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A PHYSICAL RETENTION MECHANISM FOR *NEPHROPS NORVEGICUS* LARVAE

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ABSTRACT

The fecundity of the Norway Lobster (*Nephrops norvegicus*) is comparatively modest, females producing 500 - 3,000 eggs, in comparison to other crustaceans, for example the edible crab (*Cancer pagurus*) 0.5 - 3.0 million and the lobster (*Homarus gammarus*) 1,000 - 30,000. With low fecundity, a reproductive strategy that minimises larval losses whilst in the planktonic stage would favour survival.

The geographically isolated mud patch of the western Irish Sea supports a commercially important *Nephrops* fishery (mean catch 8,136 tonnes 1990 - 1994). In spring and summer (the surface heating season) there exists a cyclonic near-surface gyre, centred on the mud patch, that circulates around a static dome of cold dense bottom water which remains beneath the thermocline from the previous winter. Release of the newly hatched larvae to the water column in spring coincides with the formation of the gyre. Recruitment depends on settlement of metamorphosed larvae onto the mud patch. Larvae distributions show a strong correspondence to the pattern of the gyre and it is probable that this is a retention mechanism maintaining the population on the mud patch.

On the European continental shelf, there are indications of seasonal gyres at seven other locations above mud patches supporting a *Nephrops* population. If gyre circulations effectively isolate a population there are important implications for stock management. In addition, a particular population may be at serious risk in the event of spring or summer contaminant spills.

Keywords: Hydrography, Seasonal stratification, Tidal stirring, Gyre circulations, *Nephrops*, Larval retention, Irish Sea, Stock management.

INTRODUCTION.

The distribution of Norway lobster (*Nephrops norvegicus*) populations corresponds to the location of suitable areas of muddy substrate in which adults construct a complex system of burrows (Farmer, 1974; Chapman, 1980). Eggs are spawned in late summer/early autumn and carried under the female abdomen until the following spring. Upon hatching, larvae are released to spend approximately 50 days in the plankton (Nichols *et al.*, 1987; Thompson and Ayers, 1989). Here, larvae metamorphose through three pelagic stages before the first post-larval stage settles to muddy substrate in order to construct or occupy burrows.

Since juveniles require the same substrate as adults and are thought to be non-migratory, planktonic larvae advected to settle on unfavourable substrate are lost to the population. Often suitable areas are sufficiently isolated, that there is little likelihood of larvae transported from one area colonising another. The fecundity of *Nephrops* is comparatively modest (Nichols *et al.*, 1987; Nichols and Thompson, 1988), females producing 500 - 3,000 eggs, in comparison to other crustaceans, for example the edible crab (*Cancer pagurus*) 0.5 - 3.0 million and the lobster (*Homarus gammarus*) 1,000 - 30,000 (Bennett and Howard, 1987). Given low fecundity, a reproductive strategy that minimises larval losses whilst in the planktonic stage would favour survival.

In this paper we consider the western Irish Sea, where the geographically isolated mud patch supports a commercially important *Nephrops* fishery. The mean catch of 8,136 tonnes for 1990 - 1994 was worth approximately £15 million per annum at first sale. Here, there is evidence that the prevailing hydrographic conditions act to limit dispersion of larvae from the area. There are indications that other *Nephrops* populations may have similar controls. A physical mechanism acting to contain larvae has a number of significant implications for stock management. Also, in the event of a spill, contaminants will be contained within such a region, exacerbating potential risk to the stock. In addition, for the purposes of setting Total Allowable Catches (TACs) it has been convenient to group a number of populations, or Functional Units (FUs), within the much larger ICES Sub-area boundaries. Inherent within this approach is the danger that one population may suffer a disproportionate fishing effort that exceeds sustainable levels, a concern highlighted by the ICES Working Group on *Nephrops* Stocks (Anon., 1990; Anon., 1994; Anon., 1995).

THE WESTERN IRISH SEA.

The western Irish Sea (Fig. 1) is taken to be bounded in latitude by 53° 20'N to 54° 40'N and longitude 4° 40'W west to the Irish coast. A deep trough (>100 m) extends along the length of the region from about 53° 30'N into the North Channel. In the Irish Sea, the tide has the form of a standing wave with its velocity node located in the western Irish Sea. For this reason tidal currents are exceptionally weak (< 0.30 m s^{-1}) compared to the rest of the Irish Sea. The combination of deep water and weak tides means that the western Irish Sea stratifies during the spring and summer heating cycle when there is insufficient tidally-generated turbulent energy to maintain mixing against the input of surface buoyancy (Simpson and Hunter, 1974). A further consequence of low tidal energy is that the region is a depositional environment over which an extensive isolated mud patch has formed. Fresh water discharge from the eastern Irish coast is maximal in November - January and minimal in June - September, which may result in the formation of a band of low salinity coastal water in the shallow (<50 m) region along the Irish coast during winter and spring. In general, however, salinity variations make only a minor contribution to the density field in the central western Irish Sea. Infrared satellite imagery (Simpson and Bowers, 1981) and a considerable body of historical data (e.g. Slinn, 1974; Lavin-Peregrina, 1984) demonstrate the pattern of summer stratification to be essentially consistent from year to year.

OBSERVATIONS.

During 13 June to 3 July 1994 a comprehensive hydrographic survey of the region was undertaken from the *RV Corystes*. Measurements of the temperature and salinity fields were made with a FSI CTD mounted in a SCANFISH towed, undulating vehicle. The 'V' shaped profiles effectively provided CTD stations at intervals of approximately 200 - 500 m, principally dependent on depth. Contemporaneous measurements of the velocity field were made with a RD Instruments 153.6 k Hz broad band acoustic Doppler current profiler (ADCP), set to record with a resolution in the vertical of 2 m (bin size) and horizontal of approximately 300 m (1 minute averages). Additionally, the Lagrangian flow field has been measured with free-floating, satellite-tracked drogued buoys.

Nephrops larvae surveys were undertaken in 1982, 1984 and 1985 for stock assessment purposes (Nichols *et al.*, 1987; Nichols and Thompson, 1988). Samples were obtained using double oblique hauls with a Lowestoft high speed sampler fitted with a 270 μm aperture mesh net and a 40 cm diameter aperture nose cone. Less intensive surveys were undertaken in 1987, 1988 and 1989. In addition, Hillis (1974) reports the results of intensive surveys made during 1969 - 1971.

THE WESTERN IRISH SEA GYRE.

The existence of a gyre was first revealed when 9 drifters, drogued at 15 m with 30 m^2 'window blinds', deployed during 11-20 July 1990 (Hill *et al.*, 1994a) described a cyclonic (anti-clockwise) circulation (Fig. 2a). Two further drifters, with Holey-sock drogues 1.5 m diameter and 7 m high and centred at 15 m, were deployed from 15 July - 15 August 1993 at locations thought to be on the southern and northern flowing arms of the gyre (Fig. 2b). Buoy 20762 drifted for 41 days and 20763 for 39 days. Initially, both buoys moved as expected, but 20763 left the region moving north into the North Channel. However, buoy 20762 demonstrated clear evidence of a cyclonic circulation for 14 days prior to leaving the gyre to the east.

Deployments in June/July 1994, again with Holey-sock drogues but centred at 23 m, revealed the full extent of the gyre circulation (Fig. 2c). The trajectory of longest duration (06374; 24 days) was remarkably similar to that of 20762 the previous year, particularly in the southern extent of the gyre. It also provided evidence of a return flow at the northern end. Buoy 20762, this time laid at the centre of the gyre, showed virtually no advection during the 16 days of deployment confirming the gyre centre as a stagnation point. The contemporaneous distribution of potential energy anomaly, ϕ, a measure of stratification defined by Simpson (1981), is derived from a detailed SCANFISH grid and presented in Figure 3. There is a marked correspondence between the drifter tracks and contours of ϕ.

A SCANFISH section (Fig. 4a) along approximately 53° 40'N clearly shows the dome of dense bottom water about which the drifters circulate. The coincident ADCP data (Fig. 4b) dramatically illustrates the circulation associated with this density field. To obtain this detided data, the appropriate depth averaged values of the dominant M_2 and S_2 tidal components and the tidal residual were first derived from a 3-D tidal model (Davies and Lawrence, 1994) with a grid resolution of order 3 km. These values were subtracted from the one minute averages of velocity in each ADCP bin. Along this line the direction of flow is essentially normal to the section. To the west (22 - 27 km) is an intense narrow southward flowing jet, the core of which is centred at approximately 35 m and has a velocity in excess of 25 cm s^{-1} (consistent with maximum drifter translation velocities). To the east (42 - 48 km) is a comparable northward jet centred at approximately 30 m.

A series of twelve transects demonstrated this picture of the density structure and non tidal residual flow to be essentially consistent across the entire region. Hill (1993) has given an account of the driving mechanism for the gyre. During spring and summer, in the western Irish Sea where tidal stirring is weak, surface heating stratifies the water column whilst the surrounding waters, which are either shallower or the tidal stirring is stronger, or both, remain mixed (Simpson and Hunter, 1974). Eventually, a body of cold (dense) water becomes trapped beneath the thermocline (Fig. 4a), being warmed only very gradually by diffusion of heat across the thermocline. Horizontal bottom fronts separate this relict winter water from the surrounding mixed waters. It is these bottom fronts which drive a baroclinic cyclonic near-surface flow in accordance with the thermal-wind balance. Indeed, the location of the continuous jet coincides with the maximum gradient in ϕ, the distribution in Figure 3 being analogous to a 'circulation map'. It can be seen (Fig. 3) that contained within the region there are two separate cells of stratification, about which drifters have a tendency to circulate (Fig. 2), although with considerable exchange.

Interaction with wind driven events remains to be fully explored. During the drifter deployments of 1993 and 1994 there were significant wind events, yet the gyre circulation remained clearly visible. Hydrographic data indicates that once formed the structure is remarkably robust until the end of summer.

Nephrops AND THE HYDROGRAPHY.

Whilst individual larvae spend approximately 50 days in the plankton, hatching begins in late March and the last of the Stage III larvae can be found toward the end of July (Nichols *et al.*, 1987). Hillis (1974) and Nichols and Thompson (1988) have reported larvae to be concentrated in the upper 35 - 40 m of the water column, consistent with the location in the vertical of the gyre circulation (Fig. 4b). Additionally, the horizontal distribution of larvae (Fig. 5) typically coincides strongly with the stratified region (Fig. 3), although in all surveys there is evidence of a southward displacement of larvae. The observations suggest a system that favours larval retention. Those at the centre experiencing little advection, whilst within the more dynamic cyclonic circulation horizontal movement will be significant, but essentially over the mud patch.

Clearly, a significant retention of larvae above the mud patch is essential for the survival of the population and the gyre would appear to provide this mechanism. *Nephrops* fecundity is comparatively low and the ovigerous females retain their eggs for up to 9 months whilst remaining confined to their burrows. This implied energy investment in offspring would apparently strongly favour a reproductive strategy which minimises larval losses.

The hypothesis that the gyre acts as a *Nephrops* retention mechanism is not without difficulties, however. Hatching commences in late March and Stage I abundance peaks in early May during the initial phase of the heating and stratification cycle when the gyre and associated retentive mechanism are comparatively weak. However, by the peak of Stage II abundance in late June stratification is well developed. The pre-gyre circulation of the region remains poorly characterised. Relatively short term and random wind driven flows undoubtedly have a significant dispersive role. Observations of larval distributions suggest some southward advection and subsequent loss from the population (White *et al.*, 1988), at least in spring. In early spring, before establishment of thermal stratification, riverine input along the shallow Irish coast may form a southward flowing, buoyancy driven coastal current. White *et al.* (1988) argued that in early spring a significant proportion of larvae might be lost by southward advection, a process which would be switched off later in spring as fresh water run off reduces and thermal stratification develops. Additionally, we now recognise the gyre as a mechanism to 'switch off' such losses.

Other questions remain to be resolved (Hill *et al.*, 1995). Central among these is why does the hatching season not begin later enabling most Stage I larvae to be entrained within the gyre circulation, thereby maximising retention? Perhaps high retention is not crucial to the life-cycle and possible advective losses in early spring are not significant. On the other hand, the mud-patch and present circulation regime only dates from the end of the last ice-age 10,000 years ago. The time is short in evolutionary terms and it may be that the *Nephrops* population has not yet become optimally adapted to the environment. A further possibility is that some losses by dispersal (e.g. early hatching) to other sites are advantageous in the survival of the gene pool. Additionally, release from mid April to mid May coincides with the onset of stratification and the necessary conditions for the subsequent initiation of the spring bloom (Gowen *et al.*, 1995), which in turn furnishes an abundant supply of food.

As yet we are unsure as to the detailed way in which the gyre acts as a retention mechanism. It may simply keep larvae circulating above the mud-patch or there may be associated transverse circulations which actively bring about convergence to the centre of the gyre. Such secondary circulations would be very small, of the order 1 cm s^{-1}, and therefore difficult to measure.

DISCUSSION.

The ICES Working Group on *Nephrops* Stocks (Anon., 1984) identified individual populations, or Functional Units (FUs), for assessment purposes. At that time, identification was based on criteria ranging from evidence of geographical isolation to spatial distribution of fishing fleets and effort. Since then, there have been comparatively minor modifications and within the region encompassed by ICES areas IIIa, IV, VI, VII and VIIIa, there are 21 FUs defined (Fig. 6), each representing what are increasingly regarded as separate self sustaining populations (Anon., 1995). The hypothesis that hydrography acts as a retention mechanism aiding recruitment reinforces the Working Group approach. There is evidence for similar cyclonic circulations about a static mass of dense water at nine of the FUs in addition to the western Irish Sea (FU 15).

Work by Danielssen *et al.* (1991), including CTD, Lagrangian and Eulerian current measurements, chemical and biological sampling, clearly demonstrated the existence of cyclonic baroclinic gyres during May and June 1990 in the region of FUs 3 and 4. Le Fèvre (1986) described a dome like density structure at the centre of FU 23, generated as a consequence of seasonal stratification in an area of weak tidal stirring bounded by stronger vertical mixing, but on a gently shelving slope. There are indications (Hill *et al.*, 1994b) that a further system exists over the topographical depression comprising the Outer Silver Pit and Botney Gut (FU 5). A density-advecting numerical model (James, 1989) clearly indicates a density driven cyclonic circulation about the margins.

A cyclonic circulation, although not closed, exists on a much larger scale (> 100 km) over the Fladen Ground (FU 7) (Turrell, 1992; Svendsen *et al.*, 1991; Bailey *et al.*, 1995). At the centre of the system lies a bottom well mixed mass of cold water overlain by a seasonal thermocline and bounded to the west, south and east by shallowing topography. In part, this is probably set-up and maintained by the Dooley Current system which is topographically steered about the depression (Turrell *et al.*, 1992). A further system probably exists about the Celtic Deep (FUs 20 - 22), bounded to the east and north by seasonal thermal fronts (Simpson, 1976). Finally, Hill (pers. comm.) has recently observed a spring cyclonic circulation at the southern entrance to the Minch (FU 12), again about a dome of dense water, but in this instance salinity differentials provide the principle forcing mechanism.

It is of course expected that regions of low tidal energy associated with topographic depressions will promote mud-patches and possibly cyclonic circulation. It could be supposed that the link between gyre circulations and *Nephrops* larvae is illusory. After all, there are 11 other FUs in this area unaccounted for. Interestingly, the majority are in regions of density contrast where significant baroclinic transports are to be expected. On a more localised scale, within areas of mud it has been observed that variations in density and size composition of *Nephrops* appear to correlate with local variations in sediment characteristics (Bailey *et al.*, 1995). These may in part be related to the details of the local hydrography.

If the majority of populations are effectively isolated, they deserve management in their own right, rather than as part of an aggregate management unit chosen for administrative reasons. For example, ICES Area IV (North Sea) encompasses six FUs, whilst Area VII contains nine FUs. It is not difficult to envisage a situation where one population suffers a disproportionate fishing effort, placing the stock in danger of over exploitation. For instance, the two isolated Irish Sea stocks (FUs 14 and 15) are considered to be fully exploited and could readily be separated from the rest of Area VII (FUs 16 - 22). The difficulty of TAC management at individual FU level was recognised by the *Nephrops* Working Group (Anon., 1990), and Management Area (MA) groupings of FUs were defined on the basis of adjacent stocks showing similar states of exploitation and requiring similar management action. Even this approach must proceed with caution.

The retentive properties of gyre circulations and isolation of populations implies that in the event of a dramatic reduction in numbers, whether through disease, contaminant spillage and subsequent prolonged exposure or fishing pressure, natural replenishment from other stocks is unlikely and time scales for recovery may be long. On a positive note, the probability of disease spreading between populations is reduced.

ACKNOWLEDGEMENTS.

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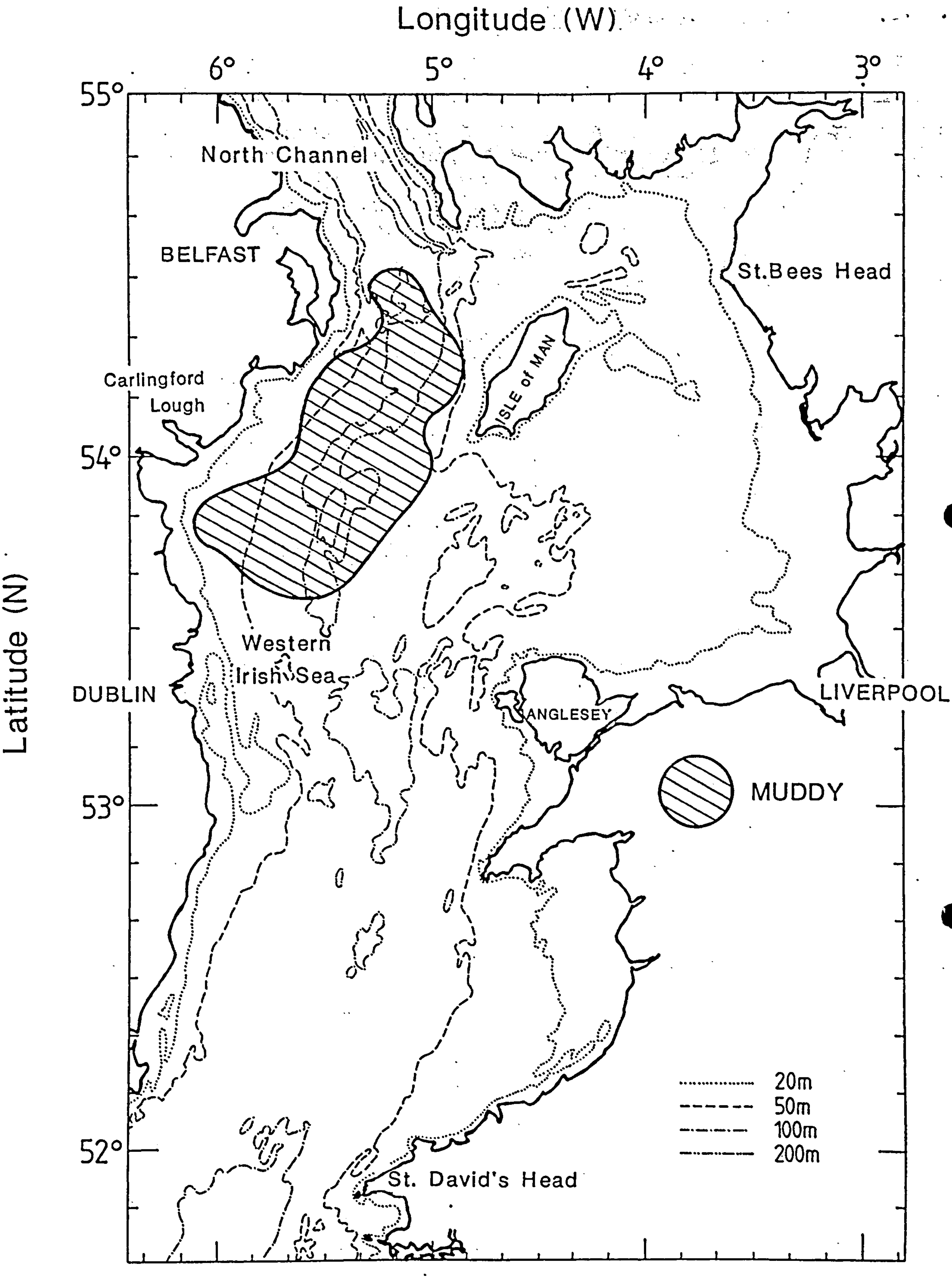


Figure 1. The Irish Sea, showing the location of the mud patch which adult *Nephrops* inhabit.

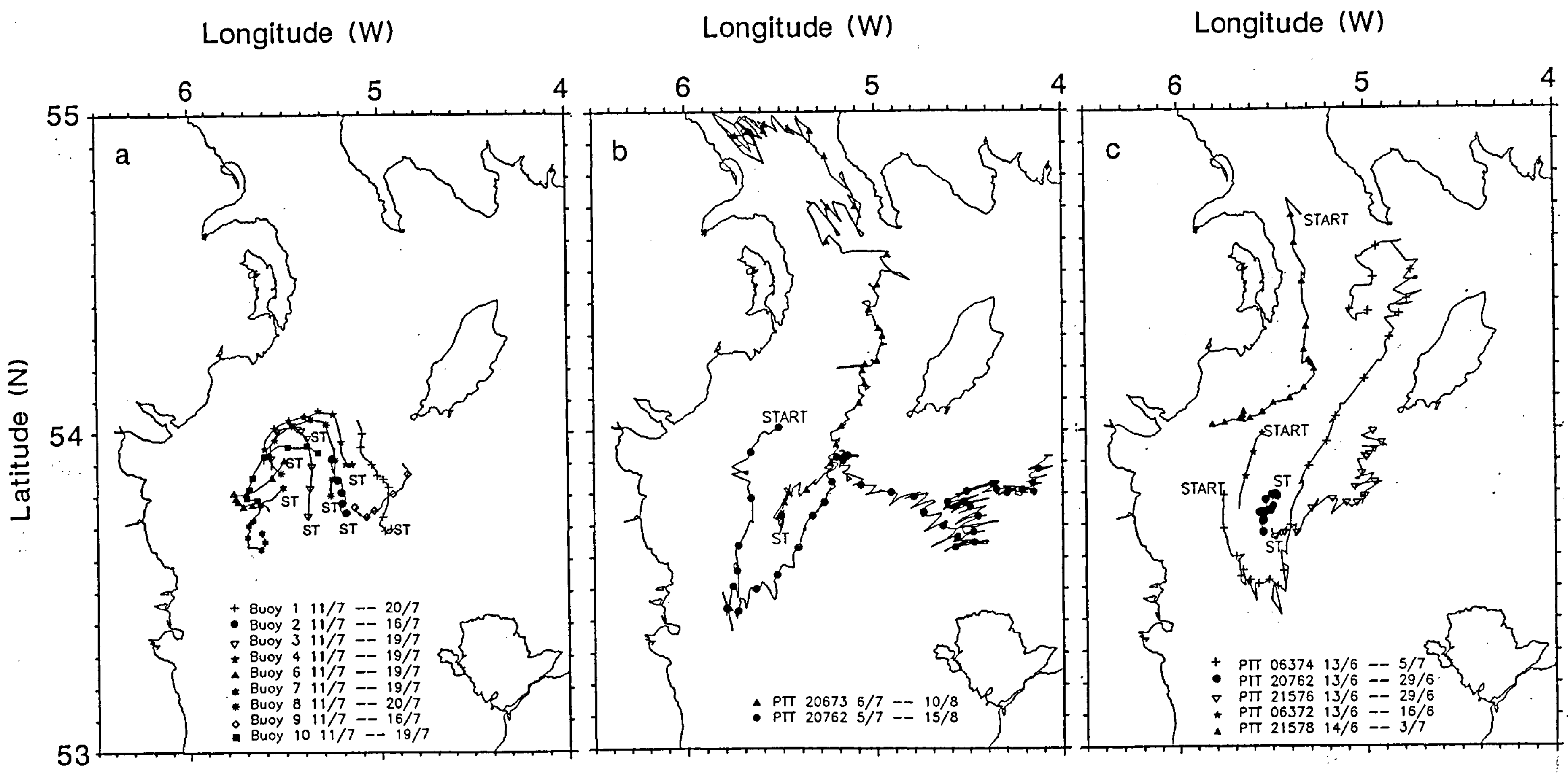


Figure 2. Trajectories of ARGOS drifters deployed in the western Irish Sea. (a) 11 - 20 July 1990; 'window blind' drogues centred at 15 m. (b) 5 July - 14 August 1993; 7 m long and 1.5 m diameter Holey sock drogues centred at 15 m. (c) 13 June - 7 July 1994; 7 m long and 1.5 m diameter Holey sock drogues centred at 23 m. Symbols indicate daily intervals.

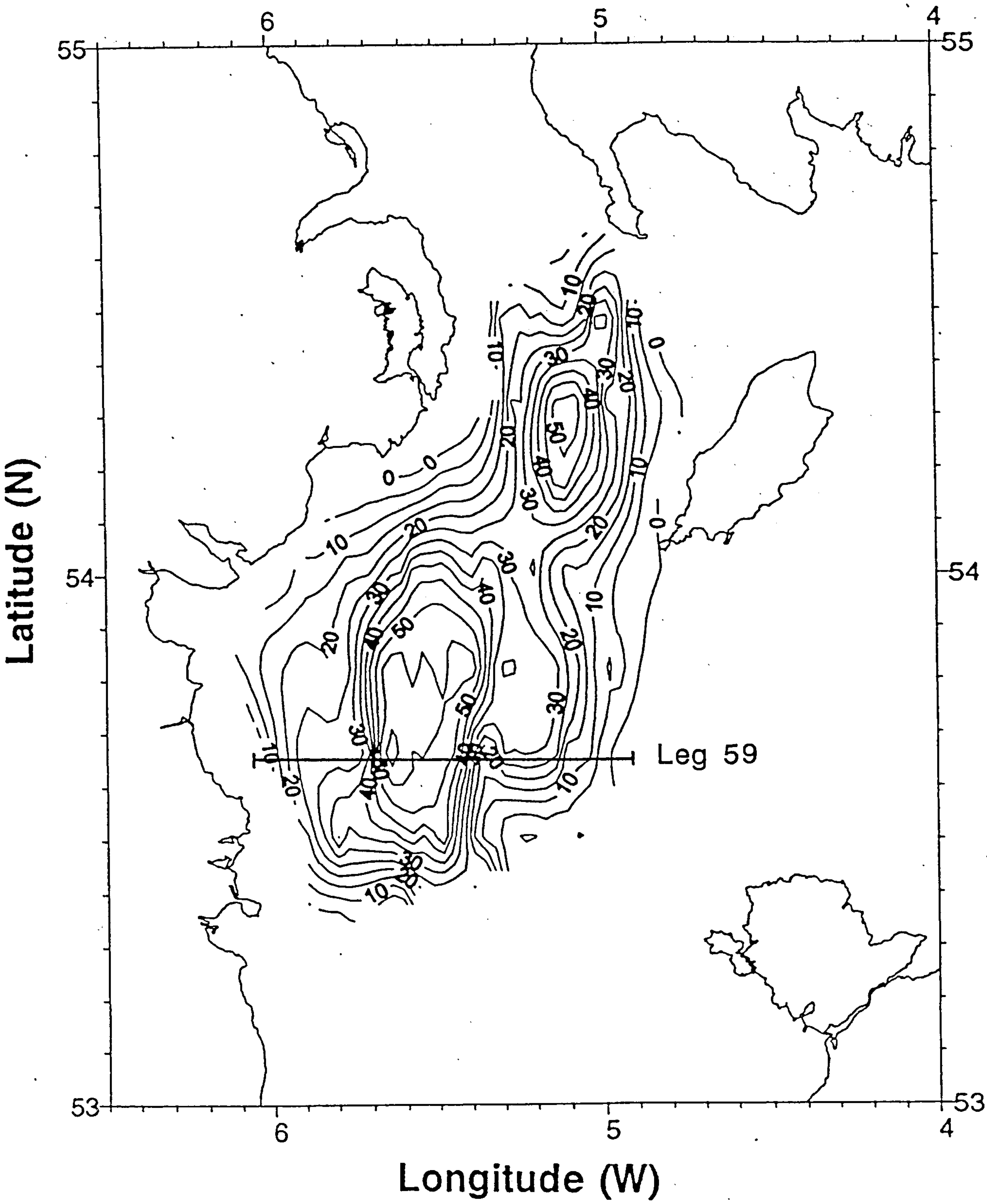
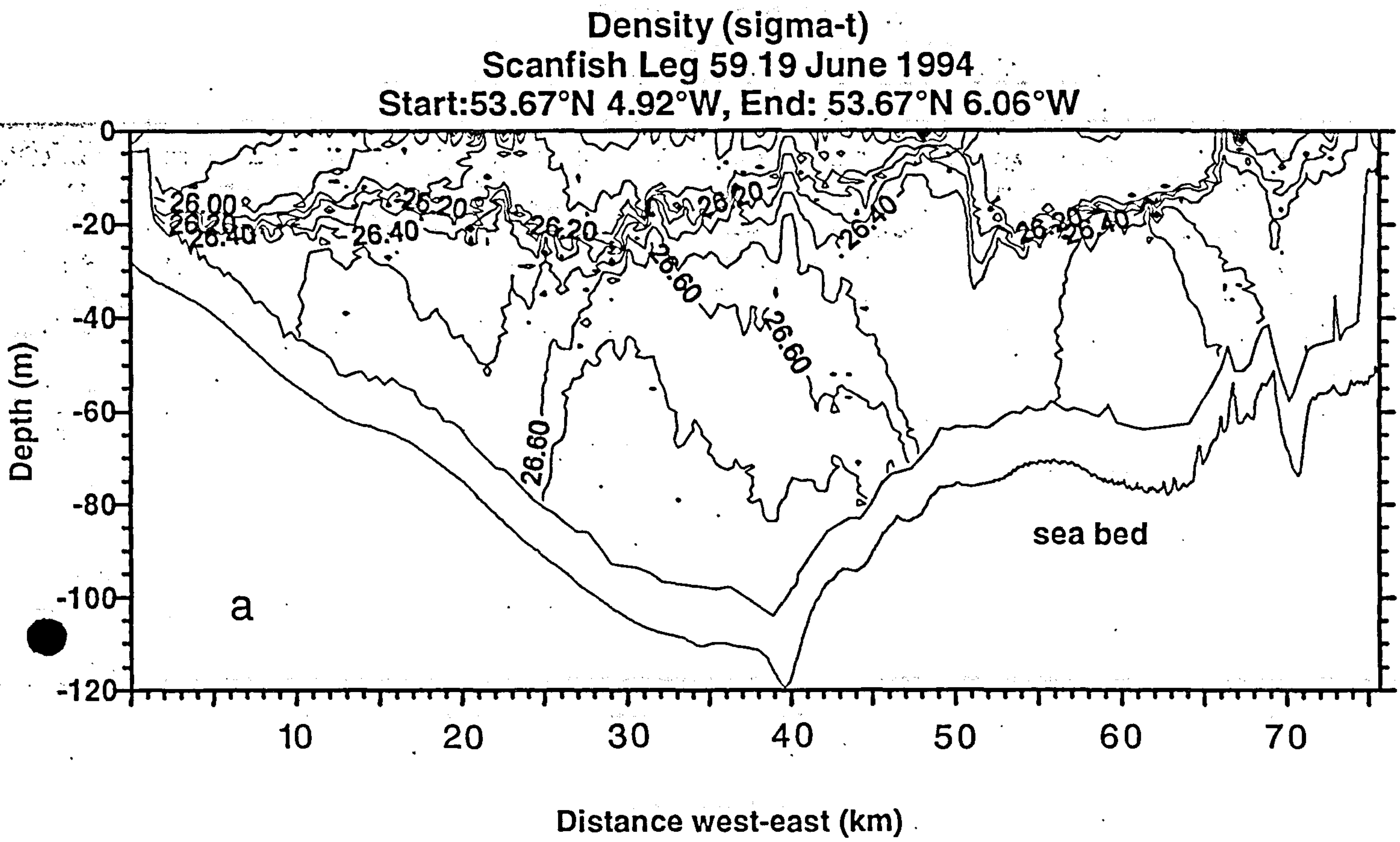


Figure 3. Stratification (potential energy anomaly, ϕ J m^{-3}), derived from a SCANFISH survey of the western Irish Sea 18 - 22 June 1994. Note the two centres of strong stratification. Leg 59 denotes the location of the sections in Figure 4.



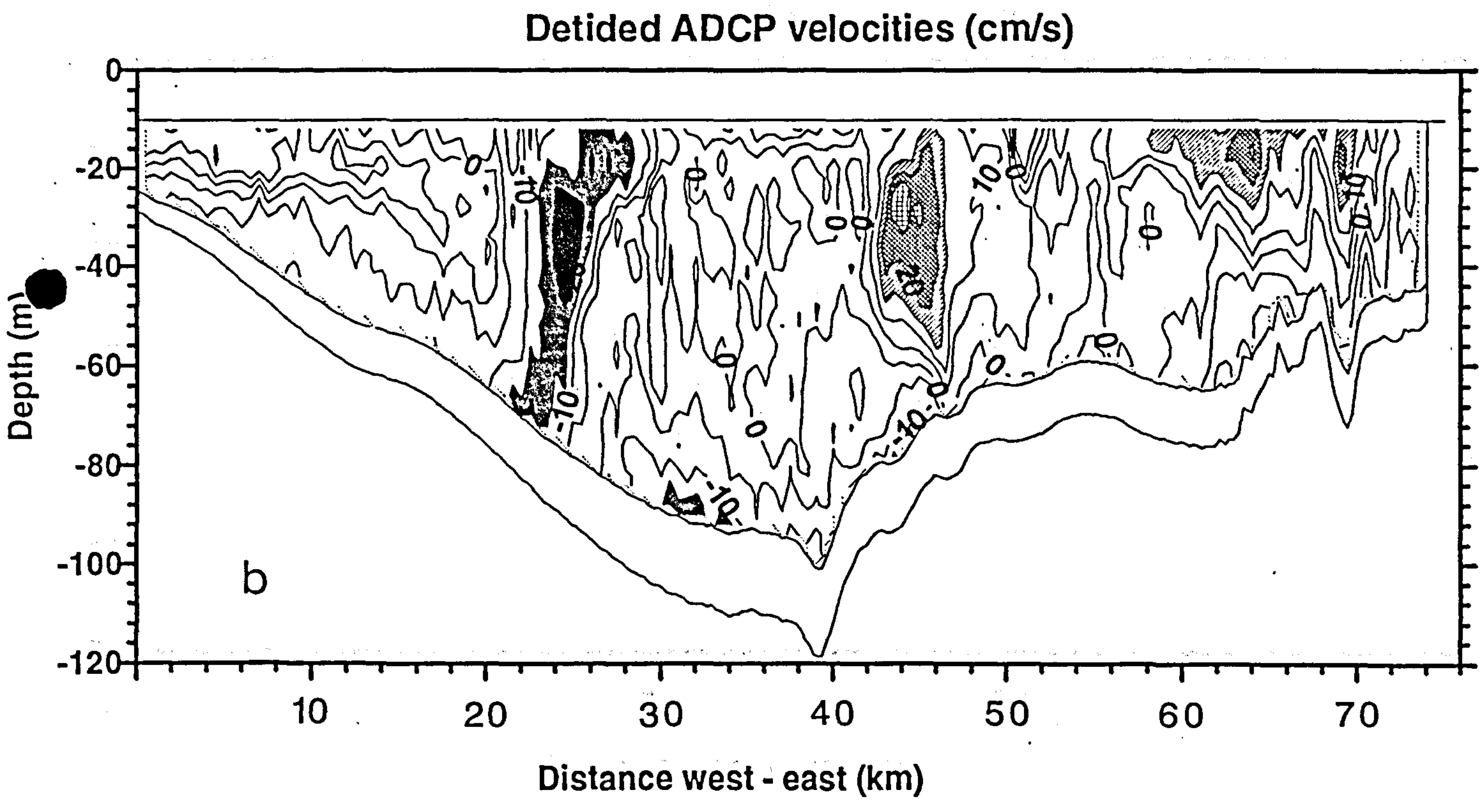


Figure 4. West - east section of the Irish Sea at latitude 53° 40′N (see Fig. 3 for location). (a) SCANFISH section of density (σ_t) illustrating the pycnocline at approximately 20 m and the dome of dense water formed over the deep central basin. (b) Detided ADCP velocities (north/south components). Note the strong southward jet on the west (22 - 27 km) associated with the dome and comparable northward flow on the east (42 - 48 km).

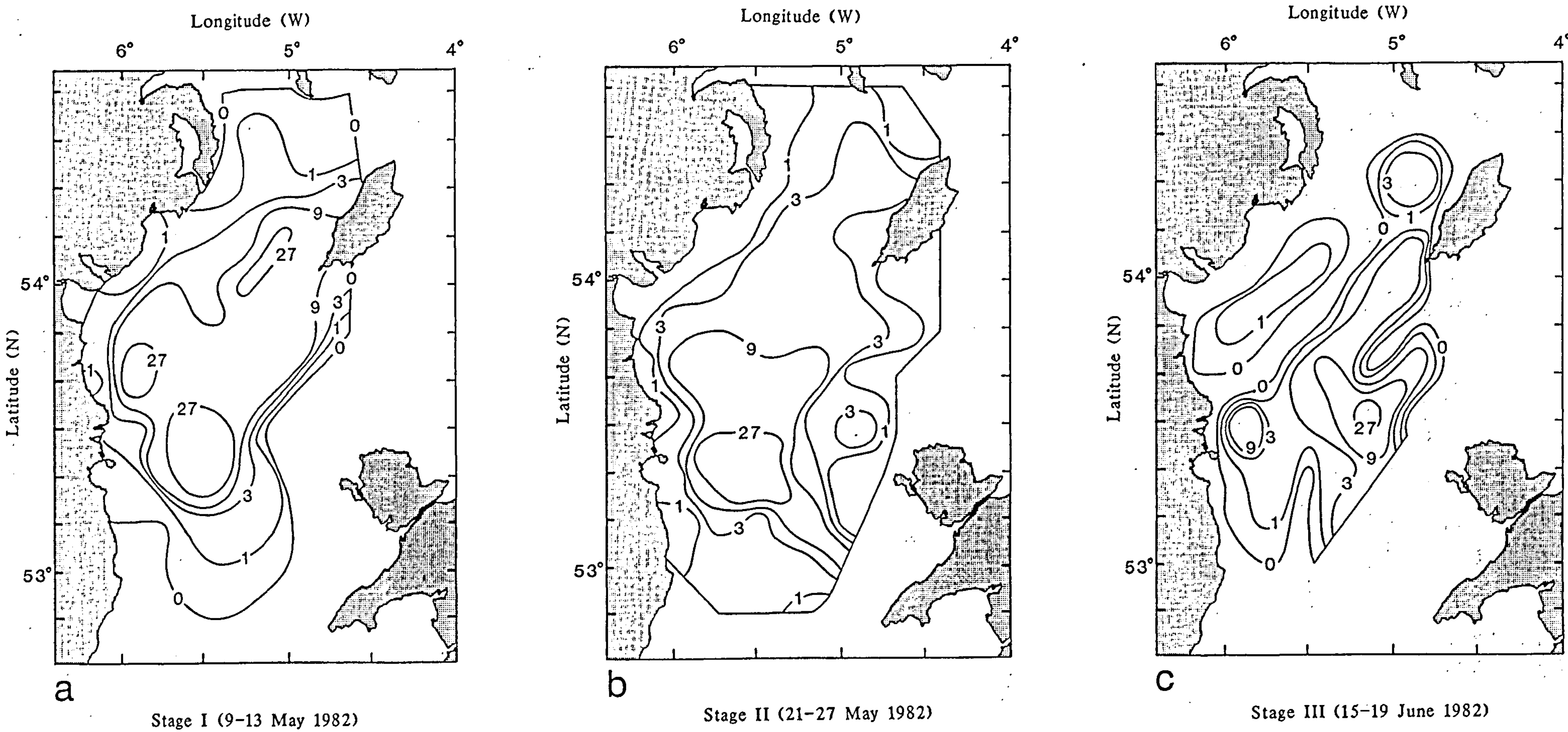


Figure 5. *Nephrops* larvae distributions as numbers (vertically integrated m^{-2}).

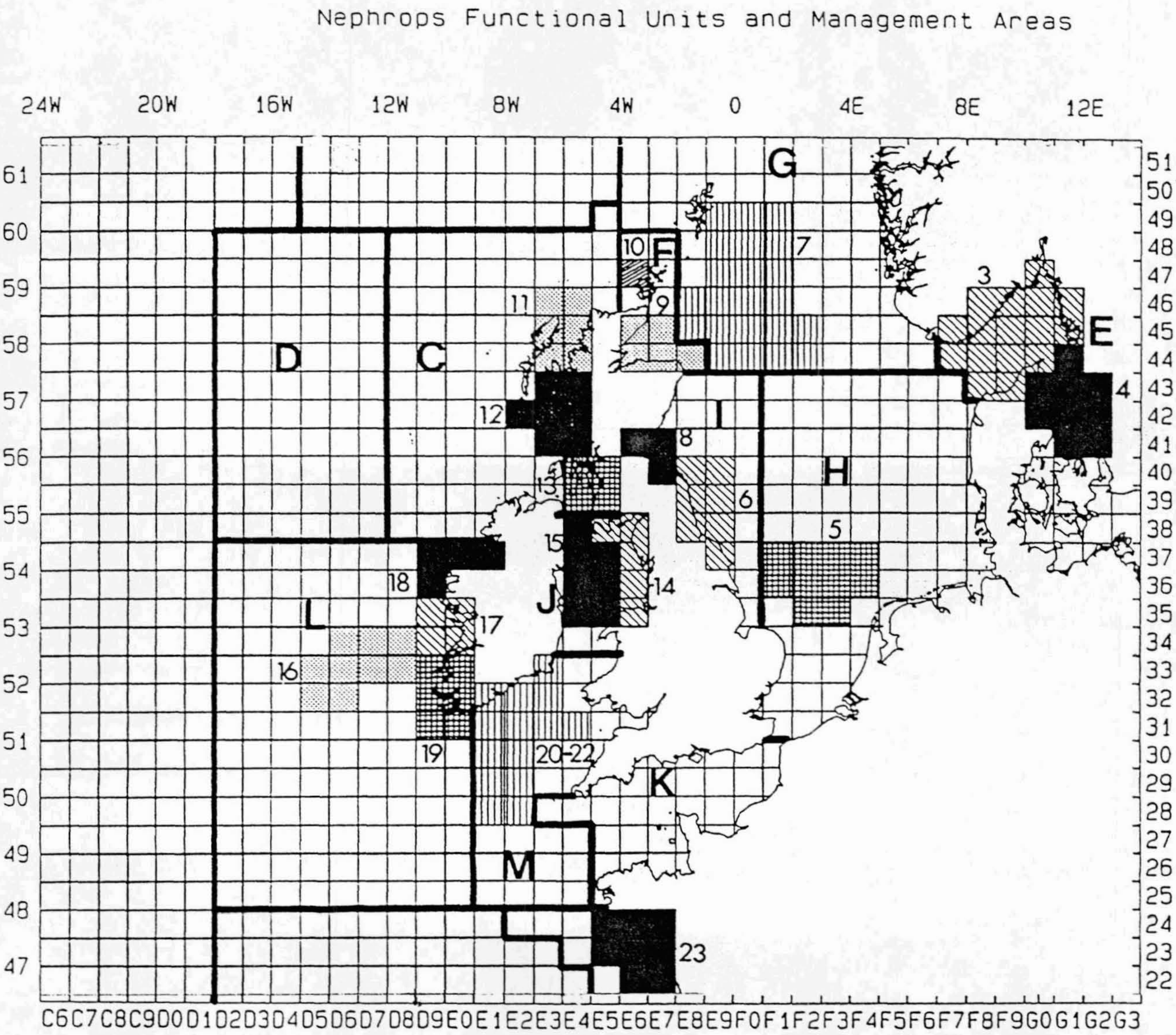


Figure 6. Functional Units (FUs; 3 - 23) and Management Areas (MAs; C - M) as defined by the ICES Working Group on *Nephrops* Stocks (Anon., 1995). FU 23 is part of MA N containing a further FU (24).