

## Seasonal variation and population dynamics of isopods inhabiting intertidal macroalgae\*

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**SUMMARY.** — Patterns of seasonal abundance and size-frequency distributions of intertidal isopods were investigated in macroalgal dominated communities (*Fucus vesiculosus*, *Gelidium latifolium* and *Cystoseira baccata*) on two semiexposed shores of North Spain. All species were found to display a seasonal cycle in abundance. In the three dominant species, *Dynamene bidentata*, *D. magnitorata* and *Cymodoce truncata*, fluctuations of density were related to reproductive biology. Macroalgae appeared to be a habitat for juveniles of these species; adults were collected in very small numbers. Oviparous females were never found. Disappearance from the algae was therefore due to mortality and migration of mature animals towards the reproductive habitat. *Dynamene bidentata* exhibited a prolonged breeding season, with a fairly continuous release of juveniles. In *D. bidentata*, differences in size-frequency distributions were found between groups of individuals collected on different algal species. In *Gelidium*, first stage juveniles formed the bulk of the recruitment. A small number of subadult and adult specimens was collected at any time. *Fucus* lacked first stage animals during most of the study and recruitment was of stage-3 juveniles. A late recruitment in *Fucus* is interpreted as an adaptation to avoid the harsher environmental condition in this community. Recruitment in *D. magnitorata* and *C. truncata* was restricted to two months (in late spring and summer) and always involved newly released individuals. Differences in synchrony of recruitment between the three dominant species might be due to location of populations within the geographical range of the species, though additional information is needed about the distribution of *C. truncata*.

**Key words:** Intertidal, isopods, macroalgae, population dynamics, seasonality, synchrony in recruitment.

**RESUMEN:** VARIACIÓN ESTACIONAL Y DINÁMICA DE LAS POBLACIONES DE ISÓPODOS DE LAS COMUNIDADES DE ALGAS INTERMAREALES. — Se ha investigado la estacionalidad y las distribuciones de talla de isópodos intermareales en comunidades dominadas por macroalgas (*Fucus vesiculosus*, *Gelidium latifolium* y *Cystoseira baccata*) en dos localidades semiexpuestas de la costa norte de España. Todas las especies recolectadas mostraron un claro ciclo estacional de abundancia. Las variaciones de densidad en las tres especies dominantes (*Dynamene bidentata*, *D. magnitorata* y *C. truncata*) estaban relacionadas con su biología reproductora. Las macroalgas probablemente constituyen un hábitat juvenil para los isópodos, ya que los adultos fueron siempre recogidos en muy bajas densidades mientras que nunca fueron recolectadas hembras en estado ovígero. La desaparición de los isópodos de las algas era, por lo tanto, debida a mortalidad y a migración de animales sexualmente maduros hacia el hábitat reproductor. *Dynamene bidentata* presenta una época reproductora prolongada, caracterizada por una liberación de juveniles continua. La distribución de tallas en esta especie era distinta para grupos de individuos recolectados en las diferentes comunidades de macroalgas. El grueso del reclutamiento en *Gelidium* estaba formado por individuos recién liberados del marsupio materno. En *Fucus*, por el contrario, el reclutamiento se realizaba fundamentalmente con individuos en el tercer estadio de desarrollo. Un reclutamiento tardío en *Fucus* se interpreta como una adaptación que evitaría a los juveniles las duras condiciones ambientales en este nivel de marea. A diferencia de *D. bidentata*, el reclutamiento en *D. magnitorata* y *C. truncata*, estaba restringido a dos meses y siempre tenía lugar con ejemplares recién liberados. Las diferencias en la sincronización en el reclutamiento entre las tres especies dominantes, podrían ser debidas a su posición dentro de su distribución geográfica, aunque se necesita información adicional sobre la distribución de *C. truncata*.

**Palabras clave:** intermareal, isópodos, macroalgas, dinámica de poblaciones, estacionalidad, sincronismo en el reclutamiento.

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## INTRODUCTION

Seasonal variation is a major feature of the dynamics of rocky intertidal communities (LUBCHENCO & GAINES, 1981; UNDERWOOD, 1981; MACLULICH, 1987). Fluctuations in animal and plant abundance are often the consequence of complex interactions between a number of factors. Thus, UNDERWOOD & JERNAKOFF (1984) showed that seasonal differences in colonization and abundance of macroalgae in intertidal pools can be explained by the interactions between grazers and the differential influence of the physical environment on recruitment, survival, and growth of the algae. Fluctuations in abundance of marine invertebrates are, in many cases, associated with seasonality of their reproductive periods. This has been found widely in nature (KOOP & FIELD, 1980; YOUNG, 1981; HEATH & KHAZAELI, 1985; DAUVIN, 1988) though cyclic and seasonal migrations are also widespread among marine animals (FISH & FISH, 1972; ALHEIT & NAYLOR, 1976; OJEDA & SANTELICES, 1984; DAUVIN, 1988).

Isopods are a major constituent of the fauna of many littoral environments, including sandy beaches, mudflats, estuaries, and rocky shores (AMANIEU, 1969; JONES, 1970; HARVEY, *et al.*, 1973; MARSDEN, 1976; SHEADER, 1977). On rocky shores, isopods have been collected in a great variety of habitats, ranging from supralittoral crevices to macroalgal dominated communities in the lowest tidal levels (HARVEY, 1968; HOLDICH, 1970, 1976; CAREFOOT, 1973; HEALY & O'NEILL, 1984). Adequate information exists on the population biology of a number of species, e.g. *Ligia* spp. (CAREFOOT, 1973; KOOP & FIELD, 1980), *Dynamene bidentata* (HOLDICH, 1968, 1970, 1976), and *Idotea* spp. (NAYLOR, 1955; SHEADER, 1977; HEALY & O'NEILL, 1984, among others). Nevertheless, seasonal variations in abundance have been emphasized only infrequently (but see HOLDICH, 1968, 1970; HEATH & KHAZAELI, 1985).

In this paper, we focus on seasonal variations in population density of isopods inhabiting macroalgae. The relationships between density cycles and population structure were also examined. Variations in the density of the isopods can be used to indicate the effect of seasonality on the fauna inhabiting macroalgae. A similar approach has been used previously to assess the effect of geographical changes in macroalgal cover on its associated fauna (ARRONTES & ANADÓN, 1990). This study also gives basic information

on the population structure of the isopods, which is necessary for subsequent studies on the ecology of this group.

## MATERIALS AND METHODS

The study sites were two localities on the shore of North Spain. Bañugues (43°38' N, 5°48' W) and Aramar (43°37' N, 5°46' W). Briefly, Bañugues has two areas differing greatly in wave exposure, the outer part has the zonation pattern described for semiexposed shores (LEWIS, 1964) but the inner part has the characteristic Fucaceae zonation of sheltered European shores (LEWIS, 1964). Aramar is a steeply sloping limestone rock platform (slope about 25-30°) exposed to moderate wave action. Zonation patterns are the same as those described for the outer part of Bañugues.

Sampling involved three macroalgal communities, those dominated by *Fucus vesiculosus* L., *Gelidium latifolium* (Grev.) Born. et Thur., and *Cystoseira baccata* (Gmel.) Silva. These are representative of extensive communities on the shores of northern Spain (ANADÓN, 1983) and were found in a previous survey to harbour large numbers of isopods (ARRONTES & ANADÓN, 1990). Samples were collected monthly, coinciding with spring tides, from July 1984 to September 1985 for *Gelidium*; August 1984 to September 1985 for *Cystoseira*; and from July 1984 to November 1985 for *Fucus*. In Bañugues, sampling involved all three macroalgae. In Aramar, only *Gelidium* was sampled. In each belt, two samples were taken from randomly located quadrats of size 50 × 50 cm for *Fucus*, 45 × 45 cm for *Gelidium*, and 60 × 60 cm for *Cystoseira*. Samples were taken by removing by hand all seaweeds present in the quadrat and scraping the rock surface clean. Special attention was paid to animals in rock crevices and holes. Sea water temperature was measured in Bañugues every two weeks from September 1984 to August 1985, and at monthly intervals thereafter.

Samples were frozen within 1-3 h after collection and stored until processed. Animals were removed by washing the algae in a big tray, the water with the animals was passed through a 0.5 mm sieve. Isopods were identified to species whenever possible and counted. For species of the genera *Dynamene* and *Cymodoce*, size-distribution for each month was obtained. Postmarsupial growth stages were considered as size-categories. The number of growth stages until reproductive age is a fixed number in some species of

isopod (HOLDICH, 1968) and their identification, at least in these two genera, is easy. Eight stages were identified in *D. bidentata* and in *Cymodoce truncata* and seven in *D. magnitorata*. Because of the different duration of each intermoult period, at least for *D. bidentata* (HOLDICH, 1968), size-distribution is not an exact substitute of age-distribution, but in the present situation appeared as the only alternative. Three major age-groups can be recognized in *D. bidentata* (HOLDICH, 1968): (i) animals in postmarsupial developmental stages 1 to 5, with no observable sexual characters (juveniles); (ii) animals in stages 6 and 7, with external sexual characters (subadults); and (iii) animals in stage 8 or reproductive specimens (adults). In *D. magnitorata*, changes in morphology and physiology are very similar to those in *D. bidentata*, though in *D. magnitorata* there are only 4 juvenile postmarsupial stages. The life-cycles of both species are very similar (HOLDICH, 1976). The sex of subadult and adult animals of both *Dynamene* species was recorded.

## RESULTS

A large number of species of isopod were collected on the three algae although only 7 species exhibited high densities (see Table 1). Species of the genus *Dynamene* were dominant in the four zones sam-

pled. *Cymodoce truncata* were also found in large densities on *Gelidium* and, during a short period of time, on *Cystoseira* (see below). There were no major differences in population dynamics for animals collected on *Gelidium* from the two localities and no further comments will be made on this. Unless specified, comments and discussion are based on data obtained from Bañugues.

### Abundance cycles

For *D. bidentata*, the patterns observed on each macroalga were markedly different (Fig. 1). A seasonal pattern was clearly observed in animals inhabiting *F. vesiculosus*, which exhibited peak abundances in late summer. Minimal abundances were recorded in mid-winter. The abundance cycle of animals from *Cystoseira* also exhibited a seasonal pattern though density fluctuations were less evident. Cycles of abundance on *Gelidium*, in the two localities, were not clear and peaks were found in winter for Bañugues, while in Aramar a small fluctuation of density was detected. Despite the different patterns observed in each community, the species was present during the whole period on the algae.

Cycles of density of *D. magnitorata* were found to be very similar in the three places where it was collected (Fig. 2). *Dynamene magnitorata* was only abundant during a restricted period. Peak abundances

TABLE 1. — Isopods collected. Maximal (M) and minimal (m) numbers recorded during the study period. The number of months in which each species was collected is given in brackets.

Species	<i>Fucus</i>		<i>Gelidium B</i>		<i>Gelidium A</i>		<i>Cystoseira</i>	
	M	m	M	m	M	m	M	m
<i>Anthura gracilis</i> (Mont.)			4	0 (4)	1	0 (3)	8	0 (6)
Anthuridae spp.			8	0 (1)				
Arcturidae spp.			3	0 (5)	6	0 (6)	12	0 (9)
<i>Campecopea hirsuta</i> (mont.)			1	1 (1)				
<i>Cyathura carinata</i> Norman & Stebbing			4	0 (5)	5	0 (7)	11	0 (8)
<i>Cymodoce emarginata</i> Leach			52	0 (15)	57	5 (16)	5	0 (2)
<i>Cymodoce truncata</i> (Mont.)	1	0 (1)	672	0 (10)	452	0 (12)	822	0 (5)
<i>Dynamene bidentata</i> (Adams)	898	40 (18)	188	13 (16)	126	16 (16)	279	37 (16)
<i>Dynamene edwardsii</i> (Lucas)			1	0 (1)				
<i>Dynamene magnitorata</i> Holdich			561	3 (16)	753	5 (16)	1847	11 (16)
<i>Gnathia maxillaris</i> Mont.					1	0 (2)	3	0 (1)
<i>Gnathia</i> sp.			4	0 (5)			1	0 (4)
<i>Idotea baltica</i> Pallas	1	0 (1)	2	0 (4)	2	0 (3)	1	0 (2)
<i>Idotea granulosa</i> Rathke							2	0 (2)
<i>Idotea</i> sp.			2	0 (3)	7	0 (1)	1	0 (1)
<i>Ischyromene lacazei</i> Racovitza			1	0 (2)			1	0 (1)
<i>Jaera</i> sp.	1	0 (1)						
<i>Jaeropsis brevicornis</i>					2	0 (2)		
<i>Munna</i> sp.			15	0 (8)	31	0 (13)		
<i>Paranthurus nigropunctata</i> Lucas			31	0 (14)	61	1 (16)	50	0 (14)
<i>Sphaeroma serratum</i> (Fab.)	2	0 (4)						
<i>Synisoma acuminatum</i> (Leach)			1	0 (4)			104	14 (16)
<i>Synisoma lancifer</i> (Leach)			28	0 (12)	8	0 (14)	46	0 (15)
<i>Zenobiana prismatica</i> Risso							1	0 (1)

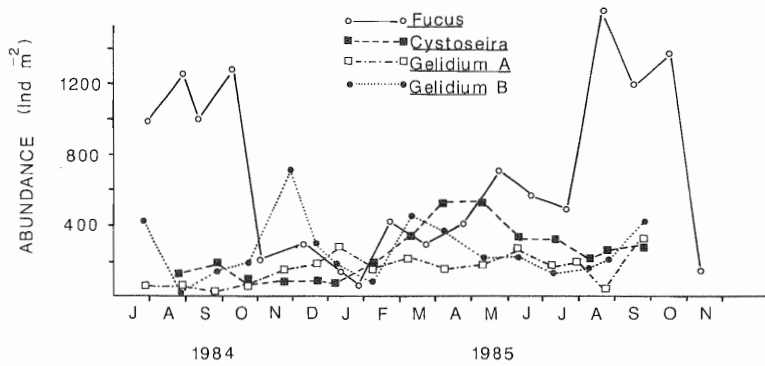


FIG. 1. *Dynamene bidentata*. Changes in population density on algae. *Gelidium* A, *Gelidium* in Aramar. *Gelidium* B, *Gelidium* in Bañugues. Abbreviations are valid for the next Figures.

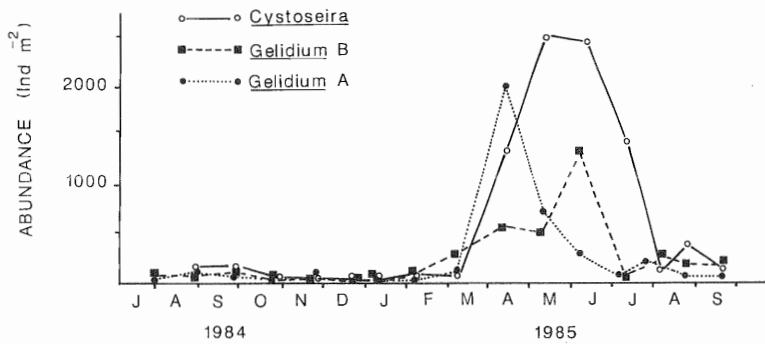


FIG. 2. — *Dynamene magnitorata*. Changes in population density on algae.

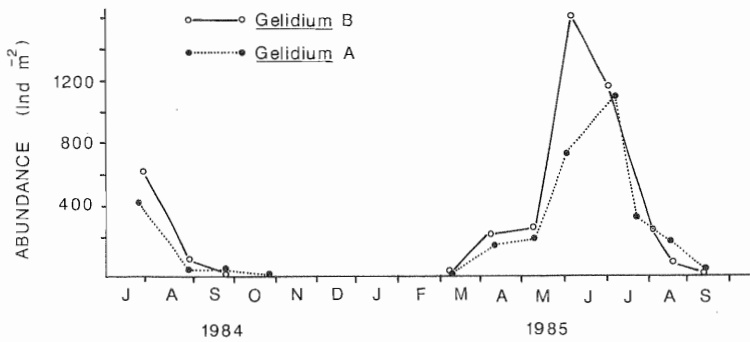


FIG. 3. — *Cymodoce truncata*. Changes in population density on algae.

were recorded in late spring-early summer. The cycle was characterized by a rapid increase of animal numbers which was followed, within the next one or two months, by an abrupt decrease in density. During late summer, autumn and winter, the number of animals collected was very small. Nevertheless, some specimens were always collected.

The density of *C. truncata* showed a very similar cycle to that of *D. magnitorata*, with one major difference. *Cymodoce truncata* was not collected on the algae during autumn and winter (Fig. 3). The cycle of abundance of *C. truncata* on the algae was highly

seasonal, with no evident differences between the two localities. This species was only collected regularly among *Gelidium*. On *Cystoseira*, *C. truncata* was collected in large numbers only in two months, so information on this species on this algae is not presented.

*Paranthura nigropunctata* (Fig. 4A) exhibited a period of large densities from late summer to autumn and a prolonged period with low densities during winter and spring. Differences between belts did not appear to be important. *Synisoma acuminatum* (Fig. 4B) had a density cycle with a period of high

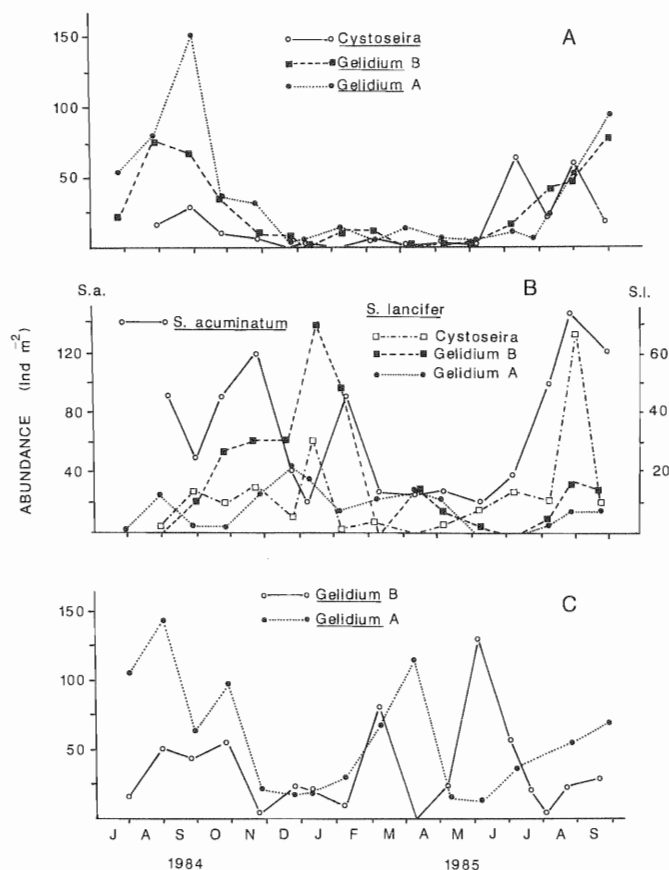


FIG. 4. — Changes in population density in non-common species of isopods. A, *Paranthura nigropunctata*. B, *Synisoma* species; S.a. *S. acuminatum*, S.l. *Synisoma lancifer*. C, *Cymodoce truncata*. Note the different vertical scale in each case.

density in late summer, autumn and early winter. The patterns exhibited by the remaining two species, *S. lancifer* and *C. emarginata* (Fig. 4C) are not easy to interpret, and more samples are necessary to describe the fluctuation patterns in these two species.

### Size-frequency distributions

#### *D. bidentata*

First stage juveniles were the dominant group in *Gelidium* during the whole study period (Fig. 5A). The age structure in *Fucus* was the opposite and juveniles of stage 1 were lacking for most of the year. Only in August were first stage specimens abundant (Fig. 5B). In this area, the bulk of the recruitment was of individuals of stages 3-4, instead of newly released animals as observed in *Gelidium* and *Cystoseira* (for simplicity, data on *D. bidentata* on *Cystoseira* are not presented). On *Cystoseira* both age-classes were found sequentially. Stage 8 individuals were scarce on all algae and invariably only males were sampled

at this stage. The time spent by the adults on the algae is probably very small (as shown by Fig. 5). No ovigerous females appeared in the samples.

Size-distributions in *Fucus* and *Gelidium* revealed another important aspect of the population dynamics of *D. bidentata*: a prolonged breeding season. Juveniles of stage 1 were collected on *Gelidium* throughout the year. Similarly, on *Fucus*, juveniles (mostly stage 3) were collected from February-March to October.

#### *D. magnitorata*

Very different size-frequency distributions were found in *D. magnitorata* (Fig. 6). There were no major differences in size-distributions between animals collected in *Gelidium* and *Cystoseira* (only data for the latter are presented in Fig. 6). Both groups exhibited a highly synchronous appearance of juveniles in April-May. On both algae, recruitment was as newly-released individuals, which remained on the algae for a short period of time. So far, it is not possible to

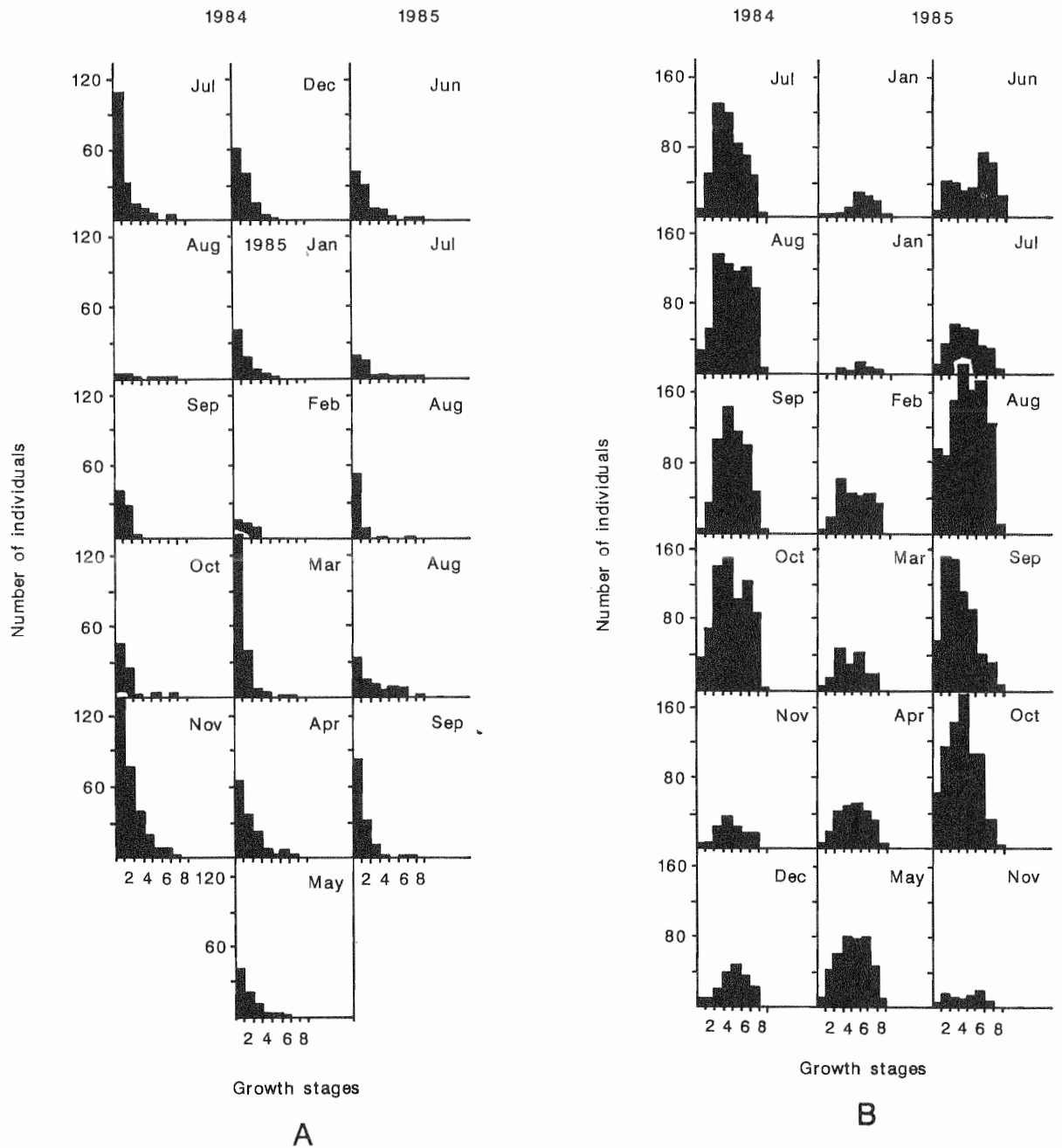


FIG. 5. — *Dynamene bidentata*. Size frequency distributions. A, *Gelidium* in Bañugues. B, *Fucus*. Obtained from total of specimens sampled in each month. August, in *Gelidium*, and January, in *Fucus*, were sampled twice. Note different vertical scales. Comments are extended to figure 6.

distinguish whether the disappearance of individuals from the algae is due to mortality, migration, or both. As in the previous species, adults were collected in small numbers. Only in July 1985 were they fairly abundant (only stage 7 males). Again, no ovigerous females of this species were collected during the study period.

The population dynamics of *Cymodoce truncata* was identical to that of *D. magnitorata* and no additional comments will be made. Stage 1 juveniles were collected from April to June. By July, subadult stages were abundant on the algae. The population collapsed in August. As in the previous two species, females carrying eggs were never found.

1984

1985

## DISCUSSION

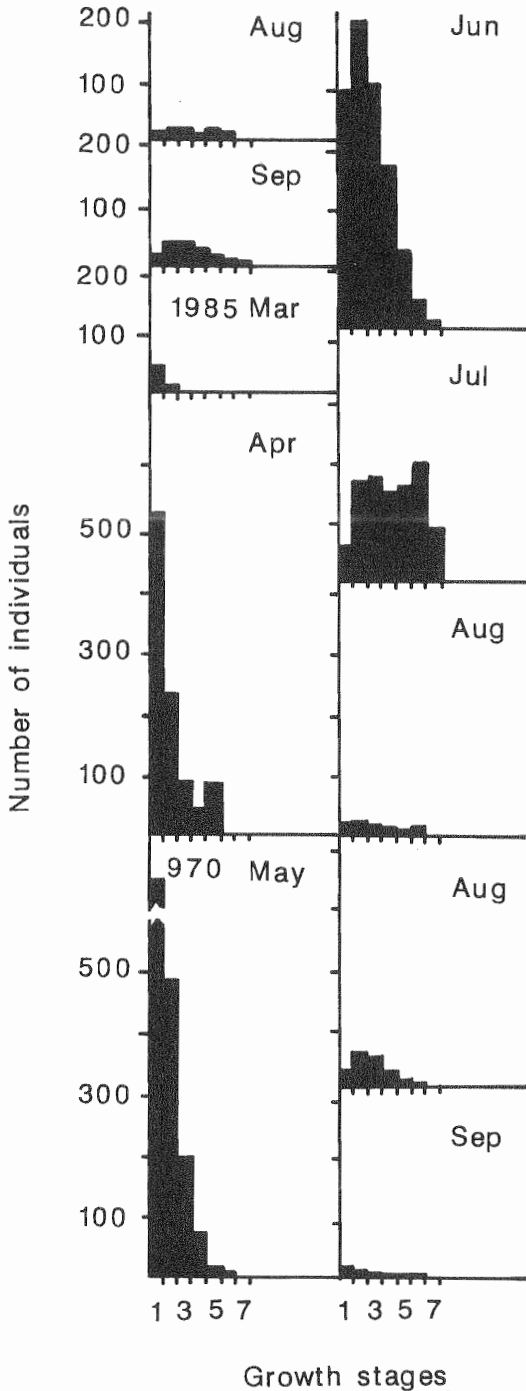


FIG. 6. — *Dynamene magnitorata*. Size frequency distributions in *Gelidium* (Bañugues). For simplicity, only months with a number significant of specimens are presented.

## Variations in abundance

All species studied exhibited a seasonal pattern of abundance to some extent. In two of them, *D. magnitorata* and *C. truncata*, populations exhibited a highly seasonal cycle. In addition to seasonal changes in the physical environment, some other aspects of macroalgal communities, with potential influences on animal populations, have been found to display clear seasonal cycles. Among others, these include changes in the abundance of algal epiphytes (D'ANTONIO, 1985; ARRONTEs, 1990), changes in the concentration of phenolic compounds, largely considered as grazing deterrents (RAGAN & JENSEN, 1978), variation in the calorific value of the algae (HIMMELMAN & CAREFOOT, 1975; MCQUAID, 1985), or seasonal changes in the concentration of storage polysaccharides (e.g. laminarans, CRAIGIE, 1974) widely utilized by marine invertebrates as energy sources (KRISTENSEN, 1972; PIVAUX, 1977). In Bañugues and Aramar, marked seasonal variations in the physical environment, abundance and composition of algae (dominant macroalgae and their epiphytes), and in the abundance and composition of other faunal species have also been reported (ARRONTEs, 1987, 1990).

In the three dominant species (*D. bidentata*, *D. magnitorata* and *C. truncata*), in addition to recruitment-mortality cycles, migration of reproductive animals may be important. A small number of mature animals was collected throughout the study, but ovigerous females never. Intertidal macroalgae, therefore, appear to be a "juvenile" habitat for these isopods, and for *C. truncata* and *D. magnitorata* for only a short time. The relative importance of mortality and change of habitat in the disappearance of specimens from the algal fraction is unknown. The precise stage at which animals shift habitat is clear for *D. bidentata* (HOLDICH, 1968, 1976); it occurs in the last growth stage for males and females. From the field data available, it is impossible to deduce the precise stages for *Cymodoce*. Duration of each growth stage is unknown and at least two options are possible: (i) fast growth and change when adults, and (ii) slow growth and progressive incorporation to the adult habitat.

In addition to *Dynamene* species (HOLDICH, 1968, 1976), change in habitat preferences has been reported in other marine isopods. FISH (1970) report-

ed an offshore movement of breeding *Eurydice pulchra*. JANSSON & MATTHIESEN (1971) and SALEMAA (1979) reported the movement of reproductive animals of the genus *Idotea* from *Fucus vesiculosus* to *Cladophora glomerata* beds, where juveniles were released. CAREFOOT (1973) has indicated that first stage juveniles of *Ligia pallasii* occur in *Enteromorpha*, low on the shore, whereas bigger specimens of this isopod were found inside rock crevices higher on the shore. In all cases described, reproductive animals were collected in cryptic (and presumably safe) sites, while juveniles were in productive habitats.

In *D. bidentata*, size-distributions in *Gelidium* and *Fucus* suggest a different change of habitat, from one macroalgal community to another during the juvenile phases. In *Gelidium*, late juvenile stages, preadults and adult animals were scarcely represented, while on *Fucus*, the bulk of recruitment was of stage 3 juveniles. Different habitat requirements at different growth stages or unequal distribution of reproductive animals, may be the reason for the observed disequilibrium in size-frequency distributions. Irrespective of the origin of the isopods, a late recruitment in *Fucus* may be an advantageous strategy to avoid the harsher physical environment of this belt (with emersion periods close to six hours twice a day) in early, presumably more sensitive, growth stages.

### Breeding pattern

*Dynamene bidentata* exhibited an extensive breeding period, possibly with two generations within the same year and with some animals (only males) mating twice. A fairly continuous release of juveniles was detected in *Gelidium*, though isopod recruitment was not found in *Fucus* from November to February. On the other hand, *D. magnitorata* and *C. truncata* exhibited a shorter breeding season with release of juveniles restricted to two or three months. Differences in the synchrony of recruitment between *Dynamene* species might be related to the relative location of the populations studied within the geographical range of the species. *Dynamene bidentata* has an Atlantic distribution, from the British Isles to the shores in South Portugal and Spain, while *D. magnitorata* has a more southerly distribution and ranges from North France to Morocco and Tunisia (HOLDICH, 1970). Virtually nothing is known about the geographical distribution of *C. truncata*. Several studies have described differences in the degree of synchrony and breeding pattern between species of

isopods of the same genus when varying environmental restrictions are imposed on the animals in different localities of their geographical range. This was suggested by HEALY & O'NEILL (1984) for *Idotea granulosa* and *I. pelagica* in South East Ireland (see also SHEADER, 1977). Differences in breeding pattern of two *Sphaeroma* (HARVEY, 1969) and two *Eurydice* species in Britain (JONES, 1970) also appeared to be related to differences in geographical distributions. The local environment can also influence population dynamics of isopods. Thus, different durations of the breeding period were found by FISH (1970) and JONES (1970) in two Welsh populations of *Eurydice pulchra* close together but with different environmental conditions (salinity and temperature), one an open sand beach the other an estuarine beach.

There are differences between the duration of the breeding period of *D. bidentata* described in this paper and that reported by HOLDICH (1968) in South Wales. In Wales, release of stage-1 juveniles occurred from May to July and only one reproductive season was found. In northern Spain, a more prolonged breeding season was found. The locality studied by HOLDICH (1968) is near to the northern limit of the distribution of this species (HOLDICH, 1970). There are large differences in environmental conditions between South Wales and North Spain, mainly in winter temperatures. These are suggested by HOLDICH (1970) to be a limiting factor in the distribution of *D. bidentata*. Considering development times for embryos (36 days at 17.5° C), and the duration of the eight postmarsupial growth stages (118 days at 17.5° C) (HOLDICH, 1968), which are strongly dependent of the sea water temperature, it is clear that in Bañugues some specimens are capable of reproducing within the year they were born. Thus, juveniles harvested in October (*Fucus*) or November (*Gelidium*) are surely descendants of animals released at the end of winter or in spring. Growth is probably fast during summer (see Fig. 7 for sea water temperatures) and was also detected during winter in



Fig. 7. — Variation in sea water temperature in Bañugues.



*Fucus* (November to January), when no recruitment of juveniles occurred.

Similar changes to those described for *D. bidentata* have been reported in the reproductive biology of *Sphaeroma serratum* in localities with different mean temperatures (CHARMANTIER, 1974; DAGUERRE DE HUREAUX, 1979). Continuous year-round recruitment is known in a number of isopods, including *Cirolana* spp. (JOHNSON, 1976; SHAFIR & FIELD, 1980), *Excirrolana braziliensis* (DEXTER, 1977), *Idotea pelagica* (HEALY & O'NEILL, 1984) and *Sphaeroma serratum* (DAGUERRE DE HUREAUX, 1979). In all of them, length of reproductive period was related to favourable temperatures.

Other factors not considered here, such as availability of feeding resources or of suitable holes for breeding, might be important in determining the population dynamics of the isopods. In this regard, KOOP & FIELD (1980) found that population dynamics of the supralittoral isopod *Ligia dilatata* was strongly dependent on availability of food. Marked differences in the composition of the diet of the isopods considered in this study were found in addition to their different response to seasonal changes in resource availability (ARRONTES, 1990).

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