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HISTORICAL PATTERNS IN THE DESCRIPTION OF NORTH EAST ATLANTIC DECAPODA

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ABSTRACT

An analysis of historical patterns in the description of North East Atlantic Decapoda is presented. The discovery curve of decapods as a whole indicates that the decapod fauna of the NE Atlantic is well known, with two major peaks in species description rates being identifiable: 1808–1830 and 1855–1890, the latter corresponding to the era of the major oceanographic expeditions. On a sub- to infraordinal level, three major periods can be discerned. An early period (1758 – mid 1880s) during which proportionally more Brachyura were described, followed by a shorter period (mid 1880s – 1920 during which more attention was devoted to Anomura and less speciose taxa (mainly deep water). From the 1920s onwards, species descriptions of Caridea have achieved prominence. Size, ecological traits, extent of occurrence, and taxonomic fashion are thought to be responsible for the early bias towards Brachyura, whilst the anomuran and caridean phase are more related to field work techniques (deep water dredging in the former) and improved observational techniques.

Following the Convention on Biological Diversity in Rio de Janeiro in 1992, much emphasis has been placed on biodiversity in the scientific literature and appropriate ways of censusing total biodiversity, including estimating the total number of species on earth. May (1990), Hamond (1992), and Stork (1993) outlined several methods for obtaining the answer to this question. Methods are either based on counting all species, extrapolations from known faunas, extrapolations from samples, extrapolations from description rates, methods using ecological criteria, and censusing taxonomists' views. One of the most frequently used of these techniques is extrapolating past trends of discovery within particular groups. It is clear that past taxonomic effort has been disproportionally allocated to certain groups, with, for instance, the period of maximum discovery rate in birds being between 1859 and 1882, but this period for arthropods (excluding Insecta) being 1956–1970 (May, 1990). Even within a certain taxon, different orders or families may have received disproportionate taxonomic effort. For instance, Strong *et al*. (1984) looked at the discovery rates of certain insect families and concluded that papilionid and danaid butterflies mirrored the bird discovery rates, whilst the discovery rate of certain families of Hemiptera and Thysanoptera (smaller, less conspicuous insects) peaked in 1920–1940. Hence, the number of described species across and within taxa is clearly not a random subset of all species, with vertebrate groups being better known than invertebrate groups, and butterflies and dragonflies being better known than other insect groups (May, 1978). However, given the fact that there will not be sufficient time to describe a large proportion of the remaining fauna before it is lost (Soulé, 1990), gaining an understanding of these nonrandom patterns and their causes may provide the key to ameliorating this bias and possibly counteracting it (Gaston, 1991).

Initially, anecdotal evidence was provided (May, 1978; Diamond, 1985) postulating a link between body size and probability of discovery, with smaller species being described later on in the discovery curve. This was empirically tested by Gaston (1991) for British beetles, and indeed confirmed. This has since been extended to birds (Gaston and Blackburn, 1994; Blackburn and Gaston, 1995), neotropical mammals (Patterson, 1994), and various other insect groups (Gaston *et al.*, 1995a, b; Allsopp, 1997; Williams, 1998). Together these studies have indicated a clear link between not only date of description and body size, but also the influence of abundance, extent of occurrence, area, conspicuousness, and behaviour. As the taxonomic bias and its underlying causes are likely to be different across various groups, it is imperative that more such studies are undertaken for a wider variety of higher taxa in order for this problem to be counteracted on a more global, inclusive scale.

Comparative studies are still largely lacking for Crustacea and for marine taxa in general, even though Wittmann (1999) and Dworschak (2000) present discovery curves for Mysidacea and Thalassinidea, respectively. In the present contribution, these patterns are further explored in North East Atlantic Decapoda. The NE Atlantic fauna is undoubtedly one of the most comprehensively known decapod fauna of the world's biogeographical regions, with a history of taxonomy starting with Linnaeus in 1758 and continuing up to the present day. Recently, d'Udekem d'Acoz (1999) provided a summary of existing knowledge on the group, enabling these patterns to be discussed. A total of 636 marine species and subspecies were listed from the area, with a discussion of their taxonomy, distribution, and ecology.

The aim of this contribution is thus to explore patterns in the taxonomic nonrandomness of the NE Atlantic fauna, contrasting the various taxa within the Decapoda, and offering likely explanations for such patterns.

Materials and Methods

Primary data (species, higher classification, authorship and dates, broad-scale geographical and depth distribution) were taken from d'Udekem d'Acoz (1999), supplemented with literature records published since then. The area studied is between 25°N and 90°N and between 35°W and 60°E (excluding the Red Sea and Persian Gulf) (see d'Udekem d'Acoz, 1999). A total of 604 taxa (species and subspecies) were included in the analysis, which excludes all Lessepsian migrants (reviewed by Galil, 1997), anthropogenic introductions (Breton *et al.*, 2002), and freshwater taxa. The year 2001 was used as the cut-off point, as no species have been described or discovered in the study area since then. A number of species also occur outside the study area (notably the western Atlantic), and a certain subset of these has been initially described from those extralimital areas. As the year in which they were described and the year in which they were discovered in the NE Atlantic need not bear any relation to each other, year of description was used, irrespective of type locality. For the analysis of authorship patterns, multiauthored descriptions were counted under the senior author only, except in the case of collaboration with nontaxonomists, where the junior author was clearly responsible for the taxonomic part of the paper.

Within the NE Atlantic fauna, a small number of cases are known in which an originally valid name was suppressed under the plenary powers of the International Commission on Zoological nomenclature and a much younger name validated. For instance, the name *Cancer squilla* Linnaeus, 1758, was suppressed in 1959 and the name *Palaemon adspersus* Rathke, 1837, validated, a difference in year of description of 79 years (for a discussion of this case, see Holthuis, 1950). However, as there are few such cases, it can be assumed that the overall patterns are not unduly influenced.

Discovery curves and description rates were calculated according to the methods of May (1990) and Hamond (1992), with the discovery rate defined as the number of known species at any given time slice expressed as a fraction of those known presently (expressed on a logarithmic scale). Median depths were calculated, based on ranges given by d'Udekem d'Acoz (1999).

Results

Although many species of Decapoda have been described since the dawn of Greek civilisation, the first author who used valid names for NE Atlantic taxa was Linnaeus, who described 29 species in 1758 (Linnaeus, 1758). This was followed by several other authors (Forskål, Fabricius, Pennant, Olivi, Petagna, Herbst) and as a result 75 species (i.e., 12.44% of today's list) were known by 1800 (Fig. 1). From then on, a rapid increase in the number of species took place with 195 species (32.34%) known by 1850, and 423 species (70.15%) by 1900 (Fig. 1). A swift increase in species numbers occurred early on in the period from 1808 to 1830, with the works of Montagu and Leach in the Atlantic, and Risso and P. Roux in the Mediterranean, nearly doubling the number of know species. This period culminated in H. Milne Edwards' monumental work Histoire Naturelle des Crustacés (H. Milne Edwards, 1834–1837) treating all known Crustacea on a world-wide basis. A second period of heightened discovery runs from approximately 1855 to 1890 (Fig. 1) with the work of many authors, such as Bate, Miers, Henderson, Bouvier, Heller, G. O. Sars, but particularly the highly productive A. Milne-Edwards, coupled with the discovery of many species, originally described from the West Atlantic by S. I. Smith, in the NE Atlantic. The latter half of this period coincides with the major oceanographic expeditions, such as the British "Lightning" and "Porcupine" expeditions, but also the French expeditions onboard the "Travailleur" and the "Talisman," the Monegasque expeditions with the "Hirondelle" and "Princesse Alice," and many more. As a result of these major expeditions, in one single decade (1880–1890), an astounding 104 species were described (Fig. 2), virtually a sixth of the known NE Atlantic decapod fauna. The most productive year during this period (and indeed during the entire period from 1758 to 2001) was 1881, with 29 species described (Bate, 1881; Miers, 1881; A. Milne-Edwards,

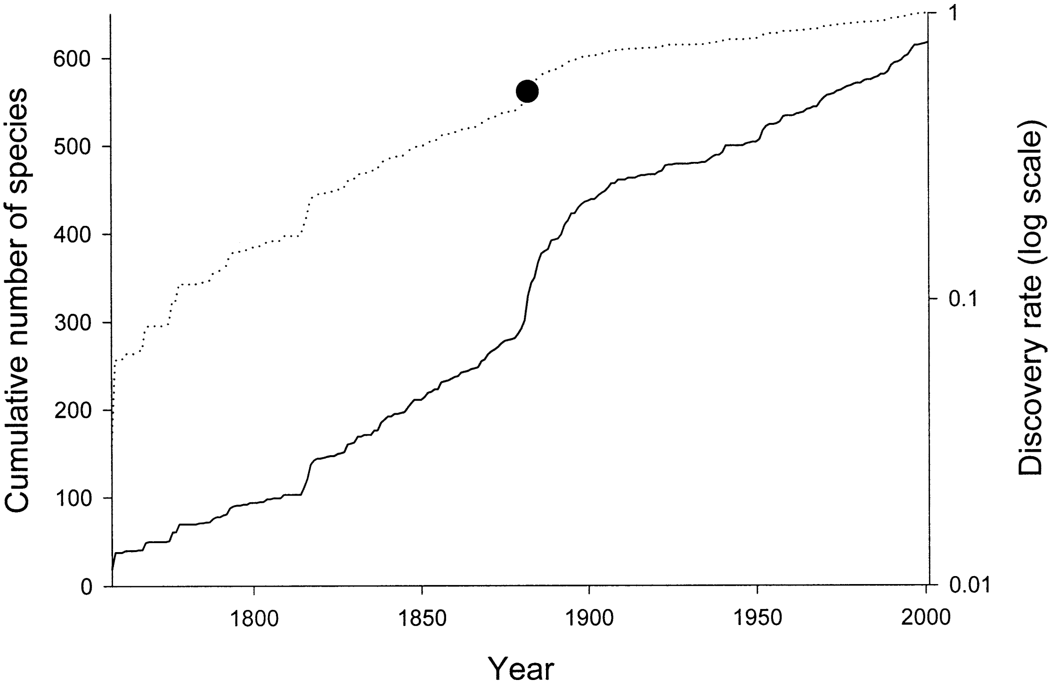

Fig. 1. Cumulative number of decapod taxa described up to 2001 in NE Atlantic waters and their discovery curve. Discovery rate (dotted line) is expressed as a fraction of those known in 2001 on a logarithmic scale, black circle indicates median date of description.

1881a, b; S. I. Smith, 1881). Although after this second period of heightened discovery, the number of taxa has continued to rise at a steady pace (Fig. 1), no periods of exponential growth can be identified.

A total of 147 authors have described species occurring in the NE Atlantic, with the majority of authors only describing a single species (Fig.

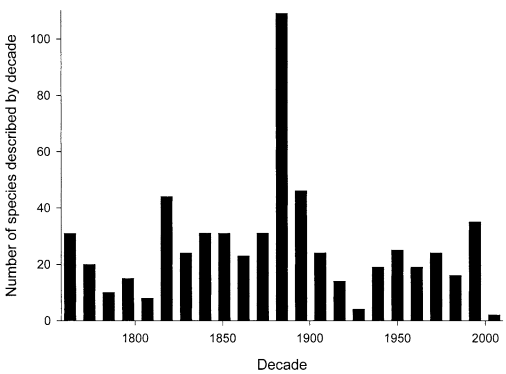

Fig. 2. Number of decapod species occurring in NE Atlantic waters described per decade. Decades were calculated from 1758 onwards (e.g., 1758–1768, 1769–1779, 1780–1790, . . .), position of each vertical bar corresponds to mid-decadal year.

3), although many of them may also have described numerous extralimital species (e.g., A. J. Bruce, who described in excess of 150 species of Indo-Pacific Pontoniinae, but only one NE Atlantic taxon). Conversely, 44.9% of all NE Atlantic decapods were described by only 10 authors. In descending order, they are as follows: A. Milne-Edwards (45 species as the sole author); Bouvier (39 species, of which 23 were jointly described with A. Milne-Edwards); Linnaeus (29); S. I. Smith (28); Holthuis (27); Risso (23); Leach (22); Miers (12); Fabricius (17); and Forest (14). Interestingly, the majority of them were active before or around the turn of the century, with only two being active in more recent years.

During the early phase of description, the majority of taxa described were shallow-water taxa (Fig. 4): although several deep-water species were also described quite early, such as *Geryon trispinosus* (Herbst, 1803) by Herbst (1782–1804), but based on shallower water specimens. This is perhaps confounded by the fact that many of the species occurring from boreal waters through to the Mediterranean occur in shallower depths in the northern part of their range (e.g., *Pontophilus norvegicus* (M. Sars,

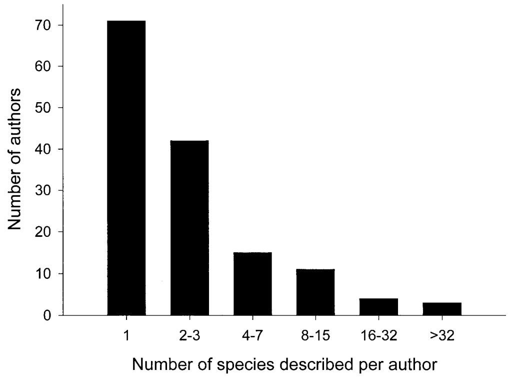

Fig. 3. Number of authors describing different numbers of species of NE Atlantic decapods. Size classes follow Gaston *et al.* (1995a).

1861), see De Grave and Diaz, 2001). Nevertheless, some deep-water species (between 300 and 1000 m) were reported upon quite early in the discovery curve by Risso (1826) and other authors. A period of deeper water exploration (as well as heightened shallow-water activity) can be identified around the early to mid 1880s (Fig. 4); this clearly corresponds to the major oceanographic expeditions. From the early 1900s onwards, species are being described/discovered from a variety of depths, although the majority are still shallow-water species. Although these three periods can be distinguished, the overall correlation between median depth and year of description is quite low (Spearman Rank Correlation 0.239), but nevertheless significant ($P < 0.005$).

It is of interest to note that the Atlanto-Mediterranean species as a whole were described much earlier (Table 1) than either exclusively Atlantic or Mediterranean species. In fact, the

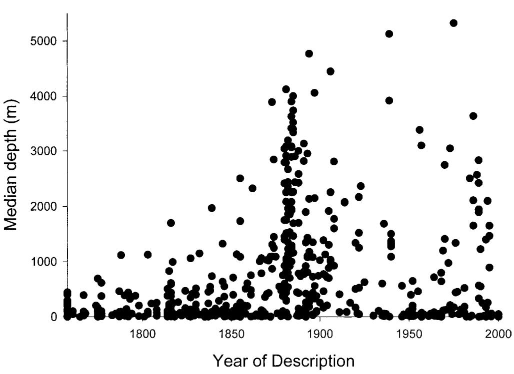

Fig. 4. Median depth (m) *versus* year of description of NE Atlantic decapods.

Table 1. Percentiles of the discovery curve of NE Atlantic Decapoda, based on large-scale distribution patterns.

	25%	50%	75%	95%
Atlantic	1877	1885	1922	1988
Mediterranean	1882	1962	1992	1998
Atlanto-Mediterranean	1808	1837	1882	1965

median date of description for exclusively Mediterranean taxa is 125 years later than the corresponding date for Atlanto-Mediterranean species, with the 75% percentile only being reached in 1992, virtually a century later than the Atlanto-Mediterranean species. Doubtless, there are regional differences within each of these three broad geographical distribution patterns, as intuitively it could be expected that more northern species (e.g., UK or Norwegian waters) were described earlier than those from more southern latitudes (e.g., African coast), not in the least due to the geographical distribution of the taxonomists themselves. However, an analysis of subregional differences is confounded by the wide extent of occurrence of the majority of species and the fact that type locality and extent of occurrence need not bear any relationship to each other (beyond the former being part of the latter).

A number of interesting comparisons can be made when the data are considered at a sub- and infraordinal level (Table 2, Figs. 5, 6). A large difference exists in the median date of description between some of the groups, with the Brachyura reaching this level earliest followed by the Nephropidea and the Palinuridea, which are both less speciose groups. The Caridea and Anomura reach this point nearly 30 years later, whilst the Stenopodidea only reach this level 50 years later (Table 2). This discrepancy becomes more pronounced if the 75th percentile is considered, with the Brachyura and Eryonidea reaching 75% nearly 70 years before Caridea, and nearly 100 years before Thalassinidea (Table 2). Later on in the description curve, these taxon differences level off between the majority of taxa, as exemplified by the 95% percentile. Nevertheless, no new Palinuridea or Dendrobranchiata have been described (nor recorded) in the area for nearly 40 years (with the exception of Lessepsian migrants), whilst the last descriptions of Caridea were in the cut-off year (2001) (Table 2). The two last taxa to be described/discovered from the area are the Stenopodidea and the deep-water Eryonidea (Table 2), although Stenopodidea were known slightly earlier (1811) from extralimital areas

Table 2. Number of species per taxonomic group in the NE Atlantic area, percentiles of the discovery curve, with the year of first and last description of a species within the taxon (95th percentiles in Palinuridea, Stenopodidea, Eryonidea, and Nephropidea could not be calculated, as too few species are present in the study area).

	Number of species	25%	50%	75%	95%	First description	Last description
Decapoda	604	1832	1881	1920	1989	1758	2001
Caridea	208	1850	1884	1951	1994	1758	2001
Brachyura	183	1801	1850	1883	1988	1758	1995
Anomura	109	1852	1887	1900	1989	1758	1994
Dendrobranchiata	50	1855	1882	1906	1936	1768	1969
Thalassinidea	22	1815	1897	1972	1997	1792	1999
Palinuridea	9	1799	1864	1921	–	1758	1963
Stenopodidea	9	1892	1905	1928	–	1827	1990
Eryonidea	8	1873	1880	1883	–	1862	1893
Nephropidea	5	1758	1865	1904	–	1758	1970

and Eryonidea since 1820 as fossils. When comparing the discovery curves of the three most speciose taxa (Caridea, Brachyura, Anomura) a number of periods of heightened species descriptions can be identified. For the Brachyura, two relatively minor periods can be identified (Fig. 5), corresponding to the work of Fabricius and Pennant in 1775–1777 and one from 1827 to 1830 corresponding to the work of Risso and P. Roux. Much more significant steps can be identified in the Anomura (Fig. 5), with a first dramatic increase in the number of species due to several species being described in the 12th edition of Linnaeus' Systema Naturae, effectively trebling the number of species; a second dramatic increase can be noted around the 1890s, mainly due to work by Bouvier. An initial increase in species description in the Caridea takes place in the period 1814–1816 due to the work by Leach and Risso; a second, less dramatic increase takes place in the mid 1880s, mainly due to the efforts of A. Milne-Edwards and S. I. Smith, the latter working in the W Atlantic, but with many of these species discovered in the NE Atlantic by Bate (1888) and other authors.

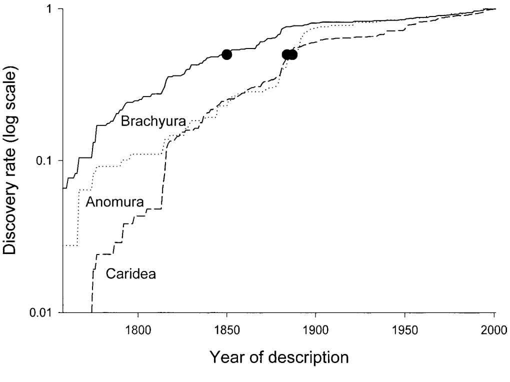

Fig. 5. Discovery curves of the three most speciose groups of NE Atlantic decapods. Black circles indicate median dates of description.

Considering the proportion of species description in the major suborders within the Decapoda over time (Fig. 6), it is clear that the initial phase of description was mainly concerned with Brachyura, with this period lasting from 1758 to the mid 1880s (Fig. 6). This period was followed by a much shorter period, lasting until the early 1920s, in which much more attention was devoted to the Anomura and the less speciose taxa (such as Dendrobranchiata, Nephropidea, and Palinuridea, see Table 2), than either Brachyura or Caridea. From the 1920s onwards, species descriptions of Caridea have become much more prominent (Fig. 6).

Discussion

Cumulative numbers of species described through time tend to follow an approximately sigmoidal function, with low rates of description early and late, although for many groups the asymptote has yet to be reached (Hamond, 1992; Gaston *et al.*, 1995a). The pattern exhibited by NE Atlantic decapods clearly demonstrates a plateau being reached in the last 50–60 years, although new species are still being added as time progresses. Compared to the graphs presented for various groups in May (1990) and Hamond (1992), the shape of the curve clearly demonstrates that the NE Atlantic decapod fauna is well inventoried (a fact which most decapod taxonomists already know). This is further supported by the fact that fifty percent of all decapods in the NE Atlantic were described by 1881, taking 123 years from the first descriptions by Linnaeus, and taking a similar time span (119 years) to describe the

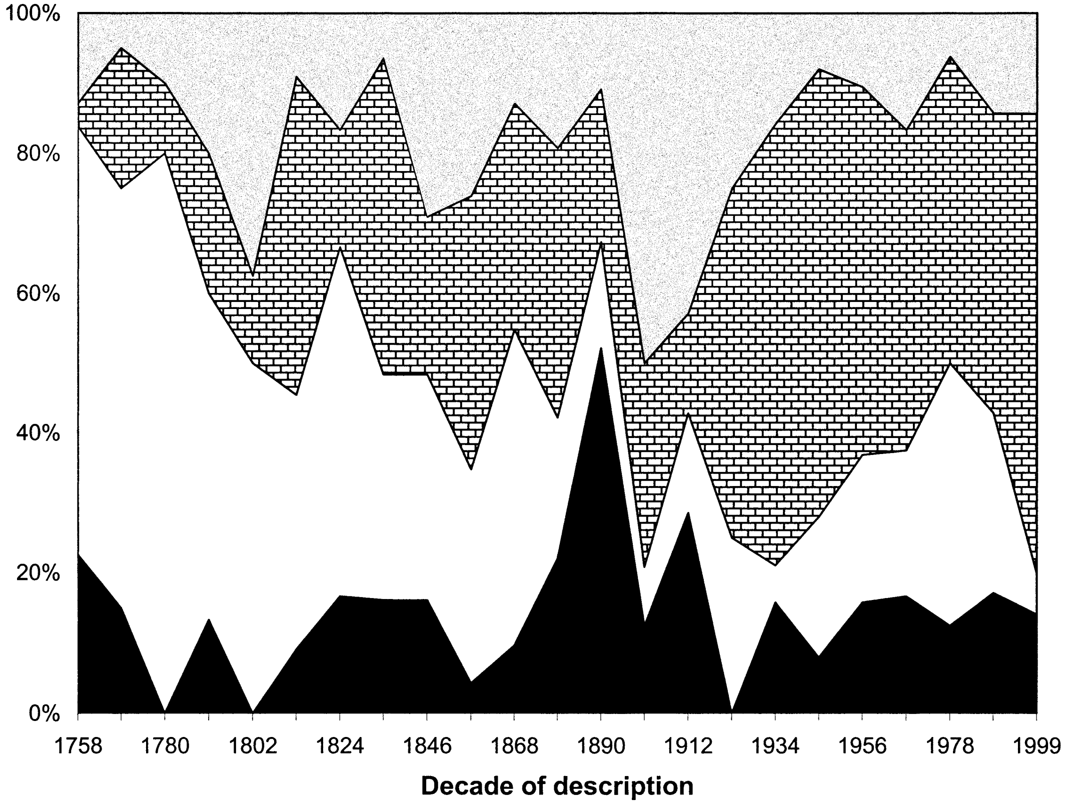

Fig. 6. Proportion of description across four groups (Anomura, Brachyura, Caridea, other) expressed per decade. "Other" category combines data for Dendrobranchiata, Thalassinidae, Palinuridea, Stenopodidea, Eryonidea, and Nephropidea. Categories as follows: Anomura (black), Brachyura (white), Caridea (blocked), other (grey). Description dates are considered per decade, with start of each decade indicated in axis.

remaining fifty percent. This is similar to the time lag in birds, considered by many to be a well-studied group in which the majority of species are described (May, 1990). The curve is in sharp contrast with the overall noninsect Arthropoda curve in May (1990), in which it took 202 years to reach the median mark and only a further 10 years to reach the presently known number of species. It is not the object of the present contribution to extrapolate how many more species will be discovered in the NE Atlantic, nevertheless it is clear that few remain to be detected. However, dramatic shifts in the number of species can occur, even in relatively well known groups or areas, due to more vigorous collecting and/or more intense revisions of certain taxa (Hamond, 1992). A recent example in the NE Atlantic is the revisionary work on *Hippolyte* Leach by d'Udekem d'Acoz (1993, 1995, 1996), which added a further four species, bringing the total number in the study area to eleven.

Many more species of Decapoda than those currently recognized have been described from the study area since 1758, especially in the first half of the 19th century. However, many of these have proven to be junior synonyms of the species presently considered valid (and here analysed). Even though the exact taxonomic status of many of these synonyms is not well understood (for instance the many varieties and formae described by Czerniawsky, 1884), it is clear that some of the earliest described, morphologically variable and/or geographically widespread species have as many as eight or nine synonyms (e.g., *Hippolyte* spp., see d'Udekem d'Acoz, 1996) and that more recently described species have none or perhaps one junior synonym. Although a cursory examination of species names does support the general trend that the number of synonyms is inversely related to the date of description (Gaston *et al.*, 1995b; Allsopp, 1997), this cannot presently be fully corroborated in NE

Atlantic Decapoda, as such an analysis is beyond the scope of the present contribution.

The NE Atlantic decapod fauna illustrates very well the effect a few productive taxonomists can have on the pattern of description and hence the number of species known, as nearly half of the total fauna was described by only 10 taxonomists, with minimal contributions by other workers when taken individually. This is of course a common theme in taxonomy, although it has not often been illustrated (see Gaston *et al.*, 1995b, for data on Lepidoptera – Geometridae).

Although a clear pattern can be discerned for decapods as a whole, on a more inclusive level (sub- and infraordinal) distinct differences can be noted. These are most notable between the three speciose groups: Anomura, Brachyura, and Caridea; with differences in less-speciose groups being more difficult to interpret. Three more or less distinct periods can be discerned, with many more species of Brachyura being described before the mid 1880s than the other two speciose groups. This was followed by a more protracted period (up to the 1920s) during which Anomura gained prominence, and during the most recent period more attention devoted to Caridea. Several explanations have been put forward in the literature to explain such trends in species discovery; these include body size, extent of occurrence, abundance, conspicuousness, and behavioural traits (Gaston, 1991; Gaston and Blackburn, 1994; Patterson, 1994; Blackburn and Gaston, 1995; Gaston *et al.*, 1995a, b; Allsopp, 1997; Williams, 1998), but trends may also be influenced by taxonomic taste and fashion, as well as ease of collection, study, and preservation (Hamond, 1992).

Due to the morphological disparity of decapods, it is impossible to derive a homologous measurement of size across all taxa, with the possible exception of body weight (data on which is lacking for the majority of species). Intuitively, however, NE Atlantic Brachyura are larger than Caridea, and this may indeed be a factor in the early emphasis on Brachyura. Equally important may have been conspicuousness and behavioural/ecological traits, perhaps prime amongst these is the depth distribution of species given the fact that the majority of early descriptions were based on shallow-water specimens (Fig. 4) which could easily be collected by naturalists. Indeed, the median depth of brachyuran species in the NE Atlantic is 71.25 m, whilst this is 450.00 m for both Caridea and

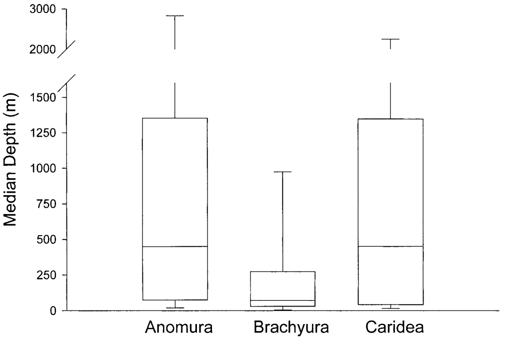

Fig. 7. Box-whisker plots of median depth in Anomura, Brachyura, and Caridea from the NE Atlantic. The box represents the interquartile range, which contains 50% of all values; whiskers extend from the box to the shallowest and deepest values, excluding outliers; median value is indicated by a line across the box.

Anomura (Fig. 7), the interquartile range further indicates the shallow water nature of Brachyura, as opposed to both Anomura and Caridea (Fig. 7). Extent of occurrence may also have played an important role in the early prominence of Brachyura, as proportionally a higher percentage of brachyuran species exhibit an Atlanto-Mediterranean distribution, compared to the other speciose groups (Table 3); this would logically allow for a higher chance of discovery.

Taxonomic taste and fashion may have played a certain, if somewhat un-quantifiable, role in this early phase of description. Certainly, the main decapod carcinologists of the era had wide ranging taxonomic interests, and many described Brachyura, Anomura, and Caridea from other geographical areas. However, as over half of the descriptions of NE Atlantic decapods were made not by these leading carcinologists, but by authors who only described a handful of species (sometimes only one or two), it is not inconceivable that taste and fashion (as well as other factors such as conspicuousness, ease of study or preservation) may have played a major role during this phase.

The second phase of species description, during which Anomura (and the less speciose groups) achieve prominence, coincides with the era of the main oceanographic expeditions, such as the "Challenger," "Travailleur," "Talisman," and many more. Although dredging of coastal waters for procuring natural history specimens was practised as early as 1832 by Thompson, in Strangford Lough (Northern Ireland), it was the deep-water dredging on board these expeditions that led to the discovery of

Table 3. Percentage of species within decapod groups exhibiting Atlantic, Mediterranean, or Atlanto-Mediterranean distributions. "Other" category combines data for Dendrobranchiata, Thalassinidae, Palinuridea, Stenopodidea, Eryonidea, and Nephropidea.

	Brachyura	Anomura	Caridea	Other
Atlantic	34.97	59.63	58.85	48.54
Mediterranean	8.74	8.25	8.13	8.73
Atlanto-Mediterranean	56.28	32.11	33.01	42.71

many deeper water Anomura (e.g., Henderson, 1888). This period also coincides (or perhaps was partially driven by) the main activity peak of two taxonomists (A. Milne-Edwards and Bouvier), who worked extensively on both Anomura and these deeper water collections. This again illustrates the effect a single taxonomist can have on the number of species described.

The third (and continuing) phase is more than likely related to both improved fieldwork techniques and improved observational techniques, but perhaps also to the fact that the other groups were already extensively studied, and new taxonomists entering the field may have wanted to concentrate on other areas of research. Indeed, of the currently active European decapod taxonomists, the majority are working on various caridean families (perhaps a new phase in taxonomic fashion?). In more recent years, specialised collecting techniques, such as yabby pumps (e.g., Dworschak *et al.*, 2000) and SCUBA diving, have provided numerous examples of new species. The majority of these are carideans, with no Brachyura having been described for over five years (Table 2). Collecting in relatively inaccessible habitats (such as deep-water caves), as well as more intense prospecting in shallow-water habitats, coupled with more revisionary work will undoubtedly yield more species. Although existing trends may indicate that these new species are likely to be carideans, a certain number of anomurans and brachyurans undoubtedly await discovery.

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