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The distribution and habitat preferences of the Afro-European species of *Dynamene* (Crustacea: Isopoda)

D. M. HOLDICH
Department of Zoology, University College of Swansea*

Introduction

Unlike most other members of the family Sphaeromatidae the genus *Dynamene* Leach is virtually restricted to the Boreal-Atlanto-Mediterranean-Black Sea region of the northern hemisphere. Seven species are now known (Holdich, 1968 c), only one of which occurs outside that geographical area, in Australia (Baker, 1908). From past records it would appear that this genus also has a limited habitat range, being restricted to intertidal or shallow water algae and crevices (Torelli, 1930 ; Colman, 1940 ; Glynne-Williams & Hobart, 1952 ; Wieser, 1952 ; Morton, 1954 ; Santini, 1961 ; Bellan-Santini, 1961, 1963, 1964, 1966 ; Ledoyer, 1962, 1964 a, b, 1966 a, b ; Kensler, 1964, 1965, 1967).

This paper aims at describing the geographical distribution of the genus in the light of the recent discovery of three new species (Holdich, 1968 c). The geographical ranges of each species are indicated and the habitat preferences, particularly that of *D. bidentata* (Adams), are discussed.

The following have generously lent material and/or offered personal observations for inclusion in this study : Professor T. Monod (Natural History Museum, Paris) ; Dr. L. B. Holthuis (Natural History Museum, Leiden) ; British Museum (Crustacea Section) ; Plymouth Marine Laboratory ; Dr. E. Fresi (Stazione Zoologica, Naples) ; Dr. M. Ledoyer (Endoume Marine Station) ; Dr. C. Edwards (Millport Marine Station) ; Dr. M. Miller (University of Auckland, New Zealand) ; Dr. K. P. Jansen (University of Canterbury, New Zealand) ; Dr. E. Naylor, Dr. C. Harvey and Dr. D. A. Jones (University College of Swansea). To all these people I am extremely grateful.

Geographical distribution

Any attempt to plot an accurate distribution of the several species of the *Dynamene* genus is hampered by the fact that so many misidentifications concerning *D. bidentata* have been made in the past (Holdich, 1968 c). However, as a basis for discussion, all previous records for *D. bidentata* (see Omer-Cooper & Rawson, 1934 ; Holdich, 1968 a) are summarized in fig. 1, and present observations, incorporating the six Afro-European species, are presented in figs. 2–5.

Present investigations around the Mediterranean have revealed no specimens of *D. bidentata* but have yielded three new species, *D. tubicauda* Holdich, *D. torelliae* Holdich and *D. magnitorata* Holdich (Holdich, 1968 c). It is likely

* Present address: Department of Zoology, The University, Nottingham.

that most Mediterranean material previously attributed to *D. bidentata*, except perhaps those in southern Spain (Kensler, 1965) (fig. 1), in fact belongs to the second of these new forms.

Distribution of individual species

D. bidentata

Although recorded from the Atlantic coast of N.W. Africa (Monod, 1932) a search through a wide variety of museum material has not confirmed this species from that area. Kensler (1965) was also unable to find it in his collections from N.W. Africa, but that author has reported *D. bidentata* from the Mediterranean coast of Spain (1964) and the Atlantic coasts of Spain and Portugal (1965). From descriptions given it would appear that the records for the Azores (Barrois, 1888) are possibly correct. Material of this species has been examined from Arosa (N.W. Spain) and the Isle de Glénans and

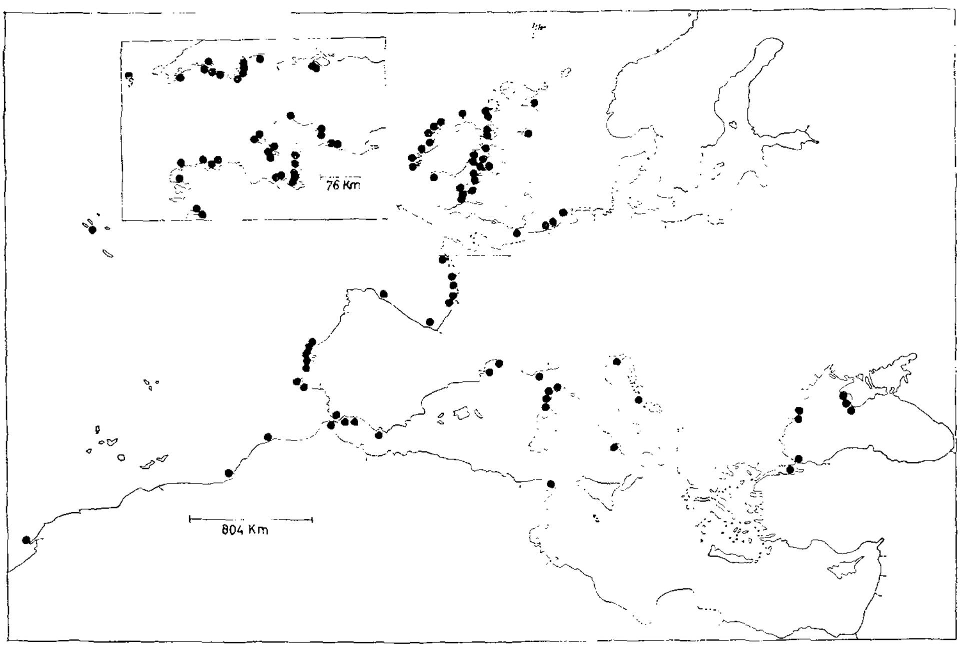

Fig. 1. Map indicating the distribution and range of *D. bidentata* (●) as determined from all known records prior to the present investigation.

Roscoff (N.W. France), and figures given by Hesse (1873) and Tristan (1809) indicate its presence in W. France. Similarly, figures and descriptions given by Caullery and Mesnil (1920), Tinturier-Hamelin (1962, 1967) and Bourdon (1964) indicate its presence in N. France. Specimens from Holland, from as far north as Fort Hassens, have been examined, but it appears that this species is not indigenous in that country (Holthuis, personal communication). Numerous records in the literature and British Museum material indicate the presence of *D. bidentata* around the British Isles and the Channel Islands (fig. 1) where no other species is recorded.

A personal survey of 111 localities around Britain during 1966–1967 and examination of recent museum material from Ireland reveals a current distribution of *D. bidentata* in the British Isles as illustrated in figs. 2–4. The main difference between present results and previous records (fig. 1) is the current lack of records on the north-western, northern, eastern and south-eastern coasts of Britain and on the South Wales coast as far west as Pembrokeshire.

D. edwardsi Lucas

The present investigation confirms the presence of this species on the Atlantic coast of Africa as far south as Port Etienne (T. Monod collection). Figures given by Hesse (1873) indicate that it may be present on the western coast of France (fig. 2) and the record of Ledoyer (1964 a), if confirmed, would

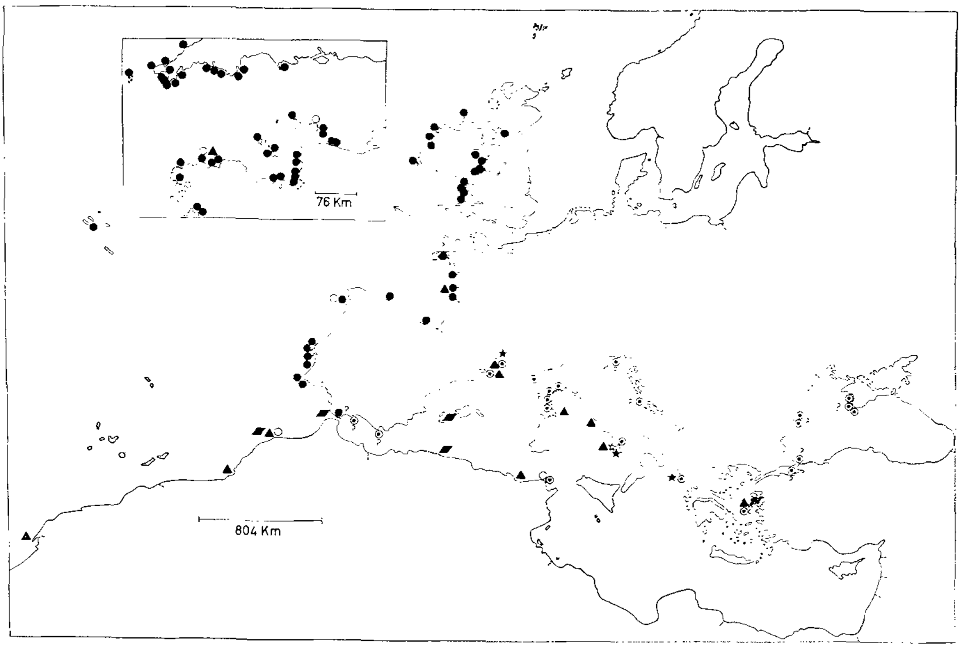

FIG. 2. Map indicating the distribution and ranges of the species of *Dynamene* occurring in Europe, and northern and north-western Africa, based on collections and examination of museum material made by the author, and from descriptive records. Symbols in the Mediterranean and Black Sea with a question mark refer to records of '*D. bidentata*' where an author has used Torelli's (1930) description (= *D torelliae*).

● *D. bidentata* ⊙ *D. torelliae* ○ *D. magnitorata*
★ *D. bifida* ☆ *D. tubicauda* ▲ *D. edwardsi*
◆ Juveniles of unidentified species.

extend the range to N.W. France (fig. 2). Specimens have been examined from the Mediterranean localities of Banyuls, Endoume, and Chios, and positive records were obtained from the majority of stations examined in Naples Bay (fig. 5). As this species is fairly distinctive, other records for the Mediterranean are undoubtedly valid (Lucas, 1849 ; Amar, 1952 ; Bellan-Santini, 1961, 1962, 1964, 1966 ; Rivosecchi, 1961 ; Ledoyer, 1962).

D. bifida Torelli

Although only a single specimen was recorded by Torelli (1930) from Cape Posillipo in the Bay of Naples, the results of the present investigation reveal that it is probably common in that general area, having been found to occur very commonly in Mergellina Harbour (fig. 5). Material of this species has also been examined from Corfu (Ionian Sea) and from Endoume (S. France).

D. torelliae

The precise distribution of this species is still in some doubt since Mediterranean, Adriatic, and perhaps Black Sea material seems to have been confused with *D. bidentata* (Torelli, 1930 ; Băcescu, 1948 ; Pauli, 1954 ; Băcescu *et al.*, 1963 ; Riedl, 1963). At any rate, museum specimens labelled *D. bidentata* from Banyuls, Endoume, Naples Bay, and Tunisia (fig. 2), have been confirmed as *D. torelliae*. In addition Pauli (1954) describes a species from the Black Sea which is based on Torelli's (1930) description of *D. bidentata* (= *D. torelliae*), as does Riedl (1963) from the Adriatic. This species was found to be common in all personal collections from the northern part of Naples Bay (fig. 5) and specimens have also been obtained from the Greek Island of Chios (Ref. 38° 23′ N, 26° 08′ E) by the University College of Swansea Diving Expedition to that island in 1967 (fig. 2).

D. tubicauda

This species was collected off Capri during the present investigation and recorded in a collection made by diving near Procida (figs. 2 and 5) by Dr. E. Fresi.

D. magnitorata

This species is so far known only from preserved material in collections from Pt. Barfleur (N. France), Roscoff, Isle de Glénans (N.W. France), Fedhala (N.W. Africa), and Tunisia (fig. 2).

D. ramuscula

This species is known only from a single male and three females from Port St. Vincent in S.E. Australia (Baker, 1908 ; Hale, 1929). I have been unable to locate this material.

Morton & Miller (1968) repeat Hale's (1929) figure of *D. ramuscula* as a species to be looked out for in New Zealand, but it has never been recorded there (Miller, and Jansen, personal communications).

Habitat preferences

As shown by Naylor & Quénisset (1964), Bourdon (1964) and by Holdich (1968 b), *D. bidentata* undergoes a change of habitat, from algae to crevices, at the onset of breeding. This also occurs in *D. edwardsi*, *D. torelliae*, and *D. bifida* which inhabit shallow water zones in the Bay of Naples. Feeding stages of these three species were found on algae, and adults in crevices.

D. bidentata ADULTS : FIELD INVESTIGATIONS

In S.W. Wales the preferred reproductive habitat of this species is within empty *Balanus perforatus* Brugière tests, a single male occurring with up to 16 females. They also occupy crevices on suitable shores and settling experiments in the laboratory suggest that crevices and barnacle tests are equally

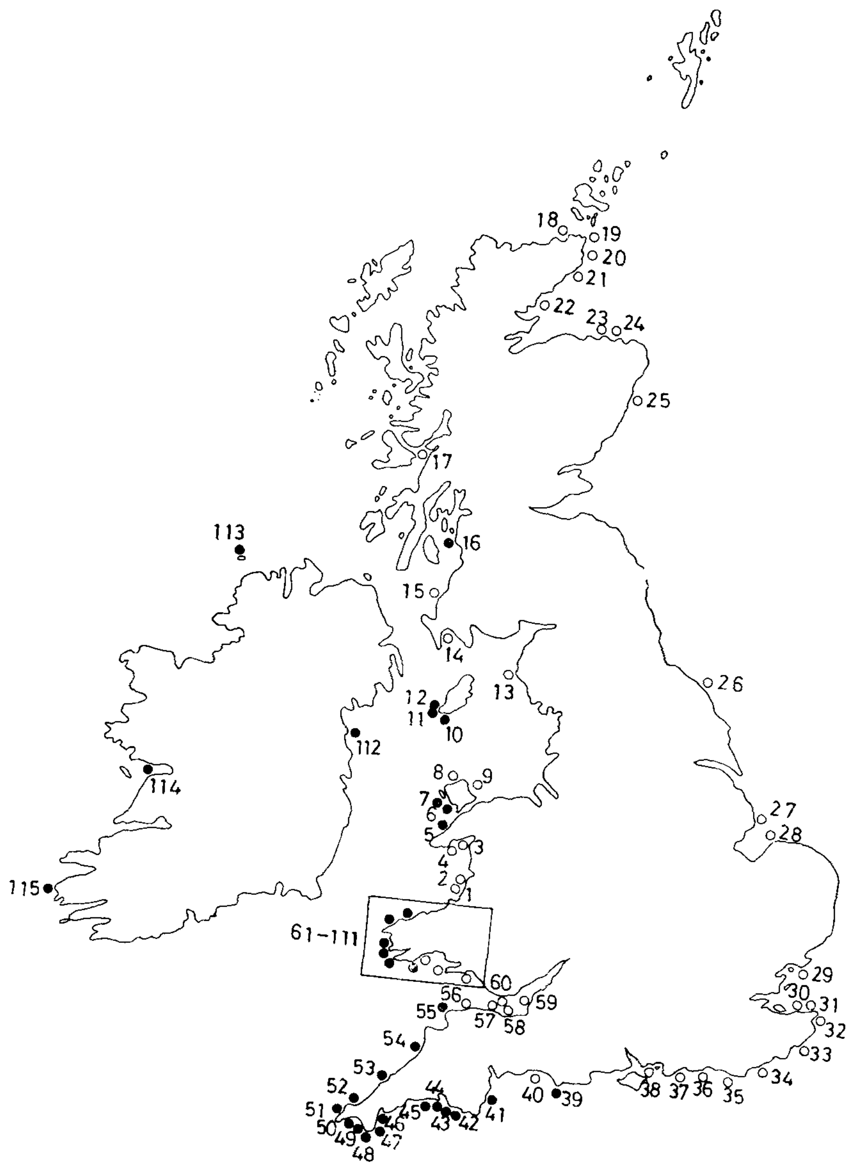

FIG. 3. Distribution of *D. bidentata* in Britain, based on collections made by the author, and Ireland, based on recent museum material. ● Present ; ○ absent. 1. Aberystwyth ; 2. Borth ; 3. Criccieth ; 4. Llanbedrog ; 5. Porth Colman ; 6. Rhosneigre ; 7. Rhoscolyn ; 8. Bull Bay ; 9. Moelfre Bay ; 10. Derby Haven ; 11. Port Erin ; 12. Fleshwick Bay ; 13. St. Bees Head ; 14. Auchenmaig ; 15. Bennane Head ; 16. Ardrossan ; 17. Oban ; 18. Thurso ; 19. John O'Groats ; 20. Sinclairs Bay ; 21. Janetstown and Helmsdale ; 22. Embo ; 23. Port Gordon and Buckie ; 24. Banff ; 25. Stonehaven and Aberdeen ; 26. Robin Hood's Bay ; 27. Gibraltar Point ; 28. Hunstanton ; 29. West Mersea ; 30. Herne Bay ; 31. Minnis Bay ; 32. Pegwell Bay (Ramsgate) ; 33. East Wear (Folkestone) ; 34. Fairlight Cove (Hastings) ; 35. Cuckmere Haven (Seaford) ; 36. Worthing ; 37. Bognor Regis ; 38. Portsmouth and Solent ; 39. Portland Harbour ; 40. Charmouth ; 41. Goodrington Sands ; 42. South Milton Sands ; 43. Wembury ; 44. Tinside and Bovisand ; 45. Whitesand Bay (Cornwall) ; 46. Falmouth ; 47. Kennack Sands ; 48. Lizard ; 49. Mullion Cove ; 50. Marazion ; 51. Cape Cornwall ; 52. St. Ives ; 53. Treyarnon ; 54. Widermouth Sand (Bude) ; 55. Ilfracombe ; 56. Lynmouth ; 57. Blue Anchor (Watchet) ; 58. Minehead ; 59. Weston-super-Mare ; 60. Barry ; 61–111. See fig. 4 ; 112. Loughshinny ; 113. Tory Island ; 114. Galway Bay ; 115. Valentia.

preferred, as happens in the field in Devon and Cornwall. The position taken up by the male in the barnacle tests is indicated in figs. 6 and 7 (♂) and that of the females in fig. 7 (♀). The cuticular pigmentation (Holdich, 1969), growths of algae on the pleotelson, and the similarity between its bidentate process (fig. 8) and the spines on the tergal plates of this barnacle species (Bassindale, 1964) form an effective concealment for the male *Dynamene*. This barnacle-dwelling habit appears to have been overlooked in Britain, except by Scott (1899), Bassindale & Barrett (1957), and Naylor & Quénisset (1964), but Hesse (1873), Koehler (1885), Dollfus (1888), Caullery & Mesnil (1919, 1920), Fage (1933), Tinturier-Hamelin (1962), Bourdon (1964), and Kensler (1965) have recorded *D. bidentata* from *B. perforatus* tests elsewhere.

Where *B. perforatus* is uncommon or absent, *D. bidentata* frequents crevices and this is the habitat from which the adults have usually been collected in

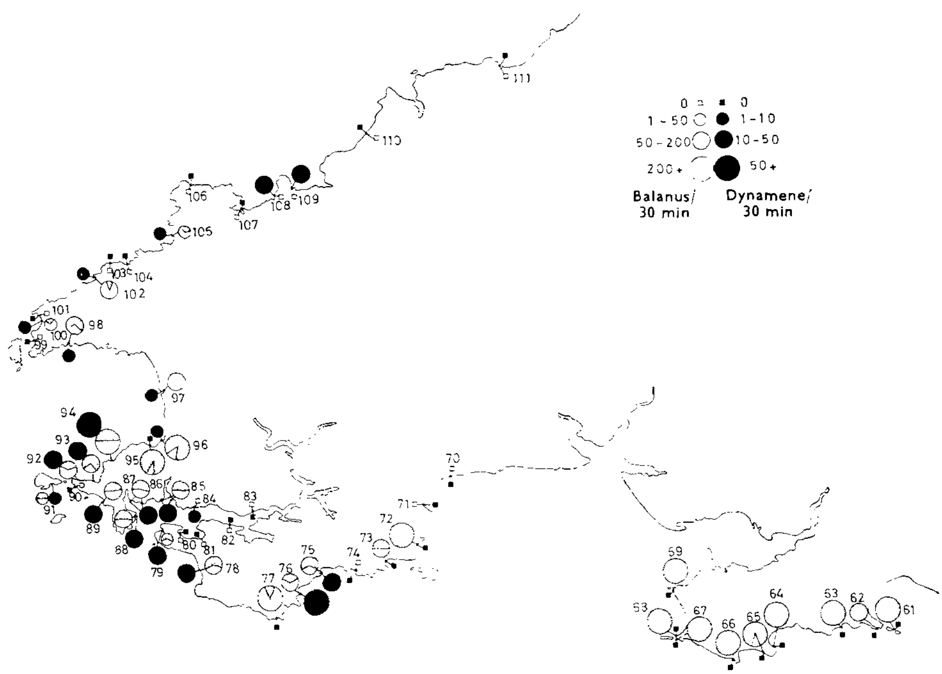

FIG. 4. Distribution and abundance of *D. bidentata* and *Balanus perforatus* in southern and south-western Wales based on 30 minute collections made by the author during 1965 and 1966. Black symbols indicate the isopod. Open or shaded circles refer to *B. perforatus*, the shading indicating the proportion which were dead. 61. Mumbles Head ; 62. Bracelet Bay ; 63. Caswell Bay ; 64. Oxwich Bay ; 65. Slade Bay ; 66. Port Eynon ; 67, 68. Rhosilli Bay (South) ; 69. Burry Holmes ; 70. Wiseman's Bridge ; 71. Saundersfoot ; 72. Tenby ; 73. Lydstep ; 74. Manorbier ; 75. Freshwater East ; 76. Stackpole ; 77. St. Govan's Head ; 78. Freshwater West ; 79. West Angle ; 80. Angle (West) ; 81. Angle (East) ; 82. Pwllcrochan ; 83. Hazelbeach ; 84. Gelliswick Bay ; 85. Sandyhaven (West and East) ; 86. Monks Haven ; 87. Musselwick ; 88. Castlebeach ; 89. West Dale Bay ; 90. Renney Slip ; 91. Skomer (South Haven) ; 92. Martins Haven ; 93. Musselwick Sands ; 94. St. Brides Haven ; 95. Little Haven ; 96. Broad Haven ; 97. Nolton Haven ; 98. Caer-fai Bay ; 99. Porthstinian ; 100. Whitesand Bay (West) ; 101. Pwlluog ; 102. Aber-Eiddy ; 103. Porthgain ; 104. Trevine ; 105. Abermawr (North.) ; 106. Porthsychan ; 107. Goodwick Harbour (Fishguard) ; 108. West Dinas Head ; 109 Cwm-yr-eglwys (East Dinas Head) ; 110. Ceibwr Bay ; 111. Aberporth.

the British Isles (Naylor & Quénisset, 1964 ; Kensler, 1967), the Channel Islands (Koehler, 1885 ; Sinel, 1906 ; Norman, 1907), and the Atlantic coasts of Europe (Saudray & Derouet, 1961 ; Kensler, 1965). There are some records of this species occurring under stones and rocks, Hesse (1873), Bonnier (1887), Barrois (1888), Tattersal (1905, 1912), Bruce *et al.* (1963), but this habitat is not typical. In the present investigation *D. bidentata* was also recorded from empty *Hiatella arctica* burrows and *Laminaria digitata* holdfasts. In addition, Scott (1899) records it from among scrapings from the hull of a ship, Holthuis (1956) records it from *Himanthalia* and from corks washed up on the shore in Holland, Monod (1932) and Bellan-Santini (1963) from *Mytilus* beds in N.W. Africa and N.W. France respectively, and Bénard (1960) has recorded it from cavities in *Lithophyllum incrustans*.

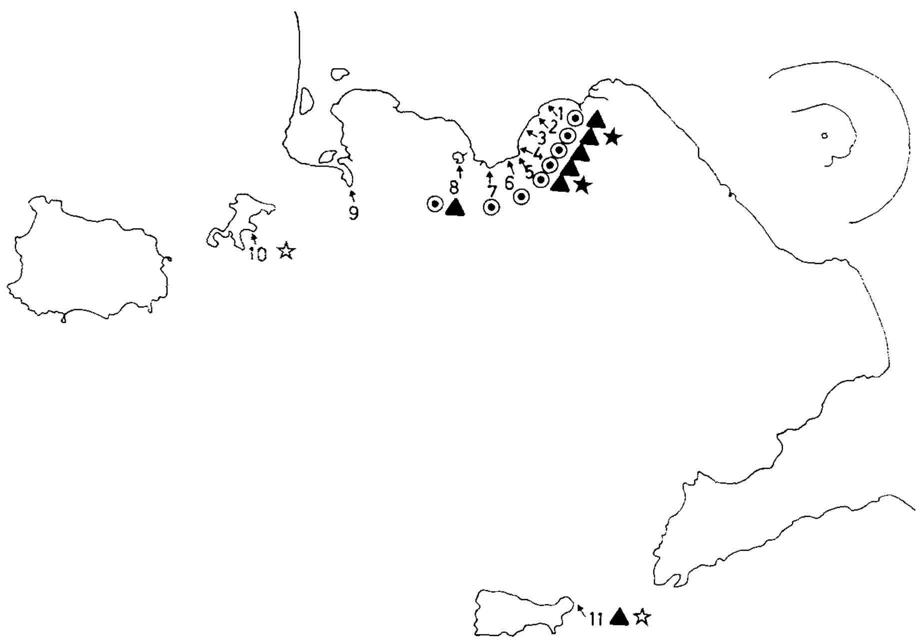

Fig. 5. Distribution of *D. edwardsi* (▲), *D. torelliae* (⊙), *D. bifida* (★), and *D. tubicauda* (☆) in the Bay of Naples based on collections made by the author. 1. Grand Hotel ; 2. Mergellina Harbour ; 3. S. Pietro ai due Frati ; 4. V. Galloti ; 5. Posillipo ; 6. Marechiaro ; 7. La Gaiola ; 8. Nisida ; 9. C. Miseno ; 10. P. Pizzago (Procida) ; 11. P. Tiberio (Capri).

Along the S. Wales coast adult *D. bidentata* were usually to be found in large numbers in empty barnacle tests (fig. 4). Where no dead barnacles were recorded (Station 97) and where the barnacles were rare (79), or absent (108, 109) crevices and mollusc borings were occupied.

In areas where the barnacle populations were largely eliminated by the adverse weather conditions during the winter of 1962/63 (Moyse & Nelson-Smith, 1964), as in the Gower Peninsula (61–69, except 66) and the Tenby region (72), *D. bidentata* was also eliminated. It seems likely that the low temperatures which killed the barnacles also adversely affected the pre-ovigerous and ovigerous females of the isopod (Holdich, 1968 b).

In conditions of extreme exposure to wave action, as at St. Govan's Head (77), *B. perforatus* was present in sheltered gullies but the isopod was absent. In only one other locality (95) where living and dead *B. perforatus* occurred was *D. bidentata* not found, probably because the dead barnacles that were available for settlement had large opercular openings and were unsuitable for the isopods (see central test, fig. 6).

Ideal conditions for settlement of both barnacle and isopod are present at St. Brides Haven (Pembrokeshire) (fig. 4) which faces N.W. and is fairly exposed, as indicated by the presence of *Fucus vesiculosus evesiculosus* and only small amounts of *Ascophyllum nodosum* on the rocks facing the direct force of the waves (Moyse & Nelson-Smith, 1963). Figure 9 indicates a transect across a moderately exposed area between the exposed conditions

FIG. 6. Surface view of a number of *Balanus perforatus* tests, some occupied by *D. bidentata* and some empty.

found at Castle Head and the more sheltered conditions of the haven itself. *B. perforatus* was present in fairly large numbers (C—kite diagram, fig. 9), ranging from MTL to near LWS and tending to be more concentrated on rocks exposed to wave action. Approximately half the barnacles throughout the whole range were dead and the majority of these were occupied by adult *D. bidentata*. The numbers of isopods in these tests varied with season (A and B—kite diagrams), but there was always a resident population of males in the summer months (Holdich, 1968 b).

In a number of quarter metre square samples of the barnacle population approximately 54% were dead and 49% of these were suitable for settlement of the isopod. Of these suitable tests, 80% were inhabited by *D. bidentata*. Other organisms occurring among the empty barnacles were those typical of crevice faunas (Morton, 1954 ; Kensler & Crisp, 1965), particularly *Gnathia maxillaris*, *Lasaea rubra*, and *Mytilus edulis*, the latter being especially common when the opercular openings of the barnacles were large. The hemipteran *Aepophilus bonnairei* was also recorded and it appeared to be feeding upon *Dynamene*. Various polychaetes were recorded, but no evidence was found that nereid polychaetes feed on *Dynamene* as was suggested by Glynne-Williams & Hobart (1952). *Acanthocottus bubalis*, which has been reported to feed on *Dynamene* (Rice, 1962), was found occasionally in crevices near populations of the isopod.

Animal parasites recorded with *D. bidentata* at St. Brides Haven and Plymouth included nematodes, the epicaridian isopod *Ancyroniscus bonnieri* (Holdich, 1968 a, b), and metacercaria of a digenian helminth probably belonging to the Fellodistomatidae.

D. bidentata ADULTS : LABORATORY INVESTIGATIONS

Although in barnacles a single male *Dynamene* was nearly always found with a number of females (fig. 7), groups of females were often found in

Table 1

Observed and expected data from a settlement experiment (two trials, A and B) in which 32 male and 122 female were released into a tank containing 25 empty barnacle tests, the number occurring in each test then being recorded after 6 hours

	Occurrences									
	A (after 6 hours)				B (after 6 hours)				Expected	
	Male		Female		Male		Female		%	
Dynamene/ test	No.	%	No.	%	No.	%	No.	%	Male	Female
0	7	28	3	12	4	16	2	8	27	1
1	10	40	2	8	13	52	3	12	35	3
2	4	16	2	8	6	24	2	8	23	8
3	2	8	2	8	1	4	5	20	10	14
4	2	8	4	16	1	4	1	4	3	18
5	0	0	3	12	0	0	0	0	1	18
6			1	4			4	16	0	15
7			2	8			2	8		10
8			3	12			2	8		7
9			0	0			0	0		4
10			1	4			3	12		2
11			1	4			1	4		1
12			0	0			0	0		0
13			0	0						
14			1	4						

crevices without a male. This suggests that males may not always remain in the microhabitat where they initially settle. To investigate this possibility, and to test for the attractiveness of males and females to each other, laboratory experiments were carried out by placing a number of empty barnacle tests in tanks and recording the settlement pattern of isopods subsequently introduced.

In one experiment (table 1), 32 male and 122 female *Dynamene* were introduced into a tank containing 25 empty barnacle tests. Counts of males and females in each barnacle were made after six hours and the percentage frequency of occurrence of the number of isopods in the tests are plotted against expected Poisson distribution in fig. 10. The distribution of males closely follows the Poisson curve, suggesting that their settlement is random. The distribution

FIG. 7. Vertical section through a dead *Balanus perforatus* test occupied by *D. bidentata* indicating the relative positions of the male and females.

of females is different from the expected Poisson distribution, in particular there being more than expected occurrences of tests without isopods. Such a pattern, if confirmed, would seem to suggest some degree of aggregation of females.

Table 2

Observed and expected data from a settlement experiment (three trials, A, B, and C) in which one male was placed in each of 32 empty barnacle tests and then 121 females were set free into the same tank, the number occurring in each test then being recorded after 24 hours

	Occurrences															Mean of three trials			
	Males							Females								Males		Females	
	A		B		C		Exp.	A		B		C		Exp.					
Dynamene/test	No.	%	No.	%	No.	%	%	No.	%	No.	%	No.	%	%		%	Exp. %	%	Exp. %
0	13	39	11	33	10	30	33	10	30	9	27	7	21	2		34	33	26	2
1	10	30	14	42	15	45	37	5	15	1	3	3	9	8		39	37	9	8
2	5	15	4	12	4	12	20	4	12	6	18	6	16	16		13	20	16	16
3	4	12	2	6	3	9	7	3	9	2	6	1	3	20		9	7	6	20
4	0	0	1	3	0	0	2	3	9	2	6	3	9	19		1	2	8	19
5								0	0	2	6	1	3	14		0	0	3	14
6								1	3	3	9	5	15	9				9	9
7								1	3	1	3	0	0	5				2	5
8								0	0	3	9	3	9	2				6	2
9								1	3	0	0	0	0	1				1	1
10								1	3	3	9	2	6	0				6	0
11								0	0									0	0
12								0	0									0	0
13								0	0									0	0
14								0	0									0	0
15								1	3									1	0
16								0	0									0	0
17								1	3									1	0
18								0	0									0	0
19								1	3									1	0

In a second series of experiments (table 2) a single male was placed in each of 32 barnacle tests, 121 females were then introduced into the tank and the distribution of both sexes was recorded after 24 hours. The procedure was repeated three times and the mean results of the three tests are plotted against expected distributions in fig. 11. Particularly striking is the close conformity of the observed and Poisson distribution of males. This indicates that although the animals were experimentally spaced out, one to each barnacle at the beginning of the experiment, they subsequently swam in the tank and distributed themselves randomly. Females again did not follow the expected Poisson distribution, there being more than expected occurrences of tests

Table 3

Data (derived from tables 1 and 2) indicating the average number of females occurring in barnacle tests occupied by 0–4 males respectively

Males	Females			
	Total observations	Mean No./test	Range	Standard deviation
0	45	3·2	0–11	±3·5
1	63	4·0	0–15	±3·6
2	23	6·5	0–19	±5·8
3	12	3·2	0– 7	±2·3
4	4	3·2	0– 8	±3·3

without isopods. Again, therefore, there is evidence of aggregation of females and it remains to determine whether this results from the mutual attraction of females or the attraction of females to males. So far as they go present observations tend not to support the latter alternative, but interpretation of the results is complicated by the fact that males may have moved from one barnacle to another. Table 3 plots the average number of females occurring in barnacles

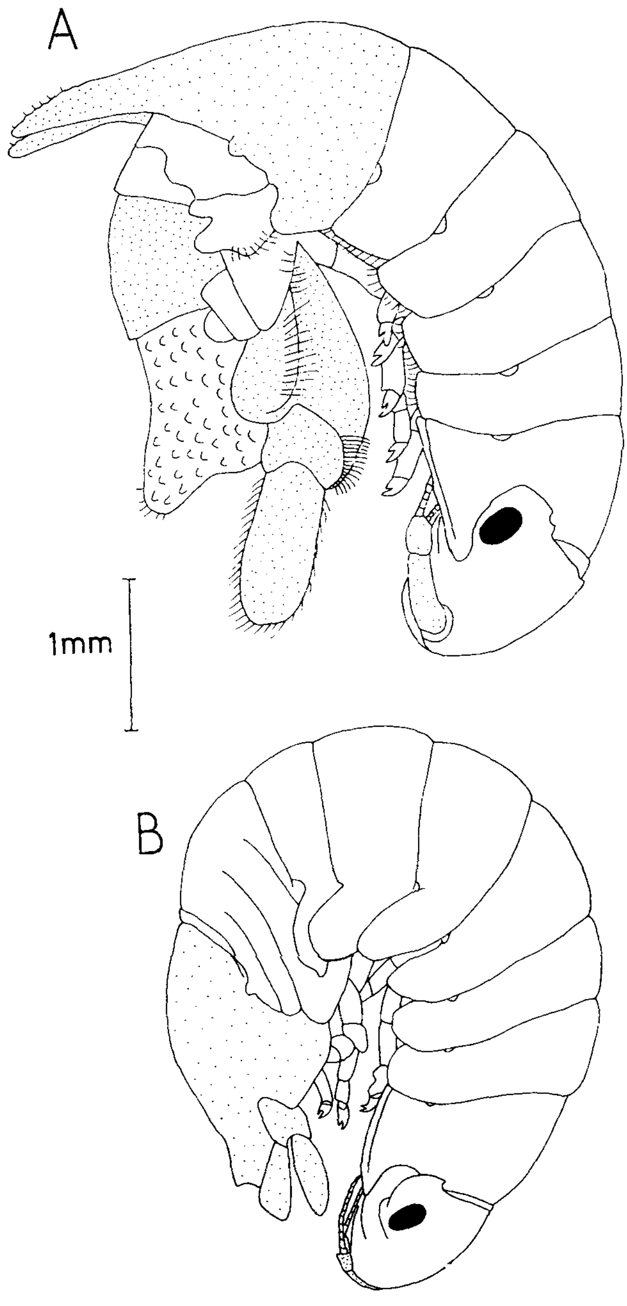

Fig. 8. Side views of adult male (A) and pre-ovigerous female (B) *D. bidentata* indicating the degree of possible folding.

occupied by 0, 1, 2, 3 and 4 males respectively, and it can be seen that, apart from a slight increase in the number of females in tests containing two males, a concentration of males is not correlated with an increased number of females.

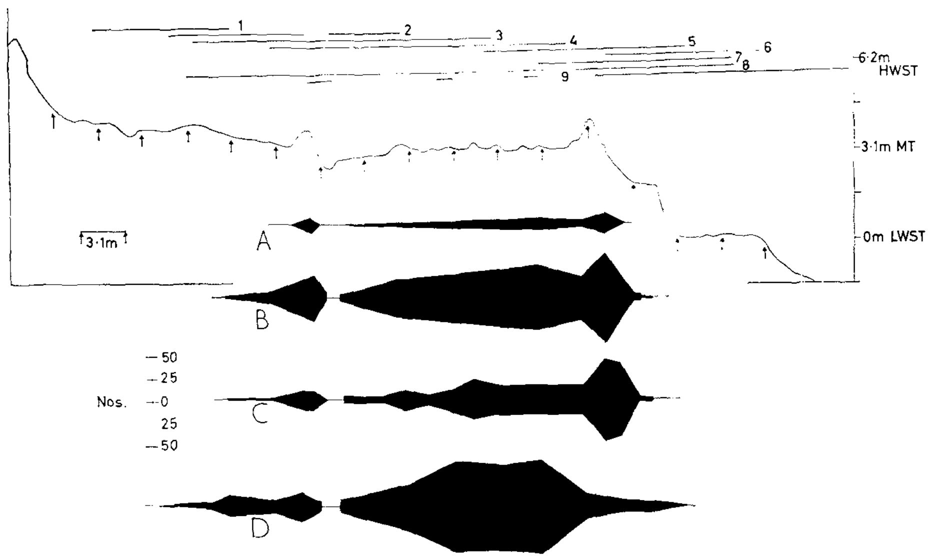

Fig. 9. Transect across a moderately exposed region of St. Brides Haven showing the relative abundance of *D. bidentata* and *Balanus perforatus* in the littoral zone as determined from ¼ m square counts between the points marked ↑ . Kite diagrams A and B refer to the numbers of isopods collected from barnacle tests in July and January respectively, and D to the numbers collected from the littoral algae (1–9) in July. C indicates the average number of *Balanus perforatus* tests recorded in all months. 1. *Pelvetia canaliculata;* 2. *Fucus spiralis;* 3. *Ascophyllum nodosum;* 4. *Fucus vesiculosus evesiculosus;* 5. *Himanthalia elongata;* 6. *Chondrus crispus;* 7. *Rhodomenia palmata;* 8. *Fucus serratus;* 9. *Laminaria digitata.*

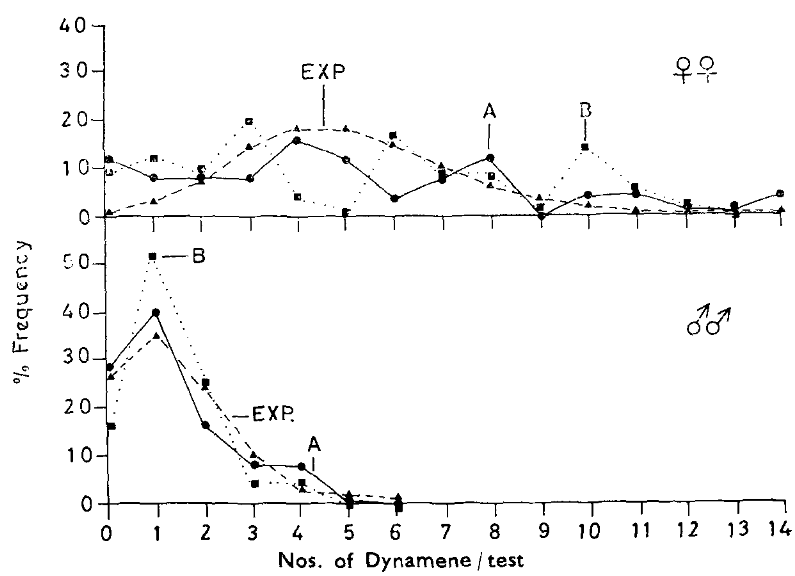

Fig. 10. Percentage frequency of occurrence of the numbers of *D. bidentata* in each barnacle test plotted against expected Poisson distribution (Exp.), using the data in table 1 (two trials, A and B).

The occurrence of large numbers of females in tests unoccupied by males tends to further the view that females aggregate by mutual attraction, but it is possible that they could have been attracted to a male which then subsequently vacated the barnacle test.

D. bidentata JUVENILES : FIELD INVESTIGATIONS

Juveniles of this species are restricted to algae and at St. Brides Haven had a greater vertical spread on the shore than the adults, ranging from above MTL to LWS (fig. 9 D). They were most concentrated in the zone of the dominant algae, *Fucus vesiculosus evesiculosus*, *Fucus serratus*, and *Himanthalia elongata*, which appear to be the most acceptable food (Holdich, 1968 a). In more sheltered regions they were also present in large numbers on *Ascophyllum nodosum* and elsewhere they have been recorded from most intertidal algae except *Pelvetia* and *Laminaria* (Colman, 1940 ; Wieser, 1952 ; Marine

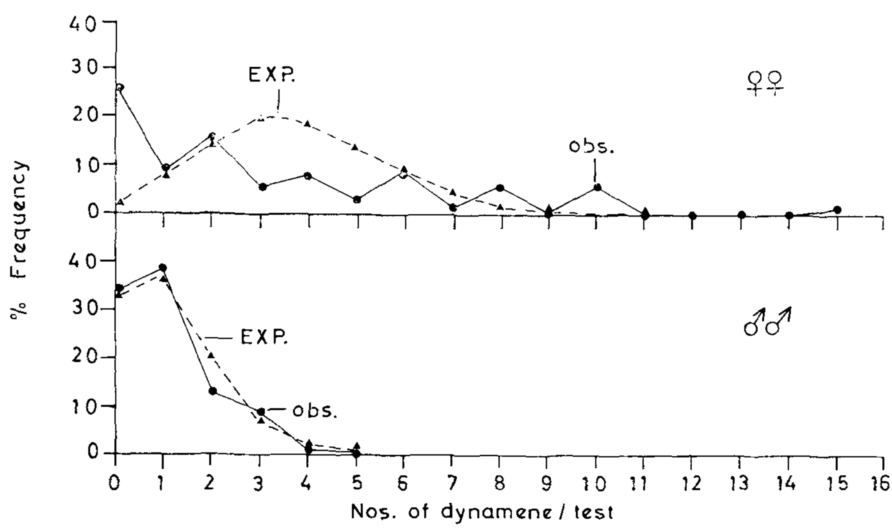

Fig. 11. Percentage frequency of occurrence of the numbers of *D. bidentata* in each barnacle test plotted against expected Poisson distribution (Exp.), mean results (Obs.) of three experiment using the data in table 2.

Biological Association, 1957). Wieser (1962) suggests that juveniles migrate on and off shore with the rise and fall of tides and in relation to this it is noteworthy that Fage & Legendre (1923), and Fage (1933), have recorded both adults and juveniles in shallow water plankton by means of a light trap at Concarneau (N.W. France). However, as shown in Holdich (1968 b), such a migration was not found to occur at St. Brides Haven. On the Atlantic coast of Europe juveniles have been recorded from similar algae to those on which they are found in Britain, although Chevreax (1883) has also recorded them from *Corallina officinalis; Bellan-Santini* (1963) from *Cystoseira granulata, Laurencia pinnatifida*, and *Petroglossum nicaense* ; and Ledoyer (1964 a) from *Zostera marina, Ulva, Corallina, Cystoseira*, and *Laminaria*.

D. edwardsi

In Naples Bay (fig. 5) juveniles of this species were frequently found on the algae *Sargassum* and *Cystoseira* at depths of 1–3 m, and adults amongst colonies of *Hydroides unicata* and occasionally in empty *Balanus perforatus* tests. One specimen was obtained from scrapings off a vertical rock face at 10 m off the Isle of Capri (fig. 5). This species also appears to be common on *Cystoseira* at Banyuls (Dr. I. Gordon, material in British Museum). At Endoume, Bellan-Santini (1962) has recorded it from *Petroglossum*, *Corallina* and crevices, and Ledoyer (1962, 1966 a) from *Ulva*, *Corallina*, and at 4 m from *Mytilus* and *Antedon*. Torelli (1930) records it from algae, rocks and *Balanus* tests in the Bay of Naples, and Rivosecchi (1961) from a colony of *Sabellaria elveolata*, which was 200 m from the shore near Rome (fig. 2). Outside the Mediterranean area (fig. 2), Monod (1932) records it from the ' Zone des Corallines ', and Ledoyer (1964 a) from *Fucus serratus* and *Cystoseira*.

D. bifida

Adults of this species were found commonly among *Hydroides unicata* colonies in the Bay of Naples (fig. 5), and Ledoyer (1962) has recorded it from *Ulva lactuca* at Endoume.

D. tubicauda

This species was obtained from among scrapings of rock, incrusting algae, and hydroids from five metres, and also caught freely swimming at 30 m (Fresi, personal communication), in the Bay of Naples.

D. magnitorata

An intertidal and shallow water species.

D. torelliae

Juveniles were found on *Cystoseira* and *Sargassum* at depths from 0·25 to 3 m in Naples Bay. Specimens were also found in material from Chios (Emborios Bay and Cape Mashka) collected off *Cystoseira* at depths from 0·5 to 33 m. Torelli (1930) records it (as *D. bidentata*) from under rocks and in empty *Balanus* tests from Naples Bay.

Discussion

The genus *Dynamene* shows an unusually restricted geographical distribution when compared with related genera (see, for example, Richardson, 1905 ; Barnard, 1914, 1940 ; Hale, 1929 ; Omer-Cooper & Rawson, 1934 ; Loyola e Silva, 1960 ; Menzies, 1961). Six out of the seven species are confined to an area comprising the Azores, N.W. Africa (as far south as Port Etienne), the Mediterranean and Black Seas, the Atlantic coasts of Spain, Portugal, France, and the coasts of the British Isles. The seventh species, for which only a single record exists, is restricted to S.E. Australia.

D. bidentata appears to have the greatest distributional range, and has previously been described from the whole area mentioned above. However, present work suggests that the majority of records for the Mediterranean and

Black Seas probably apply to *D. torelliae* or *D. magnitorata*. Its distribution has been described as Lusitanian-Mediterranean (Kensler, 1965), but it now seems more appropriate to refer to it as Boreal. Of the remaining species *D. magnitorata* and *D. edwardsi* can be termed Atlanto-Mediterranean on Kensler's (1965) scheme, while *D. bifida*, *D. tubicauda*, and *D. torelliae* are Mediterranean, with the last of these probably extending into the Black Sea.

Omer-Cooper & Rawson (1934) suggested from early records (fig. 1) that *D. bidentata* was extending its range into the North Sea via the English Channel and Northern Scotland, but present evidence suggests that its northern limit in Britain may now be retreating southwards. Although present around Ireland, it is now restricted to the south-westerly projecting peninsulas of England, Wales, Isle of Man, and perhaps S. Scotland. The apparent southward retreat of the range of *Dynamene* is perhaps correlated with the lowering of mean sea temperatures over the last few years (Marine Biological Association, Report of Council 1965–66). Hoestland (1955) has suggested that the northerly limit of *Sphaeroma serratum* is determined by the effect of the ambient temperature at the time of oöcyte formation. Similarly, for *Dynamene* it has been shown that viable broods are not produced in ovigerous females kept at 5°c (Holdich, 1968 b) and this could account for the absence of the genus from E. and S.E. coasts of Britain. Evidence for the adverse effect of cold weather on this species is also provided by observations after the 1962–63 winter (Moyse & Nelson-Smith, 1964) when sea temperatures were below 5°c, and air temperatures often much lower than this, for some time during the incubation period. At this time populations of *D. bidentata* on the eastern parts of the S. Wales coast (fig. 4) were totally wiped out and had not recovered by early 1967.* The present distribution follows closely the 6–7°c winter isotherm for surface waters (Lewis, 1964) in southern and south-western Britain. This isotherm also extends across the north of Scotland and partly down the eastern coast, but it seems likely that air temperature is more limiting for *Dynamene* in those areas.

Besides being limited geographically, the species of *Dynamene* appear to be restricted in their vertical distribution to the regions of algae and crevices in the intertidal zone and inshore waters. *D. bidentata*, which has been termed as a permanent facultative member of the crevice fauna (Kensler & Crisp, 1965), has been shown by Wieser (1962, 1963), and Kensler (1967) to be moderately well adapted to living in the lower intertidal zone. Both males and females are able to resist desiccation to some degree by rolling up (fig. 8) although they are less effective in this than *Campecopea hirsuta* (Wieser, 1963 ; Harvey, 1967), which inhabits higher regions of the shore. When occurring in crevices *Dynamene* inhabits the inner and middle crevice zones, associated with its imperfect ability to resist desiccation (Morton, 1954 ; Kensler, 1967). Because of their shape empty tests of *B. perforatus* provide a particularly suitable alternative settlement site for *Dynamene*. The male plugs the opercular opening, thus reducing desiccation when the tide is out and also being suitably positioned for ventilation of the females when the tide is in (Naylor & Quénisset, 1964). The posterior region of the body of the male (figs. 7 and 8) is heavily chitinized and usually becomes coated with calcareous

* Recent observations (April, 1969) on the Gower Peninsular have revealed that both *Dynamene bidentata* and *Balanus perforatus* have now become re-established.

algae ; it also possesses a bidentate process (fig. 6) which resembles the tergal spines of live *B. perforatus.*

The adults of the species of *Dynamene* found in the Bay of Naples were also found to occupy crevice habitats during the reproductive phase. As desiccation does not have to be contended with to any great extent in this region except perhaps in very calm weather (Colman & Stephenson, 1966), the type of habitat occupied by the adults suggests that combined with the behaviour of the male, it forms an efficient means of protecting the ovigerous females from predators and wave action.

There appears to be a great deal of overlap both in range and habitat preference of the *Dynamene* species. *D. bidentata* is entirely intertidal, as are *D. edwardsi* and *D. magnitorata* outside the Mediterranean, but in that sea the latter two species usually inhabit shallow water zones, although occasionally *D. edwardsi* has been recovered from deeper water off steep-sided islands. *D. bifida* has so far only been found in shallow water habitats in the Mediterranean, and *D. tubicauda* below 5 m off steep-sided islands. The vertical range of *D. torelliae* is by far the greatest of the six Afro-European species extending from shallow water algae down to those at 33 m off steep-sided islands. Where geographical ranges overlap (fig. 2), as in the case of *D. bidentata, D. edwardsi,* and *D. magnitorata* on the Atlantic coasts of Europe, and *D. edwardsi, D. bifida,* and *D. torelliae* in some parts of the Mediterranean, identical habitats are occupied and this poses interesting problems of intraspecific competition and mate selection which warrant further study.

Summary

The geographical distribution of the genus *Dynamene* is described in the light of the recent discovery of three new species. *D. bidentata* appears to have a Boreal distribution whilst that of *D. edwardsi* and *D. magnitorata* is Atlanto-Mediterranean. *D. torelliae, D. bifida,* and *D. tubicauda* have a Mediterranean distribution but the first species may extend into the Black Sea. Only one species, *D. ramuscula,* has been recorded outside the Afro-European region, in S.E. Australia. The ranges and habitat preferences of those species outside the Mediterranean overlap as do some of those within the Mediterranean, particularly in the Naples Bay region. Juveniles of *D. bidentata* inhabit and feed on intertidal algae while adults shelter in crevices and empty tests of *Balanus perforatus,* mainly below MTL. Settlement of males into barnacle tests appears to be random, but females show some degree of aggregation, perhaps to other females. Other species show the same change of habitat at sexual maturity and all inhabit intertidal or inshore localities.

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