate and survival has been a focal point of numerous investigations (e.g. Bergenius et al., 2002; Campana, 1996; Hovenkamp, 1992; Meekan and Fortier, 1996; Meekan et al., 2006; Rice et al., 1993; Wilson and Meekan, 2002), many of which suggest that lower growth rates during the larval and juvenile stages could result in higher mortality.

It was almost a century ago that Hjort (1914) suggested, for the first time, that larval mortality could explain recruitment variability (termed the “critical-period” hypothesis). Specifically, Hjort hypothesized that year-class size in temperate fishes was determined by larval feeding success at the time of transition from yolk to exogenous feeding. More recent theories focus on the impact of both larval growth rates and predation on the variability in survival of cohorts, over a significant portion of their pelagic stage (Bergenius et al., 2002). These theories emerged based on observations that small changes in larval growth and mortality rates can generate order-of-magnitude or greater differences in annual recruitment (Houde, 2002; Shepherd and Cushing, 1980). The premise that larger individuals are usually less vulnerable to predation and thus more likely to survive than smaller individuals (Anderson, 1988; Miller et al., 1988; Rice et al., 1993) supported a parsimonious and simple view that places great emphasis on larval size as a factor in predation vulnerability, Miller et al. (1988) “bigger-is-better” hypothesis, and on growth rate as a controller of cumulative size-dependent predation mortality (see Fuiman et al., 2005). Accordingly, as feeding success increases, growth increases and the probability of mortality due to starvation and predation decreases (Hare and Cowen, 1997). Another obvious and important advantage of fast growth is a reduction in predation mortality not by increases in size but instead by reducing the time that larvae spend in a stage vulnerable to high mortality (Houde, 1987). Termed the “stage-duration” hypothesis (Leggett and Deblois (1994),

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this theory assumes that post-settlement mortality rates are lower than larval mortality rates, and that faster-growing larvae are able to abbreviate the pelagic stage duration by achieving competence earlier than slower-growing larvae. In other words, because the cumulative probability of lethal events (predation and starvation) occurring throughout high mortality pelagic stage increases with stage duration, cohorts spending less time in the plankton should produce strong recruitment events. Collectively, these theories are known as the general "growth-mortality" hypothesis (Anderson, 1988).

In summary, both the "bigger-is-better" and "stage-duration" hypotheses claim that growth rates are a critical determinant of larval survival. That is, survival is ultimately determined by factors that affect growth rates in the plankton (Takasuka et al., 2004). This paper has three objectives. First, we test whether overall pelagic growth is related to recruitment success by comparing recruitment magnitude with larval growth up to settlement. Second, we test the "bigger-is-better" and the "stage-duration" hypotheses by comparisons of the early life-history characteristics of newly settled fishes and corresponding recruitment magnitude. The "bigger-is-better" hypothesis is supported if larvae that grow faster up to some age threshold are associated with relatively high recruitment. Specifically, we use an age threshold of 30 d post-hatch. The "stage-duration" hypothesis is supported if larger recruitment pulses are associated with shorter larval lives. To conclude, we ask if SAS is a good predictor of recruitment success, that is, if the size advantage at threshold age is preserved up to settlement.

2. Methods

2.1. Study area and species

The Azores archipelago is a chain of nine volcanic islands and several islets in the North Eastern Atlantic (bounded by 37° and 40° N lat, 25° and 32° W long) (Fig. 1). Shallow habitat is limited and the surrounding water is deep. Most of the islands shores are exposed, except for some small bays and harbors. Oceanography is influenced by the Gulf Stream jet, and its southeastern branch generates the eastward-flowing Azores Current (Klein and Siedler, 1989). In general, productivity is low but localized upwelling associated with island slopes and seamounts enhances local production (Bashmatchnikov et al., 2004; Monteiro et al., 1996; Morato et al., 2008; Santos et al., 1995).

The rainbow wrasse, *Coris julis* (Linnaeus 1758; Pisces: Labridae) is a small temperate, moderately short-lived (average 2 to 4 years) shallow-water reef fish, and one of the most abundant species in the local reef fish community (Afonso, 2002). Like most wrasses, the rainbow wrasse is a pelagic spawner with planktonic larvae. Larvae have a long pelagic larval dispersal phase lasting up to 46 d (Raventos and Macpherson, 2001, personal observation) and a reef-associated juvenile and adult phase. Upon settlement, *C. julis*, undergoes metamorphosis over a period of about 4 d, as indicated by a metamorphic band visible on the otoliths (Raventos and Macpherson, 2001, personal observation) (Fig. 2). Spawning is very seasonal in the Azores, lasting for approximately 3 months (late May through late August; Afonso and Morato, unpublished data).

2.2. Recruitment surveys

We measured recruitment on four islands, Corvo (Western group), Faial and Pico (Central group), St. Maria (Eastern group) and one islet, Formigas (Eastern group) (Fig. 1). All sampling sites were established in sheltered bays on South facing shores, over small and medium size boulders covered with turf algae. Sites on Faial, Pico and St Maria were located in relatively large bays (a few km wide) while the Corvo site was located in a smaller bay (few hundreds of meters wide). The Formigas sampling area was located on the sheltered southwest shore (a few tens of meters across). Although some evidence suggests that the Faial site is within an area of localized upwelling, overall information on local circulation and productivity patterns is unavailable. All sites are adjacent to deep water due to the very steep island slopes. Distance between sites ranged from 30 to 600 km. In August 2004 and 2005 we visually surveyed recruits on 5 to 6, 20×1 m transects. Transects were relocated in the second year using GPS and familiar topographic features. Once the transect lines were in place, the same diver would swim at a constant low speed counting all recently settled *C. julis* (<20 mm) along the 20 m^2 area.

We consider recruitment magnitude as the observed average density of recently settled fish (under 20 mm) hereafter termed "recruits" and its density as "recruit density". We assumed post-

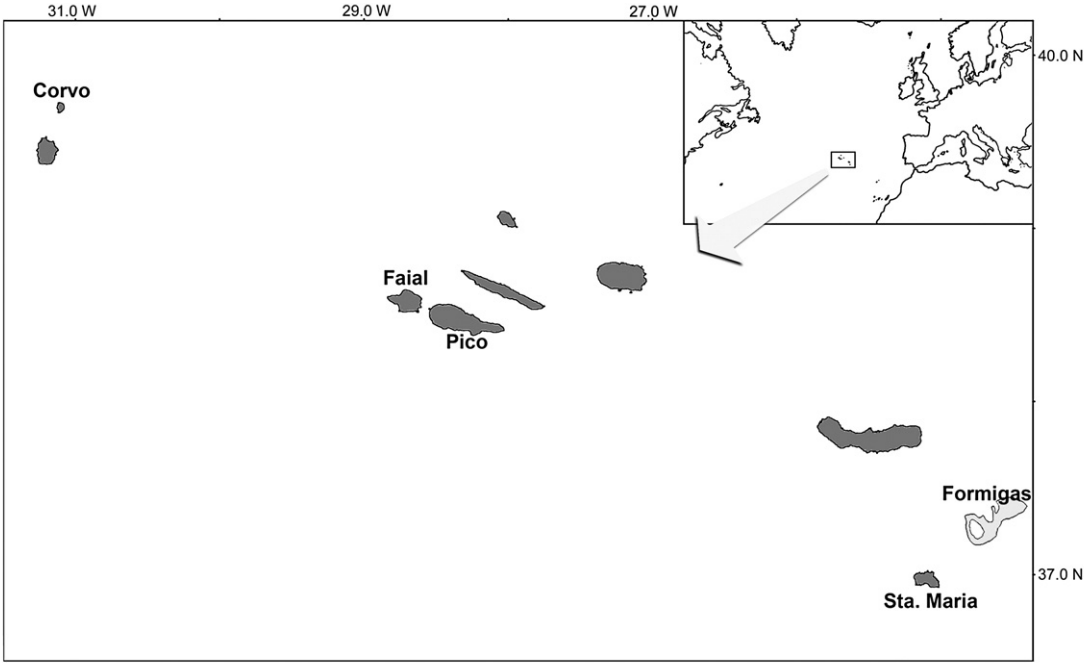

Fig. 1. Map of Azores Archipelago (NE Atlantic) showing the locations of the sites.

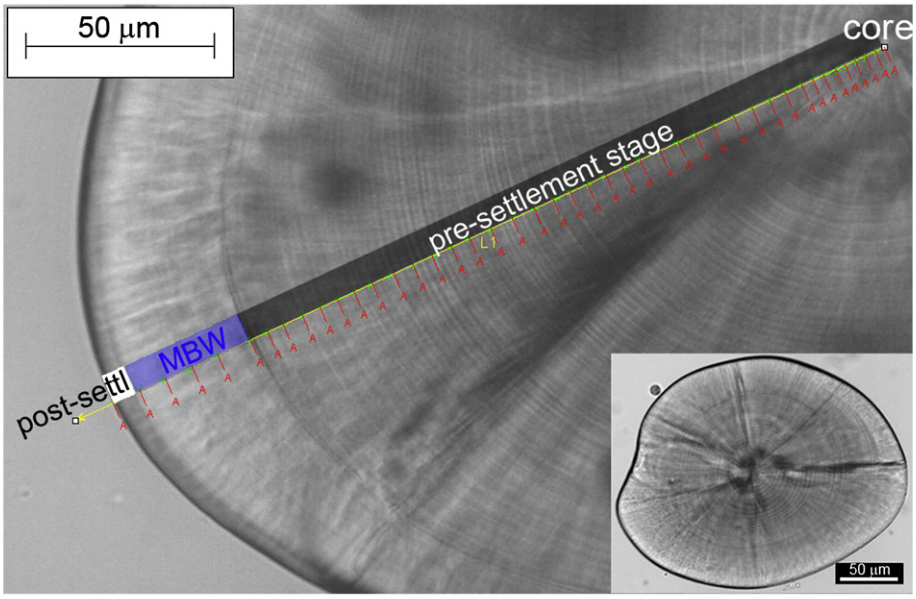

Fig. 2. Sagitta from *C. julis* recruit collected in the Azores Islands. Red tick marks indicate daily increments. MBW = metamorphic band width and post-settl = otolith material deposited after emergence.

settlement mortality and emigration to be constant between sites. If this assumption was not realistic, we would expect differential (e.g. density-dependent) post-settlement mortality to reduce any naturally occurring recruitment differences before recruits were counted, and not to generate larger differences.

In 2004, due to inclement weather conditions and limited vessel time, we collected recruits but no fish counts were possible at Formigas and Corvo. Alternatively, we estimated recruit density from the relationship between CPUE (number of recruits collected per dive time) and recruit density measured at other four sites ($R^2 = 0.72$, $p < 0.01$, CPUE = 11.08 density − 1.82). Because we cannot verify the linear nature of this relationship at higher densities than those used in the model, (approximately 30 recruits/transect) we assumed that the estimated density at Formigas should be no less than the highest density in the model, thus our estimated densities are conservative and likely underestimated (Fontes et al., 2009).

2.3. Otolith collection and analysis

Recruits were collected by divers using aquarium dip nets, kept in a fine mesh bag and placed in 50 ml plastic jars with 96% ethanol upon arrival on the boat. Recruits were collected near the transects after visual surveys were completed. Standard Length (SL) of each recruit was measured to the nearest 0.1 mm, and sagittal otoliths were dissected. The right otolith was stored in medium viscosity immersion oil. Otoliths were kept in oil for no less than two weeks (to enhance ring clarity) before excess oil was removed, after which they were embedded in thermoplastic resin and mounted on a glass slides. Embedded otoliths were later polished using (9 μm) diamond micro film.

The daily deposition of growth increments in larvae and early juvenile otoliths has been validated for numerous species, including many wrasse species and used as a proxy for somatic growth (Bergenius et al., 2002; Campana, 1996; Hare and Cowen, 1997; Searcy and Sponaugle, 2001; Takasuka et al., 2004). Raventos and Macpherson (2001) assumed that *C. julis* from the Mediterranean also formed daily increments and they classified the settlement mark as type II (a zonal settlement mark with a transition zone where post-settlement increments were wider than pre-settlement increments) (Fig. 2). Since the ring patterns we observed were very similar to those found for most wrasses that have been validated (e.g. Victor, 1982), we assumed that the increments were deposited on a daily basis. In this study, we used otolith growth as a proxy for somatic growth. We found a strong linear relationship between sagitta radius and standard length of *C. julis* recruits ranging from newly settled to over a month old ($r^2 = 0.93$; $p < 0.0001$, $n = 562$), as well as a strong positive correlation between TL of recently settled fish (0 to 2 d post emergence) with otolith radius to settlement mark ($r^2 = 0.77$; $p < 0.0001$; $n = 163$).

Daily increments were counted and measured along the longest axis of the otolith, from core to outer edge (Fig. 2), using transmitted light microscopy with a video camera connected to a PC with *ImagePro* 4.5 Image analysis tool kit. Otoliths were read once by a single reader after calibration by repeatedly reading a random set of 30 otoliths until the difference between counts was below 10%.

2.4. Larval growth, size and PLD

We randomly selected and analyzed the otolith microstructure of 20 to 30 recruits from each site. The mean PLD (pelagic larval duration) of the recruits pooled from 2004 and 2005 was 34 ± 3.6 d, which is the minimum amount of time all larvae have to be in the plankton before settling. Therefore we chose the average PLD minus the standard deviation, (i.e. 30 d), as the threshold age because this period can be compared for all recruits. Otolith radius from core to the 30th increment was used as proxy for size at age (SAA), which is directly proportional to growth to age (growth 30 d). Otolith radius from core to settlement mark (SM) was our measure of size at settlement (SAS), and PLD was given by the number of increments from core to SM (Fig. 2). Growth trajectories (Fig. 3) were derived from average daily increment widths for each site.

2.5. Statistical analysis

Linear regression analysis was used to compare recruitment with average daily larval growth (larval growth), SAA (size at age), SAS (size at settlement) and PLD (pelagic larval duration). All data were $\log_{10}(x+1)$ transformed to conform to the assumptions of normality and to address the large numbers of zeros in the recruitment data set, as suggested by Quinn and Keough (2002).

Given that daily growth data are auto-correlated because the same individuals are compared at different ages, repeated-measures MANOVA was used to test for among-site differences in growth

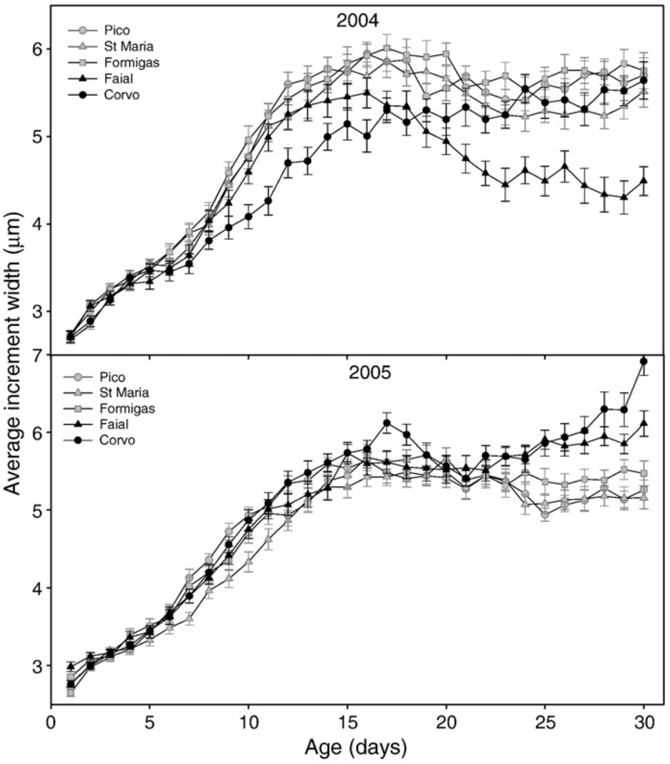

Fig. 3. Average increment width at age as measured on sagittal otoliths of larvae sampled in 2004 and 2005. Mean values ± SE are shown.

trajectory (Meekan and Fortier, 1996). We used Pillai's Trace as the test statistic because it is considered a more robust statistic than Wilk's Λ in the case of unequal sample sizes (Robert et al., 2007). Multiple regression analysis was performed between SAS (dependent variable) and PLD and growth 30 d (independent variables), for each year. Average growth from hatch to settlement could not be used in the model because averaging the width of otolith daily increments from the core to the SM is the same as dividing SAS by PLD, not conforming to the assumptions of independency.

Simple and multiple regression analysis, *t*-tests, one-way ANOVA and repeated-measures MANOVA were performed according to Quinn and Keough (2002), using JMP 7.0 statistical analysis software.

3. Results

We found that average daily growth rates, from hatch to settlement, differed among sites and between the two years (two-way ANOVA, site × year interaction, $p<0.0001$, $F=15.033$, $n=259$). Daily growth trajectories from hatch to age 30 d were initially slow, rapidly accelerated to a peak around 15 to 20 d after hatching (Fig. 3). At this point trajectories from different sites diverged, some declined, others remained the same while some increased further. Growth trajectories were significantly different among sites (repeated-measures MANOVA; 2004 $p<0.0001$, $F=2.61$, Pillai's trace $=0.68$; 2005 $p<0.0001$, $F=3.45$, Pillai's trace $=0.86$), yet the spatial pattern was not consistent between years. Recruits sampled at Faial and Corvo in 2004, showed the slowest growth trajectories in 2004, while in 2005, the same sites showed the highest growth trajectories.

Recruitment magnitude across the Archipelago was highly unpredictable between years. A clear longitudinal gradient across the Archipelago, spanning 600 km between sites, was observed in both years, but in opposite directions. For example, Corvo had the lowest overall density in 2004 and the highest in 2005. The high density observed at Formigas in 2004 was not observed in the next year (for more detail, see Fontes et al., 2009).

We found positive relationships between average larval growth from hatch to settlement, and recruitment magnitude, although the relationship was not significant in 2005 (2004: $r^2=0.86$ $p=0.02$, $F=18.83$) (Fig. 4). Average larval growth during the first 30 d post-hatch (growth 30 d) was a much better predictor of recruitment magnitude in both years (2004: $r^2=0.92$; $F=36.44$; $p=0.009$; 2005: $r^2=0.94$; $F=48.52$; $p=0.006$) (Fig. 5) despite strong inter-annual spatial variability in recruitment patterns. For example, Faial and Corvo had the lowest recruitment and lowest growth 30 d in 2004, yet in 2005 they presented both the highest recruitment and the highest growth 30 d.

In 2005 we found evidence to support the prediction that cohorts that grow faster during the first 30 d in plankton, tend to settle at relatively younger ages (shorter PLD) and in relative high numbers, as PLD was negatively correlated with recruitment ($r^2=0.91$, $F=30.43$; $p=0.017$) (Fig. 6). However, this was not the case in 2004 (Fig. 6). In 2004 between site differences in PLD were marginal (ANOVA, $p=0.04$, $F=2.59$, $n=133$), compared to 2005, when among-site differences were highly significant (ANOVA, $p<0.0001$, $F=2.59$, $n=126$). Post hoc tests revealed that average PLD observed in 2004 only differed significantly between Pico and Formigas. Inter-annual differences in PLD were also significant ($t=-2.03$; $p=0{,}042$; $n=280$).

Larger individuals at age 30 d (SAA) tended to preserve the size difference up settlement in 2004 (Fig. 7), resulting in relatively larger settlers (SAS) ($r^2=0.29$, $F=46.1$, $p<0.0001$) associated with high density sites (Fig. 8). Conversely, on the following year this relationship was best described by an inverse linear function

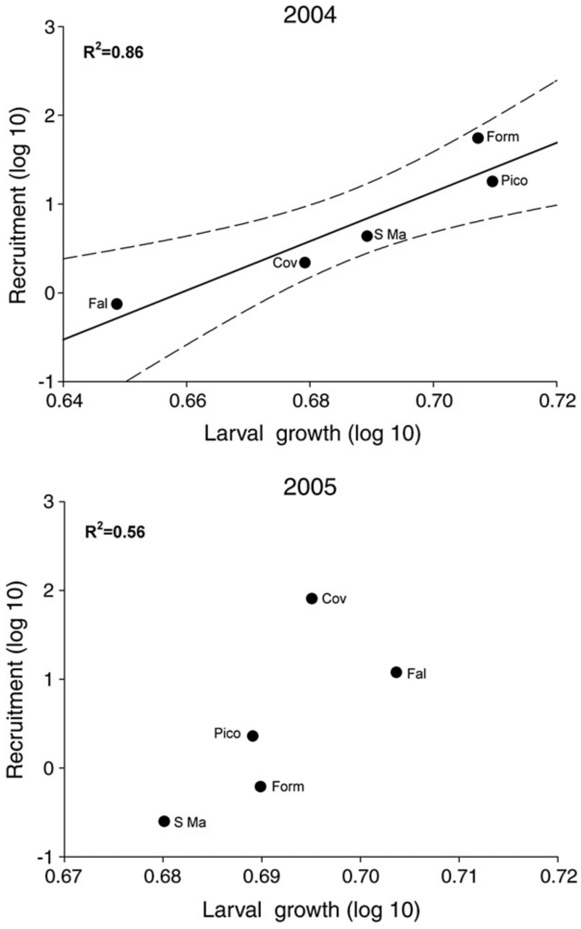

Fig. 4. Relationship between average growth rate from hatch to settlement and recruitment of *C. julis* in the Azores. Dashed curves represent the 95% confidence limits for a linear regression.

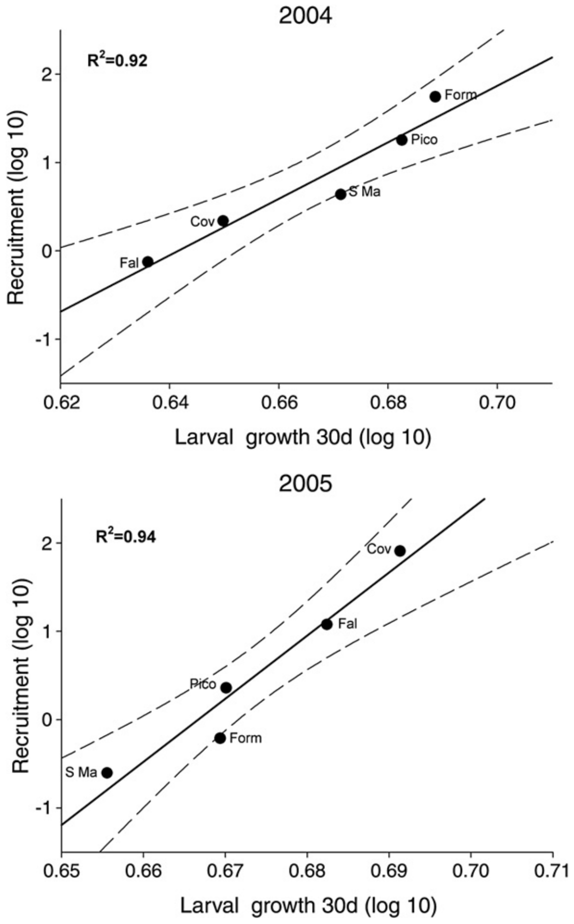

Fig. 5. Relationship between average growth rate from age 0 to 30 d post-hatching and recruitment of *C. julis* in the Azores. Dashed curves represent the 95% confidence limits for linear regressions.

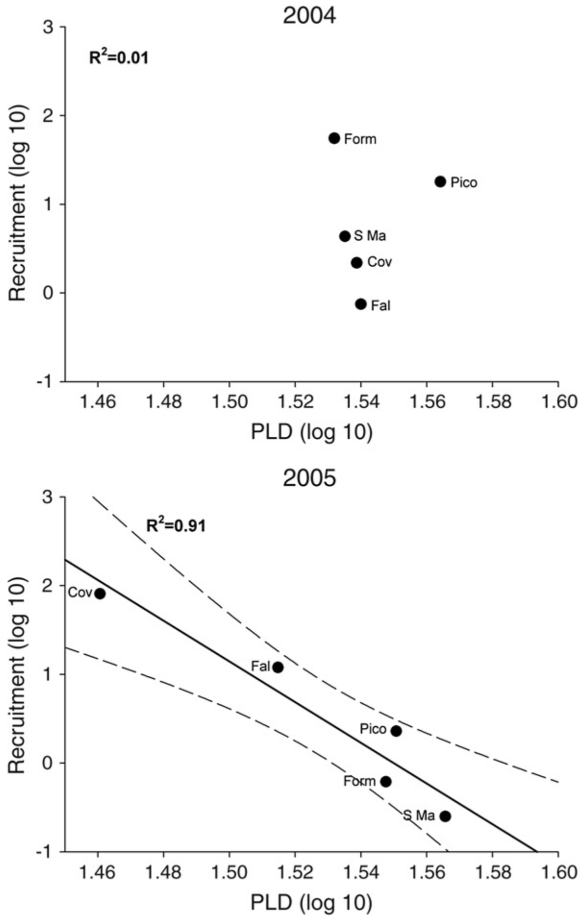

Fig. 6. Relationship between average pelagic larval duration (PLD) and recruitment of *C. julis* in the Azores. Dashed curves represent the 95% confidence limits for linear regressions.

($r^2 = 0.82$, $F = 13.5$, $p = 0.034$) (Fig. 8), while the size difference at age 30 d was not related to size at settlement (Fig. 7).

We found quite a good fit (2004, $R^2 = 86\%$ and 2005, $R^2 = 89\%$) of the variance explained by the two independent variables for both years (2004, $F = 359.23$, $p < 0.0001$; 2005, $F = 501.60$, $p < 0.0001$). The resulting standardized regression equations were: log SAS = 0.059 + 0.97 × log growth 30 d + 0.98 × log PLD and log SAS = 0.064 + 1.07 × log PLD + 0.74 × log growth 30 d, for 2004 and 2005 respectively, indicating that PLD explained most of SAS variation observed in 2005, while in 2004 both independent variables contributed in more similar proportions to SAS variation in 2004.

4. Discussion

Our data clearly support the predictions that pelagic growth is positively correlated with recruitment magnitude and, that early growth should have a disproportionally larger effect on larval survival up to settlement than pre-settlement growth. Growth from hatch to age 30 d was strongly correlated with recruitment in two consecutive years and was a better predictor of recruitment magnitude than average growth from hatch to settlement, despite the contrasting inter-annual recruitment patterns and growth trajectories observed. Still, as expected, when average PLD was similar between sites (2004), growth over the entire larval stage was a reasonable predictor of recruitment magnitude, but not when differences were large (2005).

The idea that growth during a fraction of the larval period is the main determinant of survival of marine fishes is not new (Leggett and Deblois, 1994). However, despite being widely accepted, the view that survival of a cohort is directly related to growth rates during the pre-recruitment period for marine fish (Ottersen and Loeng, 2000) is rarely straightforward to demonstrate (but see e.g. Bergenius et al., 2002; Meekan and Fortier, 1996; Meekan et al., 2006; Takasuka et al., 2003; Theilacker et al., 1996). There are many difficulties in consistently producing field evidence to unequivocally test this view. One of the potential problems is that average fast growth can either reflect fast growth of the population, under optimal conditions of temperature and food, or the removal of slow-growing larvae by predators (Robert et al., 2007). Takasuka et al. (2003) clarified this by showing that predator's stomachs contained mostly slow-growing Japanese anchovy larvae, relative to the “surviving” larvae sampled in the same area.

However, such methodologies are rarely feasible due to the difficulty of following a single cohort of pelagic small organisms over periods of weeks to months. Another reason why most field studies fail to provide clear results is the difficulty of disentangling the effects of dispersal and mortality within the plankton (Heath, 1992; Helbig and Pepin, 1998a,b). For example, when monitoring a cohort of pelagic larvae in a dynamic ocean, if sampling scales are not proportional to advection scales, mortality estimates may be corrupted by transport effects if decreasing larval density is attributed to mortality when, in fact, larvae are thriving elsewhere. Thus, dispersion out of the sampling domain should be discriminated from true natural mortality when measuring in-situ survival rates (Helbig and Pepin, 1998a). For this reason, some caution must be taken when assuming that recruit availability estimates for a given area directly reflect larval survival, especially when dispersal patterns are unknown and multiple sites are being compared.

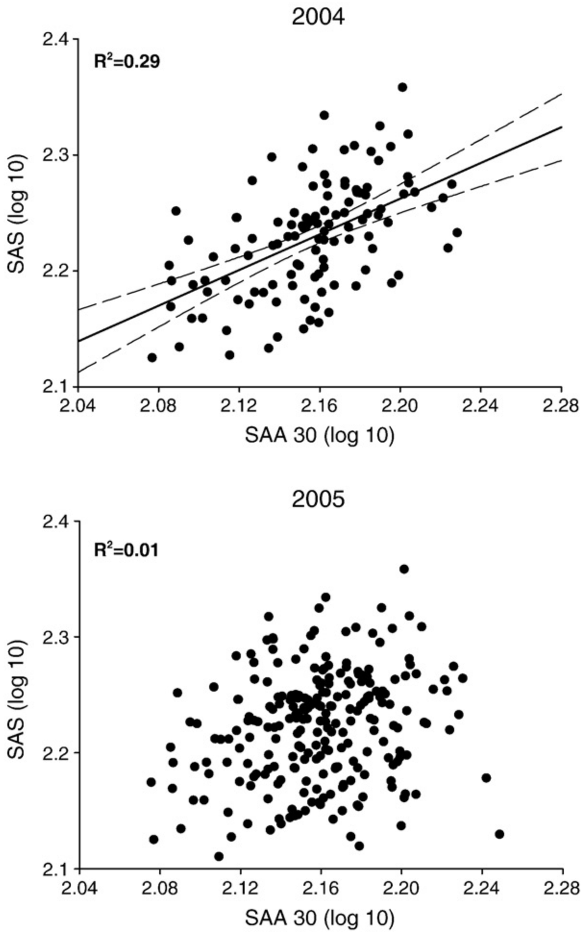

Fig. 7. Relationship between average otolith size at settlement (SAS) and otolith size at age (SAA) 30 d post-hatch (measured as otolith radius to increment 30). Dashed curves represent the 95% confidence limits for the regression.

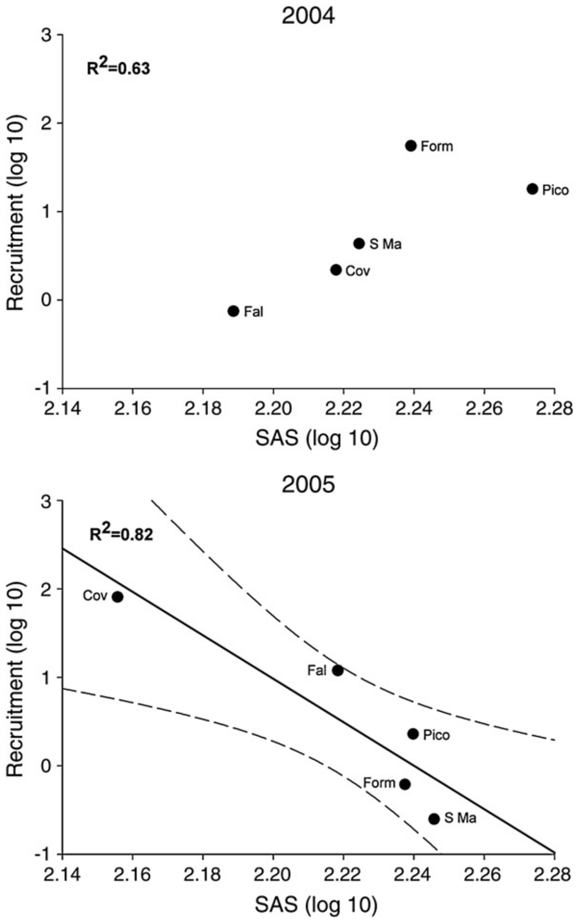

Fig. 8. Relationship between average otolith size at settlement (SAS) (measured as otolith radius from core to settlement mark) and recruitment. Dashed curves represent the 95% confidence limits for the regression.

Given that *C. julis* larval growth 30 d and recruitment were strongly correlated, it is likely that recruit abundance patterns reflect regional differences in the larval environment, which probably allowed some cohorts to grow faster and survive better (presumably due to size-related survival advantages (Bailey and Houde, 1989; Miller et al., 1988)). However, until we are able to individually track larvae in the plankton, we must also consider the possibility that growth–recruitment relationships result from co-variation with other variables. For example, the same physical features that aggregate food may also aggregate larvae and predators (Mace and Morgan, 2006; Paris and Cowen, 2004), which in turn could produce spatial differences in larval availability, as the high density food rich larval patches may favor the delivery of large numbers of fast growing larvae to some sites relative to others. This would result in a pattern of fast growing larvae associated with strong recruitment events, even in a non size-selective mortality scenario. Nevertheless, considering that size is a function of growth, i.e., fast growth up to age 30 d leads to relatively larger 30 d old larvae, it can be argued that size at age 30 d is positively correlated to the magnitude of *C. julis* recruitment, supporting the "bigger-is-better" hypothesis.

A major implication of these results is that growth and size variability following the 30 d post-hatch age threshold is probably less relevant to larval survival than earlier growth. Given that size is cumulative, and assuming that mortality is size dependent, even if growth rates decrease after size threshold is reached, individuals will only become larger and presumably less vulnerable to predation and starvation (Bailey and Houde, 1989; Miller et al., 1988). Nonetheless, even the largest larvae at threshold age still have some probability of encountering fatal events, such as predation, starvation or offshore advection (Leggett and Deblois, 1994), and that probability is cumulative, increasing with the pelagic stage duration (Cowan et al., 1996). Ultimately, high cumulative mortality resulting from long PLD, may obscure growth related survival advantages from early fast growth. According to the "stage-duration" hypothesis (Leggett and Deblois, 1994), we expect that cohorts that grew faster during the first 30 d in plankton and were able to settle at relatively younger ages should result in strong recruitment events. The strong negative correlation between PLD and recruitment found in 2005 clearly supports this idea, while the lack of relationship in 2004 probably resulted from low variability in average PLD among sites. The inability to unequivocally support the "stage-duration" hypothesis is recurring (e.g. Bergenius et al., 2002; Hare and Cowen, 1997; Takasuka et al., 2004), which is probably due to the fact that, in most cases, growth selective predation is more important than stage duration (Takasuka et al., 2004).

Size at settlement is a function of growth and larval stage duration (Denit and Sponaugle, 2004). For this reason relatively slow growing, small at age 30 d individuals may become large settlers (provided PLD is long enough), as may large at age fast growers with relatively short PLDs. However, we only expect SAS to be a good predictor of recruit abundance when SAA and SAS are positively correlated, that is, if SAS incorporates the size/growth survival advantages of large SAA, as seems to be the case in 2004. Conversely, if large SAS results from extended PLD rather than from early fast growth (large SAA), then the potential survival advantage of large body size is likely to be compensated by higher cumulative mortality expected for long PLDs (Leggett and Deblois, 1994). In addition, our results also suggest that the nature of the relationship between SAS and recruit abundance probably reflects the relative contribution of growth and PLD to size at settlement. For example, in 2005, when large size at settlement mostly resulted from long pelagic stages, SAS was negatively correlated with recruitment.

Finally it is important to note that the different combinations of early life histories resulted in two different demographic patterns, one where settlers from high recruitment sites were composed of relatively large individuals (Fig. 8/2004), and another where high recruitment sites were mostly comprised of relatively small settlers (Fig. 8/2005). Given the recent evidence that larval history and individual traits of settlers can carry over to influence individual fitness in subsequent life stages (e.g. Booth and Beretta, 2004; Hamilton et al., 2008; Miller et al., 1988; Searcy and Sponaugle, 2001), these different outcomes may have important post-settlement demographic implications with relevance for management and conservation efforts.

In summary, understanding the factors that determine recruitment and larval-survivorship patterns, in particular the role of larval growth rates, may provide the basis for prediction of recruitment with important implications for management and conservation. However, some caution must be taken when comparing recruitment success and larval growth variation; depending on what portion of early history is considered, different predictions may arise. In addition to understand the consequences of variable larval traits on pelagic survivorship and settlement, future efforts need to clarify the impact of such traits on post-settlement individual performance and future demography.

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