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## Dispersal strategies in sponge larvae: integrating the life history of larvae and the hydrologic component

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**Abstract** While known to be uniformly non-feeding, short-lived, and potentially short dispersing, sponge larvae display different behaviours (swimming ability and taxis). Our aim was to show whether sponge larvae with different behaviours exhibit different dispersal strategies under variable intensity of water movements. We first assessed the distribution of larvae of six taxa: Dictyoceratida spp., *Dysidea avara*, *Crambe crambe*, *Phorbastenacior*, *Scopalina lophyropoda*, and *Cliona viridis*, collected through plankton sampling, and the abundance of the corresponding adult sponges across three hard bottom communities and a sandy bottom from a north-west Mediterranean rocky shore. We then tested adult–larvae couplings (abundance of larvae vs abundance of adults) under increasing levels of water movements (surge) to assess the importance of this environmental factor in driving differences in dispersal strategies. Adults of Dictyoceratida spp., *D. avara*, and *P. tenacior* were most abundant in semi-dark caves (SDC), *C. crambe* and *C. viridis* in communities of sciaphilic algae (SA), whereas the distribution of *S. lophyropoda* was extremely patchy, being present almost only in the SA community of one of the five stations studied. Larvae of Dictyoceratida spp. and *P. tenacior* were more abundant in the SDC, whereas *D. avara* and *C. crambe* were homogeneously distributed across the communities. The larvae of *C. viridis* were more abundant in the SA communities and the *S. lophyropoda* larvae were mostly present in one station

and one community (SA). Increased water movement did not modify the adult–larvae coupling for Dictyoceratida spp., *D. avara*, and *C. crambe*, whereas it broke up the positive association for *P. tenacior* and to some extent *S. lophyropoda*. For *C. viridis*, possible variability in adult–larvae coupling was not tested because the larvae were collected on only one day under calm sea conditions. We confirm that efficient-swimming larvae with some cue response can actively counteract hydrodynamic forces and highlight the importance of both larval behaviour and environmental conditions in determining small-scale patterns of dispersal.

**Keywords** Behaviour · Marine invertebrates · Mediterranean Sea · Plankton · Water movement

### Introduction

Dispersal by means of propagules is a crucial stage in the life cycle of both terrestrial and marine organisms with sessile or sedentary adults (Grosberg 1987; Raimondi 1991). Seeds and spores are more often passively dispersed than other propagules such as larvae, which are capable of behaviour and can thus search to a greater or lesser degree for suitable settlement habitat.

The importance of larval behaviour in determining dispersal patterns depends on the spatial scale of the observation. On wide geographical scales (e.g. continents), dispersal can be modelled as pure passive transport (e.g. Gilg and Hilbish 2003) while behaviour becomes more important as we reduce the approximation to smaller spatial scales (e.g. habitat) (Abelson and Denny 1997; Underwood and Keough 2002). Even at the scale of the habitat, however, all larvae have a “hydrodynamic limit” (sensu Underwood and Keough 2002) beyond which they act as passive particles. It is difficult to establish this limit under field conditions because most larvae cannot be visually followed underwater (but see Olson 1985; Stoner 1990, 1992; Leis et al. 1996), and because of the complexity of larval tracking in general

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(Levin et al. 1993). Nevertheless, and independently from the spatial scale, the behaviour exhibited by larvae in natural conditions is crucial to the distance of dispersal. Depending on their inherent responses to light, gravity and chemical cues, and individual swimming ability, larvae may exhibit either wide dispersal or retention (see Olson and McPherson 1987).

It is difficult to create a generalised framework to characterise larval dispersal because of the variability of the environmental situations (Keough and Black 1996). Detailed oceanographic models can be useful tools to predict dispersal trajectories of larvae (e.g. Gilg and Hilbish 2003). However, larval behaviour may be at least as important to dispersal as oceanographic processes, and it needs to be elucidated and incorporated into models of larval dispersal (Metaxas 2001; Fisher 2005).

In subtidal rocky shores, for instance, most larvae have the ability to remain close to slow moving water layers near the substrate, avoiding being transported to the mainstream flow by eddy diffusion (Graham and Sebens 1996; Underwood and Keough 2002). With calm water movement, a boundary layer establishes close to the substrate and small particles such as larvae, which are released from the substrate, are likely to be “trapped into the layer” (Svane and Young 1989; Graham and Sebens 1996). When water flow increases (e.g. an oscillatory movement), the particles are more easily transported to the mainstream flow (Graham and Sebens 1996). Larval behaviour (namely swimming ability plus taxis) and the length of free-swimming phase become consequently especially important in determining the extent of dispersal in such environments.

While they are thought to display an ability to swim close to parental habitats to a certain extent, most marine invertebrate larvae are weak swimmers and act as passive particles on horizontal scales (Abelson and Denny 1997; Burdett-Coutts and Metaxas 2004). Hence, it is important to know their “hydrodynamic limit” in order to predict their dispersal under the different physical conditions that larvae may encounter.

Many marine invertebrates produce relatively small numbers of lecithothrophic short-dispersing larvae (Jackson 1985). Because of the reduced duration of the planktonic life and their low numbers compared with planktrophs, it is improbable that lecithothrophic larvae disperse far away from the habitats of release or hatching. Many groups include representatives with feeding and non-feeding larval stages, and differences in dispersal strategies may be strongly linked to this character. Sponge larvae are ideal organisms to test dispersal strategies because they are uniformly non-feeding and short-lived (except for rare known exceptions).

Mariani et al. (2003) have shown that assemblages of sponge larvae remain in the immediate vicinity of parental habitats on a northwest Mediterranean rocky shore. Retention seems the most probable pattern for sponge larval dispersal in the field since they reputedly live only a few hours in the plankton (Maldonado and Bergquist 2002) and have virtually never been collected in off-shore

plankton (Mariani et al. 2003). Although they lack a nervous system (Maldonado et al. 2003), sponge larvae have shown different responses to light stimuli and different swimming speeds in the laboratory (Bergquist and Sinclair 1968; Maldonado and Young 1996; Maldonado et al. 2003; Mariani et al. 2005a) and are likely to respond differently to the variable hydrodynamics that they encounter under field conditions.

We aimed to characterise the dispersal strategies for six different larval types belonging to several different sponge taxa. The sponge larvae were collected through plankton samplings conducted over 2 years across neighbouring benthic habitats, one sandy bottom and three differently illuminated rocky surfaces inhabited by different assemblages of benthic algae and invertebrates (Mariani et al. 2003). We wanted to test if sponge larvae with different behaviours showed different patterns of distribution under the effect of variable intensities of seawater movements. To this end, we first compared both the abundance and distribution of the larvae of each taxon with that of their respective adults across the habitats studied. We then ascertained the strength of adult-larvae couplings under varying magnitudes of water movement to determine the importance of such environmental factor in driving different dispersal strategies.

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## Materials and methods

### Study site and organisms

The study was conducted in the 70-year-old artificial reef that protects the Blanes Harbour (northeast Spain, northwest Mediterranean Sea). The breakwater is about 300 m long and is constituted by large boulders isolated from other rocky bottoms by a sandy-gravel bottom at 13 m. The boulders are concrete 4×2×1-m parallelepipeds colonised by rich assemblages of benthic organisms. The upper sides of the boulders were dominated by photophilic and semi-sciaphlic algae (PA), the lateral sides had a community of sciaphilic algae (SA) composed of fleshy and crustose algae and associated encrusting invertebrates (mostly sponges and bryozoans). Some boulders overlap each other to form small caves. Overhangs and lateral walls in the caves were dominated by sessile invertebrates such as sponges and bryozoans characteristic of semi-dark caves (SDC) (see Uriz et al. 1992; Mariani et al. 2005b for a description of these communities). Light diffused to different extents on different aspects of the boulder: the upper sides were the most illuminated followed by the lateral sides, while the caves received the least illumination (see Mariani et al. 2005b). Light intensity at the sandy bottom (see below) did not differ significantly from that recorded on the PA communities (Mariani 2002).

Five sampling stations ~30 m apart (from ~5 to ~40 m) were haphazardly established along the breakwater at average depths of ~8 m. Each station consisted

of three haphazardly chosen communities on neighbouring (at the same depth) boulders (a PA, a SA, and a SDC) and a portion of the sandy bottoms (SB) in front of such communities (~5 m apart). The choice of the communities and the stations as well as the effectiveness of the sampling design and methods have been illustrated and justified elsewhere (Mariani et al. 2000, 2003, 2005a, b).

The class Demospongiae comprises the highest numbers of known species among Porifera and has brooding and oviparous species with a variety of larval types (Boury-Esnault and Rützler 1997; Maldonado and Bergquist 2002). Six sponge taxa were chosen for this study from the 20 described in Mariani et al. (2005a) (5 viviparous and 1 oviparous taxa): Dictyoceratida spp., *Dysidea avara*, *Crambe crambe*, *Phorbas tenacior*, *Scopalina lophyropoda*, and *Cliona viridis*. The rationale for the choice of these organisms was established on the following features: the interest of the species (frequency and ecological importance), the current knowledge of larval natural history, a minimum number of larvae for statistical analysis, and the possibility to test differences in dispersal strategies between species phylogenetically related (see later).

The taxa studied are distributed either exclusively in the Mediterranean Sea or both in the Mediterranean and Atlantic Ocean. Larval life span is generally short (<3 days) although 15-day free-life periods have been observed in the laboratory for larvae under adverse conditions (M.J. Uriz, personal communication). The larvae of the species chosen here (see Table 1) display different behaviours in the laboratory (Uriz et al. 1998; Maldonado et al. 2003; Mariani et al. 2005a). Thus far, there is no evidence from cellular or experimental studies for the existence of chemotaxis in sponge larvae, and photoreponse is the only larval taxis to have been documented in the literature (Leys and Degnan 2001; Maldonado et al. 2003). Hence, we predict that larval dispersal strategies should vary among the species depending on the interaction between individual characteristics of larvae (i.e. taxis and swimming ability) on the one hand (see Mariani et al. 2005a) and the hydrodynamics encoun-

tered during the swimming phase on the other. The resulting dispersal strategies were tested using adult-larvae couplings as below.

The larvae of the taxon Dictyoceratida spp. very likely belonged to the species *Ircinia oros* and *Cacospongia mollior*. We could not distinguish the larvae of the two species by external features and behaviours (see Mariani et al. 2005a for details). They are actively swimming, photophobic parenchymellae (see Maldonado et al. 2003; Mariani et al. 2005a; Table 1) which are continuously released between July and September at the study site (Mariani et al. 2005a). The adults of both species inhabit the same habitats (SDC communities). For these reasons and in the context of the present study, we will consider *I. oros* and *C. mollior* as a single taxon (Dictyoceratida spp.).

The larvae of *D. avara* share both swimming ability and external morphology with larvae of the Dictyoceratida spp. (same order). Nevertheless, they show positive phototaxis in the laboratory (Mariani et al. 2005a; Table 1). At the study site, the larvae of *D. avara* were released from late June to late August. The adults seem to mainly colonise the SA and SDC communities.

The larvae of *C. crambe* can continuously change their morphology from elongated to spherical ovoids (Uriz et al. 1998, 2001; Mariani et al. 2005a). They alternate rather active swimming with passive buoyancy and do not show significant response to light during the swimming phase (Uriz et al. 1998; Table 1). Larvae are released from mid-July to early September (Mariani et al. 2005a). Adults of *C. crambe* colonise photophilic and sciaphilic habitats to different extents in the north-west Mediterranean (Becerro et al. 1994) and were more abundant in the SA communities at the study site.

The larvae of *P. tenacior* show fairly negative response to light and alternate active swimming with crawling onto the bottom of Petri dishes in the laboratory (Mariani et al. 2005a; Table 1). While to different extents, these larvae can constantly change their morphology whilst swimming. They are released almost continuously from mid-July to early November. Adults of *P. tenacior* mostly appear in the SDC communities.

**Table 1** Resume of the information available (mainly from Mariani et al. 2005a) on the morphology, main behaviour, and periods of larval release for the taxa studied

Taxon	General morphology	Phototaxis	Swimming efficiency	Release period
Dictyoceratida spp.	Brown dark ~800 µm parenchymella with posterior flagellar tuft	Negative	Very high	July to September
<i>Dysidea avara</i>	Pink whitish ~800 µm parenchymella with posterior flagellar tuft	Slightly positive	Very high	June to August
<i>Crambe crambe</i>	Red ~1.5 mm parenchymella variable in shape	Absent	Weak (passive buoyancy depending on variable morphology)	July to September
<i>Phorbas tenacior</i>	Grey whitish ~500 µm parenchymella variable in shape	Negative	High to weak (depending on variable morphology)	July to October
<i>Scopalina lophyropoda</i>	Orange ~1.2 mm parenchymella uniformly flagellated	Absent	Weak	June to August (discontinuous)
<i>Cliona viridis</i>	Yellow ~350 µm parenchymella uniformly flagellated	Absent	Weak (more a crawler)	June (very punctual)

The larvae of *S. lophyropoda* are weak swimmers and do not show any clear phototaxis (Mariani et al. 2005a; Table 1). Although taking place from late June to late August, the period of larval release is rather discontinuous (Mariani et al. 2005a). At the study site *S. lophyropoda* seems exclusively present in the SA communities.

The oviparous species *C. viridis* releases eggs very punctually in spring and larvae can be found ~2 days after spawning (Mariani et al. 2001). The tiny larvae are weak swimmers and do not show any phototaxis (Table 1). At the study site, the species was present elsewhere on the boulders, but mostly in the PA and SA communities (Mariani et al. 2000).

#### Assessing the hydrodynamics at the study site

The study site was exposed to winds blowing between 80°NE and 225°SW (Mariani 2003). Increments in wind intensity result in higher wave action toward the harbour wall, which leads to increments in underwater oscillatory movements (surge).

As a first approximation, four levels of surge were assigned to the water movements observed on each day whilst SCUBA diving (see later) over the plankton sampling period. Level 0 indicated no perceivable movements of water masses by the SCUBA diver. Level 1 indicated an increasing level of bi-directional surge, perpendicular to the breakwater wall. Levels 2 and 3 indicated strong and very strong surge, respectively. Level 3 was considered the limit condition for sampling to be accurately carried out.

The direction and velocity of water masses on the different boulder sides were measured using a liquid solution of a fluorescent sodium salt (fluorescein, Sigma products) released by a syringe a few cm from the boulder sides and the sandy bottoms. Three replicate trails (two near opposite edges and one in the middle of each boulder side) were done in each community and station under all surge conditions. Movement of the fluorescein dye along a metre stick was recorded and the current direction was recorded using a compass (see Stoner 1992, for a comparison with our method).

On the upper sides of the boulders, with surge level 0, the fluorescein dye diluted after 1 min, without moving from the release point. No movements were recorded either on the rest of boulder sides or sandy bottoms. With level 1, fluorescein followed a bi-directional, oscillatory pattern (perpendicular to the harbour wall) and effective water transit was not observed after ~1-min observations (the time fluorescein was diluted and disappeared) so that velocity was difficult to record because only opposite accelerations took place. At the edges of the boulders, with regime level 2, oscillation (and acceleration) became very intense and a pattern of ejections and sweeps (*sensu* Abelson and Denny 1997) was observed in the caves. With surge level 3, the intensity of oscillation of water masses on the boulders became too intense to allow recordings whilst SCUBA diving. Moreover, flow velocity was impossible to measure because the fluorescein

dye only oscillated near the release point before being diluted. The fluorescein flow on the sandy bottom followed the same pattern observed on the boulders and water transport was never observed either tangential or parallel to the boulder orientation.

#### Assessing adult and larval distributions

In summer 1999, ten 625-cm<sup>2</sup> quadrats were haphazardly sampled at each community (except for the SB where the studied sponges do not live) along the five stations to assess the distribution of adult sponges of the six species on the boulder sides. The quadrat was subdivided with a nylon string into 25 subquadrats of 25 cm<sup>2</sup> each. We recorded presence of adults in each 25-cm<sup>2</sup> subquadrat and calculated the percent cover (see Mariani et al. 2000, 2005b for details).

Plankton was sampled between July 1998 and June 2000, approximately every 3 days in spring, summer and fall, and at least once a week in winter. On each sampling day, at ~1100 hours, a plankton net was towed by a SCUBA diver for 2 min at ~30 cm from the substrate in each of the three communities on the boulders (PA, SA, SDC) and on the sandy bottoms in front of the reef (SB), and along the five stations. Sponge larvae are known to release during morning and daylight hours (Amano 1986, 1988; Lindquist and Hay 1996; Linquist et al. 1997). To perform the samplings in a single dive the net was connected to a 60-ml syringe by means of a plastic funnel. After each sampling the net contents were extracted while underwater with a syringe that was used as container for samples (see Mariani et al. 2000, 2003, 2005a for more details). The samples were transported to the laboratory immediately after collection and sorted *in vivo* to identify the sponge larvae.

The general design was a mixed-model ANOVA with the five sampling stations as the random factor and the four communities (three for the adults) the fixed factor. The analysis to test for differences among abundance of larvae were done using data from 2 years (1998, 1999) with year as a second fixed factor. For the larvae of *C. viridis* we had a randomised block design with five replicates (stations) for each habitat because the larvae were collected only once (see also Mariani et al. 2000).

Prior to analysis, data were tested for normality (Kolmogorov–Smirnov test) and Cochran's *C* test was used to check for the assumptions of homogeneity of variances. When these assumptions were violated, logarithmic [ $\log(x+1)$ ] or square root transformations were applied to meet them. We used SNK tests for a posteriori multiple comparisons of the means ( $\alpha=0.05$ ).

#### Adult–larvae couplings

We hypothesised that in days with higher surge, especially weakly-swimming sponge larvae ought to be more mixed among the different habitat studied than on calm days. The strength of adult–larvae couplings, that is the extent to which larvae tended to remain close to adult

conspecifics under increasing levels of surge, was assessed by correlating adult and larval abundance for each taxon. These relationships were tested using three data sets. The first corresponded to the mean abundance of larvae of each species over the whole sampling period. This was taken as a reference. Then, we separated larval abundance data corresponding to the days of calm sea conditions (surge levels 0–1) from those of days of higher surge (levels 2–3). For each species, the correlation analysis were done plotting adult abundance corresponding to the average percent cover obtained from ten replicate quadrats calculated at each of the four communities in the five stations ( $n=20$ ) versus each of the three data sets of larval abundance above. For *C. viridis*, because the larvae were collected on a day of calm sea conditions, only one data set was used for the analysis. Since differences in the correlation coefficient were found for most of the species depending on the data set used (see **Results**), we tested whether such differences (a decrease in the correlation coefficient from days of calm to rough sea conditions) were significant using a randomisation procedure. To this end, we randomly reassigned the observation dates to days of calm and rough water, totalling the same days of each condition as in the original data, and keeping all other data structure (e.g. stations and communities) unchanged. We then recomputed the correlation coefficients between adult and larvae distributions for the newly generated “calm” days and “rough” days and calculated their difference. The data series was randomised 5,000 times and the distribution of differences in correlation coefficients generated was compared to the actual difference observed. The percentage of values in the randomised series that equalled or exceeded the observed value was taken as the significance of the observed

decrease in correlation (i.e. in strength of larval–adult coupling).

## Results

### Adults and larvae distributions

The abundance of adults and larvae varied across communities and stations depending on the taxon and differences between years were also found for the larvae (Tables 2, 3).

Sponges of the taxon Dictyoceratida spp. (i.e. *Ircinia oros* and *C. mollior*) were significantly more abundant in the SDC communities (SNK test: SDC > SA = PA) and such differences were especially remarkable at stations 3 and 5 (Fig. 1). The larvae of Dictyoceratida spp. were overall more abundant in the SDC communities (SNK test: SDC > SA > PA = SB) and in the second year of sampling (SNK test: 2 > 1). Station 5 had the highest numbers of larvae.

The adults of *D. avara* were significantly more abundant in the SDC communities (SNK test: SDC > SA > PA) except at station 4 where they were more abundant in the SA community (Table 2). As regards the larvae, there were significant differences among communities, stations, and years (Table 3). Overall, there were less larvae in the PA community (SNK test: SDC = SA > PA; PA = SB), in the first year of sampling, and at stations 1 and 2.

*Crambe crambe* was significantly more abundant in the SA communities (SNK test: SA > SDC > PA) of stations 1, 2, and 4 than in the rest of the stations (Table 2). We found no significant differences in the

**Table 2** Mixed ANOVA table summarising significance in the differences found in adult abundance among communities (fixed factor) and stations (random factor) for each taxon

Taxon	A) <i>Dictyoceratida</i> spp.				B) <i>Dysidea avara</i>			C) <i>Crambe crambe</i>		
	df	MS	F	p-level	MS	F	p-level	MS	F	p-level
Source of variation	ANOVA				ANOVA			ANOVA		
Community = C	2	2052.6	17.74	0.001	1869.2	6.98	0.017	13639.2	23.08	<0.001
Station = S	4	142.3	2.4	0.05	241.86	1.83	n.s.	1545.9	13.68	<0.001
C × S	8	115.65	1.95	0.05	267.82	2.03	0.04	590	5.23	<0.001
Residual	135	59.26			131.95			113		
	C test: 0.42 Transformation: None				0.37		$p>0.05$	0.22		$p>0.05$
					None			None		
Taxon	D) <i>Phorbas tenacior</i>				E) <i>Scopalina lophyropoda</i>			F) <i>Cliona viridis</i>		
	df	MS	F	p-level	MS	F	p-level	MS	F	p-level
Source of variation	ANOVA				ANOVA			ANOVA		
Community = C	2	5074.3	112	<0.001	600	19.9	n.s.	98.27	10.39	0.0059
Station = S	4	52.79	0.75	n.s.	506.66	1.18	<0.001	25.12	5.69	<0.001
C × S	8	45.27	0.6	n.s.	506.66	19.9	<0.001	9.45	2.14	0.034
Residual	135	70.06			25.42			4.41		
	C test: 0.28 Transformation: None				0.89		$p>0.05$	0.17	Square Root	$p>0.05$
					None					

Variable transformation, when necessary, and Cochran's C test are shown  
 $P > 0.05$  was considered non-significant (NS)

**Table 3** Mixed ANOVA table summarising significance in the differences found in larval abundance among communities and years (fixed factors) and stations (random factor) for each taxon excepting *Cliona viridis*

Taxon	A) <i>Dictyoceratida</i> spp.				B) <i>Dysidea avara</i>				C) <i>Crambe crambe</i>			
Source of variation	ANOVA				ANOVA				ANOVA			
	df	MS	F	p-level	df	MS	F	p-level	df	MS	F	p-level
Year = Y	1	39.5	71.17	0.001	1	20.49	43.53	0.002	1	24.91	32.06	0.004
Community = C	3	46.1	55.51	<0.001	3	3.94	15.32	<0.001	3	0.71	2.39	n.s.
Station = S	4	7.13	12.21	<0.001	4	4.58	5.63	<0.001	4	1.19	3.53	0.007
Y × C	3	1.04	1.26	n.s.	3	0.68	1.37	n.s.	3	0.03	0.1	n.s.
Y × S	4	0.55	0.94	n.s.	4	0.47	0.577	n.s.	4	0.77	2.3	n.s.
C × S	12	0.83	1.42	n.s.	12	0.25	0.32	n.s.	12	0.29	0.877	n.s.
Y × C × S	12	0.84	1.42	n.s.	12	0.49	0.61	n.s.	12	0.33	0.975	n.s.
Residual	520	0.58			377	0.81			466	0.3		
	C test: 0.04 Transformation: log (x+1)				p>0.05 0.05 log (x+1)				p>0.05 0.06 log (x+1)			

Taxon	D) <i>Phorbas tenacior</i>				E) <i>Scopalina lophyropoda</i>			
Source of variation	ANOVA				ANOVA			
	df	MS	F	p-level	df	MS	F	p-level
Year = Y	1	0.098	0.376	n.s.	1	0.002	0.08	n.s.
Community = C	3	12.11	9.53	0.001	3	0.23	1.067	n.s.
Station = S	4	1.04	2.39	0.048	4	0.343	8.32	<0.001
Y × C	3	0.61	1.3	n.s.	3	0.01	0.45	n.s.
Y × S	4	0.26	0.6	n.s.	4	0.02	0.64	n.s.
C × S	12	1.27	2.92	<0.001	12	0.21	5.21	<0.001
Y × C × S	12	0.46	1.07	n.s.	12	0.034	0.84	n.s.
Residual	789	0.43			361	0.04		
	C test: 0.06 Transformation: log (x+1)				C test: 0.24 None			
	p<0.05				p>0.05			

Variable transformation, when necessary and Cochran's C test are shown  
 $P > 0.05$  was considered non-significant (NS)

abundance of larvae among communities (Table 3). Again more larvae were collected in the second year and stations 2 and 3 had significantly more larvae.

Adults of *P. tenacior* were significantly more abundant in the SDC communities (SNK test: SDC > SA = PA) (Table 2). There were also significant differences among communities (SNK test: SDC > SA > PA = SB) and stations (2 and 3 with more larvae than the rest) for larvae but not between years (Table 3).

The adults of *S. lophyropoda* exclusively colonised the SA communities at of station 3 and 5 and at a different extent (Fig. 1). The distribution and abundance of adults across communities and stations matched that of the larvae and there were no differences between years (see Tables 2, 3).

Finally, *C. viridis* was more abundant in the SA communities, although the different growth forms ( $\alpha$ ,  $\beta$ , and  $\gamma$ ) distinctive of the species colonised the boulder sides to different extents (see Mariani et al. 2000 for details of the results). The larvae of *C. viridis* were significantly more abundant in the SA communities and were not found over the sandy bottoms (see Results in Mariani et al. 2000, and Fig. 1b)

In sponges, intra- and inter-annual variability in the abundance of adults can be found. As part of a larger study, photographic and visual monitorings were carried out in the summers 2000 and 2001. Although they are not presented here because of the different methods used, the

results of both monitorings reflect the same patterns of adult distribution recorded in 1999 (see Mariani 2002).

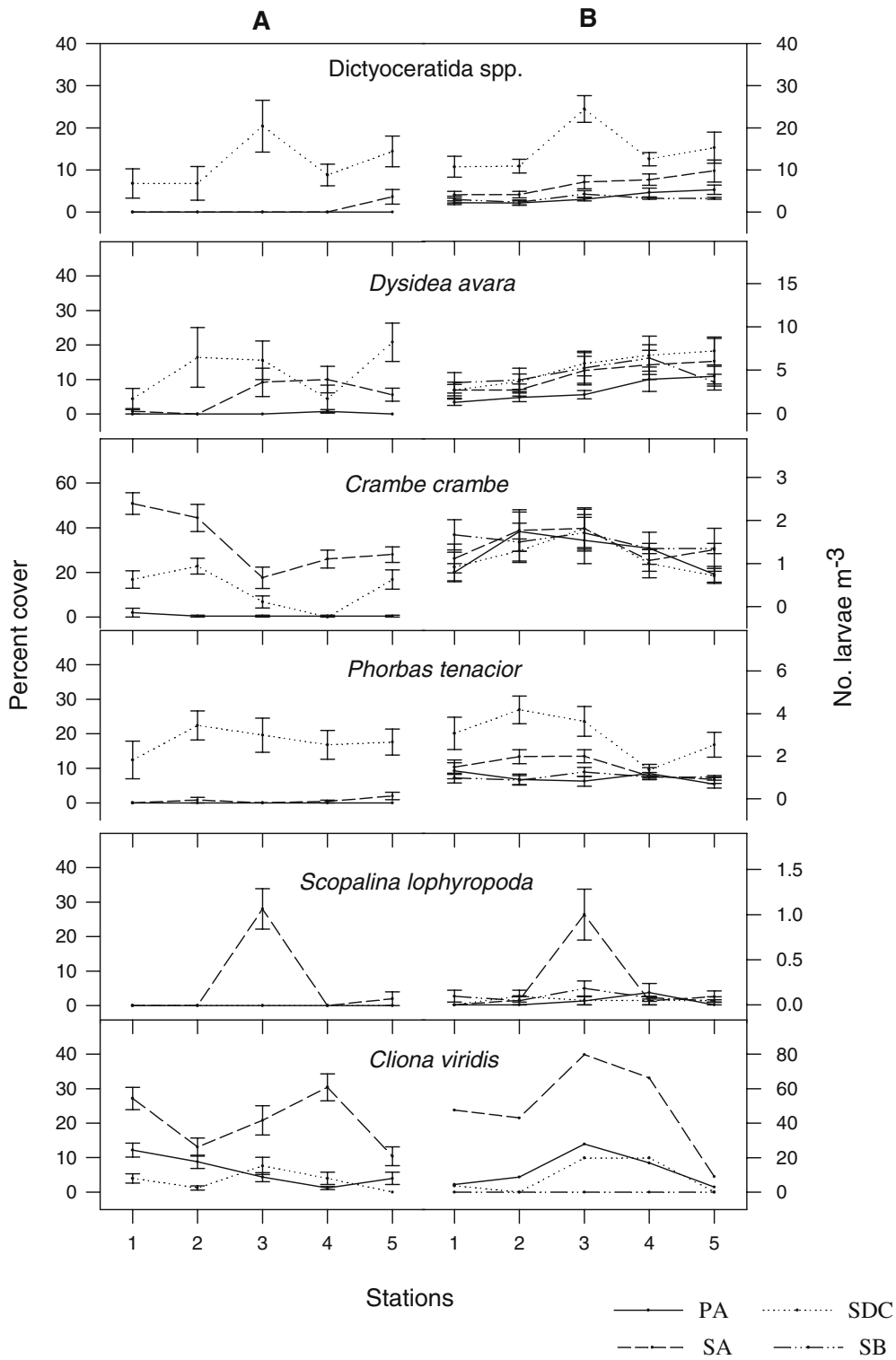
#### Adult-larvae couplings

The surge level varied over the release periods of the taxa studied and the days of high surge were 19.6% of the total of days in which larvae were collected. In the case of *C. viridis* the day of larval release corresponded to surge level 1.

The results of the regression analysis are shown in Table 4 (Fig. 2). Averaging larval abundance of all sampling dates, adult and larval abundance showed a significant relationship for the Dictyoceratida spp., *D. avara*, *P. tenacior*, *S. lophyropoda*, and *C. viridis* ( $P < 0.05$  for all comparisons). For *C. crambe*, the relationship was negative and not significant. The same pattern was found when considering days with absent or low surge (levels 0–1).

With rough sea conditions (surge levels 2–3), the associations became weaker (except for *C. crambe*, see Table 4), although they were still significant if *S. lophyropoda* was excluded. The adult-larvae couplings could not be tested with strong surge for *C. viridis* because larvae were only collected with surge level 1.

The randomisation test showed that the difference in the correlation coefficients corresponding to low and high surge for *P. tenacior* was highly significant

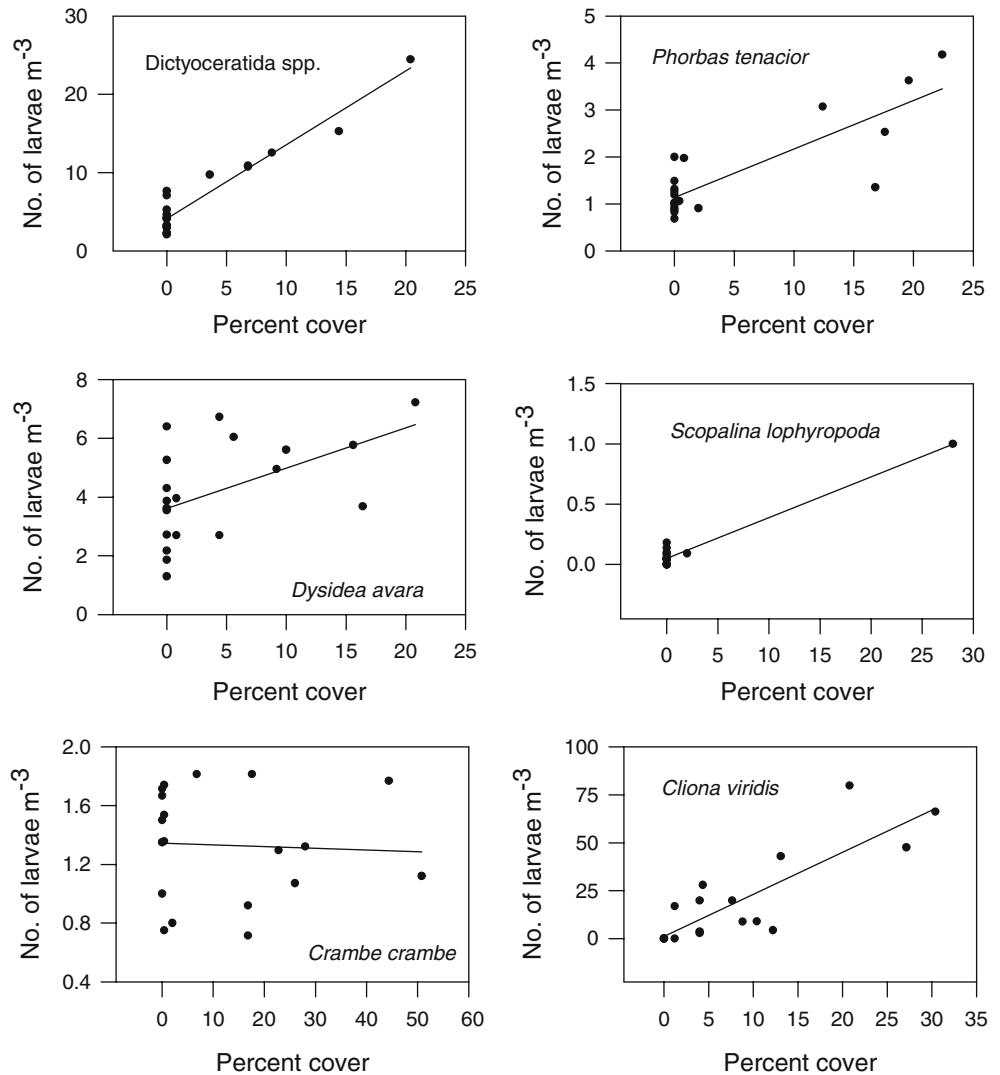


**Fig. 1** Adult percent cover (mean of ten quadrats) for the six taxa studied, in the three communities of the reef and along the five stations (a); mean larval abundance of the six taxa in the four communities (PA, SA, SDC, and SB) and along the five stations (b). Error bars are SE

( $P=0.018$ ) (Table 4). No significant differences were found for the other species with the exception of *S. lophyropoda*. This is a special case, since the association between adults and larvae depended on a single data point. Although for this reason the results of the

randomisation test are to be considered with the necessary caution, we must acknowledge that the point specifically refers to the exact coupling between the highest abundance of adult and larvae in one community of one station, which is worth noting. Since our test was

**Fig. 2** Relationships between adult (mean percent cover of the ten quadrats) and larval abundance for the six taxa studied. Data on larval abundance correspond to the whole period of sampling (both calm and rough sea conditions)



**Table 4** Correlation values for the abundance of adults and larvae averaging larval abundance over all observational days, and separately for low- and high-surge conditions

Taxon	Dictyoceratida spp.	Dysidea avara	<i>Crambe crambe</i>	<i>Phorbas tenacior</i>	<i>Scopalina lophyropoda</i>	<i>Cliona viridis</i>
R (all days)	0.95*	0.46*	-0.12	0.83*	0.97*	-
R (low surge)	0.95*	0.44*	-0.12	0.86*	0.97*	0.88*
R (high surge)	0.87*	0.36*	-0.048	0.57*	0.38	-
<i>P</i> difference	0.53	0.46	NA	0.018*	0.138	-

*P* difference refers to the results of the randomisation test used to assess significance in differences between the correlation coefficients corresponding to low- and high-surge days

NA Test not applicable (see text)

Asterisks indicate significant correlation. Terms were considered not significant at  $P > 0.05$

one-tailed, it was not applicable to *C. crambe*, which showed lower correlation values in calm than in rough water days.

## Discussion

For marine larvae, the magnitude of a dispersal pattern depends mainly on three factors: the length of larval life,

the swimming behaviour, and the hydrographic regimes that the larvae encounter during the planktonic phase (e.g. Young and Chia 1987; Graham and Sebens 1996; Paris and Cowen 2004). None of these factors alone can explain a distribution. Long-lived larvae, the most likely to disperse widely, may remain close to local parental populations by means of specialised behaviours limiting their horizontal diffusion (see Paris and Cowen 2004) and/or because they are poorly dispersed or even aggre-

gate near the point of release (Keough and Black 1996). It is likewise possible to argue that once transported to a mainstream flow, even short-lived larvae (typically short-dispersing) incapable of efficient swimming can be dispersed over relatively large distances by currents.

The parenchymella larvae of the demosponge studied display different swimming abilities and taxis (Mariani et al. 2005a; Table 1). These species-specific characteristics cannot be inferred from the phylogenetic relatedness among species. The Dictyoceratida spp. larvae (*C. mollior* and *I. oros*) are virtually identical to those of *D. avara* (both belong to the Order Dictyoceratida) in terms of their morphology and swimming ability. Nevertheless, the first taxon shows negative response to light in the laboratory (Maldonado et al. 2003; Mariani et al. 2005a) whereas the second is rather photophilic (see Mariani et al. 2005a). The distribution of the larvae of Dictyoceratida spp. appeared not to be affected by the intensity of water movements since larvae remained mostly close to the parental habitats (the SDC) within the magnitude range of hydrodynamic forces found in this study. The larvae of *D. avara* are much less specific than those of Dictyoceratida spp. as regards the habitat preference and were found with equal probability close to or away from the habitats where adults live (Table 5). Hence, it seems that the swimming ability alone cannot explain a dispersal strategy if we know nothing about larval phototaxis, for instance.

Larvae of *P. tenacior* and *C. crambe* belong to the same order (Poecilosclerida) yet display very different dispersal strategies perhaps as a result of the differences in their morphologies and behaviour. The distribution of adults and larvae of *P. tenacior* is almost coincident with that of the Dictyoceratida spp. Overall, the larvae of *P. tenacior* tend to remain close to the sciaphilic habitats where the adults live as their negative response to light suggests (see Mariani et al. 2005a), but such coupling is lost when the intensity of water movements increases. This is likely because the larvae of *P. tenacior*, unlike those of Dictyoceratida spp., are not such efficient swimmers (i.e. have a lower “hydrodynamic limit”), thus are more easily washed away from parental habitats when hydrodynamics increase (Table 5). Overall, our findings strengthen the hypothesis that actively swimming parenchymellae with posterior tufts of flagella (Order

Dictyoceratida) can direct swimming more efficiently than parenchymellae with no posterior tuft (e.g. *P. tenacior*) and may thus possess much higher hydrodynamic limits (see Maldonado et al. 2003).

The larvae of *C. crambe* were homogeneously distributed among communities and were the only species found in higher numbers over the sandy bottoms than on the reef, although the difference was not significant. This indicates that the lower (or even null in *C. viridis*) abundance of larvae of the other species on the sandy bottoms cannot be due simply to passive transport or dilution from the nearby reef. The larvae of *C. crambe* are weak swimmers and can be seen with the naked eye in the water column during the release period. While visual monitoring is difficult to carry out because larvae are too small to carefully follow underwater (1 mm), their presence has often been noticed in diverse sublittoral areas and habitats like rocky and sandy bottoms and seagrass meadows along the coastline (authors’ personal observation). It is likely that this distributional pattern is influenced by the peculiar morphology of larvae, which literally transform into spherical, free buoyant balls with very limited swimming abilities, and on their neutral response to light (see Uriz et al. 1998; Mariani et al. 2005a). Therefore, the larvae of *C. crambe* are an example of sexual propagules which can be passively dispersed by currents and wide dispersal is possible (Table 5).

Larvae of *S. lophyropoda* (Order Halichondria) and *C. viridis* (Order Hadromerida) show rather unspecialised morphologies compared to the other larvae above (see Mariani et al. 2005a). They are weak swimmers, but show different and distinctive behaviours. Due to their bright orange colour and relatively large size (up to 1.5 mm) larvae of *S. lophyropoda* can be observed whilst SCUBA diving in the immediate vicinity of parental sponges where they can remain for several minutes (Uriz et al. 1998; authors’ personal observation). Larvae of *C. viridis* alternate free swimming with demersal crawling in the laboratory and are also certainly unable to counteract strong water flows because of the reduced size and short flagella (350 µm; Mariani et al. 2000, 2001). For both species, the most likely strategy is short dispersal (Table 5). However, our study indicates that with calm sea conditions, the larvae of *S. lophyropoda* remain efficiently close to the adults, whereas such coupling is

**Table 5** Resume of the conclusions on the possible dispersal strategies arising from this study for each taxon studied

Taxon	Possible strategy	Taxon	Possible strategy
Dictyoceratida spp.	Actively counteract hydrodynamic forces. Prefer the habitats where adults live	<i>Phorbas tenacior</i>	Can counteract hydrodynamic forces to some extent. Prefer the habitats where adults live
<i>Dysidea avara</i>	Active dispersal with no strong preference for the habitats where adults live	<i>Scopalina lophyropoda</i>	Swim in the vicinity of adults. Cannot actively counteract strong hydrodynamic forces
<i>Crambe crambe</i>	Stochastic distribution among habitats (passively transported)	<i>Cliona viridis</i>	Do not disperse over the habitat unsuitable for settlement

lost when water movement increases. Hence, it is probable that in areas where strong hydrodynamic forces exist, such larvae will be easily dispersed relatively far from parental habitats thus depending upon the duration of larval life. In the case of *C. viridis*, whose larvae hatch punctually (over few days a year; see Mariani et al. 2001) from eggs which adhere to the substratum surrounding mother sponges, phylopatry seems the only conceivable dispersal pattern. Nevertheless, we do not know what would happen if either spawning or larval release or both occurred during days of rough sea conditions.

Much emphasis has been paid to the role of larval behaviour in determining the distribution of adults among different habitats in invertebrates with short-lived larvae (see Stoner 1990, 1992 for ascidians; Keough 1986; Mariani et al. 2005b for bryozoans) and notably in sponges (Bergquist et al. 1970; Maldonado and Uriz 1998; Uriz et al. 1998). It is true that larval behaviour may predict adult distributions in some cases. *S. lophyropoda* is known to distribute in clumped patches among sublittoral habitats in the northwest Mediterranean, whereas *C. crambe* is more homogeneously distributed (Uriz et al. 1998). Moreover, different larval behaviours may also be reflected in different gene flow between neighbouring populations. Nevertheless, larval dispersal is only *one of* the many factors influencing the adult spatial distributions of marine sessile invertebrates. Settlement and post-settlement processes, which we have not dealt with in this study, can be important in determining the final distribution of sponges across the different communities studied.

Larval dispersal is one step in the process of supply of new individuals into any population and its importance in directly determining adult distributions for many non-opportunistic, long-lived organisms need to be assessed for each case study. In sponges recruitment rates have been found to be generally low (Zea 1993) especially when compared with those of other sessile invertebrates such as bryozoans (Mariani 2003; Mariani et al. 2005b). For example, species such as *C. crambe*, which is the least selective among the studied species with regard to the habitat colonised, is the only one to recruit in appreciable numbers on artificial settlement plates at the study site (Mariani 2003) thus behaving in a rather opportunistic way. Yet both recruit and adult distributions are not uniform across the community studied (recruits are few in the PA communities) indicating that settlement and post-settlement processes are important even for this species. Yet, sexual dispersal by larvae must play a role as long as different morphologies and behaviours have evolved and, hence, different dispersal strategies have emerged as a way for larvae to cope with the environmental situations encountered during the planktonic phase.

The number of larvae produced is also variable among species (e.g. *C. crambe* produces five times more larvae than *S. lophyropoda* per surface unit; Uriz et al. 1998; see Table 1) and this may determine different larval survivorship and settlement rates. Selective predation on

the larvae of one species over the other is also possible (Uriz et al. 1996), although sponge larvae are known not to be particularly affected by such mortality (Lindquist and Hay 1996). Finally, the study of the demography of sponge populations is further complicated by the issue of asexual reproduction. It is not always easy to figure out whether an increase in population size is the result of immigration of sexual propagules or asexual propagation from the same population. It is perhaps naïve to attempt to directly relate larval dispersal strategies with adult distributions of sponge populations.

Our results (the first of this kind obtained with sponge larvae in the field) confirm that pelagic larvae showing efficient swimming and some cue response (light intensity, in this case) can actively counteract hydrodynamic forces. In short-lived, non-feeding larvae such as those of sponges (e.g. Dictyoceratida spp.) this may favour retention near parental habitats, thus enhancing self-seeding and probably self-recruitment. Weak-swimming larvae, on the contrary, lacking relevant phototaxis (e.g. *C. crambe*) may randomly distribute in the water column and across benthic habitats. Since they are more easily passively transported by currents, they may also critically disperse wider or accumulate in some place, which may be predictable by oceanographic models.

In spite of the hints from the literature about the importance of larval behaviour to predict a realised dispersal (e.g. Keough and Black 1996; Metaxas 2001; Paris and Cowen 2004), models of larval dispersal in the sea often consider hydrographic variables, larval swimming speeds, and planktonic life duration as the main variables, paying scant regard to behavioural differences. Integrating life history (including behaviour) of larvae and the hydrographic component certainly requires a considerable effort but may make possible more realistic predictions of planktonic and benthic distributions that go beyond the intrinsic limitations of case studies.

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## References

- Abelson A, Denny M (1997) Settlement of marine organisms in flow. *Annu Rev Ecol Syst* 28:317–339
- Amano S (1986) Larval release in response to a light signal by the intertidal sponge *Halichondria panicea*. *Biol Bull* 171:371–378
- Amano S (1988) Morning release of larvae controlled by the light in an intertidal sponge, *Callyspongia ramosa*. *Biol Bull* 175:181–184
- Becerro MA, Uriz MJ, Turon X (1994) Trends in space occupation by the encrusting sponge *Crambe crambe*: variation in shape as a function of size and environment. *Mar Biol* 121:301–307
- Bergquist PR, Sinclair ME (1968) The morphology and behaviour of larvae of some intertidal sponges. *NZ J Mar Freshw Res* 2:426–437
- Bergquist PR, Sinclair ME, Hogg JJ (1970) Adaptation to intertidal existence: reproductive cycles and larval behaviour in Demospongiae. *Symp Zool Soc Lond* 25:247–271

- Boury-Esnault N, Rützler K (1997) Thesaurus of sponge morphology. *Smith Contr Zool* 596:1–55
- Burdett-Coutts V, Metaxas A (2004) The effect of the quality of food patches on vertical distribution of the sea urchins *Lytechinus variegatus* (Lamarck) and *Strongylocentrotus droebachensis* (Muel-ler). *J Exp Mar Biol Ecol* 308:221–236
- Fisher R (2005) Swimming speeds of larval coral reef fishes: impacts of self-recruitment and dispersal. *Mar Ecol Prog Ser* 285:223–232
- Gilg MR, Hilbish TJ (2003) The geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. *Ecology* 84:2989–2998
- Graham KR, Sebens KP (1996) The distribution of marine invertebrate larvae near vertical surfaces in the rocky subtidal zone. *Ecology* 77:933–949
- Grosberg RK (1987) Limited dispersal and proximity-dependent mating success in the colonial ascidian *Botryllus shlosseri*. *Evolution* 41:372–384
- Jackson JBC (1985) Distribution and ecology of clonal and aclonal benthic invertebrates. In: Jackson JBC, Buss LW, Cook E (eds) *Population biology and evolution of clonal organisms*. Yale University, New Haven, pp 297–356
- Keough MJ (1986) The distribution of a bryozoan on seagrass blades: settlement, growth, and mortality. *Ecology* 67:846–857
- Keough MJ, Black KP (1996) Predicting the scale of marine impacts: Understanding planktonic links between population. In: Schmitt RJ, Osenberg CW (eds) *The design of ecological impact studies: conceptual issues and application in coastal marine habitats*. Academic, Orlando, pp 199–234
- Leis JM, Sweatman HPA, Reader SE (1996) What pelagic stages of coral reef fishes are doing in the blue water: daytime field observations of larval behavioural capabilities. *Mar Freshw Res* 47:401–411
- Levin LA, Huggett D, Myers P, Bridges T, Weaver J (1993) Rare-event tagging methods for the study of larval dispersal by marine invertebrates. *Limnol Oceanogr* 38:346–360
- Leys SP, Degnan BM (2001) Cytological basis of photoresponsive behavior in a sponge larva. *Biol Bull* 201:323–338
- Lindquist N, Hay ME (1996) Palatability and chemical defence of marine invertebrate larvae. *Ecol Monogr* 62:547–568
- Lindquist N, Bolser RC, Laing K (1997) Timing of larval release by two Caribbean demosponges. *Mar Ecol Prog Ser* 155:309–316
- Maldonado M, Bergquist PR (2002) Phylum porifera. In: Young CM (ed) *Atlas of marine invertebrate larvae*. Academic, London, pp 21–50
- Maldonado M, Uriz MJ (1998) Microrefuge exploitation by subtidal encrusting sponges: patterns of settlement and post-settlement survival. *Mar Ecol Prog Ser* 174:141–150
- Maldonado M, Young CM (1996) Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. *Mar Ecol Prog Ser* 138:169–180
- Maldonado M, Durfort M, McCarty DA, Young CM (2003) The cellular basis of photobehavior in the tufted parenchymella larva of demosponges. *Mar Biol* 143:427–441
- Mariani S (2002) Larval supply and recruitment of invertebrates in the western Mediterranean: patterns in contrasting benthic communities. PhD thesis, University of Barcelona
- Mariani S (2003) Recruitment in invertebrates with short-lived larvae: the case of the bryozoan *Disporella hispida* (Fleming). *Helgol Mar Res* 57:47–53
- Mariani S, Uriz MJ, Turon X (2000) Larval bloom of the oviparous sponge *Cliona viridis*: coupling of larval abundance and adult distribution. *Mar Biol* 137:783–790
- Mariani S, Piscitelli M, Uriz MJ (2001) Temporal and spatial co-occurrence in spawning and larval release of *Cliona viridis* (Porifera: Hadromerida). *J Mar Biol Assoc UK* 81:365–367
- Mariani S, Uriz MJ, Turon X (2003) Methodological bias in the estimations of important meroplanktonic components from near-shore bottoms. *Mar Ecol Prog Ser* 253:67–75
- Mariani S, Uriz MJ, Turon X (2005a) The dynamics of sponge larvae assemblages from northwestern Mediterranean nearshore bottoms. *J Plankt Res* 27:249–262
- Mariani S, Alcoverro T, Uriz M-J, Turon X (2005b) Early life histories in the bryozoan *Scizobrachiella sanguinea*: a case study. *Mar Biol* 147:735–745
- Metaxas A (2001) Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Can J Fish Aquat Sci* 58:86–98
- Olson RR (1985) The consequences of short-distance larval dispersal in a sessile marine invertebrate. *Ecology* 66:30–39
- Olson RR, McPherson R (1987) Potential vs. realized larval dispersal: fish predation on larvae of the ascidian *Lissoclinum patella* (Gottshaldt). *J Exp Mar Biol Ecol* 110:245–256
- Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnol Oceanogr* 49:1964–1979
- Raimondi PT (1991) Settlement behavior of *Chtamalus anisopoma* larvae largely determines the adult distribution. *Oecologia* 85:349–360
- Stoner DS (1990) Recruitment of a tropical colonial ascidian: relative importance of pre-settlement vs. post settlement processes. *Ecology* 71:1682–1690
- Stoner DS (1992) Vertical distribution of a colonial ascidian on a coral reef: the roles of larval dispersal and life-history variation. *Am Nat* 139:802–824
- Svane I, Young CM (1989) The ecology and behaviour of ascidian larvae. *Ocean Mar Biol Annu Rev* 27:45–90
- Underwood AJ, Keough (2002) Supply-side ecology. The nature and consequences of variations in recruitment of intertidal organisms. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer, Sunderland, pp 183–200
- Uriz MJ, Rosell D, Martin D (1992) The sponge population of the Cabrera archipelago (Balearic Islands): characteristics, distribution, and abundance of the most representative species. *PSZNI Mar Ecol* 13:101–117
- Uriz MJ, Turon X, Becerro MA, Galera J, Lozano J (1996) Feeding deterrence in sponges. The role of toxicity, physical defences, energetic contents, and life-history stage. *J Exp Mar Biol Ecol* 205:187–204
- Uriz MJ, Maldonado M, Turon X, Martí R (1998) How do reproductive output, larval behaviour, and recruitment contribute to adult spatial patterns in Mediterranean encrusting sponges? *Mar Ecol Prog Ser* 167:137–148
- Uriz MJ, Turon X, Becerro MA (2001) Morphology and ultrastructure of the swimming larvae of *Crambe crambe* (Demospongiae, Poecilosclerida). *Invertebr Biol* 120:295–307
- Young CM, Chia FS (1987) Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrogeographic factors. In: Giese AC (ed) *Reproduction of marine invertebrates*, vol 9. Blackwell, Palo Alto, pp 385–464
- Zea S (1993) Recruitment of Demosponges (Porifera, Demospongiae) in rocky and coral reef habitats of Santa Marta, Colombian Caribbean. *PSZNI Mar Ecol* 14:1–21