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Authors

Aguzzi, Jacopo
Maynou, Francesc
Company, Joan Baptista
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The dimensional units of *Nephrops norvegicus* (L.) distribution: from burrows to populations

JACOPO AGUZZI*, FRANCESC MAYNOU, JOAN BAPTISTA COMPANY,
GUIOMAR ROTLLANT, FRANCESC SARDÀ

*Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta 37-49,
08003 Barcelona (Spain)*

**e-mail: jaguzzi@cmimLa.csic.es*

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SUMMARY

Nephrops norvegicus is a burrowing decapod inhabiting muddy bottoms of the continental shelves and slopes of European Atlantic and the Mediterranean seas. Several aspects concerning *N. norvegicus* geographical and bathymetric distribution are revised in relation to its biology. Burrows are considered the ultimate small-scale unity of distribution, while patches the intermediate one. Larval migration among patches determines the geographic and bathymetric distribution of populations. Ecological factors determining patchiness are considered along with implication for morphology and genetics of populations. Issues for further researches concerning *N. norvegicus* distribution and commercial exploitation are proposed.

INTRODUCTION

The biogeographical aspects of *Nephrops norvegicus* (L.) distribution are intriguing for three main reasons. As a first instance, its distribution range is mainly known due to the commercial fishing fleet and to survey projects of research (see below), which identify the exploitable grounds where density meets commercial criteria required by the fishery. In this sense, for those few areas where the commercial fishery is absent, no conclusion on *N. norvegicus* presence can be drawn. As a second instance, a two-dimensional aspect in the species distribution should be considered: the species occupies a wide geographic range (from the European Atlantic Ocean, down to the Mediterranean including Morocco), and a wide bathymetric range (spanning from the subtidal regions of the upper shelf in the Atlantic and North Sea, to the slopes of the western-central Mediterranean)

(Farmer, 1975; Sardà, 1995). As a third instance, *N. norvegicus* exhibits an endobenthic lifestyle, being therefore strictly linked to the substratum. Individuals do not undertake migrations, therefore they spend all the post-larval life cycle in the same area (Chapman, 1980b; Chapman and Bailey, 1987). Consequently, the populations' demography and genetics are affected by larvae dispersal.

In the last decade, the growing importance of *N. norvegicus* for the demersal trawl fishery in the Mediterranean area justified the planning of a series of research projects devoted to increase the knowledge on its biology for stock management purposes (Sardà, 1998a; Maynou and Sardà, 2001; Abello et al., 2002a). Most of these projects were developed over the Spanish and Italian fishing grounds. Only recently the body of knowledge on *N. norvegicus* biology was expanded eastward by adding new data on fishery of Greek populations (Mytilineou et al., 1992; 1998; 2002). In particular for the Spanish Mediterranean, the GEOESC project (Maynou and Sardà, 1997) analysed population distributions and demography in the Catalan Sea, in relation to substrate typology and the occurrence of other decapod species (Maynou et al., 1996; Maynou and Sardà, 1997; Maynou, 1998; Maynou et al., 1998). The NEMED project (Sardà, 1998b) dealt with other biological parameters of the populations inhabiting different areas of the Mediterranean such as growth and reproduction (Mytilineou et al., 1998; Orsi Relini et al., 1998), feeding (Cristo and Cartes, 1998), morphology (Castro et al., 1998), genetics (Maltagliati et al., 1998) and fishing techniques in the involved countries (Sardà, 1998c). For the Italian grounds, many data on *N. norvegicus* distribution were gathered by the GRUND project (Relini et al., 1999). The pluriennial EU funded MEDITS project (Bertrand and Relini, 2000; Abello et al., 2002b), estimated abundance indices and population characteristics of demersal target species in the European Mediterranean Sea, including *N. norvegicus*. Then, other useful data on geographic and bathymetric distribution and population structure were obtained for this species in the whole Mediterranean area.

NEPHROPS NORVEGICUS DISTRIBUTION

Geography and bathymetry

N. norvegicus geographical distribution can be subdivided into a northern range (Gulf of Biscay to Norway and Iceland) and a southern range (Portugal, Mediterranean and Morocco) (Fig. 1) (Farmer, 1975). In particular in the Mediterranean basin, *N. norvegicus* is abundant in the Western area, in the Adriatic Sea and in the North Aegean Sea, whereas it is less abundant in the East Mediterranean (Holthuis, 1987; Abello et al., 2002a). In the south Mediterranean, it is present from the Straits of Gibraltar to the Nile delta, but it is absent from the Levantine coasts (Holthuis, 1987).

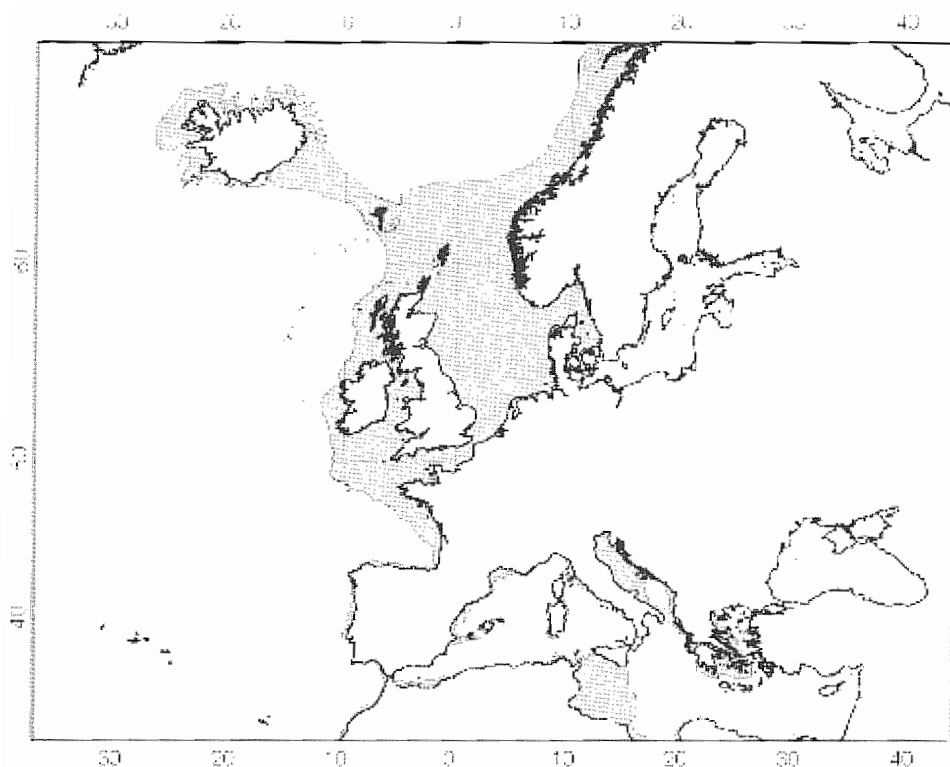


Fig. 1 - *Nephrops norvegicus* geographic distribution (courtesy of Food and Agriculture Organization, FAO, Rome). Dense areas in the map indicate zones of species presence

In the Mediterranean basin, the species bathymetric range of distribution spans from depths shallower than 100 m (the shelf) in the Adriatic Sea, in the North Euboikos Gulf and in the Ebro (and to a lesser extent, the N Aegean Sea, Gulf of Lions and Corsica) (Frogliia, 1972; Maynou and Sardà, 1997; Mytilineou et al., 1998; Abelló et al. 2002a), down to 870 m (the slope), typical of the western-central Mediterranean area (Abelló et al., 1998; 2000, 2002a; 2002c). While in the Adriatic Sea, the North Euboikos Gulf, and the Ebro delta maximal densities are found at around 100 m depth, in the central-western Mediterranean the species reaches a maximum in its distribution between 245 and 485 m (Abelló et al. 1988; 2002a; 2002b; Cartes and Sardà, 1993; Maynou and Sardà, 1997; Maynou et al., 1998; Aguzzi et al., 2003b).

The small scale distribution: the burrow

The burrow is the primary element of *Nephrops norvegicus* distribution, since it acts as the centre of a strong territorial behaviour (Chapman and Rice, 1971;

Rice and Chapman, 1971; Farmer, 1974b; Sardà, 1998a). Two lobsters are virtually never found in the same shelter (Cobb and Wang, 1985), although no spatial segregation between juveniles and adults occurs (Maynou and Sardà 1997). No nursery areas are reported for this species (Briggs, 1987). Juvenile burrows independent from those of adults were not noted in the field, suggesting that the majority of juveniles form adult-juveniles burrow complexes (Tuck et al., 1994). As the burrow system becomes more complex, and juveniles grow, each individual develops its own section and links between the burrow sections can no longer be maintained (Tuck et al., 1994).

Territoriality in this species, at least for the adult part of the life cycle, justifies the equivalence: one burrow, one animal. This observation was often taken into account to estimate *N. norvegicus* densities on Atlantic fishing grounds by means of visual methods of sampling. Burrows present strict morphological features allowing their easy individuation on bottoms (i.e. a main crater-like entrance opens into a tunnel, that ends into several rear small holes of ventilation) (Rice and Chapman, 1971, Tuck et al., 1994; Froglija et al., 1997; Hugens and Atkinson, 1997; Aguzzi et al., 2005b). Underwater surveys, directly made by scuba divers, or by means of underwater television (i.e. towed sledges endowed with videocameras), provided highly variable results on density estimates (numbers of burrows per m²) and typology of distribution (random, aggregated, ordered). Density estimation presented uncertainties mainly produced by two factors: juvenile may share burrows with adults (Briggs, 1987); burrows may persists for a certain period of time if not occupied, depending from fishing activity and hydrodynamism occurring on a particular *N. norvegicus* ground (Tuck et al., 1997). In Tab. I a bibliographic compen dium of these results is reported as an example.

Tab. I - Density of *Nephrops norvegicus* (kg/km²) as recorded by underwater direct estimates in the Scottish (Sc), Irish (Ir), Italian (I) and Spanish (S) seas.

Source	Zone	Density (num. burrows/m ²)
Chapman and Rice (1971)	Loch Torridon (Sc)	2.1
Rice and Chapman (1971)	Loch Torridon (Sc)	2.5
Hillis (1974b)	Dublin bay (Ir)	1.0-2.5
Atkinson (1974)	Loch Aline (Sc)	0.15-0.16
Chapman (1979)	Sound of Jura (Sc)	3.0-5.0
	Firth of Forth (Sc)	0.4
	Clyde (Sc)	0.9-1.4
	Linn of Morven (Sc)	8.0
Chapman (1985)	Linn of Morven (Sc)	0.15-0.31
Tuck et al. (1994)	Loch Sween (Sc)	0.092
Tuck et al. (1997)	Firth of Forth (Sc)	0.46-1.48
Hugens and Atkinson (1997)	Cumbran Coasts (Ir)	0.1-1.3
Froglija et al. (1997)	Pomo Pit (I)	0.66-0.72
Aguzzi et al. (2005b)	Ebro delta (S)	0.81

Direct, underwater visual estimates on *N. norvegicus* density disagreed with indirect records provided by trawl fishing activity, being the former higher than the latter (Tuck et al., 1997). This disagreement was explained by considering that marked *N. norvegicus* emergence rhythms may produce biases in animals sampling. In fact, animals are captured by trawl gears only when out of their burrows (Chapman and Howard, 1979; Main and Sangster, 1985; Newland et al., 1992). Peaks in catches occur at different hours at different depths following an optimum light intensity range (e.g. Chapman et al., 1972; 1975; Farmer, 1974a; Moller and Naylor, 1980; Aguzzi et al., 2003b; Aguzzi et al., 2004a). Chapman (1980a), by comparing indirect (trawl fishing) and direct (visual census) data, stated that only 10-30% of animals exit from their burrows on a daily base, being therefore captured in nets, the others remain always concealed. However, recent data in the Mediterranean on *N. norvegicus* behaviour under laboratory controlled conditions (Aguzzi et al., 2003a; 2004b) do not support such a low proportion of animals emerging from their burrows at each activity cycle. Reproductive biology may account for the differences observed, since berried females remain hidden for long periods of time, as revealed by sex ratio seasonal fluctuations in catches recorded both in the Atlantic (Figuereido and Thomas, 1967; Rice and Chapman, 1971; Farmer, 1974c, 1975; Chapman, 1980) and in the Mediterranean (Sardà and Lleó, 1993; Sardà, 1995; Orsi-Relini et al., 1998; Aguzzi et al., 2004a).

The intermedium scale distribution: the patch

The main ecological factor influencing the species distribution is the availability of suitable substrate to dig burrows. Substrate particulate dimensions of bottoms inhabited by *N. norvegicus* correspond to those typical of silt and clays. Particulate of this size usually deposited on bottoms in a context of low hydrodynamism (Bailey et al., 1995). Temperature and salinity are considered less relevant in limiting the species distribution (Maynou and Sardà, 1997), although both affect larval development and mortality (Figuereido and Vilela, 1972; Dickey-Collas et al., 2000a).

The relationship between substrate characteristics and *N. norvegicus* distribution was extensively studied both in the Atlantic (Bailey et al., 1995; Tully and Hillis, 1995) and in the western Mediterranean (Maynou and Sardà, 1997). Maynou and Sardà (1997) reported that density of dwelling animals was higher in fine-grained sediments of slope areas, being lower in coarse sediments on the continental shelf. In particular, a marked discontinuity of the distribution was revealed concomitantly to changes in substrate typology (Maynou et al. 1998). A highly complex aggregated patterns made by high-density patches (6-10 Km) was recorded off the Catalan coasts (Maynou et al., 1998; Sardà, 1998a).

On the other hand, Maynou and Sardà (1997) found that *N. norvegicus* distribution is not only affected by substrate typology, but also by the occurrence of competitor species. In the western-central Mediterranean slope, the extensive segregation between patches of *N. norvegicus* and *Pasiphaea sivado* or *Solenocera membranacea* occurs: high-density patches of one species coincide with low-density patches of the other (Maynou et al., 1996). Predator-prey relationships, as source of patchy distribution, are not known in this species. While for the Atlantic, the cod (*Gadus morrhua*) is the major predator of *N. norvegicus* (de Clerk and Sterk, 1979; Fannon and Hillis, 1982; Armstrong et al., 1991), no major predator is known in the Mediterranean area. For example, Bozzano et al. (1997) did not observe remains of *N. norvegicus* in the stomachs contents of a major predator such as *Merluccius merluccius*.

The large scale distribution: relationship among patches

Different ecosystems of a geographic area can be distinguished basing on the growth-form of dominant species, usually plants. A classification of the marine ecosystems is more complex since it may or may not be based on ecological determinants such as the hydrodynamism, temperature gradients, pressure, salinity, etc. (Aguzzi and Abello, in press). Many marine species follow a metapopulation pattern, with subpopulations (demes) being connected by larval dispersal. This is the case of most benthic species, whose individuals are strictly related and fixed to the bottom substrate at adult life stage. Adults constitute sedentary subpopulations connected by dispersing larval stages (Botsford et al., 1998).

N. norvegicus releases newly hatched larvae from spatially well-defined muddy areas into the overlying water column. In the Atlantic, larvae are generally sampled near the surface, in the upper part of the water column (Williamson, 1956; Hillis, 1972; 1974a; Linedley et al., 1994; Angelico, 1999). Larval biology is mostly known for the Irish Sea, where this life stage was object of studies for stock assessment purposes (Thompson, 1986; Nichols et al., 1987; Dickey-Collas et al., 2000b). In that area, larval distribution is apparently restricted to adults' high density patches (Garrod and Harding, 1980). Scarce data are available for the Mediterranean, where larvae were rarely captured (Santucci, 1926), being the species distribution generally deeper than in the Atlantic. Larvae may be released in the water column a few meters above the patch, without displacing too far away from it, due to the low hydrodynamism typical of shelf and slope grounds. However, larvae present a marked phototaxis (Farmer, 1975), possibly forcing them to reach upper levels. There, they could be exposed to a wide array of hydrodynamic factors affecting both their mortality and dispersal (White et al., 1988; Bailey et al., 1995). Additionally, a period up to 50 days is required before settlement (Hill and White, 1990). As a result, larvae could

redistribute over large areas, effectively contributing to populations' dispersal. Depending from patch geographical proximity, the level of connectivity may change: a metapopulation dynamic may take place when connectivity between patches is low, whereas losses of larvae in one patch could allow recolonization by migrants from a neighbouring one, in case of high connectivity. In a sense, the survival of adult populations depends from a balance between a sufficient larval dispersal, after advective losses, and retention (White et al., 1988).

Changes in morphology on a geographical base could be produced by a reduction in the gene flow among populations, leading to a genetic differentiation, or at the contrary they could be the result of phenotype plasticity (reaction norm: similar genotypes express different morphological features due to local environmental effects) (Wright, 1978). Genetic isolation and reaction norm are not easily distinguishable in *N. norvegicus*. Differences in the animals' size among populations were generally attributed to phenotype plasticity rather than genetics. An unclear relationship between local substrate grain size and animals mean size was found in the Atlantic (e.g. Chapman and Bailey, 1987; Hillis, 1988; Chapman and Howard, 1988). Competition for food and space may differently affect the growth rate of animals in different patches, depending from respective demography (Farmer, 1974a; Neil and Ansell, 1995; Fariña et al., 1999). Fishing activity may also be of local importance in determining difference in size. Generally, for a locally based fishery like the Mediterranean one (i.e. each harbour possesses its independent fishery fleet), a differential fishing exploitation increasing mortality rates, could lead to a variation in mean size of populations of different ground areas (Figuereido, 1987; Sardà and Leonart, 1993; Abello et al., 2002a; Sardà, 1998d). Properly designed biometric studies, planned to discriminate Atlantic and the Mediterranean populations on a biographical base, failed to show any significant trend (Castro et al., 1998).

The genetic structure of *N. norvegicus* stocks was analysed by Passamonti et al. (1997) who compared allozyme variation of Scottish and Aegean stocks of *Nephrops*. The authors did not report significant genetic differences. Later, Maltagliati et al. (1998), in a similar study involving Atlantic and Mediterranean populations, found no clear patterns of geographic stock structure. Negligible genetic differentiation was also observed at a smaller geographical scale, between two separated Adriatic stocklets showing different growth and reproductive parameters (Mantovani and Scali, 1992). Recent studies on DNA polymorphisms in two different Portuguese populations indicated their genetic similarity (Streiff et al., 2001).

CONCLUSIONS

Several aspects of *Nephrops norvegicus* distribution are currently still unknown. The definition of levels of population structure, from continuum to patches, is

crucial for a correct fishery management of this species. A series of indication for further researches is accordingly proposed below.

The existence of a pelagic larval stage makes the case of genetic isolation difficult to accept without further proof (Castro et al., 1998). Larvae of *N. norvegicus* are scarce in plankton reports. They are uneasily found in the Mediterranean, making any attempt to trace their dispersal through geographical and bathymetric sampling, very difficult. Larvae are subjected to a wide array of oceanographic dynamics (White et al., 1988; Hill and White, 1990) whose origin and development through time and space are mostly unknown. More scientific effort is needed to assess distances of larval dispersal and their bathymetry of distribution, in relation with hydrography. Additionally, since larval survival is strictly linked to the available nourishment (Rotllant et al., 2001), studies on dispersal in relation to nutrients are needed as well as those on predator avoidance. These data are essential to discriminate a metapopulation structure from a more continuous one. Fishing policy should discriminate patches based on the demography and migration rates of populations inhabiting those patches. Large shelf-sustained populations, acting as steady reservoirs for neighbouring satellite populations, should carefully be exploited for fishing purposes, since their disappearance could determine a collapse of an entire local network.

A modest migration rate among small subpopulations favours the occurrence of phenotypic plasticity (Kingsolver et al., 2002). Up to date, the results of the biometric and genetic studies are not indicative of any clear geographical pattern of the populations studied. Further results could be drawn by the direct analysis of DNA sequences, since electrophoresis of proteins could not be sensitive enough to detect small variation at the DNA level. Nuclear and mitochondrial DNA analyses should also be undertaken to estimate the effective population size (N_e) of *N. norvegicus* stocks (V. Sbordoni, pers. comm.).

Behavioural studies focusing on *N. norvegicus* chemical communication are also needed. If the absence of genetic differentiation among patches is confirmed, a high rate of larval dispersal over large geographic areas should be assumed. This species does not rely on the production of higher number of larvae and eggs are incubated carefully for several months (Sardà, 1995). Settling should not occur at random, especially by considering that *N. norvegicus* survives only on suitable bottom substrates. How larvae can make their way from one patch to another remains unknown. A possible chemical intraspecific communication may occur among adults and larvae. This intraspecific chemical communication may also be responsible of a lowering in the aggressive territorial behaviour taking place during the mating season, when soft-shell males and females approach for reproductive purposes on bottom surface, after moulting (Farmer, 1974c). At this time, stage IV larvae could successfully settle, possibly occupying adults burrows at the beginning, because of a general reduction in territorial aggressive behaviour occurring at that time.

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