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Spatial variation in the recruitment of the intertidal barnacles *Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli) (Crustacea: Cirripedia) over an European scale

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Abstract

Spatial variation in the recruitment of the intertidal barnacles *Chthamalus montagui* and *Chthamalus stellatus* was examined over an European scale. The study was carried out using

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standardised protocols at a series of locations. The five locations chosen (SW Ireland, NW Spain, SW Portugal and NW and NE Italy) span a large part of the range of these species in Europe. The spatial scales were location (hundreds of kilometres) and shore (thousands of metres).

Estimates of total cumulative recruitment (cyprids and metamorphs) summed over the year (April 1997 to March 1998) showed substantial variation between locations which was dependent on the species. Recruitment was highest in SW Portugal for *C. montagui* and in SW Ireland and NW Spain for *C. stellatus*. Overall recruitment of *C. montagui* was higher than that of *C. stellatus* at all locations except SW Ireland, where recruitment of the two species was not significantly different. There were significant differences among shores in each location.

The recruitment period of both species varied with location, with recruitment beginning earlier further south. In general, recruitment of *C. montagui* and *C. stellatus* was recorded in 8 months in NW Spain and NE Italy, while only in 7 months in SW Ireland. Recruitment of *C. montagui* occurred in 10 months in SW Portugal, but no recruits of *C. stellatus* were found. In all locations there was at least one distinct peak of recruitment. In SW Ireland both species showed only one peak of recruitment, a month after initiation. At the more southerly Atlantic locations, as well as in the Mediterranean, two unequal peaks of recruitment were generally seen. During recruit census, the number of cyprids, in comparison to metamorphs, found at any location was very low. In SW Ireland and NW Spain cyprids of both species were found, while in SW Portugal and in the Mediterranean, only cyprids of *C. montagui* were found.

Keywords: Barnacles; *Chthamalus*; Recruitment; Spatial variation

1. Introduction

Underwood (2000) has highlighted the necessity for increasing the spatial scale and the range of places and types of habitats over which intertidal experiments are carried out. In order to gain an understanding of the scales at which important ecological processes are acting, it is necessary to make comparisons of ecological processes between different geographical regions (hundreds of kilometres) (Levin, 1992; Underwood, 2000). In addition, an understanding of the role of early life history stages in determining the distribution of benthic invertebrates requires studies covering a wide range of habitats at multiple scales (Satumanatpan et al., 1999). The settlement rate (the rate at which the planktonic larvae of sessile species establish permanent contact with the substrate) depends on a number of different processes which operate over different spatial and temporal scales. Consequences of spatial variation of settlement and recruitment have been increasingly incorporated into models of population and community regulation (e.g. Caffey, 1985; Gaines and Roughgarden, 1985; Gaines et al., 1985; Raimondi, 1990). Recruitment can be defined as the point in time when the larva has permanently attached and metamorphosed and has survived for a specified period of time (Connell, 1985). Several workers have commented on the importance of recruitment as an influence on the community structure of rocky shores (see, for example, Connell, 1961; Denley and Underwood, 1979; Underwood and Denley, 1984; Caffey, 1985; Gaines and Roughgarden, 1985; Roughgarden, 1986; Menge and Sutherland, 1987; Judge et al., 1988; Hoffmann, 1989; Menge, 1991; Roberts et al., 1991). Recruitment is a process that establishes pattern, while factors such as competition, predation, facilitation or disturbance modify patterns of abundance and distribution (Menge, 2000).

Barnacles are key space-occupiers in rocky shore communities on European coasts (Lewis, 1964) and interact with other species (e.g. Hartnoll and Hawkins, 1985; Jenkins et al., 1999) and hence affect overall biodiversity. The intertidal barnacles *Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli) overlap extensively in geographic range, occurring along the Atlantic coasts of Ireland, Britain, France, Spain and in the Mediterranean and Black Seas (Crisp et al., 1981). Although both species occur along the Portuguese coast, *C. stellatus* is significantly less abundant there than *C. montagui* (Sousa et al., 2000; Range and Paula, 2001). The southern mainland distributional limit of the two species is not clear, although Crisp et al. (1981) suggested that *C. montagui* extends at least to Mauritania and *C. stellatus* may extend farther south than *C. montagui* along the W. African coast, but more investigation is needed in this region. Both species reach the northern limit of their distribution in the British Isles (Crisp et al., 1981). In Britain and Ireland, the distributions of the adults of *C. stellatus* and *C. montagui* may overlap considerably in terms of shore height and wave exposure. *C. montagui* is usually more common in the upper barnacle zone, than it is lower down, where *C. stellatus* may be dominant (Crisp et al., 1981). *C. stellatus* is often abundant on wave-exposed coasts whereas *C. montagui* is more commonly found in embayed situations, but there is still extensive overlap (Southward, 1976; Crisp et al., 1981).

Although these two species co-occur on many European shores, the processes controlling the distribution patterns of these species are as yet unknown. Since the realisation that there were two European species of *Chthamalus* (Southward, 1976), a number of researchers have investigated the reproduction, settlement and recruitment of the two species (e.g. SW Ireland (Myers et al., 1978, 1979, 1980; Cross and Southgate, 1983; O'Riordan et al., 1991, 1992, 1995; Power et al., 1999a), SE Ireland (Healy, 1986; Healy and McGrath, 1998), N Scotland (Lewis et al., 1982; Lewis, 1986), mid-Wales (Kendall and Bedford, 1987), SW Britain (Burrows et al., 1992, Pannacciulli, 1995), NW Spain (Miyares, 1986), Portugal (Cruz, 1999; Range and Paula, 2001) and in the Mediterranean (Pannacciulli and Falautano, 1999; Pannacciulli and Relini, 1999)). However, this work was done at different times using disparate methodologies. Recently differences between the two species in settled cyprid density relative to metamorph abundance have been demonstrated by Power et al. (1999a). It has been suggested that post-settlement mortality may control adult barnacle abundance rather than settlement (Delany et al., 2003; O'Riordan et al., 2002a) and that desiccation pressure (despite exposure to wave splash) on shores along the Atlantic coasts of Spain, Portugal and N Africa may inhibit the survival of *C. stellatus* (Power et al., 2001). Hyder et al. (2001) used data from a pan-European recruitment study of *C. montagui* to test the assumptions of a model of open populations with space-limited recruitment.

The overall aim of the present work was to investigate spatial variation (over a year) in recruitment of the intertidal barnacles *C. montagui* and *C. stellatus* in Europe. We wanted also to examine any latitudinal differences in the periodicity of recruitment of the two species over their geographical range. Thus, the study was carried out using standardised protocols at a series of locations. The five locations were chosen as representative of a large part of the geographical range of both species in Europe and included high, mid and low latitudes on the Atlantic coast (SW Ireland, NW Spain and SW Portugal, respectively) and open and more enclosed seas in the Mediterranean (Ligurian and Adriatic Seas). The spatial scales were location (hundreds of kilometres apart) and shore (thousands of metres apart). The general hypothesis to be tested was that there was variation in recruitment at any considered scale and between species. Recruitment was defined as the number of cyprids and living metamorphs (i.e. all juvenile stages of a species) attached to an area of substrate, which had been cleared 1 month before census.

2. Methods

2.1. Study sites

This study was carried out in the Atlantic Ocean on shores in Cork, SW Ireland, on the Asturian coast near Oviedo, NW Spain, near Sines, SW Portugal and in two areas of the Mediterranean Sea: the Gulf of Genoa in the Ligurian Sea, NW Italy and the Gulf of Trieste in the northern part of the Adriatic Sea, NE Italy (Fig. 1).

Three shores and three sites/shore were studied at each location. The shores at each location were as follows: SW Ireland—(1) Castlepark, (2) Bullens Bay West, (3) Garrettstown; NW Spain—(1) Artedo, (2) Campiello, (3) Oleiros; SW Portugal—(1) Oliveirinha, (2) Queimado, (3) Nascedios; NW Italy (Ligurian Sea)—(1) Capo S. Chiara, (2) Pontetto, (3) Punta Chiappa; and in NE Italy (Adriatic Sea)—(1) Barcola, (2) Santa Croce, (3) Aurisina. Shores at each location were thousands of metres apart and sites tens

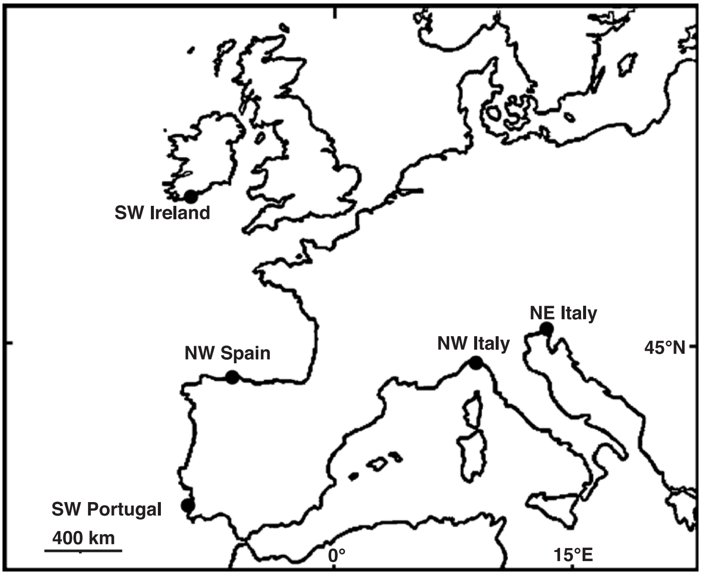

Fig. 1. Map showing the five study locations.

of metres apart. Each shore (at least 50–100 m long) was sampled 1 day/month, within 5 days either side of the lowest spring tide, between April 1997 and March 1998. At each of three sites (1–4 m^2) per shore, six quadrats (5×5 cm=25 cm^2) were cleared of all fauna each month with a paint scraper and then rinsed with seawater. Only areas, which, prior to clearing, had at least 25% barnacle cover, were used. Sites were sampled in the *C. montagui*-dominated zone, except at the shores in NW Italy where they were sampled in the *C. stellatus* zone, since *C. stellatus* is more abundant than *C. montagui* at all levels there.

Quadrats were cleared first in March 1997 and the first samples were collected in April 1997. Sampling continued on a monthly basis until March 1998. After 1 month, all attached cyprids and metamorphs were collected, from the cleared squares using fine forceps and preserved in absolute alcohol. The same sites were sampled each month, but new randomly selected squares were cleared within sites each month. Each month the number of *C. stellatus* and *C. montagui* recruits in each quadrat was counted.

When barnacle density was very high, subsampling was carried out for metamorphs. The total number of metamorphs per replicate was counted, then the first randomly selected 50 individuals from each replicate were identified. Where more than 100 metamorphs could be collected from <25 cm^2, subsampling was permitted by using five randomly selected 1-cm^2 quadrats. Subsampling was not permitted for cyprids.

If on any sampling window it was not possible to sample/clear a shore, that shore was sampled/cleared at the next possible date, but the next scheduled window was adhered to.

2.2. Identification of cyprids and metamorphs

In the laboratory, with the chthamalid cyprid lying on its side, length was measured to 25 μm precision from the anterior to posterior carapace margins using an ocular micrometer on a dissecting microscope. The *Chthamalus* cyprids were identified to species-level based on their carapace length, following O'Riordan et al. (1999, 2001) (see also Power et al., 1999b). The *Chthamalus* metamorphs were identified using criteria outlined in Burrows (1988).

2.3. Analysis

Since chthamalid cyprids can metamorphose faster in more southerly locations such as Portugal (Cruz, 1999) and Italy (within a few hours, FGP) than on shores in Britain and Ireland (Delany et al., in prep.), the numbers of cyprids and metamorphs collected on a given date were summed for each species. This allows direct comparison of results from different locations. By using cleared quadrats, all cyprids and metamorphs, which had settled and survived since the previous month's collection, were collected.

The hierarchical sampling programme was adopted to allow measurement of variation in recruitment at the spatial scales of location and shore, using nested ANOVA (Underwood, 1981, 1997). Cumulative recruitment over the whole year (April 1997 to March 1998) was examined for the two species at the four locations, with three shores per location and three sites per shore. Due to adverse weather conditions, as well as algae covering replicate quadrats, samples could not be collected in NW Italy on a number of shores and dates, so this location was excluded from ANOVA. In the three-factor ANOVA, the factor species (two levels) was fixed and orthogonal, as was location (with four levels (SW Ireland, NW Spain, SW Portugal and NE Italy)), while shore was random (three levels, nested within location). Although the number of *C. stellatus* and *C. montagui* recruits was counted in each of the six quadrats per site, to maintain independence of samples for statistical purposes, only three of the six quadrats were used for counts of *C. stellatus* recruits and three for *C. montagui*. Since random quadrats had been used on each date, "total recruitment" was calculated for each site per shore. For each species, recruitment to 1 month in a site was thus the mean recruitment after 1 month on the three quadrats of 25 cm^2. Cumulative recruitment was the sum of the 12-month data for each site. Data were tested for heterogeneity of variances, using Cochran's test and data were then transformed using ln(x+1), and re-tested. The dataset was homogenous after transformation. Cochran's test for heterogeneity of data, ANOVA and, subsequently, Student–Newman–Keuls (SNK) were all done using GMAV5 for windows (Institute of Marine Ecology, Sydney, Australia).

3. Results

3.1. Cumulative recruitment of C. montagui and C. stellatus to 1 year

Analysis of the total cumulative levels of recruitment of both species over 1 year allowed examination of variation at the spatial scales of location and shore (Table 1 and

Table 1
Analysis of variance of total cumulative recruitment (cyprids and metamorphs) of *C. montagui* and *C. stellatus*

Transformation: ln(x+1), Cochran's test C=0.1430, NS

Source of variation	*df*	MS	*F*	P	F versus
Species	1	129.2238	194.82	0.0000	Sp×Sh(Lo)
Location	3	7.5755	3.10	0.0890	Sh(Lo)
Shore(Location)	8	2.4408	4.74	0.0003	RES
Species×Location	3	29.4504	44.40	0.0000	Sp×Sh(Lo)
Species×Shore(Location)	8	0.6633	1.29	0.2724	Res
Residual	48	0.5151			
Total	71				

SNK test of Species×Location, S.E.=0.2715

Species	Location	Location	Species
C. montagui	SW Portugal>NW Spain=NE Italy>SW Ireland	SW Ireland	Cm=Cs
		NW Spain	Cm>Cs
		SW Portugal	Cm>Cs
		NE Italy	Cm>Cs
C. stellatus	NW Spain=SW Ireland>NE Italy=SW Portugal		

Fig. 2). Shore did not interact with species, indicating that the relative recruitment of the species at each shore within a location did not differ. There were significant differences among shores in each location. Total recruitment over the year varied with species. For the largest scale location, there was a significant interaction with species, indicating the effect of this spatial scale varied between *C. montagui* and *C. stellatus*. The results of multiple comparisons (SNK tests) on the location with species interaction are shown in Table 1. The SNK examining the effect of species within each location showed that recruitment of *C. montagui* was significantly higher than that of *C. stellatus* at all locations except SW Ireland, where recruitment was not significantly different. For *C. montagui* recruitment was significantly greater in SW Portugal than NW Spain, which was not significantly different to NE Italy. Recruitment of *C. montagui* was significantly less at the most northerly site, in SW Ireland, than at the other three locations. For *C. stellatus*, recruitment was not significantly different between the two more northerly locations (SW Ireland and NW Spain), but it was significantly greater at these two

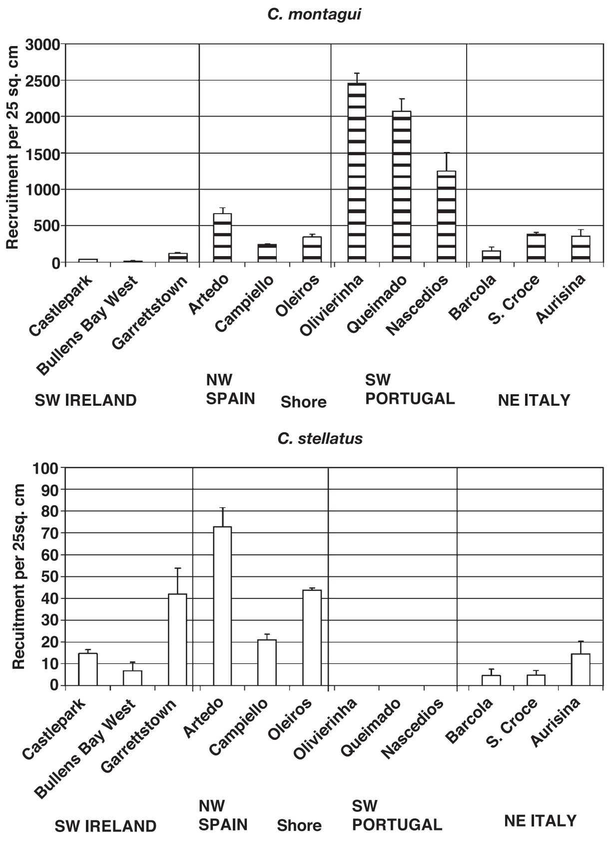

Fig. 2. Mean cumulative recruitment (+S.E.) per shore, calculated as the number of cyprids and metamorphs in 12 monthly samples of 25 cm^2. N.B. different scales for *C. montagui* and *C. stellatus*.

locations than in the Mediterranean (NE Italy), with no recruitment of this species in SW Portugal.

Cumulative recruitment over the whole year was summed over the 12 months for each site/shore/location. For *C. montagui*, cumulative recruitment over the year (mean of the three shores/location±S.E.) was approximately 35 times higher in SW Portugal (1924.1±203.19 25 cm^{-2}) than in SW Ireland (53.8±16.28 25 cm^{-2}). While recruitment was between 3.5 and 8.5 times greater in SW Portugal than in NW Spain (414.5±69.05 25 cm^{-2}) and NE Italy (297.4±48.02 25 cm^{-2}) (Fig. 2). For *C. stellatus* recruitment was about twice as high in NW Spain (45.8±7.96 25 cm^{-2}) than in SW Ireland (21.2±6.42 25 cm^{-2}) and nearly six times greater in NW Spain than in NE Italy (8.0±2.58 25 cm^{-2}).

3.2. Number of cyprids and metamorphs

The cumulative number of cyprids and metamorphs of each species collected per location in the 54 quadrats/month (18 quadrats at three shores/location) summed over the whole year is shown in Table 2. Some cyprids were too damaged to be measured or were lost (either in the field or laboratory) before measurement so their identification to species-level could not be determined.

In SW Ireland and NW Spain, low numbers of cyprids (<2% of recruitment) of both *C. stellatus* and *C. montagui* were found, with the percentage of cyprids out of the total recruitment being higher in *C. stellatus* than in *C. montagui*. All 175 cyprids identified in SW Portugal were *C. montagui*, but this represented only 0.2% of recruitment. In the Mediterranean, only *C. montagui* cyprids were identified from the shores in NW and NE Italy, although metamorphs of both species were found.

Table 2
Cumulative number of cyprids and metamorphs of each species collected per location in the fifty-four 25 cm^2 quadrats/month summed over the whole year

Location	Cyprids (unidentified cyprids)	Metamorphs	% cyprids out of total recruits
SW Ireland	20 *C. stellatus*	1009 *C. stellatus*	1.9
	7 *C. montagui*	2337 *C. montagui*	0.3
	(30)		
NW Spain	13 *C. stellatus*	3088 *C. stellatus*	0.4
	18 *C. montagui*	23,205 *C. montagui*	0.1
	(95)		
SW Portugal	0 *C. stellatus*	0 *C. stellatus*	0.0
	175 *C. montagui*	91,470 *C. montagui*	0.2
	(148)		
NW Italy	0 *C. stellatus*	7684 *C. stellatus*	0.0
	11 *C. montagui*	3130 *C. montagui*	0.4
	(12)		
NE Italy	0 *C. stellatus*	429 *C. stellatus*	0.0
	31 *C. montagui*	16,938 *C. montagui*	0.2
	(54)		

3.3. Patterns in recruitment to 1 month over the year

Figs. 3 and 4 show the mean number (+S.E.) of *C. montagui* and *C. stellatus* recruits 25 cm^{-2} between April 1997 and March 1998, on the three shores at each location. Counts are the mean of 18 quadrats (i.e. three sites with six stratified quadrats each) per shore.

3.3.1. C. montagui

3.3.1.1. SW Ireland (Fig. 3a). Recruitment had started at low levels (<1.4 recruits 25 cm^{-2}) by August in SW Ireland. Peak recruitment (maximum $\pm$ S.E.: 67.9 $\pm$ 8.22 recruits 25 cm^{-2}) occurred 1 month after the start and then decreased sharply (<17.0 recruits 25 cm^{-2} in October). Recruitment continued at very low levels in autumn and winter (e.g. <0.5 recruits 25 cm^{-2} in January); however, cyprids were found from August to October only. Only very low levels of recruitment occurred in February, with none in March. Thus, in SW Ireland, recruitment of *C. montagui* occurred for a maximum of 7 months of the year only (Table 3), with a single sharp peak.

3.3.1.2. NW Spain (Fig. 3b). In contrast to SW Ireland, recruitment of *C. montagui* was present at low levels (<2.5 recruits 25 cm^{-2}) in NW Spain on the first date of sampling in April. Recruitment maintained moderately high levels ($\geq$38 recruits 25 cm^{-2}) over 4 months (June–September), with peaks (maximum: 197.6 $\pm$ 18.04 recruits 25 cm^{-2}) in June/July and August/September. Recruitment lasted for a maximum of 8 months. Cyprids of *C. montagui* were found in May, June, September and October only, but unidentified cyprids were found from April to October. No recruitment was found between December and March.

3.3.1.3. SW Portugal (Fig. 3c). In contrast to the more northerly locations described above, in SW Portugal very high levels of recruitment occurred on the first sampling date, April 1997 (maximum: 545.3 $\pm$ 95.71 recruits 25 cm^{-2}). Recruitment levels had dropped by the following month, but then started to rise again in June, with a second peak, greater than that seen in April, between July and September. In general, in SW Portugal recruitment maintained relatively high levels (>95 recruits 25 cm^{-2}) over 7 months (April–October), although after September recruitment decreased. Low levels were found in December, but no recruitment occurred in January or February. Low levels (range: 4.0–11.0 recruits 25 cm^{-2}) were seen again in March, indicating the start of a new year's recruitment, while none was seen further north. Both cyprids and metamorphs were found from April to October and March, but in November/December only metamorphs were present.

3.3.1.4. NW Italy (Fig. 3d). Recruitment of *C. montagui* was seen in April in NW Italy, increasing to reach a plateau in June/July before decreasing in August. In comparison to the Atlantic shores, only very low levels of recruitment occurred (<28.0 recruits 25 cm^{-2}), with a maximum in June/July. Recruitment continued at very low levels until October/November, although due to adverse weather conditions or algae

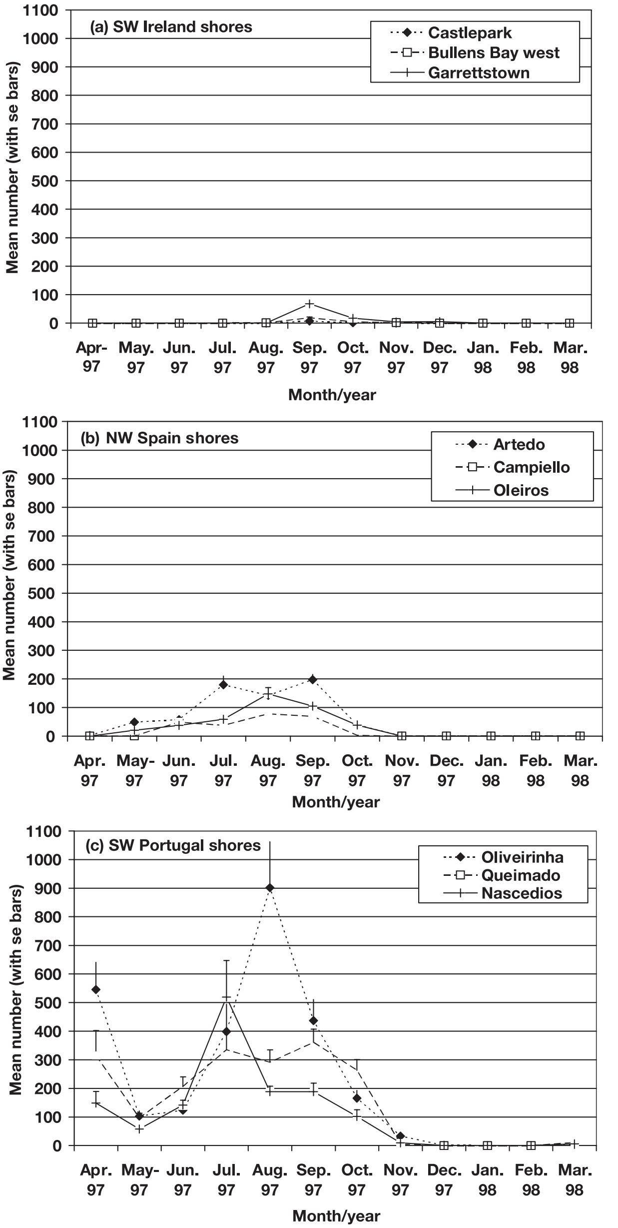

Fig. 3. Mean number (+S.E.) of *C. montagui* recruits 25 cm^{-2} to 1 month between April 1997 and March 1998, on shores at the five locations: (a) SW Ireland, (b) NW Spain, (c) SW Portugal, (d) NW Italy and (e) NE Italy. N.B. Different scale to Fig. 4. Counts are the mean of 18 quadrats per shore.

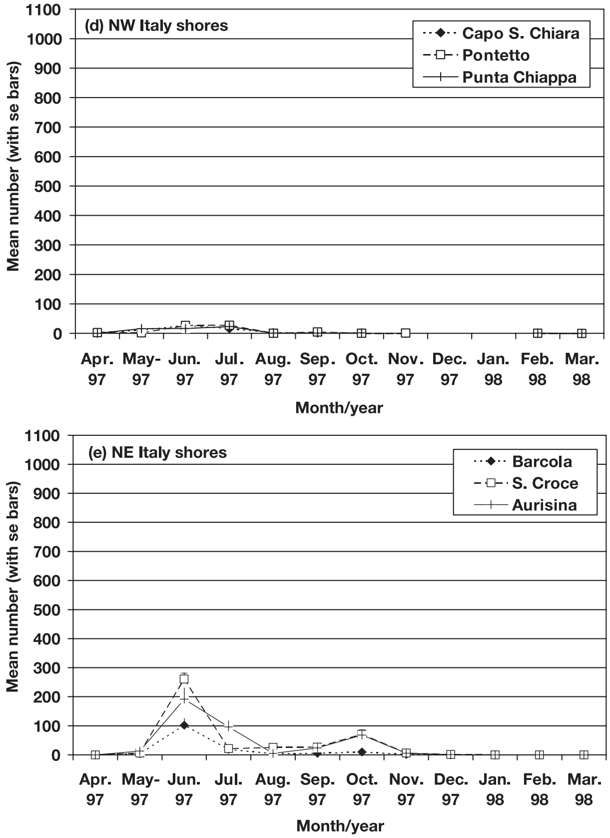

Fig. 3 (*continued*).

covering the replicates, there are missing data for October/November and no data were collected at this location in December and January. Low levels (range: 0.1–0.7 recruits 25 cm^{-2}) of recruitment occurred in February and March (0.1$\pm$0.06 recruits 25 cm^{-2}), but, due to the missing data, it is unclear whether at this location this was the end of recruitment from 1997 or the start of 1998. Cyprids of *C. montagui* were found in May, June, August and September only.

3.3.1.5. NE Italy (Fig. 3e). Recruitment, albeit at a low level (range: 3.8–12.6 recruits 25 cm^{-2}), was first observed in May, followed by peak (maximum: 260.8$\pm$20.45 recruits 25 cm^{-2}) recruitment in June. Recruitment then declined in July–August, before increasing slightly in September. A second much smaller peak in recruitment was seen in October (range: 9.8–70.7 recruits 25 cm^{-2}). Cyprids were found in May, June, September and October only. In December, recruitment was very low, while no recruitment of *C. montagui* was observed in the 3 months (January, February and March) sampled in 1998.

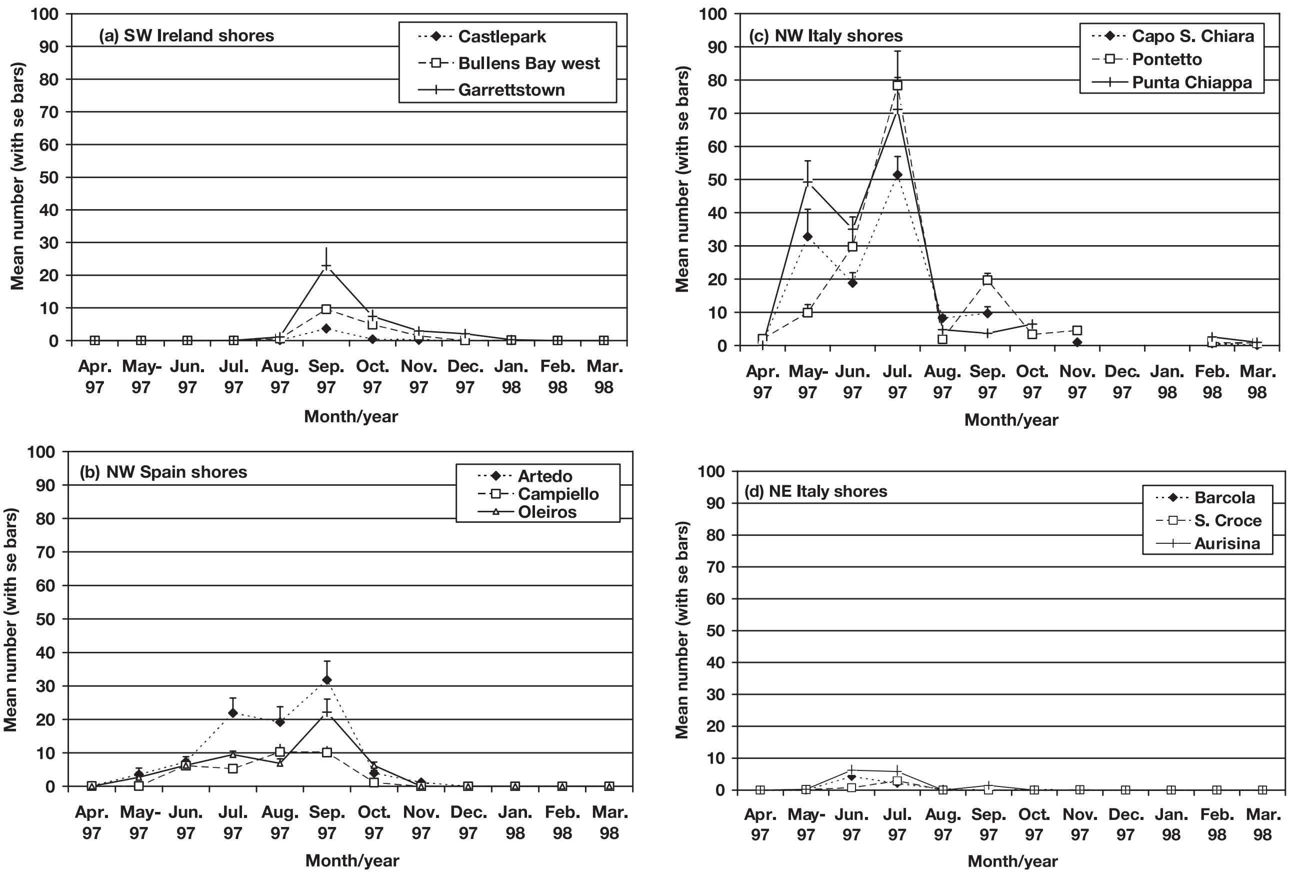

Fig. 4. Mean number (+S.E.) of *C. stellatus* recruits 25 cm^{-2} to 1 month between April 1997 and March 1998, on shores at the four locations: (a) SW Ireland, (b) NW Spain, (c) NW Italy and (d) NE Italy. N.B. Different scale to Fig. 3. Counts are the mean of 18 quadrats per shore.

Table 3
Timing of recruitment of *C. montagui* and *C. stellatus* at the five locations between April 1997 and March 1998

Location	*C. montagui*	*C. stellatus*
SW Ireland	August – February	July – January
NW Spain	April – November	April – November
SW Portugal	April – December, March	N/A
NW Italy	April – November February – March (N.B. no data for December/January)	April – November February – March (N.B. no data for December/January)
NE Italy	May – December	May – November

3.3.2. C. stellatus

3.3.2.1. SW Ireland (Fig. 4a). In SW Ireland, recruitment of *C. stellatus* was first observed in July/August, with peak recruitment (maximum: 23.0±5.43 recruits 25 cm^{-2}) in September, followed by a sharp decline in subsequent months but with low levels continuing into autumn/winter. September, the peak recruitment month, was the only month in which *C. stellatus* cyprids were found. Recruitment occurred in a maximum of 7 months only, with none observed in April to June nor February and March.

3.3.2.2. NW Spain (Fig. 4b). Unlike in SW Ireland, recruitment of *C. stellatus* had started by April (maximum: 0.2±0.11 recruits 25 cm^{-2}), with increasing but still low levels in May and June. June was the only month in which cyprids of *C. stellatus* were found. Two small peaks of recruitment of *C. stellatus* were seen in July and September or June and August, with in each case the second peak (maximum: 31.8±5.56 recruits 25 cm^{-2}) being greater than the first. Recruitment continued until October/November. Similar to *C. montagui,* no recruitment of *C. stellatus* was seen in NW Spain from December to the following March, so recruitment occurred in a maximum of 8 months only.

3.3.2.3. SW Portugal. No recruitment of *C. stellatus* was recorded in this study at this location.

3.3.2.4. NW Italy (Fig. 4c). In NW Italy, *C. stellatus* recruits (metamorphs only) were found in all months sampled, but there are missing data for between October and January. Very low levels of recruitment were recorded in April (range: 0.1–2.0 recruits 25 cm^{-2}). Two peaks of recruitment (maximum: 78.3±10.38 recruits 25 cm^{-2}) were seen. Some recruitment was still present in November. Low (<3.0 recruits 25 cm^{-2}) levels of recruitment occurred in both February and March.

3.3.2.5. NE Italy (Fig. 4d). Very low levels (maximum of 6.2±1.66 recruits 25 cm^{-2}) of *C. stellatus* recruitment (metamorphs only) were recorded in NE Italy. In general, recruitment occurred from May to August and, after a gap of a month, in another month between September and November. Peak recruitment was in June/July. No recruitment was found in April nor between December and March.

Table 3 shows a summary of the timing of recruitment of *C. montagui* and *C. stellatus* at the five locations between April 1997 and March 1998.

4. Discussion

The present study, using the same methodology at different locations, allowed spatial variation, as well as the timing, length and intensity, in the recruitment of *C. montagui* and *C. stellatus* to be examined.

In this study, of the four locations compared using ANOVA, cumulative recruitment was highest in SW Portugal for *C. montagui* and in NW Spain for *C. stellatus*. One explanation for the observed patterns across locations and between species could be related to the supply of larvae that may be potentially higher on a coast where adults are very abundant, or potentially lower on a coast where adults are less abundant. Of the locations studied, highest densities of adult *C. montagui* have been recorded in SW Portugal where highest recruitment was recorded. Up to a mean density of 32.0 cm^{-2}, adult *C. montagui* may occur in SW Portugal (Sousa et al., 2000), in comparison to 5.5 cm^{-2} in SW Ireland (Power, 2000), 3.4 cm^{-2} in NW Spain (Crisp et al., 1981) and 4.0 cm^{-2} in NE Italy (Pannacciulli and Relini, 2000). The patterns of recruitment of *C. stellatus* found in the present study also follow the trends in adult abundance. Recruitment was not significantly different for this species in SW Ireland and NW Spain (up to a mean density of 5.0 cm^{-2} adult *C. stellatus* has been recorded in SW Ireland (Power, 2000) and 3.2 cm^{-2} in NW Spain (Crisp et al., 1981)). Lowest recruitment of *C. stellatus* was found in NE Italy, with none in SW Portugal, where the mean number of adults of this species on both coasts was only 0.2 barnacles cm^{-2} (Pannacciulli and Relini, 2000; Sousa et al., 2000). For the SW coast of Portugal, Sousa et al. (2000) suggested that the reduced number (in comparison to *C. montagui*), and percentage cover, of *C. stellatus* adults may be due to lower egg production and limited supply of settling larvae compared with *C. montagui*. However, it must be reiterated that at all of these locations, in the present study, recruits were collected in *C. montagui*-dominated zones only. Previous studies, but using different methods in different sampling years and at different times of year, have reported a wide range of recruitment densities, with no discernible latitudinal pattern. Densities of 30–50 cm^{-2} *Chthamalus* spat have been recorded at Kintyre, Scotland (Southward and Crisp, 1954), 10–15 cm^{-2} at Plymouth, England (Burrows, 1988), 20–25 cm^{-2} at the mouth of the Gironde, France (Crisp and Fischer-Piette, 1959), 20 cm^{-2} in NW Spain (Miyares, 1986) and 17 recruits cm^{-2} on the central west coast of Portugal (Range and Paula, 2001). At Aberystwyth, Wales, Kendall and Bedford (1987) reported a maximum density of 4 *C. montagui* spat cm^{-2}, while Myers et al. (1979) observed up to 26 *C. montagui* spat cm^{-2} at an exposed site in Bantry Bay, SW Ireland.

In one of the few comparable studies over broad spatial scales, Jenkins et al. (2000) reported substantial variation in barnacle recruitment with location. Recruitment was significantly higher in the arctic-boreal barnacle *Semibalanus balanoides* (L.) near the centre (SW Ireland/SW England) of its European range than further north in the Isle of Man or Sweden. As in the present study, Jenkins et al. (2000) also reported significant variation in the level of recruitment at the smaller spatial scale of shore. Reports of some shores being more abundantly colonised than others are common in the literature. Greater larval supply or flow rates at more open coast situations (Southward and Crisp, 1956; Bennell, 1981; Caffey, 1985; Bushek, 1988), propagule availability (Gaines et al., 1985; Kendall et al., 1985; Raimondi, 1988; Minchinton and Scheibling, 1991; Bertness et al., 1992; Carroll, 1996), larval retention at certain shores (Bennell, 1981) or specific local conditions (Connell, 1985) have been suggested as the cause of this variability. In the present study, despite the variability between shores within location, shore did not interact with species, indicating that the relative recruitment of the species at each shore within a location did not differ.

From ANOVA, the effect of species within each location showed that recruitment of *C. montagui* was higher than that of *C. stellatus* at all locations except SW Ireland, where recruitment was not significantly different (but it was lower in *C. stellatus* than *C. montagui*). As in the present study, on two shores in SW Ireland, Power et al. (1999a) found that the relative abundance of the recruits (metamorphs only) of these two species did not differ significantly in 1996–1997. In Britain and Ireland, the distributions of the adults of *C. stellatus* and *C. montagui* may overlap considerably in terms of shore height and wave exposure (Crisp et al., 1981). In SW Ireland, *C. montagui* increases in abundance in sheltered locations and towards the high-water neap-tide level on all shores where chthamalid species occur. *C. stellatus* may be found on all such shores and, with increasing exposure, extends upwards into the *C. montagui* zone (Delany et al., 2003). *C. stellatus* and *C. montagui* are approaching the northern edge of their geographical limit in SW Ireland and they have been suggested to be recruitment-regulated due to the sub-optimal conditions imposed by increased environmental stress at the limits of their range (Kendall and Bedford, 1987; Healy and McGrath, 1998).

In the present study, the cyprids of *C. stellatus* and *C. montagui* were identified based on carapace length, following the work of O'Riordan et al. (1999, 2001) and Power et al. (1999b). Cyprids of these species are also distinguishable genetically (see Power et al., 1999b), as well as at the ultrastructural level using scanning electron microscopy (Jensen et al., 1994; O'Riordan et al., 2002b). In comparison to metamorph numbers, few cyprids were found on the shores in NW Italy and NE Italy. Based on their size, the cyprids were identified as *C. montagui*. However, *Euraphia depressa* (Poli) occurs on the shores which we sampled, so these cyprids may have been this species, whose cyprids cannot yet be distinguished from those of *C. montagui*, although no metamorphs of *E. depressa* were found on these shores during the study period. On these shores, *E. depressa* lives in crevices and seldom enters into the formation of the barnacle belt and our sampling was on open rock where *Chthamalus* is more abundant. Although metamorphs of both species of *Chthamalus* were found on the Mediterranean shores, no cyprids of *C. stellatus* were recorded. O'Riordan et al. (2001) had previously found a single *C. stellatus* cyprid from one of the NE Italy shores (Santa Croce) out of a sample of 186 cyprids.

Cruz (1999) has ascertained that the cypris larvae of *Chthamalus* species can metamorphose during one tidal cycle. According to Range and Paula (2001), this would explain their relatively low abundance (compared with metamorphs) on Portuguese shores, which was also seen in the present study. Since our sampling regime was only monthly, the ability to metamorphose within hours of attachment in certain locations, as well as the effect of temperature (and how it varies seasonally with location) on the rate of metamorphosis may in part explain why cyprids were only found in a subset of the months in which recruitment was recorded. But cyprids were missing in winter months when metamorphosis may take longer, but this was also when recruitment was low. The lack of cyprids in winter might have been expected since the ratio of cyprids/metamorphs, even at peak recruitment, was low. In the present study, in both SW Ireland and NW Spain, the percentage of cyprids out of the total recruitment was higher in *C. stellatus* than in *C. montagui*. Power et al. (1999a), Power (2000) and O'Riordan et al. (2001, 2002a) have reported that on Irish shores cyprids of *C. stellatus* are much more abundant than those of *C. montagui*. Power et al. (1999a) and Delany et al. (2003) have suggested that *C. montagui* may have a faster rate of metamorphosis than *C. stellatus* as well as a higher metamorphic success.

Range and Paula (2001) suggested a latitudinal variation in the recruitment period of *Chthamalus* spp. on the Atlantic coast of the Iberian peninsula and this latitudinal trend has now been confirmed for both *C. montagui* and *C. stellatus* and expanded with data from sites spanning a large part of the range of these species in Europe. For *C. montagui*, recruitment on the Atlantic coast was seen to begin later and had a shorter season further north (in SW Ireland than in NW Spain than in SW Portugal). A similar pattern was seen for *C. stellatus* in SW Ireland versus NW Spain.

In SW Ireland, the summer initiation and overall period of recruitment was approximately the same in *C. montagui* and *C. stellatus*, with both species showing peak recruitment in September. Further north, on Clare Island, Mayo, Ireland (O'Riordan et al., 2002a), settlement began at the end of July or in September. As in the present study, in 1996/1997 settlement in SW Ireland was greatest from August to October, but continued at a low level until the following April (Power et al., 1999b). Similarly, further south, in SW Britain, Burrows (1988) and Pannacciulli (1995) found that settlement began in July/August and continued into September (the month of peak settlement of *Chthamalus* in 1991/1992), while a chthamalid cyprid was seen in November in 2001 (SJH, pers. obs.).

Unlike in SW Ireland, in NW Spain neither species recruited from December to March. However, the recruitment period was actually 1 month longer than in SW Ireland. Our results are broadly comparable to those reported for NW Spain by Miyares (1986) and Macho et al. (2000). Both reported recruitment beginning in May, which continued until the end of Autumn (Macho et al., 2000) or until October, with a single settler found in November (Miyares, 1986). The timing of recruitment is linked to the reproductive period. In SW Ireland, O'Riordan et al. (1995) reported the majority of ripe embryos occurring from April/May to October, but with a few chthamalid barnacles containing fertilised embryos as late as December and February/March, while none were found outside March to September in NW Spain (Miyares, 1986). So, the main period of both reproduction and recruitment start earlier in NW Spain, but they may continue into the winter in SW Ireland. In SW Ireland, *Chthamalus* barnacles were observed releasing larvae in January, soon after being brought into the laboratory (AAM, pers. obs.), but it is not known whether these were capable of settling.

C. montagui is the most abundant intertidal barnacle on the Portuguese mainland (Range and Paula, 2001). According to Sousa et al. (2000), in the mid intertidal rocky shores of Portugal, *C. montagui* is very abundant and *C. stellatus* is much less abundant and is more frequent in the low intertidal and on very exposed shores. Our results for *C. montagui* near Sines, in SW Portugal are comparable to those of Range and Paula (2001) who found that, further north on the central west coast of Portugal, in 1996/1997 *Chthamalus* spp. recruited almost continuously during the year, with a peak between July and September and a gap of 2 months (February and March).

Initiation and timing of recruitment may be influenced by such inter-related factors as latitude, temperature and food availability, as well as shore height. Range and Paula (2001) suggested that seasonal recruitment intensity in *Chthamalus* spp. may be related to intertidal temperature fluctuation, as well as food availability affecting reproduction. Burrows et al. (1992) noted that the main effect of latitude appears to be on the onset of breeding, with 4 months separating the beginning of the breeding season in the Mediterranean in February and in SW Scotland at the beginning of June. As seen in the present study, this is then clearly reflected in the commencement and length of the recruitment period. Southward (1976) and Burrows et al. (1999) suggested a possible failure of early broods or slower development times near the northerly limits of the species range. Burrows et al. (1992) have related the release of the larvae of *Chthamalus* spp. to blooms of flagellates. They noted that in southern latitudes, these flagellates occur over a longer period of the year, which allows for a longer season for the successful development and recruitment of *Chthamalus* larvae.

As well as biological processes (e.g. variations in timing and intensity of reproduction), variations in processes involving the physical transport of larvae on-and off-shore among locations could explain the differences in timing, intensity and length of recruitment. It is known that local settlement and recruitment rates are partly decided by large-scale factors (e.g. offshore hydrodynamic processes, Barnes, 1956; Raimondi, 1990) and partly by small scale factors (e.g. local water turbulence). In the Northeast Pacific Ocean, Connolly et al. (2001) found that a very large transition in recruitment rates of intertidal invertebrates occurred near Cape Blanco in southern Oregon. Recruitment was significantly and markedly higher north of this headland, where upwelling is weak, than south of it, where upwelling is strong. This is consistent with the hypothesis of Connolly and Roughgarden (1998) that regional differences in upwelling intensity are a major cause of corresponding differences in benthic community structure. Stronger upwelling (and thus offshore flow) to the south was hypothesized to transport larvae further offshore and thereby reduce larval supply to nearshore benthic communities. On the west coast of USA, transport of larvae onshore has been related to the cessation of coastal upwelling (Farrell et al., 1991). Upwelling also has an indirect effect on zooplankton, by increasing the biomass of phytoplankton. Upwelling is very intense during the summer at two of the locations we studied, SW Portugal (Fiúza et al., 1982) and NW Spain (Botas et al., 1990). In Portuguese coastal waters, Mendes (1997) reported phytoplankton biomass peaks associated with upwelling events in February, August and October, which links with recruitment first being recorded in March with peaks in the summer. Benedetti-Cecchi et al. (2000) pointed out that understanding causal processes initially relies on appropriate description of pattern. Now that we have described the pattern, the next logical step would be to study the processes (physical and/or biological), which may be causing the observed variations in recruitment of these two chthamalid species among locations along the Atlantic coast of Europe.

Recruitment of *Chthamalus* was studied in two locations in the Mediterranean, in NW (Ligurian Sea) and NE (Adriatic Sea) Italy. It is difficult to compare these shores with the Atlantic locations. In general the Mediterranean is calmer than the Atlantic and has warmer seas, with an earlier algal bloom and consequently a more protracted season for larval release (Stubbings, 1975). Furthermore, the shores in NE Italy are located in the Gulf of Trieste, which is more enclosed and has lower winter temperatures (which can limit the length of the reproductive season) than the shores in NW Italy, in the Gulf of Genoa (Pannacciulli and Falautano, 1999). The two areas also differ in tidal range and hydrodynamics, the former having limited wave action and 1-m tidal range, while the latter has quite strong wave action and tidal range of 30 cm.

Like the Atlantic shores, the shores in NE Italy were dominated by adults of *C. montagui*. In NE Italy, recruitment for both species began in May, which follows the latitudinal pattern of recruitment being earlier than in SW Ireland but later than in NW Spain. Pannacciulli and Relini (1999) had commented that in Italy the settlement period of *Chthamalus* appears to be longer than that that observed for the same species in the Atlantic. The present study has shown this to be true in comparison to recruitment for the populations of *C. montagui* at the most northerly Atlantic location (i.e. in SW Ireland), but the recruitment period lasted for the same number of months (8) in NW Spain and NE Italy, while recruitment was shorter than at the most southerly Atlantic location, in SW Portugal. Similar to both NW Spain and SW Portugal, two peaks of recruitment of *C. montagui* occurred, but in NE Italy, the first was larger than the second peak. In comparison with *C. montagui*, only very low levels of *C. stellatus* recruitment were seen. A study in the same location by Pannacciulli and Falautano (1999) suggested that larvae are released into the plankton by *C. montagui* from April to September, while only from June to September for *C. stellatus*. von Kolosváry (1947) reported *Chthamalus* brooding embryos in the Adriatic Sea from July to December.

Unlike at the other locations, the shores in NW Italy (Ligurian Sea) were *C. stellatus*-dominated (see Pannacciulli and Relini, 2000). Interestingly, dissimilar to elsewhere, high numbers (>7500) of *C. stellatus* metamorphs (although no cyprids) were found. However, the dataset is incomplete due to problems with sampling during a number of months, with data completely lacking for December and January. The timing of recruitment broadly agrees with Pannacciulli and Falautano (1999) who had suggested that in NW Italy *C. montagui* larvae are released into the plankton in March–October, while *C. stellatus* releases larvae from May to September. However, in the same areas, Relini (1983) reported the two *Chthamalus* species brooding all year round except October and November, with *Chthamalus* settling from March to May and September to January. Pannacciulli and Relini (1999) suggested that differences in timing could be related to interannual variations. Benedetti-Cecchi et al. (2000) reported considerable variation at different temporal and spatial scales in the recruitment and mortality of *C. stellatus* in the Mediterranean.

According to Carroll (1996), temporal and spatial recruitment variation has been recorded in or near the centre of species' geographic ranges and thus tells us little about the importance of recruitment regulation on populations existing near their geographic limits. The present study was concerned with spatial variation in the recruitment of the chthamalid barnacles, *C. stellatus* and *C. montagui*, over a large part of their range in Europe, not just at the centre. Jenkins et al. (2000) examined the spatial and temporal recruitment of the barnacle *S. balanoides* over an European scale as part of the EURO-ROCK programme. In comparison to the chthamalids, *S. balanoides* releases its larvae in spring after brooding over the winter months and settles during a relatively short period of time (Jenkins et al., 2000). As in the present study for chthamalids, Jenkins et al. (2000) found that settlement of *S. balanoides* varied in length and timing among locations. For the arctic-boreal *S. balanoides* settlement was earliest and shortest at the most northerly location (Sweden), while for the Lusitanian *C. montagui* and *C. stellatus* recruitment was earliest, as well as longest, at the most southerly locations (SW Portugal and NW Spain respectively). Further studies on an European scale, using the same methodology, examining recruitment of both *Chthamalus* species at a number of shore heights or where one or other of the adults dominates may prove interesting, although post-settlement mortality, rather than larval supply, was deemed to be the more significant factor in determining the characteristic patterns of these chthamalid species on SW Ireland shores (Delany et al., 2003).

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