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VLIZ (vzw)
VLAAMS INSTITUUT VOOR DE ZEE
FLANDERS MARINE INSTITUTE
Oostende - Belgium

Distribution of *Nephrops norvegicus* (L.) larvae in the western Irish Sea: an example of advective control on recruitment

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R.G.White, A.E.Hill and D.A.Jones

School of Ocean Sciences, Marine Science Laboratories, Menai Bridge, Gwynedd LL59 5EY, UK

Abstract. Results of a survey of *Nephrops norvegicus* larvae conducted in the western Irish Sea during May 1984 are discussed. The larval distributions show a pronounced tongue of high numbers extending southward from the muddy area where they are hatched. The inferred density-driven circulation at the time of the survey is consistent with the southward transport of larvae. Because *N.norvegicus* requires a muddy substrate for successful larval settlement, the processes which influence the circulation may provide an important control on the level of recruitment.

Introduction

Nephrops norvegicus (commonly known as the Dublin Bay prawn or Norway lobster) is a marine benthic decapod and is one of the important, commercially fished, demersal species within the Irish Sea. The distribution of adults is tightly controlled by their requirement for a muddy substrate in which to construct burrows (Farmer, 1975). The distribution of their planktonic larval stages, on the other hand, is more likely to be determined by the oceanographic controls on the pelagic environment.

In this paper observations are presented of the larval distributions of *N.norvegicus* in the western Irish Sea in May 1984 which indicate that, during this period, larvae were advected a considerable distance southward of the muddy region suitable for juvenile recruitment. There is some evidence that this was not an isolated occurrence of the phenomenon, and some of its general implications for the *Nephrops* fishery are discussed.

Biology and ecology of the larvae

The distribution of adult *Nephrops* is confined to regions of muddy substrate where burrows can be constructed (Farmer, 1972). There are two such muddy areas within the Irish Sea, a small region off the Cumbrian coast of northwest England and a much larger area in the western Irish Sea, both of which are shown in Figure 1. The nature of the mud region in the western Irish Sea has been described by Banner *et al.* (1979). The location of mud in this area is probably related to the low energy tidal regime of the western Irish Sea which prevents scouring of the sea floor in a similar manner to that discussed by Pingree and Maddock (1977). Stock biomass estimates of adult *Nephrops* have hitherto been rather difficult to obtain. Nevertheless, the known location of commercial fishing activity for *Nephrops* (O'Riordan, 1964) may be used to infer the adult distribution. The fishing grounds for *Nephrops* are superimposed on Figure 1 and show that the adult population is indeed closely confined to the muddy region of sea floor in the western Irish Sea.

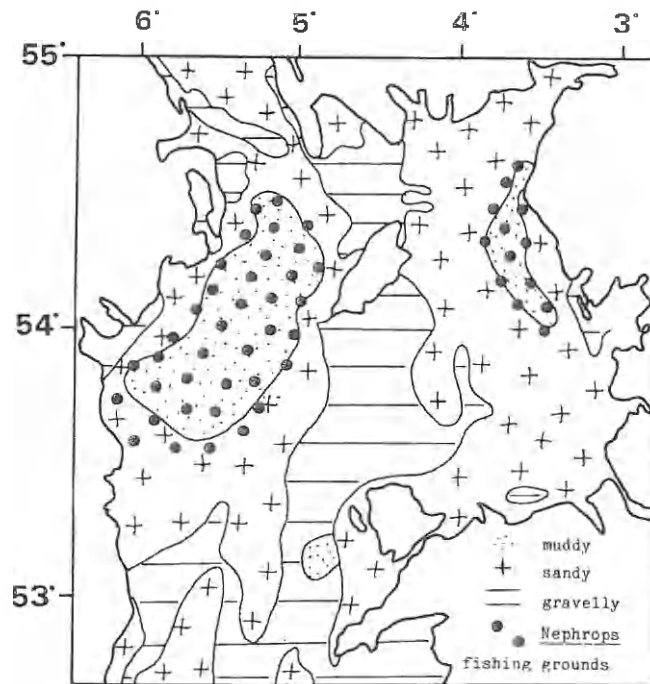


Fig. 1. Simplified distribution of surficial sediment types in the northern Irish Sea, based on the British Geological Survey 1:250000 series. Superimposed are the *N. norvegicus* fishing grounds in the Irish Sea.

Accounts of the reproductive cycle of *N. norvegicus* have been given by Farmer (1974). Generally, the adult female moults during spring and mating takes place whilst the exoskeleton is still soft. During the summer, eggs are laid and attached to the pleopods where they are incubated for 6–10 months. Whilst carrying the eggs, the ovigerous females are confined to their burrows. In the Irish Sea, the female *Nephrops* mature at 3 years and the males at an unknown age (Hillis, 1979).

Hatching takes place from March to July with a peak of larval occurrence in May (Thomas, 1964). The newly hatched larvae pass through three pelagic larval stages (I, II and III) before metamorphosing to the juvenile or post-larval stage (IV). The post-larval stage resembles the adult in most features and commences a benthic existence by settling on the sea bed (Figueiredo and Thomas, 1967; Farmer, 1975). Few reliable observations of development of larvae in relation to temperature have been made, but it is estimated that they spend ~60 days in the plankton (Nichols *et al.*, 1987).

Materials and methods

The economic importance of the *Nephrops* fishery has motivated attempts to estimate the spawning stock of the organisms from the production of the larvae.

Larval abundance surveys have been carried out by the Ministry of Agriculture, Fisheries and Food, Lowestoft, in the western Irish Sea and these have been reported by Nichols *et al.* (1987) and Thompson *et al.* (1986).

A *Nephrops* larval survey was conducted during a cruise of the research vessel 'Cirolana' from 25 to 27 May 1984. The larvae were sampled using a net of 270 μ m aperture with a multipurpose Lowestoft High Speed sampler (Milligan and Riches, 1983) combining a 76-cm-diameter MG82 tow-net with a 40-cm nose cone, based on the tow-net described by Beverton and Tungate (1967). Both internal and external flowmeters were attached to the sampler in order to assess its efficiency. The results of the calibrations of the sampler and flowmeters are given in Milligan and Riches (1983).

A CTD unit was attached to the sampler which continuously monitored (every 2 s) the conductivity ratio, temperature and depth. Temperature and salinity values were averaged into 1 m-depth bands and a corresponding value of density was computed using the international equation of state for sea water (UNESCO, 1981).

Planktonic larvae were collected using double-oblique hauls of the tow-net starting from the surface, sampling the total water column to within 3 m of the bottom, and then back to the surface. The net was usually towed at a speed of 4–5 knots for an average of 20 min. Data obtained from tow-net hauls are presented at nominal stations, the positions of which are determined as the mid-point of a surface–bottom–surface undulation; these positions have also been tidally corrected. Nominal station positions obtained by this procedure are superimposed on a bathymetric map of the region in Figure 2. Upon retrieval of the net, plankton samples were immediately fixed in a solution of 4% buffered formaldehyde and returned to the laboratory for sorting.

Nephrops larvae were picked out from the total plankton samples and separated according to the three zoeal stages and the post-larval stage (Williamson, 1983). Studies of the vertical distribution of the larvae (Hillis, 1974; Harding and Nichols, 1987) have indicated that they spend most of their planktonic life within the surface 60 m. The numbers in each stage per haul were thus converted to numbers per square metre of sea surface using calibrated flowmeter readings. An alternative, and essentially equivalent, approach would be to compute the numbers per cubic metre of sea water and correct these for depth to account for the concentration of larvae in the surface 60 m; the two methods produce similar distributions.

Results

The distributions of stage I, II and III *Nephrops* larvae observed in May 1984 are shown in Figure 3. The highest concentrations of each of the larval stages are found in an area close to the Irish coast, north-east of Dublin (~53°30'N and 05°40'W), which corresponds to the location of the adult population described previously. A zone of high numbers, however, extends southwards, for each of the larval stages, in a band overlying the deep channel of the central Irish Sea (see Figure 2 for bathymetry). As a result stage I larvae were found a

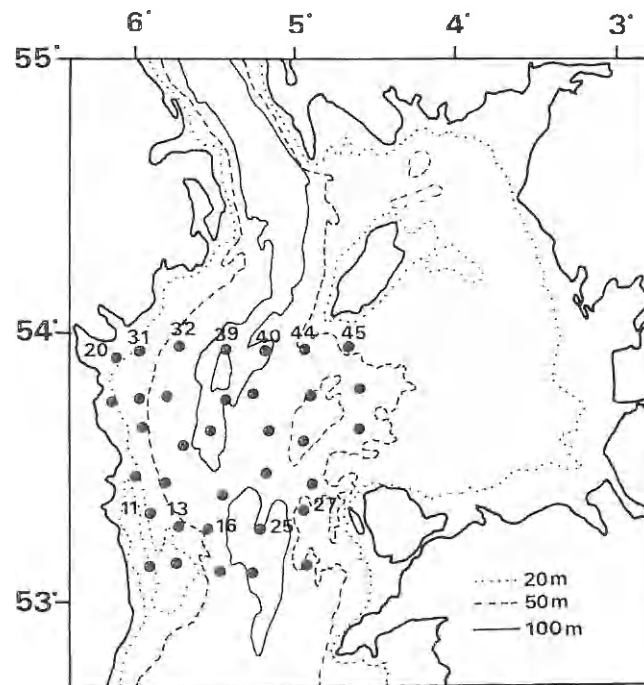


Fig. 2. Bathymetry of the northern Irish Sea showing the tidally corrected sampling positions.

considerable distance (40 km) south of the observed region to which the adult population is confined. High larval concentration probably extended further south than this although sampling was limited to north of 53°10'N. Stage III larvae appeared to be dispersed further southward than the earlier stages, suggesting that the extent of the southward excursion increased with age. Figure 3 also shows that areas of maximum larval population density tend to occur south of the centre of adult distribution.

In order to assess the possible mechanisms controlling the observed distribution of larvae, the corresponding temperature, salinity and density fields have been examined and are shown in Figure 4.

A core of high salinity water in the deep central channel of the Irish Sea separated lower salinity water close to the Welsh and Irish coasts. This general pattern of surface salinity in 1984 is consistent with previously published observations such as those described by Bowden (1950). Reduced salinity on the eastern side of the Irish Sea results from fresh water discharge into Liverpool Bay whilst that close to the Irish coast is caused by local fresh water discharge from rivers along the Irish east coast. The fresher water, close to the Irish coast, was also warmer during the observation period so that the combined temperature and salinity effects resulted in a low density water mass against the Irish coast. The accompanying vertical structure of the thermohaline field is

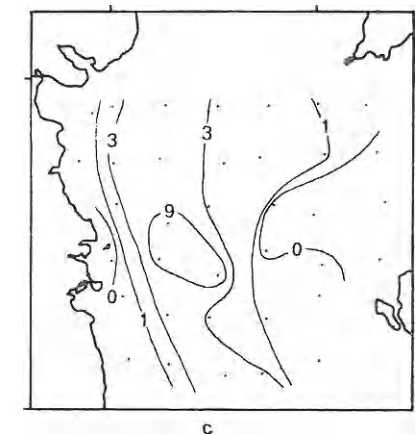
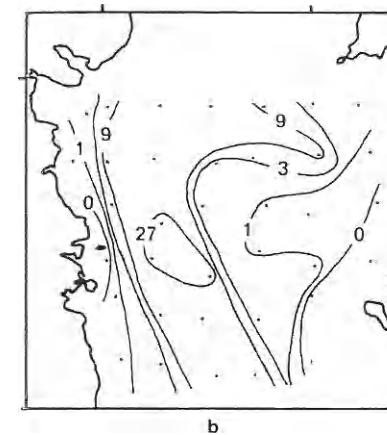
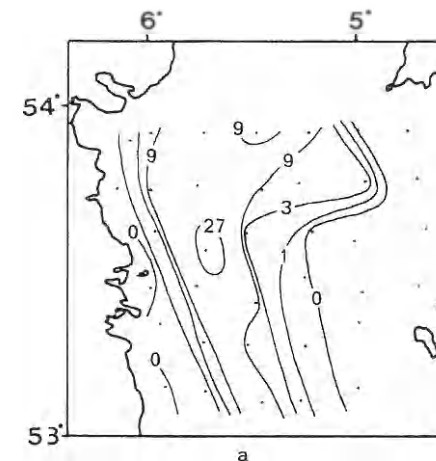


Fig. 3. Distribution of *Nephrops* zoea as numbers (m^{-2}) in the western Irish Sea in May 1984: (a) stage I *Nephrops* zoea; (b) stage II *Nephrops* zoea; (c) stage III *Nephrops* zoea. Each of these distributions shows a pronounced band of high larval numbers extending southwards.

illustrated in Figure 5. Figure 5a shows an approximately east-west section in the southern part of the survey area. Here temperature, salinity and density gradients were essentially horizontal with warm fresh water confined to within 20 km of the Irish coast (inshore of about station 16). There is little evidence of thermal stratification in this section and the density field is dominated by salinity. The physical structure on the northern section, however, is rather different as shown in Figure 5b. Here, again low salinity water was found close to the coast but the density field was determined primarily by temperature. Thermal stratification was well developed on the section with a seasonal thermocline established at a depth of 50 m.

The extent of the stratified region is shown in Figure 4d, which shows contours

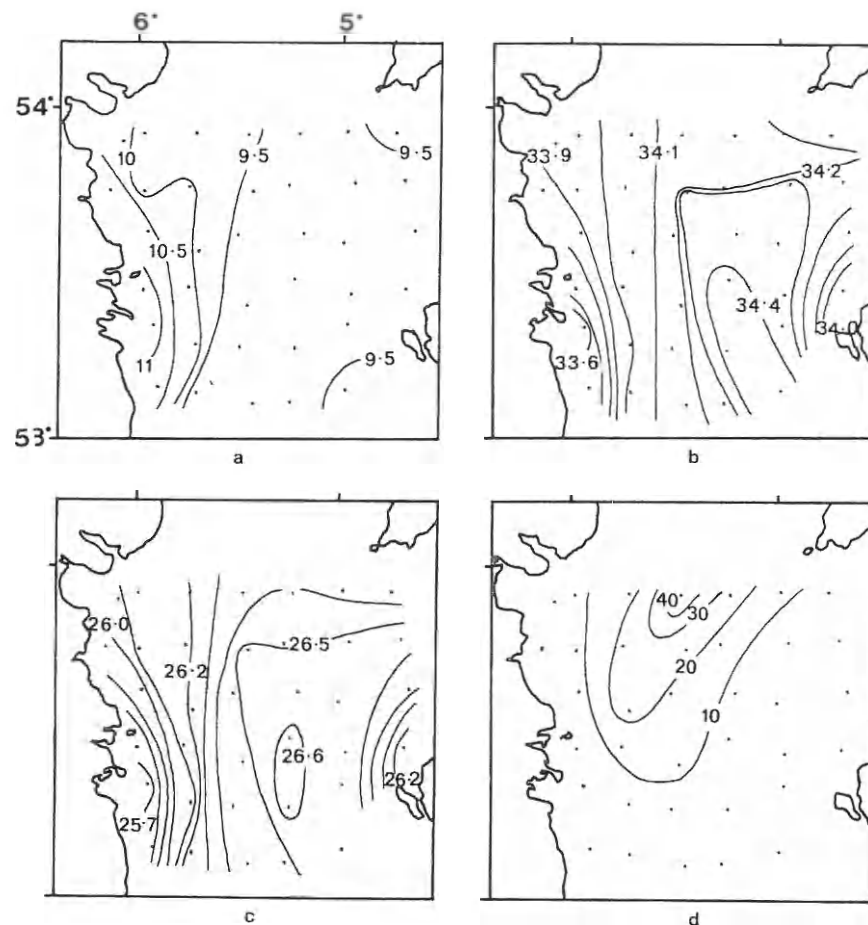


Fig. 4. Distribution of (a) surface temperature ($^{\circ}\text{C}$); (b) surface salinity; (c) surface density (σ_t); (d) stratification parameter (ϕ) in the western Irish Sea during 25–27 May 1984 showing warm fresh water close to the Irish coast. Thermal stratification was weakly developed over most of the region except for at the northern limit of the survey area.

of the potential energy anomaly ϕ , defined by Simpson (1981) and which is obtained from the vertical density profile, $\rho(z)$, according to

$$\phi = \frac{1}{h} \int_{-h}^0 g z (\bar{\rho} - \rho(z)) dz$$

where z is the depth beneath the sea surface (negative), h is the total water depth, $\bar{\rho}$ is the depth average density, i.e.

$$\bar{\rho} = \frac{1}{h} \int_{-h}^0 \rho(z) dz$$

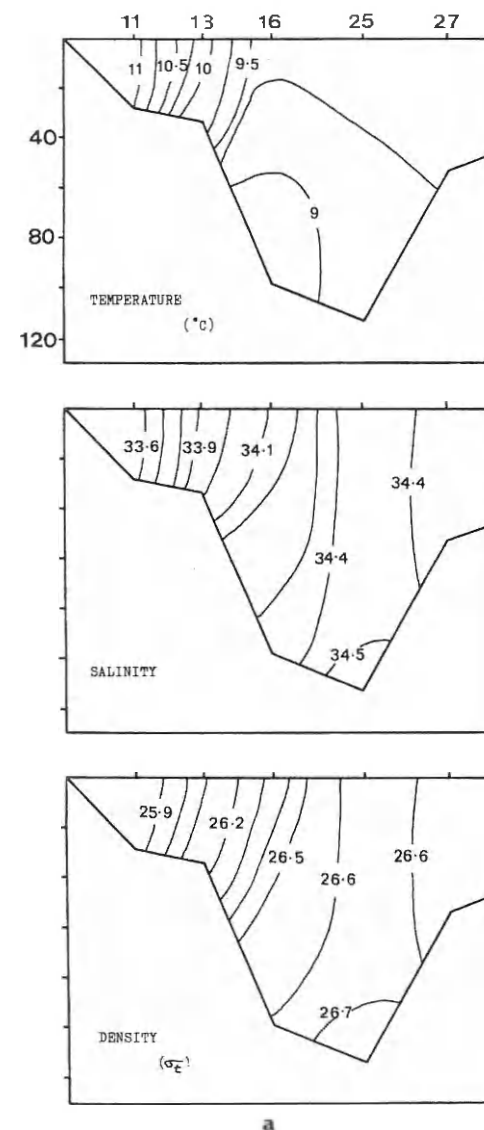


Fig. 5. Temperature, salinity and density sections in an approximately east-west direction in May 1984. (a) Southern transect showing warm fresh water close to the Irish coast in which property gradients are principally horizontal. Refer to Figure 2 for station positions.

Physically, ϕ represents the amount of energy required to vertically mix a water column to a completely homogeneous state and ϕ increases with increasing stratification with $\phi = 0$ representing complete vertical homogeneity. In the fully stratified regime in the western Irish Sea, ϕ typically has values of

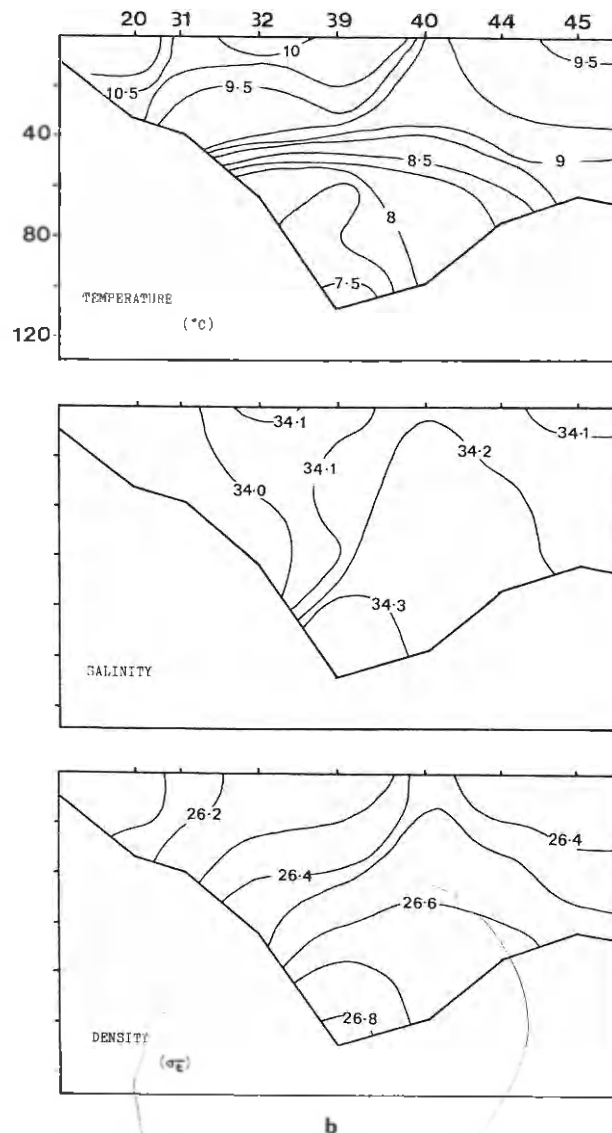


Fig. 5. (b) Northern transect in which thermal stratification is well developed. Refer to Figure 2 for station positions.

$80\text{--}100 \text{ J m}^{-3}$ (Simpson and Bowers, 1981; Lavin-Peregrina, 1984). In the present case, therefore, stratification is only weakly developed over most of the region except at the northern margin of the survey area. Dynamically, the presence of low density water close to the Irish coast may be expected to induce

a southward flowing geostrophic current. The observed density distribution has been used to estimate the depth mean, density driven current field by using the vertically averaged thermal wind relation

$$V = \frac{gh}{2Lf} \frac{(\bar{\rho}_1 - \bar{\rho}_2)}{\bar{\rho}}$$

and

$$\bar{\rho} = \frac{(\bar{\rho}_1 + \bar{\rho}_2)}{2}$$

where $\bar{\rho}_1$ and $\bar{\rho}_2$ are the average water column density for stations 1 and 2 respectively (kg m^{-3}), L is the distance between nominal station positions (m), g is the acceleration due to gravity (9.81 m s^{-2}), h is the water depth (m), f is the coriolis parameter ($1.4 \times 10^{-4} \text{ s}^{-1}$) and V the depth mean current velocity (m s^{-1}). The computed density current vectors are depicted in Figure 6 which shows that the strongest southward currents, $\sim 11.5 \text{ km day}^{-1}$ are associated with the maximum density gradient in deep water off the Irish coast. The inferred current field is thus consistent with the distribution of *Nephrops* larvae which suggests them to be transported southward away from the region of adult distribution. In contrast with the southern margin of the survey area, the distributions of larvae and adults conform quite closely in the eastern region, suggesting very little dispersion away from the hatching area in an easterly direction. This is, indeed, consistent with the current field shown in Figure 6 which shows that the currents have a very weak east-west component in that area.

Discussion

The distribution of the three larval stages of *N. norvegicus* during May 1984 shows that larvae are transported some considerable distance southward of the muddy area in the western Irish Sea where they are hatched. Southward transport of larvae is consistent with the inferred density driven current field in the region at the time of the 1984 survey. The extensive temperature and salinity data set presented by Slinn (1974) suggests that the presence of water of low salinity and density confined close to the Irish coast (as in Figure 5a) is a common feature of the hydrographic regime of the western Irish Sea during winter and early spring. A southward flowing coastal current, similar to that inferred from the present observations, may therefore be a typical feature of the winter and early spring regime although there are insufficient direct current observations to verify this. In late spring and summer, however, pronounced thermal stratification develops in the western Irish Sea as described by Simpson (1971) and Simpson and Hunter (1974), and a marked frontal system separates the stratified water in the western Irish Sea from the vertically homogeneous (mixed) water to the south and east. Stratification develops in the western Irish Sea during late spring and summer because the supply of turbulent kinetic

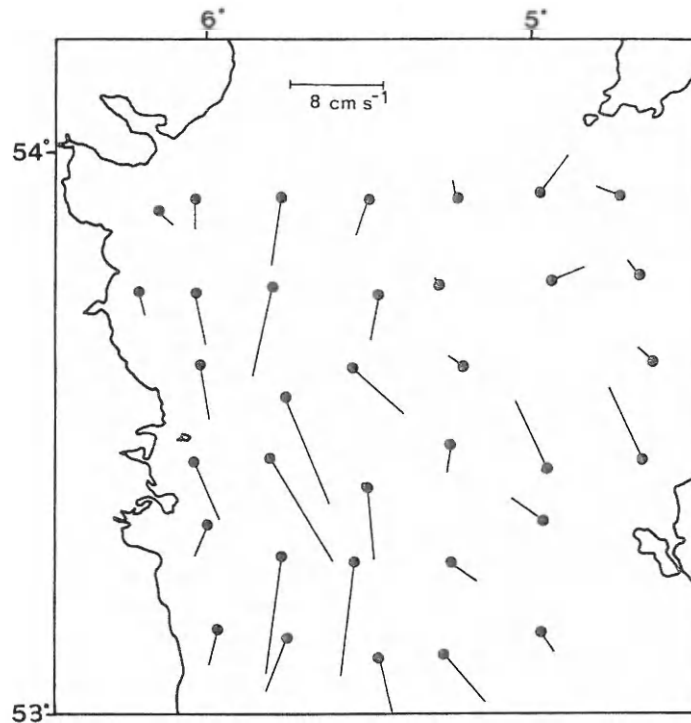


Fig. 6. Depth-mean geostrophic current vectors inferred from the observed density field. The current distribution is consistent with southward transport of larvae from the hatching area suggested by the observed larval distributions.

energy, generated by relatively weak tidal streams in the deeper waters of the western Irish Sea, is insufficient to maintain vertical mixing against the supply of buoyancy at the sea surface due to solar heating (Simpson and Hunter, 1974). The present set of observations are transitional between the winter and summer regimes. The southern section (Figure 5a) displays features typical of the winter and early spring season whilst the northernmost section (Figure 5b) exhibits thermal stratification. During the summer season, the combined effects of reduced fresh water discharge from the Irish coast and strong thermal stratification cause the density field to be controlled principally by temperature (Simpson and Hunter, 1974; Lavin-Peregrina, 1984). In these circumstances, a southward flowing density current, close to the Irish coast, would be expected to be severely reduced. Although a locally southward density-driven flow has been inferred close to the Irish coast it is widely accepted that the long-term, basin-wide, mean transport is northward in the Irish Sea, as indicated by the budgets of salinity and caesium (Bowden, 1950; Wilson, 1974). This is because other forcing agents, besides density, are also important in driving the mean circulation in the Irish Sea. A numerical model simulation undertaken by

Pingree and Griffiths (1980), for example, shows that a northward flowing coastal current close to the Irish coast is the response to a steady, mean wind stress from the south-west (the prevailing wind direction). The May 1984 survey was undertaken during a period of light winds, however, so that the meteorologically driven component of circulation may be expected to have been rather small at the time. The observations of May 1984 taken together with historical data sets (e.g. Slinn, 1974) suggest that a locally southward flowing density current may be a feature of the early spring situation in the western Irish Sea. Such a flow pattern, however, is likely to be severely modulated both on a seasonal basis (as a result of the onset of thermal stratification) and intermittently as a result of changing patterns of meteorological forcing. The presence of locally southward density-driven flow close to the Irish coast is also supplemented by tidally induced residual currents in the region. These currents, which arise because of the non-linearity in the propagation of the tidal wave in shelf seas, have been computed using a three-dimensional numerical hydrodynamic model of the north-west European shelf by Davies (1983). The model shows southward tidally induced residual flow of $4-6 \text{ cm s}^{-1}$ at the sea surface and $2-4 \text{ cm s}^{-1}$ at the sea bed close to the Irish coast in the southern region of the survey area presented here. The tidally driven residual flow is unaffected by changes in meteorological forcing so that it forms a persistent component of the flow regime subject only to modulation in magnitude over a springs-neaps cycle. The picture which thus emerges of the mean circulation in the region is one of a comparatively weak but persistent local southward tidally induced flow, a rather stronger quasi-persistent density driven flow caused by the mean offshore density gradient arising from the influence of coastal freshwater discharge. The latter flow component is, however, probably severely modulated on a seasonal time scale by the onset of thermal stratification. Superimposed on the quasi-steady flow components is a highly variable (both in magnitude and direction) meteorologically driven circulation which nevertheless tends to drive a mean northward flow because the prevailing direction of wind forcing is from the south. The net transport of water averaged over the width of the Irish Sea basin is northward although in a relatively narrow zone close to the Irish east coast the indications are of a local southward flow.

The observations presented here have interesting implications regarding recruitment to the adult stock of *Nephrops* in the western Irish Sea. Larval survival is generally regarded as a critical factor influencing the magnitude of recruitment in a given year. Because *Nephrops* populations are substrate specific, and do not migrate before spawning, another critical factor is retention of larvae within suitable settling out areas. The two comprehensive *Nephrops* larvae surveys conducted by MAFF in 1982 (Nichols *et al.*, 1987) and 1985 (Thompson *et al.*, 1986) over the complete hatching season (early April to late June) also exhibit distributions broadly in accord with the present data; in particular they display southward transport of larvae away from the hatching area. Furthermore, these data sets indicate that the peak of larval occurrence in the western Irish Sea is in May. Survival of the adult population depends upon sufficient larval retention despite the advective losses to the system. The

southward advection by the coastal current is clearly an important control on the level of recruitment to the adult population. It is apparent, however, that the level of recruitment may be rather critically determined by processes that influence the current. A combination of events such as exceptional coastal runoff conditions (controlling the magnitude of the density current), wind conditions (affecting wind-driven coastal flows) or early or late development of stratification may result in either anomalously high advective losses from the juvenile recruitment area or, conversely, especially favourable conditions for retention in that area; these influences would correspondingly be revealed in the abundance of a particular year class. *Nephrops*, however, are not readily separated into year classes as there are no distinctive physiological indicators of age in the adult. Present statistics of the *Nephrops* fishery in the western Irish Sea are also inadequate for assessing changes in larval recruitment.

An alternative approach to assessing changes in larval recruitment involves predicting (or hindcasting) periods of high or low advection on the basis of meteorological observations. The difficulty which arises here, however, is that the dynamics of the coastal flow is affected by a range of coupled meteorological influences (fresh water discharge, solar heating and wind stress) so that a dynamical model incorporating all these influences will probably be necessary to properly predict the modulations of the coastal current which control recruitment.

It is of interest to consider the fate of the advected post-larvae once out of suitable settlement areas of muddy substrate. The most probable outcome is they fall prey to other organisms and are completely lost to the system, as evidenced by the lack of any reports of adult *Nephrops* found outside the known fishing grounds. However, very little is known of the behaviour of stage IV larvae and a question arises in this regard concerning whether it is possible for juveniles to migrate back along the sea bed to the suitable settlement areas. An extensive migration of this kind is known to occur, for example, in the benthic juvenile edible crab *Cancer pagurus* (Nichols *et al.*, 1982) where they apparently travel distances along the sea bed of up to 50 km in the North Sea, prior to recruitment to the commercial fishery.

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