The western Irish Sea gyre: a retention system for Norway lobster (*Nephrops norvegicus*) ?

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ABSTRACT

Recently a cyclonic, near-surface, gyre has been discovered above the deep (> 100 m) western basin of the Irish Sea. The gyre is present each year only during spring and summer (the surface heating season), and circulates around a static dome of cold bottom water left beneath the thermocline after the previous winter. The mud substrate of the western Irish Sea is geographically isolated and is the habitat for adult Norway lobster (*Nephrops norvegicus*). In spring, newly hatched larvae are released into the water column, spending approximately 50 days in the plankton. Recruitment depends upon settlement of metamorphosed larvae onto the mud patch. Larval distributions show a strong correspondence to the field of stratification and it is probable that the gyre acts as a retention mechanism, helping to maintain the population on the mud patch.

RÉSUMÉ

Le tourbillon de la Mer d'Irlande occidentale : un système de rétention pour la langoustine (*Nephrops norvegicus*) ?

Un tourbillon cyclonique superficiel a été récemment découvert au-dessus du bassin occidental profond (> 100 m) de la Mer d'Irlande. Ce tourbillon ne se présente que durant le printemps et l'été, c'est-à-dire pendant la saison de réchauffement superficiel ; il circule autour du dôme statique d'eau froide, situé au-dessous de la thermocline qui s'établit en fin d'hiver. Les fonds vaseux de la Mer d'Irlande occidentale sont géographiquement isolés et constituent l'habitat des langoustines (*Nephrops norvegicus*) adultes. Au printemps, les larves récemment écloses gagnent la colonne d'eau pour mener une vie planctonique pendant environ 50 jours.

Le recrutement dépend de l'établissement des larves métamorphosées sur la vase. La distribution des larves est fortement reliée au champ de stratification, et cette correspondance suggère que le tourbillon agit comme un mécanisme de rétention pour maintenir la population sur la vase.

INTRODUCTION

Many marine organisms have complex life-histories which include a pelagic larval phase. In these circumstances it is possible that life-cycle closure is governed, not only by biological factors, but also by the physical dispersal processes that control whether larvae reach suitable habitats at critical stages of their development (Sinclair, 1988; Heath, 1992; Le Fèvre and Bourget, 1992). Before the impact of oceanographic processes can properly be examined, however, it is essential that the key elements of life-history (including spawning time, spawning location, larval duration, larval behaviour and juvenile nursery location) are fairly well known. All too often basic spatial information, such as the location of the spawning or recruitment area is uncertain and, for this reason, there is a strong motivation to study estuarine and substrate-specific benthic invertebrates for which the spatial constraints on lifecycle closure often are more clearly defined.

Whilst a number of studies have focused on species which are confined to the rather special circulation regimes of estuaries, much less is known about organisms which spend all, or part, of their larval phase in the open sea. Within this broad context the aim of this paper is to draw attention to the case of a decapod crustacean, the Norway lobster *Nephrops norvegicus* (Linnaeus; 1758) in the western Irish Sea, where we explore the evidence for a direct link between the prevailing oceanographic conditions and the requirements of life-cycle closure.

In the following sections the important aspects of the physics and *Nephrops* life-history specifically relevant to the Irish Sea are briefly described, followed by presentation of the observational evidence for the existence of a summer gyre in the region. The results of a diagnostic circulation model which reproduces the observed gyre are presented and compared with observations. Finally the distribution of *Nephrops* larvae in the area are described in relation to the gyre. The discussion considers some of the important biological and physical questions raised by this case study.

BACKGROUND TO THE STUDY AREA

The western Irish Sea (Fig. 1) will be taken to include the region bounded by (53°20' N - 54°30' N, 4°40' W - 6°W). A deep (> 100 m) trough extends along the length of the Irish Sea from about 53°30' N into the North Channel. Annual mean fresh water discharge from the eastern Irish coast (south of Carlingford Loch) is 9855×10^6 m^3 (MAFF, 1987) with peak runoff in November-January and the minimum in June-September. Fresh water input results in the formation of a band of low salinity coastal water in the shallow (< 50 m) region close to the Irish coast. In late spring and summer, however, salinity variations make only a minor contribution to the density field in the central western Irish Sea (Lavin-Peregrina, 1984) which is then dominated by temperature effects. The crucial aspect of the physics in the western Irish Sea is the development of seasonal thermal stratification, the spatial distribution of which is controlled principally by topography and tidal dynamics through the Simpson and Hunter (1974) h/U^3 criterion

(h, water depth; U, tidal current amplitude). In the Irish Sea, the tide has the form of a standing wave with its velocity node located in the western Irish Sea where, consequently, tidal currents are exceptionally weak (< 0.3 m s^{-1}) compared with the remainder of the Irish Sea (see Fig. 5 *a* later). The combination of deep water and weak tides means that the western Irish Sea stratifies during the spring and summer heating season when there is insufficient tidally-generated turbulent kinetic energy to maintain vertical mixing against the input of surface buoyancy (Simpson and Hunter, 1974). Pronounced tidal mixing fronts separate thermally stratified and tidally mixed waters (Simpson and Hunter, 1974; Simpson, 1981).

Associated with the onset of seasonal thermal stratification is the formation of a dome of cold (dense) bottom water in the deeper parts of the western Irish Sea. The dome is composed of water, left over from the previous winter, which becomes trapped beneath the thermocline as stratification develops in May/June each year. The cold dome is warmed only very slowly by weak diffusion of heat across the thermocline. This body of isolated, relict, winter water is separated from warmer, surrounding mixed waters by horizontal bottom fronts. Low oxygen values within the dome (Davies, 1972) confirm the limited exchange with surrounding waters. The dome breaks down each year in October/November when autumn gales and surface cooling return the Irish Sea to its winter mixed state. Similar seasonally isolated bodies of relict winter water have been observed in a number of shallow seas world-wide and the
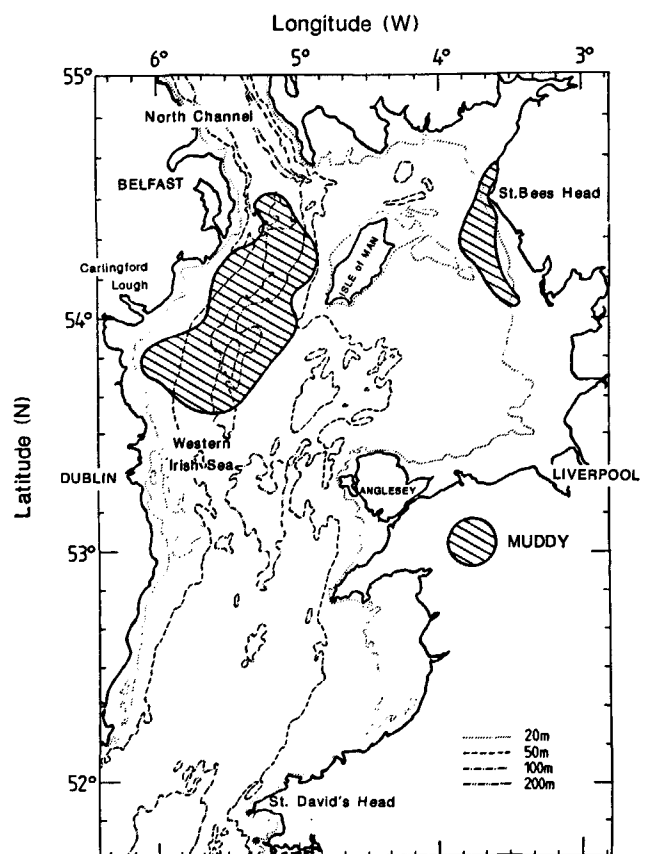

Figure 1

The Irish Sea showing the location of mud patches which are adult Nephrops *habitats. Adapted from MAFF (1987).*

term "bourrelet froid", meaning a cold cushion, has been used to describe them (Vincent and Kurc, 1969; Le Fèvre, 1986). In North America the term "cold water pool" has been used to describe a similar structure on the Mid-Atlantic Bight shelf (Houghton et al., 1982).

To date, little has been known of the mean circulation in the western Irish Sea although, in general, it has been thought to be weak because the tidal mixing fronts would be significantly displaced from their observed h/U^3 locations by mean flows greater than 1-2 km d^{-1} perpendicular to them (Simpson, 1981). Importantly, however, this does not preclude the existence much stronger mean flows parallel to density contours. Bowden's (1950) estimate of a basin-averaged, mean, northward flow through the Irish Sea of about 1-2 km d^{-1} has been widely accepted. However, the capacity of cold water pools to generate significant baroclinic (density-driven) circulation in coastal seas has been largely overlooked and, as we shall see, this simple picture of the circulation in the region requires revision for the summer season.

Another consequence of the low tidal energy regime is that the western Irish Sea is a depositional environment which has accumulated an isolated patch of Holocene muds in a layer up to 33 m thick over a subsurface of glacial origin (Belderson, 1964; Fig. 1). This muddy area supports a valuable Nephrops fishery (a mean 8,252 tonnes between 1989-1993). Adult distribution is tightly constrained by their requirement for a muddy substrate in which they construct an elaborate system of burrows (Farmer, 1974; Chapman, 1980). In the Irish Sea, female Nephrops mature at age 3 years. The adult female moults during spring and mating takes place whilst the exoskeleton is still soft. During summer, eggs are laid and attached to the pleopods where they are incubated for 6-10 months. Hatching of larvae into the water column takes place from late March to July. Newly hatched larvae spend approximately 50 days in the plankton, dependant on temperature (Nichols et al., 1987; Thompson and Ayers, 1989). Whilst in the water column, larvae metamorphose through three pelagic stages (I, II and III) which are found in the upper 40 m of the water column. Peak stage I and stage III larval occurrences are found in May and June respectively. The postlarvae (stage IV) resemble adults in most respects and commence their benthic existence by settling onto a muddy substrate where they construct or occupy burrows. It is not thought that juveniles undertake significant migrations along the bed after settling.

OBSERVATIONAL METHODS

Physical measurements

The flow field in the western Irish Sea has been measured using free-drifting, satellite-tracked drogued buoys. Drifter measurements were made covering the following periods: nine drifters from 11-20 July 1990; two from 5 July-15 August 1993; five from 13 June-7 July 1994. These respective deployments were made using the research vessels RRS Challenger, RV Prince Madog and RV Corystes. In 1990 Argos-Decca buoys were used with a position fix

obtained every 10 min (Roberts et al., 1991; Hill et al., 1994) and each buoy was drogued at 15 m depth with a 30 m^2 "window-blind". In 1993 and 1994, Argos buoys were used, giving nominally 8-12 satellite fixes per day. Holey-sock drogues, 1.5 m diameter by 7 m length, were used with drogues centred at depths of 15 m and 23 m in 1993 and 1994 respectively. Measurements of the temperature/salinity field were made in 1994 using a CTD mounted in a Scanfish towed, undulating vehicle.

Larval surveys

Data from Nephrops larval surveys undertaken as part of a stock assessment programme have kindly been made available by Dr. John Nichols (MAFF Directorate of Fisheries Research, Lowestoft). 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. Details of the sampling and handling methods are described by Nichols et al. (1987).

THE IRISH SEA GYRE

Drifter observations

In July 1990, a gyre was discovered in the western Irish Sea with nine free-drifting Argos-Decca buoys. These results have already been discussed in detail by Hill et al. (1994) who showed that the cyclonic circulation is consistent with geostrophic flow around a dome of cold, dense bottom water in the deep western basin which is discussed further below.

In July/August 1993, two drifters were laid at the northern (54° N, 5°30' W) and southern (53°40' N, 5°30' W) limits of the observed 1990 gyre to see whether they would drift southwards and northwards respectively, if caught in the gyre. Buoy 20762 (solid circles) drifted for 41 days, buoy 20763 (solid triangles) for 39 days (Fig. 2 a). Although both buoys initially moved in the expected directions, 20763 left the gyre region to the north without returning southwards as expected. Buoy 20762, however, showed clear evidence of cyclonic flow for a period of 14 days before it also left the gyre (to the east). The latter drifter also revealed the southern extent of the gyre, a feature not shown by the 1990 drifters.

In June-July 1994, five drifters showed the gyre circulation (Fig. 2 b). The longest duration trajectory (buoy 6374; 24 days) showed remarkable consistency with the track of 20762 in 1993, particularly in delimiting the southern extent of the gyre. The implied time to make a complete circuit of the gyre would seem to be at least 30 days on the basis of the 6374 track. In 1994, buoy 20762, laid in the middle of the gyre (Fig. 2 b), showed virtually no displacement over a 16 day period, confirming that the gyre centre is indeed a flow stagnation zone.

The spatial extent of the seasonally stratified region is depicted by Simpson's (1981) potential energy anomaly, Φ (Fig. 3), derived from a comprehensive Scanfish grid in June 1994 (during the time of the drifter experiment).
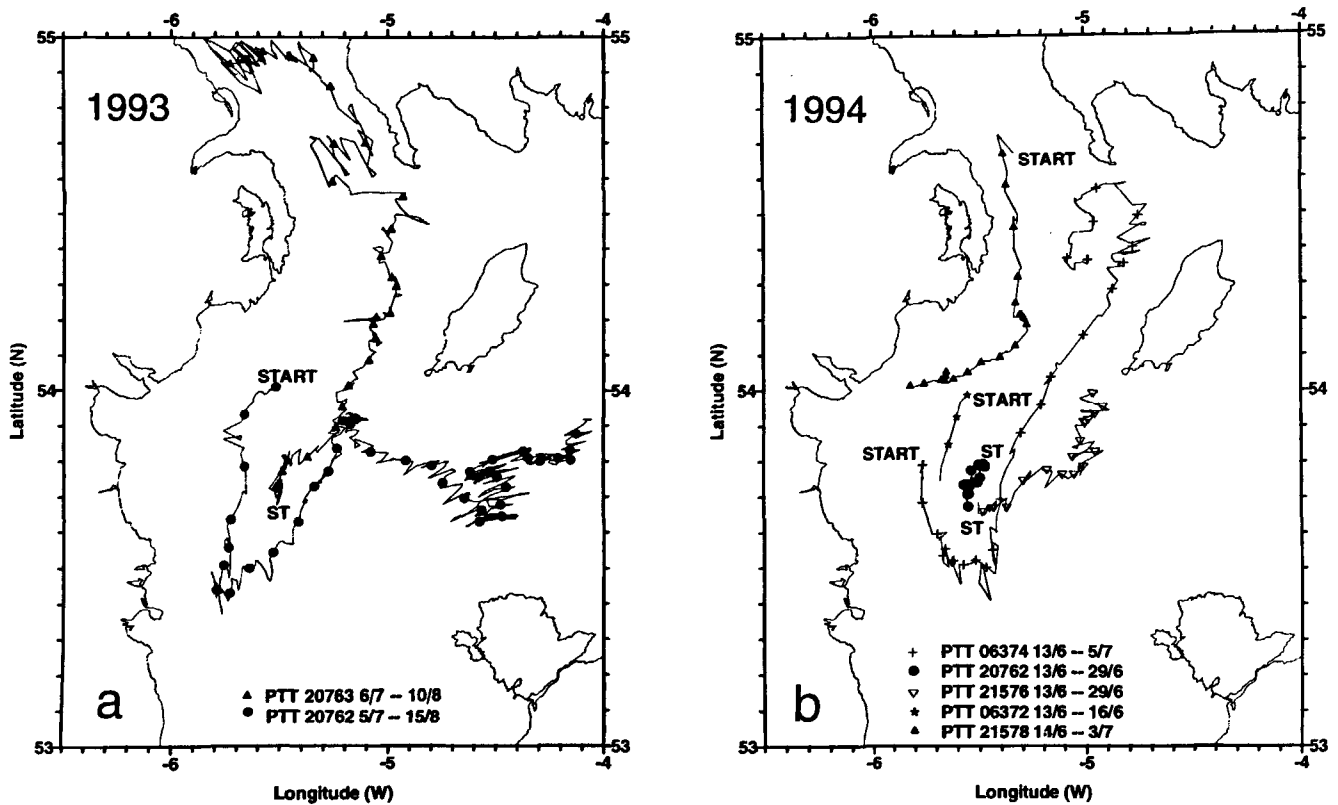
Figure 2

Trajectories of Argos drifters with holey sock drogues deployed in the western Irish Sea. (a) 5 July-14 August 1993: drogues centred at 15 m depth. (b) 13 June-7 July 1994: drogues centred at 23 m depth. Symbols indicate daily intervals.

Because this survey was made early in the stratification season, the peak values of Φ were only 60 J m^{-3}, whereas values of about 100 J m^{-3} are expected during the height of summer. In addition to showing the overall spatial extent of stratification, this figure also provides evidence for two centres of higher ($\Phi > 30$ J m^{-3}) stratification within the main stratified area. Evidence of two high Φ centres can also be found in the earlier distributions of Nichols *et al.* (1993). There is fair correspondence between contours of Φ and several of the drifter trajectories which show circulation around the stratified region.

The density structure enables us to comprehend the driving mechanism of the gyre (Hill, 1993). The cold dome that forms in spring/summer is separated from the surrounding waters by horizontal near-bottom density gradients. This can be seen in Fig. 4 *a* which shows a Scanfish section (Leg 59 in Fig. 3 at approximately 53°40' N) in which the dome can be identified as water with density, $\sigma_t > 26.6$. It is the *bottom* density gradients that are dynamically significant and drive baroclinic, cyclonic, *near-surface* flow in accordance with thermal-wind balance assuming zero flow parallel to the density contours at the bottom; the latter condition is equivalent to a condition no net 'cross-front' transport (Garrett and Loder, 1981). The dynamical effect of the density structure can be seen in Fig. 4 *b* which shows geostrophic velocities computed from the Scanfish section (Fig. 4 *a*), relative to an assumed level of no motion at the sea-bed. The geostrophic currents show flows up to 0.2 m s^{-1} circulating in the cyclonic sense. As the heating season proceeds, the mixed waters are expected

Figure 3
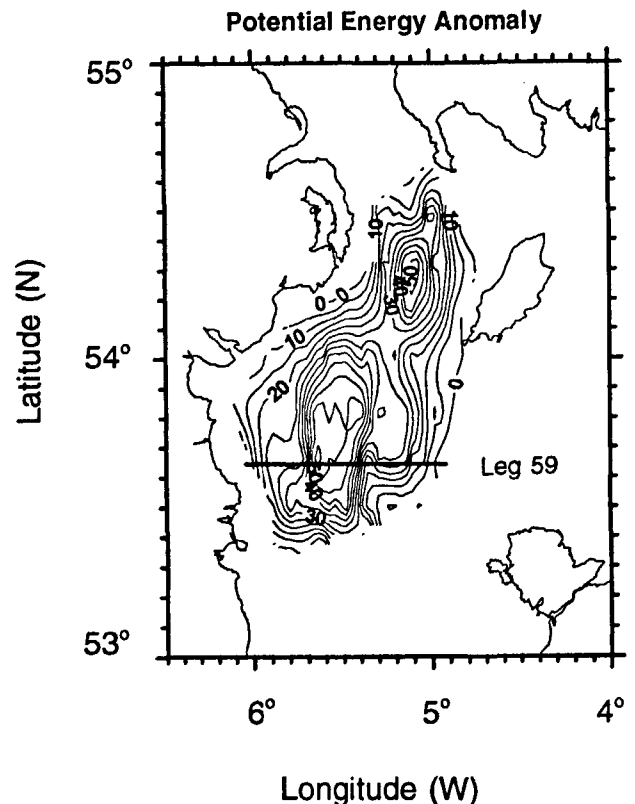
Stratification (potential energy anomaly, Φ J m^{-3}), derived from a Scanfish survey of the western Irish Sea 18-22 June 1994. Note the two centres of strong stratification in the region during the survey.
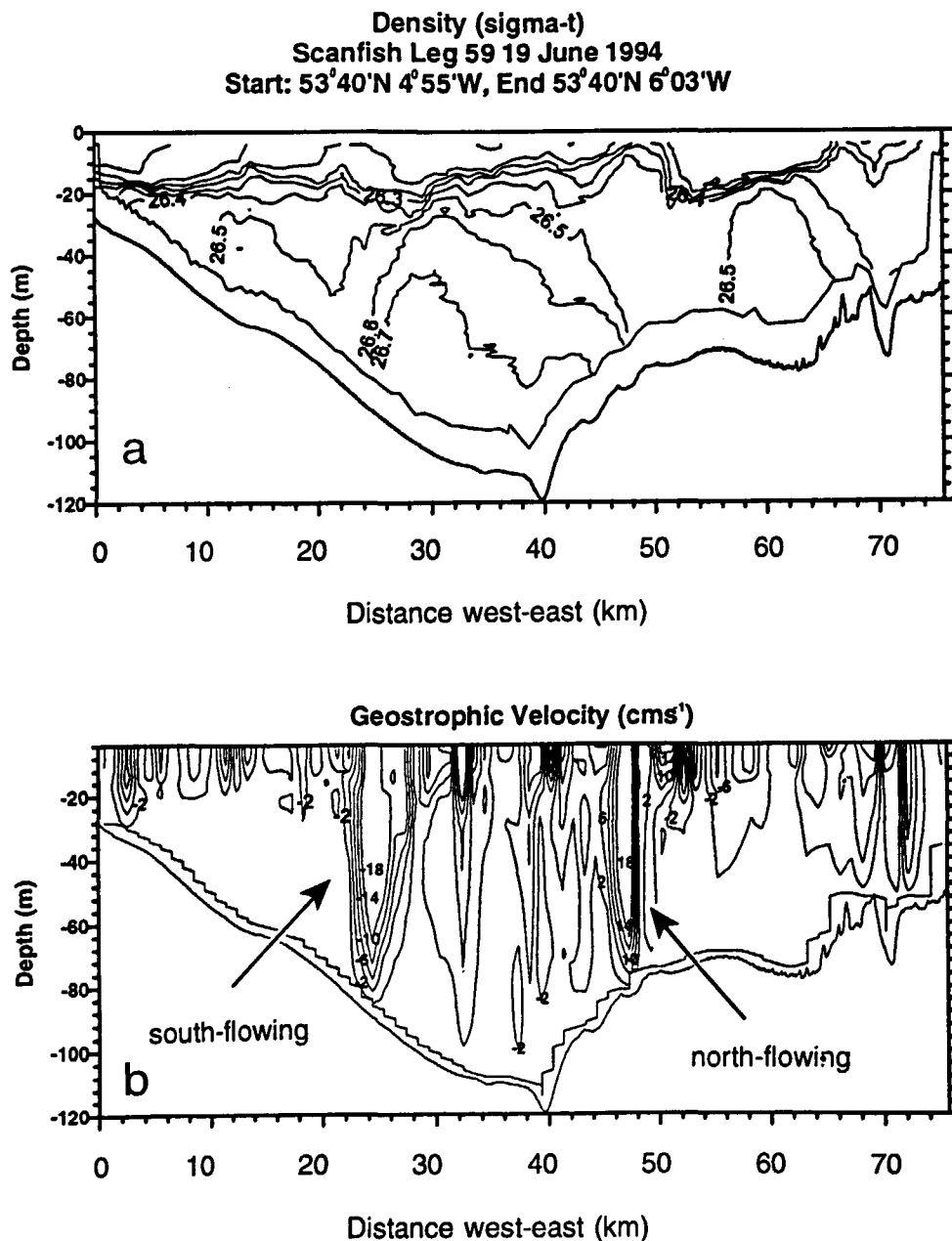
Density (sigma-t)
Scanfish Leg 59 19 June 1994
Start: 53°40'N 4°55'W, End 53°40'N 6°03'W

Geostrophic Velocity (cms⁻¹)

Figure 4

West-east Scanfish section of the western Irish Sea at latitude 53°40' N showing (a) density (σ_t) and (b) geostrophic velocity computed relative to an assumed level of no motion at the sea bed. Positive isotachs indicate flow into the page.

to become progressively warmer whilst the cold dome warms much more slowly. Consequently, the gyre is expected to become progressively faster as bottom fronts sharpen over the heating season.

The gyre driving mechanism described above is a baroclinic one. There are, however, barotropic processes, particularly tidal rectification, which might be expected to generate cyclonic flow around a topographic depression all year round. In the western Irish Sea, however, it seems very unlikely that tidal rectification plays a significant role. The buoy tracks (Fig. 2) show fast flows (> 0.1 m s⁻¹) in parts of the southern flank of the gyre where tidal currents are very weak (Fig. 5 a). In general the rectified current is expected to be at least an order of magnitude smaller than the amplitude of the tidal current generating it. However, the most compelling evidence against tidal rectification in

the western Irish Sea is the failure of high-resolution, barotropic tidal models to show any such currents.

Persistence of the gyre

Drifter trajectories obtained in the gyre to date are of relatively short duration (up to 24 days). Despite this, there is reason to expect that the gyre is a persistent circulation feature over the duration of the stratification season each year. Firstly, the dome-like density structure (which it has been argued above, on dynamical grounds, is the key driving mechanism for the gyre) is present throughout spring and summer each year as shown by a large body of historical temperature/salinity data (e.g. Slinn, 1974; Lavin-Peregrina, 1984; Nichols et al., 1993). Secondly, drifter observa-
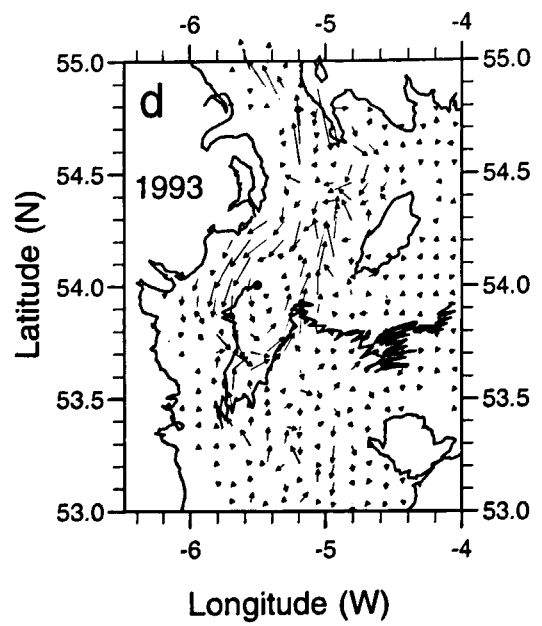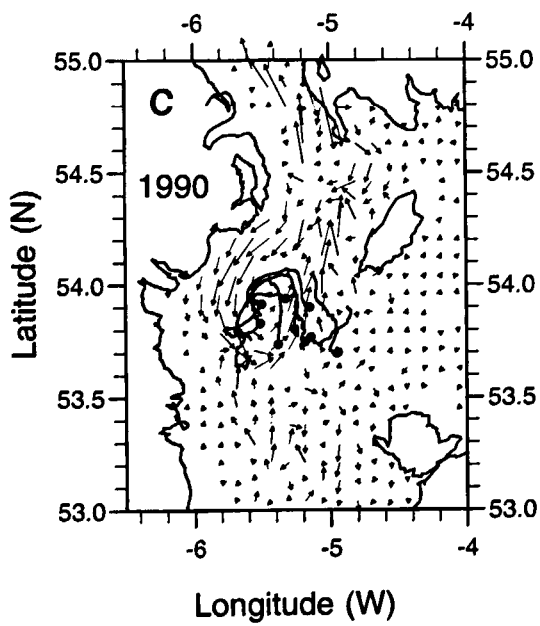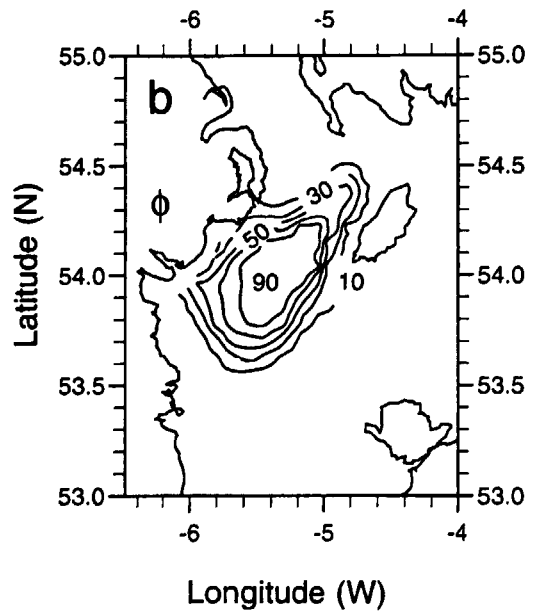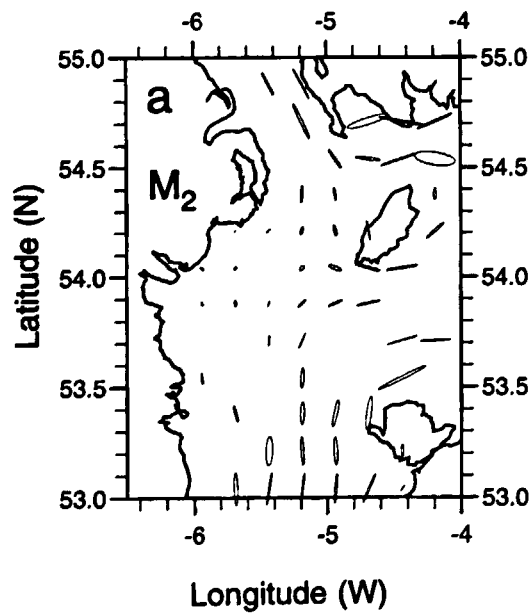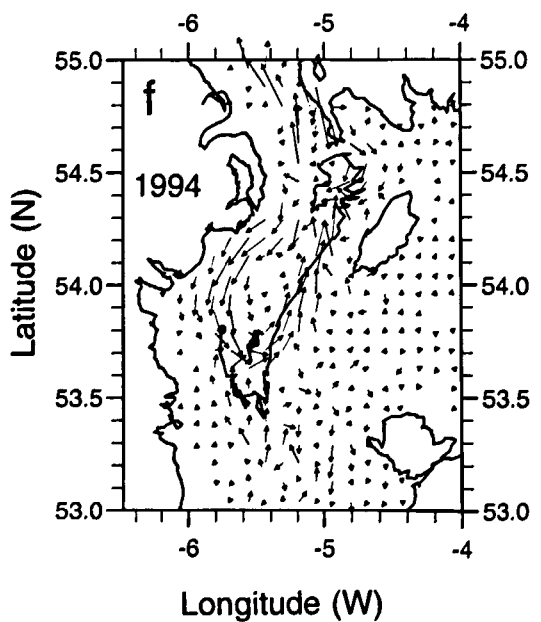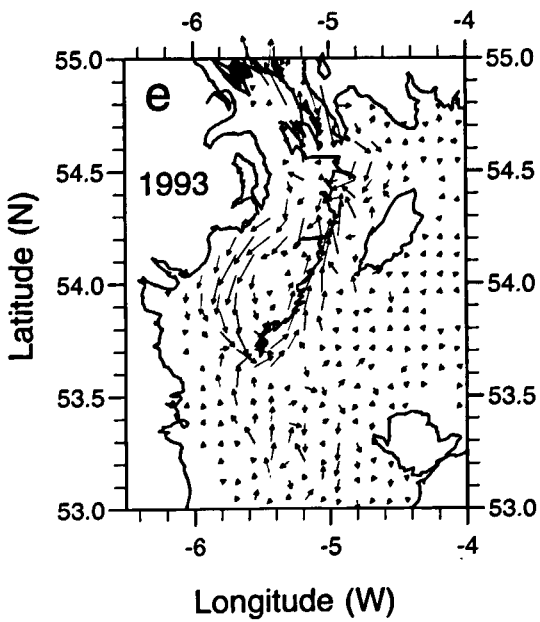
◀ Figure 5

Diagnostic circulation model results.
(a) Input M_2 tidal current ellipses (b) predicted field of stratification, Φ ($J\,m^{-3}$). Predicted surface current vectors together with drifter tracks from
(c) 1990, (d) buoy 20762, 1993, (e) buoy 20763, 1993, (f) buoys 20762 and 6374, 1994.

tions have been made in both June and July and, with hindsight, the gyre is also visible in the track of a single radio-tracked drifter deployed in September 1971 by Hunter (1972). On the basis of the available drifter data, therefore, it seems that cyclonic flow can be observed at a variety of times during the summer, lending support to the view of a seasonally-persistent circulation feature. There are also indications from current meter records obtained in 1981, 1993 and 1994 in the western (southward-flowing) flank of the gyre that, as the system stratifies in May-June, a more persistent southward surface flow emerges from a previously more erratic pattern of residual currents. Near bottom residual currents appear to be weak at all times and un-correlated with surface currents. Taken together, therefore, the observed density structure, current meter records and the four sets of drifter tracks in 1971, 1990, 1993 and 1994 are consistent with the picture of a stably-located gyre which is persistent over the summer season.

A DIAGNOSTIC CIRCULATION MODEL

In the light of the physical insights provided by the observations we can begin the task of modelling the gyre flow field. This is important because the existence of the Irish Sea gyre has never been predicted by any of the numerous coastal ocean models yet applied in the region. The reason is that circulation models have so-far failed to account for the dynamical implications of the crucial fact that the density field in the western Irish Sea is primarily maintained in summer by the competition between surface heating and tidal mixing. As a first step towards simulating the flow field, therefore, a three-dimensional, diagnostic, circulation model has been employed. Whilst more sophisticated approaches are possible, the present reduced-physics model is restricted only to those elements necessary to reproduce the essential features of the circulation. In particular, the model utilizes a density field generated by heating-stirring processes. The diagnostic method computes flow from the density field in a way which is dynamically consistent (with the equations of motion and continuity) but does not allow density to be advected by the resulting flow. The diagnostic approach is particularly appropriate in the present case because advection of density is likely to be a secondary influence in comparison with the dominant effect of local vertical (tidal) mixing in maintaining the density structure.

Description of the model

As the technique is well-known, details of the model are not given here. The approach is broadly similar to that described by Lynch et al. (1992), except that the calculations are performed on a finite difference grid (Hukuda et al., 1989). In the present application, the 3-D density field is

generated from a series of 1-D mixed layer models, based on the 1-D model of Simpson and Bowers (1984). The mixing model predicts the vertical density structure at a point in response to tidal mixing and climatological cycles of surface heating and wind mixing, based on prescriptions by James (1977). Flow is computed from the density field using the steady, linearised form of the equations of motion including rotation, surface slope, the baroclinic pressure gradient, internal friction (with constant vertical eddy viscosity) and linear bottom friction (Lynch et al., 1992). The flow calculation comprises two steps. First, the so-called "global problem" is solved by computing the surface-elevation field from a governing elliptic equation (Schwing, 1992) which ensures the final flow field is consistent with continuity. Once the surface elevation field is known the "local problem" is solved, to give the velocity structure in the vertical at each grid cell, by integrating equations of motion in the vertical, subject to a condition of zero surface stress and linear bottom drag. The basic inputs to the model are bathymetry and two data-bases of M_2 and S_2 tidal current amplitudes which are derived from outputs of a 2-dimensional vertically-averaged tidal model of the European shelf on a grid $1/8°$ longitude x $1/12°$ latitude developed at the Proudman Oceanographic Laboratory (UK) and described by Elliott (1991).

Model Results

Using climatological forcing, the model has been run forward from homogeneous winter conditions to predict the density distribution in mid-July when most drifter measurements have been made. The tidal currents (Fig. 5 a) input to the model provide the basic source of mixing power which is proportional to U^3 where U is the tidal current amplitude (M_2 only is shown because the spatial pattern of S_2 is almost identical). The predicted density field, summarized by the potential energy anomaly Φ (Fig. 5 b), shows an overall spatial pattern of stratification (and values of Φ) that agrees well with observations (e.g. Lavin-Peregrina, 1984; Nichols et al., 1993 and Fig. 3) and, thus gives confidence that the mixed-layer part of the model reproduces a reasonable density field. In particular, notice the correct prediction of the southern extent of stratification and the presence of stratified water between the Isle of Man and Ireland. A single predicted surface current field (Fig. 5 c-f) for the mid-July shows a gyre circulation pattern which is essentially contained within the stratified area, with the strongest flows in regions of the most pronounced horizontal density gradients (also strong Φ gradients). A feature of the predicted flow is that, on the eastern flank of the gyre (where density gradients are sharper), the flow is both narrower and stronger than on the western flank of the gyre which is characterised by a broader, more sluggish, southward return flow. We shall have cause to refer to this aspect of the flow later.

Superimposed on the predicted current pattern are some of the longer-duration drifter trajectories. It should be borne in mind, of course, that drifter tracks from individual years are here compared with a model circulation field based on climatology representing an "average year", so some inter-annual variability is to be expected. The drifter tracks from 1990 (Fig. 5 *c*) compare least favourably with the model and show the northern arm of the gyre to be located west of the southern tip of the Isle of Man, much further south than the northernmost limit of gyre predicted by the model. A possible explanation for this is offered later. The correspondence of the predicted flow with drifter 20762 (July 1993) is more impressive (Fig. 5 *d*). The correspondence between observation and model of the southern extent of the gyre is fair and the north-moving segment of the drifter track matches precisely the predicted location of the narrow northward-flowing flank of the gyre referred to above. Although drifter 20763 (Fig. 5 *e*) did not return southwards as predicted by the model, the portion of the track within the gyre again corresponded remarkably well with the location of the predicted narrow eastern flank of the gyre. The trajectory of drifter 6374 from 1994 (Fig. 5 *f*) showed excellent agreement with model predictions of: (a) the southern limit of the gyre, (b) the narrow north-flowing eastern flank and (c) the northern turning region. More-over, drifter 20762 (1994), also shown in Fig. 5 *f*, remained fairly static within the southern part of the predicted central gyre stagnation region.

The model simulation provides some clues concerning behaviour of the 1993 drifters. For example, the two drifters that left the gyre (20762 in Fig. 5 *d*; 20763 in Fig. 5 *e*) both did so in regions where the tidal currents (Fig. 5 *a*) are perpendicular to the main gyre flow, that is in regions where tides would tend to pull drifters out of the system. Moreover, 20762 (Fig. 5 *d*) left the gyre in a region where the gyre flow is particularly narrow and thus probably more susceptible to losses due to tidal or wind-driven motions transverse to the main gyre flow. The eastward motion of drifter 20762 (Fig. 2 *a*, Fig. 5 *d*) shows evidence for large tidal excursions in the tidally energetic (Fig. 5 *a*) eastern Irish Sea and the net eastward motion is probably influenced by wind-forcing. More puzzling is the behaviour of the 1990 drifters (Fig. 5 *c*), which showed the northern arm of the gyre to be much further south than predicted. Close inspection of the predicted current field (Fig. 5 *c*) does suggest that there could be a more southern branch of the return flow within the main body of the gyre. More significant, however, is the observational evidence over several years which shows two Φ maxima within the stratified region (*e.g.* Fig. 3). One hypothesis, therefore, is that in 1990, the drifters circulated around the southern centre whilst in 1993 and 1994 the trajectories encompassed both centres. Why this should be and whether such a major shift in the path around the gyre from year to year is due simply to the differences in drogue depth (or type) or due to some more fundamental seasonal, interannual or intermittent variability of the system remains open to question at present.

The model may have an inherent tendency to over-estimate density-driven flows because the density field is generated by a series of local 1-D models, with no horizontal mixing, which causes density gradients to be sharper than they otherwise would be. However, it is not the magnitude of the flow, but the spatial pattern of the currents that is of primary interest. In spite of the many possible sources of variability, the overwhelming impression is one of a good comparison between observations in particular years and a model prediction based on climatology. This strongly suggests that the gyre is a robust system which is, after all, to be expected given that it is controlled principally by topography and tidal mixing.

A *NEPHROPS* RETENTION HYPOTHESIS

From what is known of the *Nephrops* life history, it would appear that some retention of larvae above the Irish Sea mud-patch is required for the survival of the population and the gyre would seem to provide a suitable mechanism. The larval duration of 50 days, corresponds to somewhere in the range of 1-2 gyre circuits, although the gyre is "leaky" as evidenced by losses of drifters from the system. In contrast, a mean northward flow of only 1-2 km d^{-1} (the best observational estimate of the circulation prior to our knowledge of the gyre) would, over the 50 day larval duration, lead to significant (possibly total) loss from above the western Irish Sea mud patch.

The close linkages between various aspects of the physical environment and the Nephrops life-history in the western Irish Sea demonstrate how the physical conditions help to promote retention and thus improve the prospects for maintenance of a population in the region (Fig. 7). Noteworthy is the pivotal role of the low-energy tidal regime. Weak tides have at least three effects: (1) they create a depositional environment helping to form and prevent erosion of the mud substrate which is the habitat of both juvenile and adult *Nephrops*, (2) low tidal mixing promotes stratification which sets up the density field necessary to drive the gyre, (3) small tidal currents prevent frictional damping of flow, enabling the gyre to stand out as a major circulation feature. There is some evidence that *Nephrops* populations in other regions also may be associated with similar gyre-type circulations on account of the same basic underlying physics (Hill, 1993; Brown *et al.*, 1995). However, for several populations, such those off St. Bees Head (Fig. 1), or in deep continental slope regions, this particular retention mechanism does not apply.

The common link, however, is the association of mud substrates with low tidal energy and consequent stratification, so that some form of baroclinic (*density-driven*) circulation is likely to be found over all *Nephrops* grounds. The baroclinic circulation, either alone, or in combination with aspects of larval behaviour (such as vertical migration) could provide alternative means for retention in other locations.

The hypothesis that the gyre provides a *Nephrops* larval retention mechanism in the western Irish Sea is not without difficulties, however. Central among these is the issue of the timing of *Nephrops* hatching in relation to the spin-up of the gyre. The available evidence from larval surveys (Nichols *et al.*, 1987; Thompson *et al.*, 1986), indicates that hatching commences in late March, before the onset of
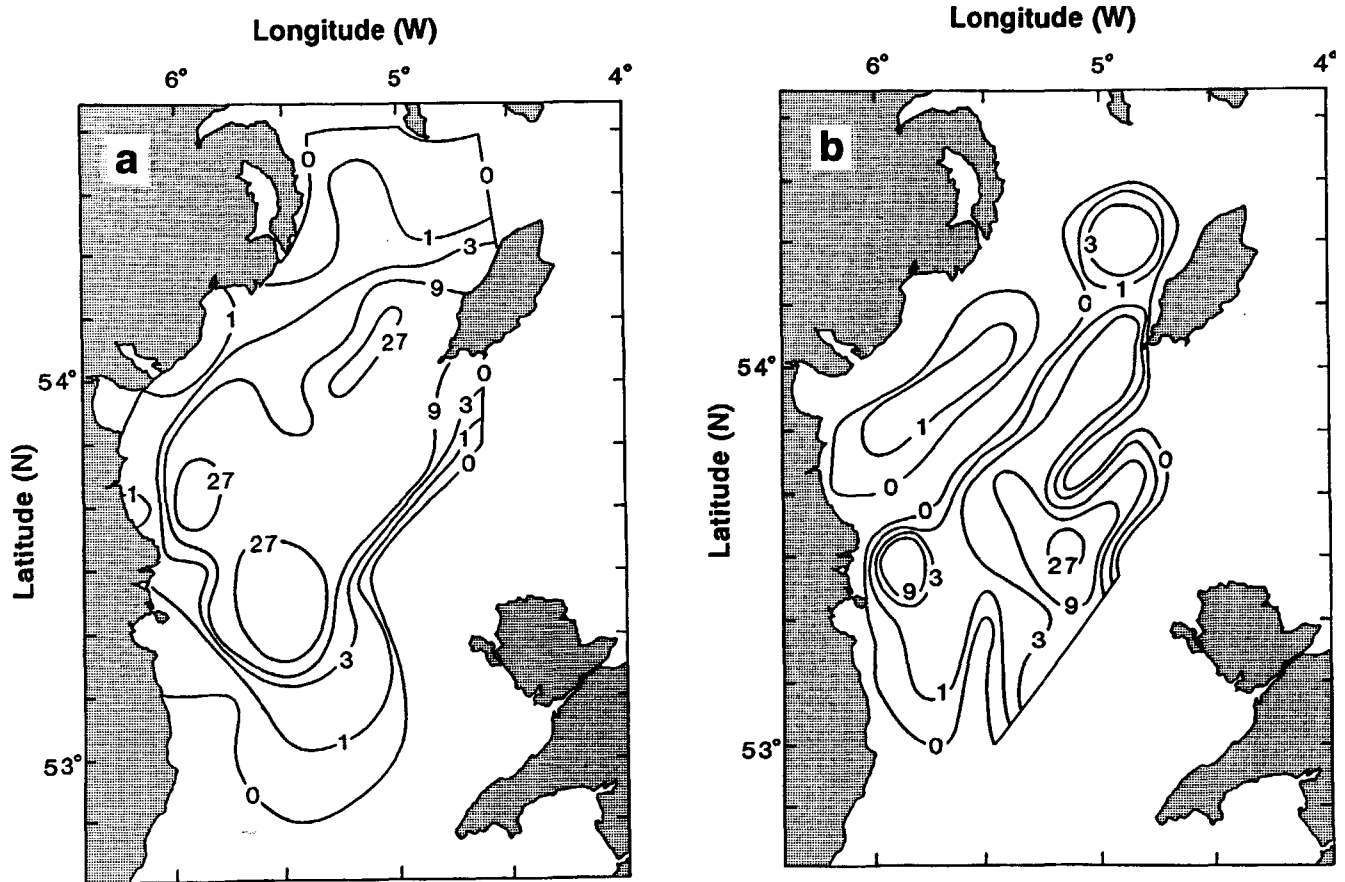
Figure 6

Nephrops *larvae distributions as numbers* (m^{-2}), *(a) Stage I, 9-13 May 1982, (b) Stage III, 15-19 June 1982.*

stratification and gyre development (in May or early June). Even at the time of peak stage I larval abundance, the gyre is only just beginning to be established. Only late hatching is likely to release larvae into the water column when the gyre is fully developed. Larvae distributions in 1982, 1984 and 1985 respectively have been described by Nichols *et al.* (1987), White *et al.* (1988) and Nichols and Thompson (1988). Whilst these show that the distribution of the centre of high larval density coincides closely with the stratified region, there is also a suggestion (in all surveys) that some larvae are displaced southwards from the main mud area (*e.g.* Fig. 6). This observation has led to the suggestion that there may be advective losses from the western Irish Sea population (White *et al.*, 1988), at least in early spring. Whilst little is known of the pre-gyre circulation of the western Irish Sea, White *et al.* suggested that in early spring, before the establishment of stratification, the higher levels of freshwater runoff (referred to in a previous section) combined with heating in shallow Irish coastal waters could form a southward-flowing, buoyancy-driven coastal current. Certainly, there is a body of evidence which supports the notion of southward flow near the Irish coast (Brown and Gmitrowicz, 1994), although intriguingly, in the light of the evidence presented above, at least part of this may be associated with what we now know to be the southward-flowing arm of the Irish Sea gyre !

White *et al.* (1988) argued that, in early spring, larvae would be subject to advective losses to the south which

would only be switched off in late spring and summer by the reduction of fresh water discharge and the onset of stratification. We now know that the gyre provides a mechanism to arrest the possible southward advective losses.

DISCUSSION

Nephrops fecundity is relatively low (500-3 000 viable eggs per season) (Nichols *et al.*, 1987) and ovigerous females retain their eggs for a long duration prior to hatching (up to ten months) during which time they are confined to their burrows. Low fecundity and the obvious energy investment in offspring would seem to favour adoption of a reproductive strategy which minimizes subsequent larval losses. However, this raises a number of questions which are yet to be resolved. Uppermost among these is why does the *Nephrops* hatching season begin so early when a later start would ensure most larvae were caught in the fully-developed gyre, maximizing retention ? Perhaps this suggests that, despite the relatively low fecundity, enough larvae are produced to withstand the early spring losses and that gyre-retention is actually not crucial to life-cycle closure. On the other hand, the existence of the mud-patch (and the present circulation regime) only dates from the end of the last ice-age 10 000 years ago. This time is short in evolutionary terms and it simply may be that the *Nephrops* which have colonised this region since the last
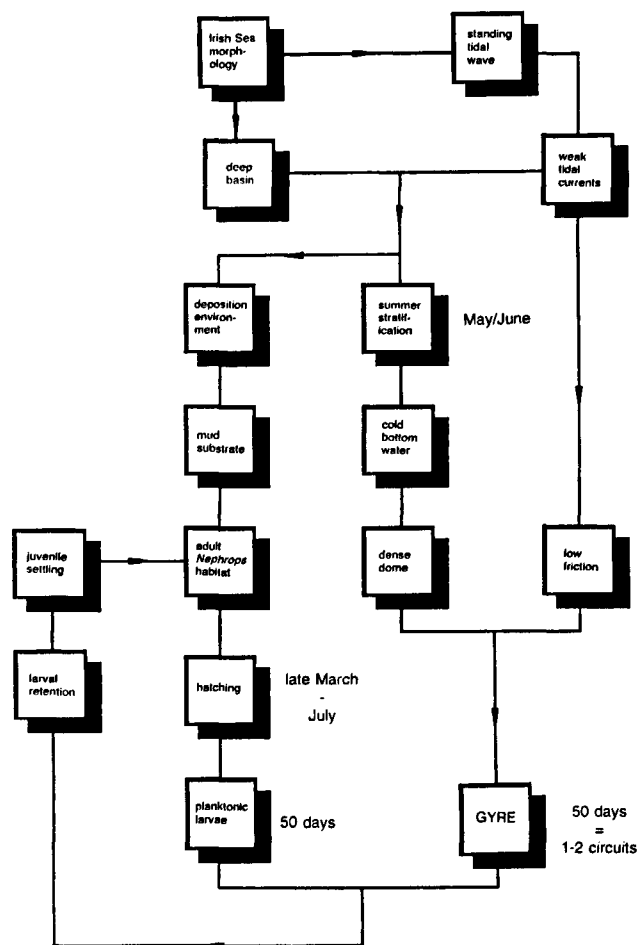
Figure 7

Physical controls on the Nephrops *population in the western Irish Sea. Note the pivotal role of the low tidal energy regime. The timing of the onset of stratification, larval hatching and larval duration are indicated against the respective boxes.*

glaciation have not yet become optimally adapted to their environment. A similar situation, raised by the spawning strategy of penaeid prawns in the Gulf of Carpentaria in northern Australia, was discussed by Rothlisberg *et al.* (1983). Another possibility is that some losses by dispersal are advantageous. In evolutionary terms, genes promoting dispersal (*e.g.* early-hatching in this case) will survive in the gene pool if dispersal leads to colonisation of remote habitats. Such genes could fare particularly well under conditions of significant interannual variability or in times of great environmental change when some habitats may be eliminated. A further consideration is that, for marine species in general, retention/dispersal is only one of many factors influencing life-cycle closure so that consideration of retention in isolation may give a distorted picture. Larval food availability (associated with the spring primary production bloom) and larval growth rates (associated with water temperature) are just two other important influences. A successful life history trajectory, in some sense, represents an optimization involving the many determinants affecting life-cycle closure. Both of the factors mentioned above are ultimately controlled by the same physical processes (related to the onset of stratification) that are also responsible for spin-up of the gyre. Given the complex

non-linearity of the actual physical system, it is almost certain that events such as the onset of the spring bloom and the timing of maximum gyre retention capacty will not coincide. Indeed, the relative timing of these events may also change in subtle ways from year to year. This is precisely the kind of problem where future generations of coupled physical-biological models (including zooplankton and larval dynamics) may usefully help to unravel and quantify some of the complex interactions between the physical and biological components of a system.

The emerging understanding of the circulation physics of the western Irish Sea points towards: (a) possible high losses of larvae in early spring when a fresh water coastal current may be present and (b) gyre spin-up which will promote retention above the mud region in late spring/summer. Setting aside the details of the precise nature of the way in which the physics impacts upon *Nephrops* life history, the key aspect of the new physical understanding is that, in a general way, it may help explain why, at some times and in some places, larval recruitment is relatively higher than at other times and locations. The physical system thus provides a basis to begin defining the effective spawning population for *Nephrops* in the region by identifying the spatial and temporal component of the population (late hatchers most favourably located within the gyre system) that contribute disproportionately to the next generation.

Another key biological question concerns the stability of the adult *Nephrops* population. The available fisheries data (Anon., 1994 *a*) suggest that both the total stock biomass and recruitment are fairly stable, though increased fishing effort in recent years may be reducing stock biomass. *Nephrops* live for several years, the majority of adults are between three and six years old (Anon., 1994 *a*) and variations in annual landings are probably the result of changed availability, rather than year class strength. The relatively constant recruitment may be indicative of the inherent robustness of the physical retention system. On the other hand, adult population stability, is characteristic of other benthic species (*e.g.* Thiébaut *et al.*, 1994) and perhaps indicates that the important population controls occur, not during the pelagic phase, but after settlement. In the case of *Nephrops*, recruitment is limited to the area of the mud patch, with carrying capacity limited by territoriality and maximum borrow density (Anon., 1994 *b*). Such density-dependant processes might mean that losses of larvae out of the gyre are insignificant in recruitment terms, as long as spawning stock biomass is maintained at a sufficiently high level.

Although this paper has focused on *Nephrops*, the western Irish Sea is an important spawning ground for other species and spring surveys in the region by Nichols *et al.* (1993) have shown high densities of fish eggs including those of cod (*Gadhus morhua*), haddock (*Melanogrammus aeglefinus*), sprat (*Sprattus sprattus*) and whiting (*Merlangius merlangus*). Clearly the distribution of all eggs and larvae present in spring/summer will be influenced by the gyre circulation regime although the possible effects, if any, upon recruitment in other species is unknown at present.

A number of important questions concerning the oceanography of the region remain unanswered. Foremost among

these is what is the nature of the early-spring circulation regime ? Obviously it would be of considerable interest to seed the region with drifters in this season to learn more about the transition from pre-gyre to gyre circulation. A second question relating to the physics is precisely how does the gyre act as a retention system ? Does it simply act to keep larvae circulating above the mud-patch, preventing them from being swept away by larger-scale mean advection, or do transverse circulations associated with the gyre actively bring about convergence towards its centre? Dynamically, a circular gyre bounded by bottom-dominant fronts would be expected to bring about flow divergence near the bottom and convergence nearer the surface (e.g. Garrett and Loder, 1981). Such secondary circulations would be very weak (order 1 cm s^{-1}) and so hard to measure and not readily apparent in the model simulations. Related to the retentive capacity of the gyre, it is interesting to note that drifters were observed to leave the gyre both to the east and to the north. Possible reasons why these locations may be especially "leaky" were given in the section dealing with the diagnostic model predictions. Are these sites also prone to larval losses ? If so, it is of interest to consider the possible fate of such larvae. A second, smaller, mud-patch supporting a Nephrops fishery, lies in the eastern Irish Sea, off St. Bees Head (Fig. 1), and the 1993 drifter track, 20762, suggests the possibility that larvae could leave the gyre in the east and so might ultimately reach it. Of equal interest is the possibility that larvae may leave the northern end of the gyre to enter the Clyde Sea. Buoy 20763, which left the gyre in 1993, eventually entered the Clyde Sea (adjacent to the eastern side of the North Channel). On this basis, there is direct evidence that some larvae lost from the western Irish Sea may enter the Nephrops population of the Clyde Sea.

The interaction between the density-driven gyre and other flow components, such as wind-driven flows remains to be investigated. Whilst the 1990 drifter experiment was conducted in near wind-free conditions, the 1993 and 1994 studies occured during periods when there were wind events. Even so, the gyre circulation was still clearly visible and was certainly not masked by wind-driven currents. Winds also interact with the gyre circulation by mixing the water column, thereby changing the density structure and affecting the density-driven flow. A detailed investigation of wind response thus requires a fully 3-D, density-advecting turbulence-closure model to simulate the complex coupling between mixing and advection. This is beyond the scope of the present study, but clearly is an important task for the future.

Seasonal baroclinic gyres, like that in the Irish Sea, are probably found in many shelf regions and Hill (1993) has identified several candidate sites. Some of the Nephrops populations off the coasts of Brittany and Scotland are also located beneath cold bottom water domes where similar gyre circulations may occur. A potentially important consequence of seasonal gyres is that, just as they may act as retention systems for marine plankton, so they will retain conservative contaminants introduced into them. For this reason, populations (and fisheries based upon them) associated with seasonal gyres may be at particular risk in the event of spring or summer oil and chemical spills.

Acknowledgements

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