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## The role of hydrodynamics in explaining variability in fish populations

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### Abstract

A review of the physical processes present in coastal regions and their effect on pelagic stages of flatfish populations is presented. While quantitative understanding of processes affecting cross-shelf transport and exchange continues to be a fundamental problem shared by physical oceanographers and fisheries scientists studying the early life history of flatfish, advances in hydrodynamic and coupled physical–biological models have made it possible to begin to examine population-level implications of environmental processes. There is now a need to rank these processes in terms of their impact on recruit strength. Existing paradigms provide testable frameworks for explaining the role of physical variability in the observed population patterns, abundance and variability. Identifying explicit links between physical variability and recruitment could result in new approaches to fisheries management strategies.

*Keywords:* recruitment; variability; hydrodynamics; transport; retention; larvae

### 1. Introduction

The question of whether interannual variability in hydrodynamics can explain interannual variability in recruitment was a theme of the 3rd Flatfish Symposium. This particular question has been pondered since the turn of the century, when Otto Pedersen in the early days of ICES identified the importance of physical processes to understanding fluctuations in fish populations (Fig. 1). Today, these ideas continue to be an integral component of national and international research efforts studying population regulation of marine species (e.g., GLOBEC, Mare Cognitum, FOCI, SABRE).

Physical processes affect recruitment directly or indirectly and lie at the core of present-day hypothe-

ses explaining population pattern, abundance and/or variability through transport (Harden Jones, 1968), feeding environment (Lasker, 1975; Rothschild and Osborn, 1988), population integrity (Sinclair, 1988) and match–mismatch (Cushing, 1974). In the case of many flatfish and estuarine-dependent species, whose juvenile nursery habitats are spatially distinct from spawning locations, the influence of planktonic transport processes is explicit during the early life history stages (e.g., Boehlert and Mundy, 1987; Hare and Cowen, 1996).

This paper discusses some of the physical processes operating during the pelagic phase of flatfish and other marine species, and the variability in populations that may arise from physical variability. While our discussion focuses on physical processes affecting early life history stages (pre-demersal stages in flatfish), the matter of year-class

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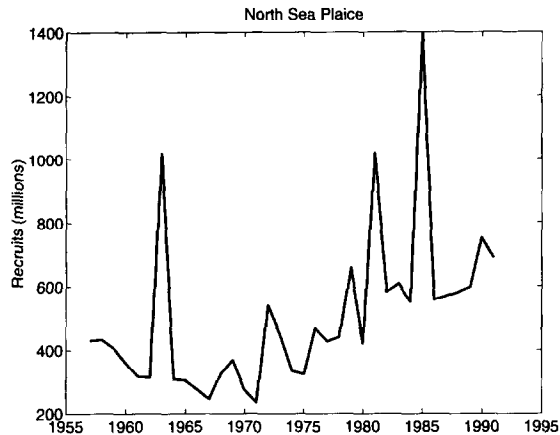


Fig. 1. Year-class strength of North Sea plaice from 1957 to 1991 (from Myers et al., 1995).

strength being set during larval stages (e.g., Hjort, 1914; Van der Veer et al., 1990; Bailey et al., 1996) or post-larval (demersal stages in flatfish) is unresolved (e.g., Sissenwine, 1984; Leggett and DeBlois, 1994). A typical scenario for the life history of fishes under consideration is that adults spawn offshore, and through a combination of drift, retention and behaviour, larvae 'use' the time-varying three-dimensional flow field to recruit into estuaries in which they will continue development as juveniles (Weinstein et al., 1980; Miller, 1988). The success of a particular cohort of larvae (as measured by the success or failure in reaching the nursery grounds) will be affected by various physical and biotic processes along their transit.

The layout of this paper is as follows. Section 2 presents concepts in marine fish population dynamics. These are intended to provide the basic framework for discussions of the role of physics in recruitment variability. Section 3 provides an overview of physical processes operating in four regions (the outer-shelf, mid-shelf, inner-shelf and near-inlet) occupied by pelagic larvae. A synthesis of these processes, likely sources of variability and main effects are presented in Section 4. Selected recent case studies linking recruitment and physical variability in the early life history of marine fishes are summarised in Section 5, and finally, Section 6 presents observations, conclusions and some directions for future research.

## 2. The role of hydrodynamics — concepts and paradigms

This section reviews four of the main paradigms relating physics to population pattern, abundance or variability (see also Heath, 1992; Cushing, 1995; Sinclair and Page, 1995). Two of the four (hydrographic containment and stable ocean hypotheses) rely on biological intermediates, the other two (encounter rate and member/vagrant hypotheses) have direct physical mechanisms in operation. We summarise these in Table 1.

### 2.1. Hydrographic containment

This hypothesis is a combination of Harden Jones' migration triangle (Harden Jones, 1968) and Cushing's match/mismatch hypotheses (Cushing, 1974). It recognises spatially separate adult feeding grounds, spawning grounds and juvenile nursery areas between which fish must migrate during certain phases of their life cycle and the importance of the overlap between production of appropriate prey and peak spawning activity. Cushing (1990, 1995) noted that feeding and spawning grounds of different plaice stocks in the North Sea are located along different tidal current streamlines. He argues, while pointing to the modelled paths of particles along these streamlines, that these paths are sufficiently distinct to keep stocks segregated in the North Sea, in effect using time invariant hydrodynamics (residual current streamlines) to explain the pattern of plaice stocks in the North Sea. This hypothesis combines both small- and large-scale physical processes: transport toward productive areas along with physical conditions conducive to the development of plankton blooms. The operative physical mechanisms are the residual tidal currents and the seasonal development of a stratified water column.

### 2.2. Stable ocean

Lasker's stable ocean hypothesis (Lasker, 1975) examined the distribution of planktonic prey for larval northern anchovy in relation to water column stability. He found that relatively thin layers of appropriately sized prey items in abundances high enough to support larval survival could indeed be

Table 1  
Paradigms explaining population pattern, abundance or variability

Hypothesis	Population pattern Individual stocks kept distinct by:	Abundance Mean population level set by:	Variability Fluctuations in abundance due to:
Hydrographic containment ( <i>migration triangle match/mismatch</i> )	the presence of tidal current streamlines between spawning and nursery grounds;	density-dependent growth and survival associated with food availability along larval drift route;	timing in onset of stratification and subsequent plankton bloom relative to spawning date;
Stable ocean	(not explained)	(not explained)	frequency and intensity of mixing such that prey aggregations at the pycnocline are disrupted;
Encounter rate	(not explained)	(not explained)	the influence of small-scale turbulence on relative motion between predator and prey;
Member/vagrant	retentive hydrographic structures which result in limited dispersal of early life history stages.	the size of the hydrographic structure associated with spawning location.	food-web and physical loss from appropriate habitat are both possible.

Adapted from Sinclair and Page (1995).

found, but the existence of these layers was related to local wind stress through turbulent mixing. Here, we have a small-scale physical process (turbulent mixing) mediating a biological phenomenon (development of prey patches).

### 2.3. Encounter rate

Rothschild and Osborn (1988) included small-scale turbulence and its effect on predator–prey encounter rates during the feeding process. The effect of turbulence was found to enhance contact rates and hence increase the effective prey concentration available to larvae (Sundby and Fossum, 1990). The recent literature suggests that a dome-shaped curve exists for capture success with respect to turbulent intensity (MacKenzie et al., 1994). Local turbulence can be influenced by a number of factors including proximity to surface or bottom boundaries, wind speed, stratification, etc. The proper parameterisation of turbulence in the encounter rate hypothesis is still debated (Denman and Gargett, 1995; Dower et al., 1997).

### 2.4. Member/vagrant

This hypothesis deals with the issue of the number of stocks (species richness) of marine organisms,

but can also explain abundance and variability (Sinclair, 1988). It requires that spawning take place in regions with persistent, predictable hydrodynamic regimes (such as gyres, tidally energetic areas, or coastal embayments) which allow a population of larvae, with appropriate behaviours, to remain coherent for the first few months of life. Here it is the maintenance of population integrity, rather than drift, that is important in defining self-reproducing populations. Sinclair (1988) and Sinclair and Page (1995) discuss the implications of this hypothesis regarding abundance and variability. They state that mean abundance is related to the size of the retentive hydrographic feature used by the population to limit dispersal. Variability can be density-dependent without a trophically based argument if vagrancy is a function of stock size (though trophic linkages are not discounted).

## 3. Hydrodynamics — an overview of key processes

In this section we present hydrodynamic processes which characterise the regions that flatfish and estuarine-dependent fish occupy during their early larval (pelagic) stages. The successful recruitment to estuarine nursery grounds depends on cross-shelf

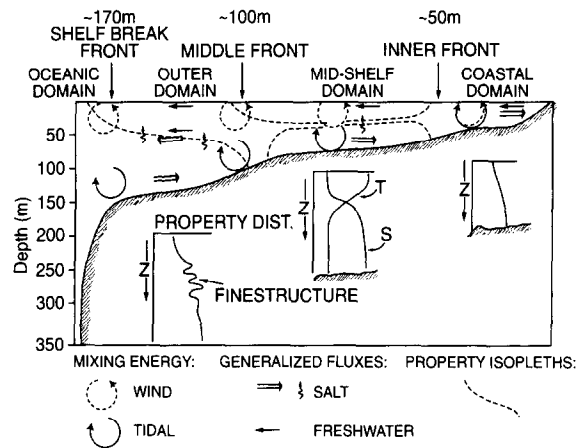


Fig. 2. Schematic of physical processes across an idealised shelf (from McRoy et al., 1986).

transport processes. A review of some of these processes can be found in Wroblewski and Hofmann (1989). A schematic of some of the physical dynamics found in the cross-shore direction is shown in Fig. 2.

The program Coastal Ocean Processes (CoOP) states as its goal “to obtain a new level of quantitative understanding of processes that dominate the transport ... and fates of biologically, chemically, and geologically important matter on the continental margins” (Brink et al., 1992). They go on to state that: “... Understanding cross-margin transport is central to achieving this goal ...”. These statements reflect the state of the art in continental shelf oceanography where our understanding and ability to quantitatively model and predict processes that advect or transport material (larvae) along isobaths is greater than for those processes which transport them across isobaths. Many of the strongest and most persistent signals are associated with along-shore/along-isobath flows. Exceptions are meanders and filaments for deep ocean currents, Ekman layers, frontal instabilities, internal waves, freshwater plumes and tidal currents. A fundamental problem shared by coastal physical oceanographers and fisheries scientists studying the early life history of flatfish, is that processes affecting cross-margin transport (i.e., the processes linking the deep ocean, the coastal ocean, and land) are not well understood.

### 3.1. Outer-shelf

We define this region as the seaward edge of the continental shelf, near the shelf break, where the physics of offshore (deep ocean) current systems are dominant. This region has been identified as a spawning area for several species of estuarine-dependent fish (see Parrish et al., 1981; Boehlert and Mundy, 1987; Hettler and Chester, 1990). There are significant differences in the hydrodynamics depending on whether the location of interest is near an oceanic western boundary system (e.g., near the Gulf Stream or the Kuroshio), or whether the particular study-site is near an eastern boundary current system (e.g., the California or the Benguela Current system). In either case, describing and modelling local dynamics cannot be accomplished without consideration of larger-scale (even basin-scale) processes.

#### 3.1.1. Western boundary current systems

Driven by basin-scale wind systems and required balances between vorticity input by winds, planetary vorticity (due to the variable Coriolis parameter) and relative vorticity (the horizontal shear) of the flow itself, these systems are characterised by energetic [ $O(1) \text{ m s}^{-1}$ ] poleward warm currents. Instabilities or fluctuations in these currents can be in the form of meanders, rings, eddies, filaments or streamers (Bane, 1994). These may affect larval populations

(and eggs) differently. For those larvae (or eggs spawned) within the main current, advection away from the site is likely with concomitant loss to the adjacent deep ocean. Some instances have been documented where fish populations have left the main current trapped (or entrained) in a ring or eddy that impinged back on the neighbouring continental shelf or coastal sea (Hare and Cowen, 1991, 1996).

Instabilities of western boundary currents also affect neighbouring embayments and shelf regions. The effects of meanders on inshore regions is reduced for wide embayments/shelves (on the order of 50 to 100 km). Meanders can be a source of different water masses; they may advect larvae on or off the shelf (Flierl and Wroblewski, 1985; Glenn and Ebbesmeyer, 1994; Stegmann and Yoder, 1996), or they can provide nutrients for phytoplankton and zooplankton populations (Hofmann and Ambler, 1988). During winter months, when shelf waters are typically cooler than oceanic waters, the warm waters associated with the filaments have been suggested to trigger spawning in certain species (e.g., Checkley et al., 1988).

There are also shifts in the 'mean' position of western boundary currents (Miller, 1994; Bane, 1994). For reasons that are not yet understood, the streams may remain in their onshore or offshore positions for 2 to 3 months. The frequency of meanders impacting the shelf is generally reduced during an 'offshore' position but the size of the meanders can increase.

### 3.1.2. Eastern boundary current systems

These systems are also driven by large-scale wind fields, but are weaker than western boundary currents, with currents flowing equatorward off western continental margins. They are best known for their proximity to upwelling centres and large fisheries off the west coasts of the US, South America and Africa.

Superimposed on the equatorward flows is a rich structure of seasonal jets, eddies and 'squirts' (see Brink and Cowles, 1991). Summer conditions are typically upwelling-like with surface outcropping of isopycnals, equatorward surface jets and poleward subsurface (although sometimes surface) countercurrents. Eddies, jets and filaments are present year-round and contribute to cross-shore exchanges. The alongshore scale of these features can be O (100–

300) km, the cross-shore scale of O (50) km, and the vertical extent of O (200) m. The occurrence of these mesoscale structures appears to be related to coastal features with the result that their frequency and strength vary alongshore. Alongshore transport of anchovy eggs and larvae in frontal systems of the Benguela system has been suggested by Shelton and Hutchings (1982). Squirts, jets and filaments are likely to affect the on- and offshore transport of pelagic larvae suggesting that behavioural adaptations (e.g., vertical migration within a sheared current) can increase retention and residence times in coastal regions (see Hofmann et al., 1991; Botsford et al., 1994). Sinclair et al. (1985) suggest that during El Niño years reduced offshore transport off California can result in reduced offshore losses of certain larvae and hence increased survival.

### 3.1.3. Other shelf-edge regions

Shelf-edge domains, such as the Middle Atlantic Bight off the US east coast and the European continental shelf-edge, are not part of either an eastern or western boundary current system. Some generalisations may be made in that the shelf-edge is usually a hydrodynamically complex region, with sampling and modelling attempts made difficult by the abrupt topography of the shelf-break, and the disparity in scales found at the juncture between coastal current dynamics and deep ocean current dynamics. There is typically a persistent density front between the deep ocean and shelf water masses which will generate (unstable) baroclinic flows and internal waves resulting in exchanges (losses and gains) between the shelf and the offshore regions (see Pingree and Mardell, 1981; Csanady, 1990; Flagg et al., 1994; Hare and Cowen, 1996). Shelf-break upwelling (e.g., Heaps, 1980) and shelf-break fronts can result in regions of increased prey aggregation (Franks, 1992; Perry et al., 1993; Munk et al., 1995) favourable to larval growth and survival.

### 3.2. Mid-shelf and shallow seas

We consider these as regions not within the direct, or continuous, influence of deep ocean current systems, but seaward of the 20 m isobath. Typical depths range between 20 and 150 m. The broad North Sea shelf can be considered a shallow sea

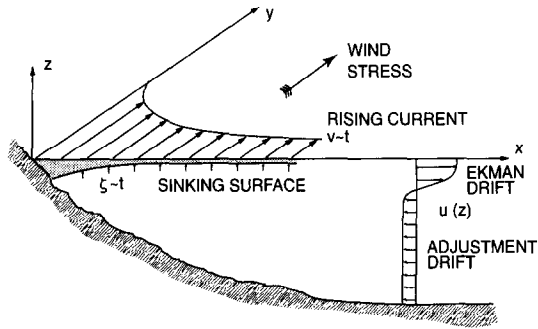


Fig. 3. Wind-driven current generated by the longshore wind-stress (from Csanady, 1981). The near-surface offshore Ekman drift is balanced by interior onshore transport during spin-up of the coastal alongshore current. The alongshore current is in geostrophic balance with the sea surface set-down at the coast.

rather than a component of a 'shelf' system. The physical processes that tend to dominate are wind-driven dynamics and seasonal fluctuations in buoyancy input (freshwater discharges or heating and cooling cycles). The tidal signal can contribute most of the variability in the measured signal (Moody et al., 1984; Pietrafesa et al., 1985) and set the local turbulence levels in the water column. Local topographic features modify this flow and determine location of fronts (Simpson and Hunter, 1974), generate tidal residuals (Loder, 1980), etc. The physical oceanography of mid-shelf regions is perhaps the most studied component of the continental shelf (see Brink, 1987; Huyer, 1990).

### 3.2.1. Wind-driven circulation

Our best understanding and descriptions are for the alongshore wind-driven flow component. This flow component is largely in geostrophic balance with the cross-shore sea surface elevation gradient resulting from the alongshore wind-induced convergence or divergence of mass at the coast (Fig. 3). Coastlines in general are not straight, and for a particular wind-stress field, the currents' response can be understood in large part by examining the effective magnitude of the alongshore wind component. Cross-shore winds, even if comparable in magnitude to along-shore winds, will generate weaker currents due to the absence of the sea-surface set-up/set-down associated with the on/offshore transport in the surface Ekman layer.

While there is cross-shelf flow in frictional Ekman layers, the flow component over most of the water column is mainly in the direction of the alongshore wind stress. Thus, any consideration of the on/offshore flow must also explicitly consider the down-wind current. The thickness of the Ekman layers  $\delta_E$  is given by  $\delta_E = \sqrt{2A_v/f}$ , where  $A_v$  is the vertical eddy viscosity and  $f$  is the local value of the Coriolis parameter. The value of  $A_v$  is a measure of local turbulence levels, with values commonly in the range of  $0.001\text{--}0.05\text{ m}^2\text{ s}^{-1}$ , resulting in typical layer thicknesses of 5 to 30 m. The levels of turbulence increase with the strength of the currents (including non-wind-driven currents such as tidal currents), the wind-stress, and decrease in the presence of stratification.

During the spin-up phase of the coastal current there is cross-shore flow in the interior due to the acceleration of the alongshore current (see Fig. 3). However, in steady wind-driven cases, cross-shelf circulation is confined to the surface and bottom Ekman layers, with the interior (away from the Ekman layers) flowing in the alongshore direction. To generate an on/offshore flow within the inviscid interior other forces or mechanisms are needed in the steady-state case. This external force can be an alongshore pressure gradient force which will balance an on/offshore interior flow, e.g., by a slope of the sea-level (or the density field) parallel to shore (Csanady, 1981; Werner and Hickey, 1983). For narrow (and deep) shelves the pressure gradients associated with deep ocean currents may be impressed across the shelf, while shelves wider than 50 to 100 km (and of depths of 50 m or less) are generally isolated from forcing by the deep ocean regime. Alongshore pressure gradients may also arise due to the variation of sea surface set-ups or set-downs forced by local winds in the presence of irregular coastlines. Hence, variation in cross-isobath transport due to mass divergences may arise from variation in coastal orientation (Werner et al., 1993a).

Remote wind forcing can also contribute to observed currents (e.g., Battisti and Hickey, 1984) and upwelling (Gill and Clarke, 1974). The remotely forced signal can propagate alongshore as a trapped long wave (a Kelvin or a shelf wave) requiring consideration of larger domains to understand locally observed phenomena (Vested et al., 1995).

### 3.2.2. Buoyancy-driven circulation

Buoyancy-driven flows result from differences in temperature or salinity fields. Large-scale buoyancy currents tend to be broad and relatively weak, and to follow isobaths (or  $f/h$  contours), e.g., the equatorward flow component in branches of the Greenland and Labrador currents along the western North Atlantic shelf (Loder et al., 1997). Polachek et al. (1992) invoked the increased magnitude of the outflow of the St. Lawrence discharge to explain the observed increase in off-bank transport of Georges Bank haddock larvae in 1987.

On shelves where salinity increases seaward, there is an additional buoyancy component of along-shelf circulation due to the geostrophic balance of the baroclinic pressure gradient (Leetmaa, 1976). Winter-time cooling off the US east coast has been suggested to generate a cross-shelf 'cell-like' circulation pattern whereby (cold and dense) water sinks at the coast crossing isobaths during its offshore transit and is replaced (by continuity) with onshore flowing water in the mid- and upper-layers. Checkley et al. (1988) suggested that menhaden larvae in the upper water column might use this flow component in their cross-shelf transit.

Examples of smaller-scale buoyancy effects are tidal fronts and internal waves. Seasonal (spring/summer) heating combined with tidal mixing results in the formation of temperature fronts (Simpson and Hunter, 1974; Loder and Greenberg, 1986; Naimie, 1996). This well-known effect generates local circulation features that have been associated with enhanced productivity and retention or aggregation of larvae near the frontal zones (Loder et al., 1988; Sinclair, 1988). The onset of vertical stratification allows for the propagation of internal waves, which has been proposed as a mechanism for cross-isobath transport by Shanks (1983) and Pineda (1991).

### 3.3. Inner-shelf

We define the inner shelf as regions inside the 20 m isobath. Due to the proximity to freshwater (buoyant) discharges, the inner shelf is often characterised by the presence of plumes and coastal fronts (Blanton, 1986; Simpson and James, 1986; Sharples and Simpson, 1993). Tidal currents and mixing tend

to be strong, and in this region behaviours such as orientation to chemical cues (Creutzberg, 1961) and selective tidal stream transport (e.g., Rothlisberg et al., 1983; Rijnsdorp et al., 1985) become viable due to ontogenetic changes in larval behaviour.

Another definition of the inner shelf of depth  $h$  can be the region where the surface and bottom Ekman layers merge. The vertical Ekman number  $E_v$  provides a measure of the relative strength of vertical mixing and rotational (Coriolis) effects,  $E_v = A_v/(fh^2)$ . When  $E_v$  is large  $O(1)$ , frictional forces become dominant and rotational (geostrophic) flow components are weakened (Garrett and Loder, 1981). Wind-driven flows and transport of eggs and larvae on the inner shelf are in the direction of the wind (e.g., Nielsen et al., 1997). However, because  $E_v$  can be large, the water column will be 'dragged' as a slab; the role of Ekman layers in generating on/offshore currents is reduced compared to mid-shelf regions (e.g., Csanady, 1981; Blanton et al., 1995) and two-dimensional studies of wind-induced variability in population are valid (e.g., Van der Veer et al., 1997). Leggett et al. (1984) found a correlation between onshore winds and regulation of year-class strength of capelin (whose life-cycle includes spawning in the nearshore and beaches). In the inner shelf and in small embayments the variability of the on/offshore winds is increased compared to the mid-shelf and offshore regions.

The structure of inner-shelf frontal zones depends on the strength of freshwater discharge and vertical mixing within the inner shelf. If mixing is strong ( $E_v$  is large) there will be seaward flow in surface layers and landward flow at depth, i.e., with lighter water tending to 'spill' over denser water as in gravitational estuarine circulation. As  $E_v$  decreases ( $A_v$  is small or  $h$  is large) the along-front flow increases (Garrett and Loder, 1981) and instabilities in the frontal zone (Ruddick et al., 1995; Wheless and Valle-Levinson, 1996) contribute to exchanges between the inner shelf and mid-shelf. While coastal frontal zones inhibit cross-frontal exchange, some phasing between larval vertical migration and the currents' shear may also be necessary to remain within the inner shelf (e.g., Peterson et al., 1979).

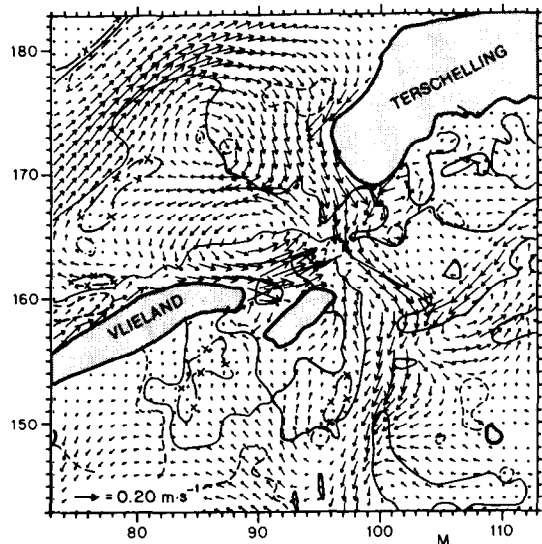


Fig. 4. Mean (residual) circulation in the vicinity of an inlet in the Wadden Sea (from Ridderinkhof, 1990). Spacing between grid points is 500 m.

### 3.4. Near-inlet

We define this as the region within a few tidal excursions of the inlet mouth and dominated by strong tidal currents, nonlinearities and tidal residuals. The small scales of the flows (eddies, fronts, residuals, etc.) makes this region difficult to sample and model (Fig. 4). Additional complications are flood and ebb channels, tidal ebb deltas, sills, dredged channels and other features (e.g., Wiseman et al., 1988; Seabergh, 1988). The effect of these topographic features is very important as tidal shear dispersion is maximised when the length scale of these features becomes comparable to the length scale of tidal excursions (see Zimmerman, 1986; Ridderinkhof and Zimmerman, 1990).

Kapolnai et al. (1996) found that larval ingress into estuaries may depend on location relative to the inlet mouth, the phase of the tide at the time of arrival by the larvae to the inlet mouth, and the presence of a buoyant plume. In the absence of stratification, the most favourable region for ingress is on either side of the inlet. The presence of a buoyant plume modifies this result due to trapping of larvae inside the plume, making them available to ingress for longer periods. Stratification also appears to diminish the potential

for ingress for particles located to the right of the inlet (viewed from the inlet mouth looking seaward). This is related to the Coriolis effect on the plume and in the Southern Hemisphere the effect would be to the left side of the inlet mouth. These results may have pronounced implications on larval ingress if jetties and other structures are constructed to aid navigation or beach sand replenishment (see also Wang, 1988).

### 4. Variability in physical factors and recruitment

Recruitment to the estuary will be a function of the processes discussed in Section 3. In Table 2 we provide a synthesis of physical processes by region, the source of variability and the effect of the processes during the cross-shelf transit of the larvae. Note that not all references provided deal with flatfish species. Although the references we provide show relationships between environmental variability and the survival, dispersal or transport of larvae, these studies tend to focus on small windows of the life cycle and/or on small subsets of the population. To date, no study has been able to follow for any particular year (or set of years) the variability in physical processes and explicitly link it with variability in populations.

By dividing the continental margin into four regions, offshore, mid-shelf, inner-shelf and near-inlet regions, we suggest that larvae move sequentially through one or more regions. Variability in physical processes in one region can affect larval characteristics (number, size, condition, age, etc.) available to the next region along the transport path. In this way variability can be introduced at any point along the pathway to the nursery ground. How this variability is manifested in the recruiting population will depend on, among other things, when it was introduced and what the distribution of larval characteristics may have been. For example, small-scale turbulence becomes relatively less important as larvae grow, making variability in local turbulence a significant process for small larvae and less so for larger larvae.

An analogy between points in space and time at which variability may be introduced to recruitment and the obstacles of a steepchase race may be appropriate. The best times in the race are usually set



Table 2

Physical processes on the continental shelf, sources of variability and their effect on pelagic stages of marine species including flatfish

Region and physical process or system	Source of variability	Effect	References
<i>Shelf edge</i>			
Western boundary currents	Mean position, meanders, eddies	Cross-shelf transport, expatriation, nutrient supply	Hare and Cowen (1996); Hofmann and Ambler (1988); Stegmann and Yoder (1996); Checkley et al. (1988)
Eastern boundary currents	Instabilities, jets, squirts, winds	Cross-shelf transport, nutrient supply	Hofmann et al. (1991); Botsford et al. (1994); Parrish et al. (1981); Sinclair et al. (1985)
Others (shelf-edge fronts and upwelling)	Winds, rings, tidal turbulence, internal tides	Cross-front exchange, transport, expatriation, nutrient supply, prey aggregation	Hare and Cowen (1991); Heaps (1980); Munk et al. (1995); Shelton and Hutchings (1982)
<i>Mid-shelf and shallow seas</i>			
Wind-driven flows	Wind direction and intensity, storm frequency	Transport, turbulence intensity (encounter rates)	Bartsch et al. (1989); Hermann et al. (1996); Sundby and Fossum (1990); Lasker (1975)
Frontal zones	Wind intensity, heating, tidal mixing	Prey aggregation, retention areas	Cushing (1974); Sinclair (1988); Simpson and Hunter (1974)
Heating and cooling	Diurnal and seasonal cycles	Absolute temperature, growth, spawning location, stratification, internal wave transport	Brander (1995); Frank et al. (1990); Denman and Gargett (1995); Shanks (1983)
Tides	Spring-neap cycle, nodal cycles	Intensity of residuals, frontal location, turbulence, transport	Garrett and Loder (1981); Parker et al. (1995); Metcalfe et al. (1993)
<i>Inner shelf</i>			
Wind-driven flows	Wind direction and intensity	Transport, upwelling/nutrient supply	Boehlert and Mundy (1988); Nielsen et al. (1997); Nelson et al. (1977); Yoder (1983); Leggett et al. (1984)
Buoyancy-driven flows	Freshwater discharge	Transport, retention, chemical cues	Ruddick et al. (1995); Creutzberg (1961)
Tides	Spring-neap cycle, nodal cycles	Intensity of residuals, formation of fronts, turbulence, transport	Loder and Garrett (1978); Rothlisberg et al. (1983); Metcalfe et al. (1990)
<i>Near-inlet</i>			
Wind-forcing	Wind direction and magnitude	Transport	Wang (1988); Epifanio et al. (1989)
Tides	Spring-neap cycle, lunar phase, shifting bathymetry	Transport, residuals	Ridderinkhof and Zimmerman (1990); Roessler and Rehrer (1971); Rijnsdorp et al. (1985)
Buoyancy-driven flows	Freshwater discharge	Plumes, fronts, two-layer gravitational flow	Kapolnai et al. (1996); Wheless and Valle-Levinson (1996)
<i>Banks</i>			
Tides	Spring-neap cycle, nodal cycle, internal tides	Intensity of residuals, turbulence, transport	Loder et al. (1988); Werner et al. (1993b, 1996); Perry et al. (1993)

Table 2 (continued)

Region and physical process or system	Source of variability	Effect	References
<i>Banks</i> (continued)			
Fronts	Winds, heating, tidal mixing	Transport, retention, prey aggregation	Naimie (1996); Incze et al. (1996)
Neighbouring currents and remote forcing	Upstream inflow, deep ocean currents	Transport, retention	Flierl and Wroblewski (1985); Polachek et al. (1992)
Wind-forcing	Wind direction and intensity, storms	Transport, retention, prey supply	Lough et al. (1994); Lewis et al. (1994); Hannah et al. (1997)

by competitors who do not trip or stumble over the obstacles and hurdles. This would be akin to all the physical factors being favourable to the cross-shelf transport of the larvae, hence resulting in strong recruitment to the estuary (all other conditions being equal, e.g., spawning stock biomass, etc.). Knocking down a hurdle may result in slower times, but the race is still completed. For example, a storm event may alter the feeding environment leading to a change in growth rate or survival that would result in a change in larval condition (or numbers) at the inlet. Finally, the worst-case scenario results from tripping over one or more hurdles and not completing the race. The poorest recruitment to the estuary may be either a catastrophic event (e.g., extreme cold affecting eggs at a spawning site) or due to a combination of adverse factors in a given year: washout events, unfavourable winds, etc.

### 5. Case studies of physical and population variability

There are many case studies linking physical variability to variability in marine fish populations. On decadal time scales, fluctuations associated with aperiodic climatic signals such as El Niño/Southern Oscillation and North Atlantic Oscillations are well known and discussions can be found in textbooks such as Mann and Lazier (1991). Possible responses of fish-stocks to future climate change scenarios are explored in Frank et al. (1990). The physical mechanisms include basin-scale changes in wind fields and water mass distributions, shut-off of nutrient supply, etc. Deterministic low-frequency signals such as the 18.6 year nodal tidal cycle are beginning to be recog-

nised and await longer time series to determine their importance (e.g., Loder and Garrett, 1978; Parker et al., 1995).

On interannual periods, winds are perhaps the most intensely studied abiotic factor contributing to variability in populations. Nelson et al. (1977) and Yoder (1983) examined the wind as a driving mechanism in recruitment variability of fish species off the US east coast, and similar attempts off the US west coast are given in Parrish et al. (1981). These studies are largely based on bulk indices. Recently more mechanistic studies have appeared in the literature and a more integrated picture has emerged using three-dimensional descriptions of the flow fields.

Checkley et al. (1988) argued that spawning, subsequent development, and onshore transport of menhaden larvae would be aided by a sequence of events triggered by winter storms near the western wall of the Gulf Stream in the US South Atlantic Bight. These storms, with a strong northeastward wind component, would cause upwelling of warmer waters at the shelf edge that may subsequently be entrained on the shelf. Larvae spawned into these higher-temperature and nutrient-enriched waters would develop more rapidly, and encounter favourable feeding conditions associated with the influx of upwelled nutrients from offshore. Subsequent cross-isobath transport would be driven baroclinically by the density difference between the cold inshore waters and the warm offshore waters. Population fluctuations in this scenario would arise from the interannual variability in the wind field, cold-air outbreaks, the frequency of upwelling events, the position of the Gulf Stream, etc.

Bartsch et al. (1989) modelled North Sea circulation to investigate the effect of varying wind fields on larval herring transport from spawning grounds in the west to nursery areas in the east. They simulated the 1987/1988 recruitment season using a 3-D model which included tidal forcing, baroclinicity, surface wind stress, atmospheric pressure fields, as well as simulated diurnal larval migrations. They found that meteorological events for this period differed from long-term means and resulted in significant changes in residual circulation. This circulation is suggested to have resulted in loss of a portion of the year class in the Norwegian coastal current and therefore to have contributed to fluctuations in recruitment.

Hermann et al. (1996) modelled the Shelikof Strait region in an attempt to understand recruitment variability in walleye pollock *Theragra chalcogramma*. Their results suggested that both winds and runoff influenced recruitment variability. However, (dissimilar) similar physical conditions resulted in (similar) dissimilar recruitment, suggesting that the mechanism governing recruitment variability was not completely isolated.

Lough et al. (1994) explored interannual variability of cod recruitment by using wind fields and upstream inflows for two different years 1982 and 1985 considered as 'bad' and 'good' cod years, respectively) with a three-dimensional hydrodynamic model of Georges Bank. They concluded that larvae lost from Georges Bank were primarily in the surface layers, and that the loss depended upon the magnitude, timing and direction of wind stress. However, high retention and recirculation on the Bank was demonstrated for larvae near the bottom and no clear results were obtained to account for the observed variation in the 1982 and 1985 year classes (Fig. 5).

The model-based studies of Bartsch et al. (1989), Lough et al. (1994) and Hermann et al. (1996) attribute interannual variability mainly to differences in large-scale transport pathways or the occurrence of retentive features. In the previous sections we have discussed other mechanisms, some at very small scales, which contribute to recruitment variability (Table 2). An example of the intersection of large- and small-scale physics affecting recruitment is given in Werner et al. (1996) in which the effect of the feeding environment — modified by turbulence at the smallest scales — on larval growth

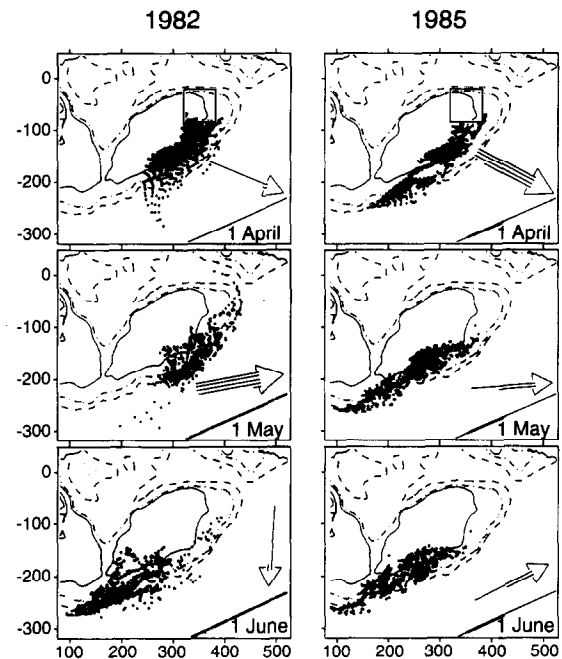


Fig. 5. Particle locations corresponding to modelled larval cod distributions on Georges Bank for 1982 and 1985 under observed mean monthly (March through June) winds. Spawning occurred in the square box on 1 March. The 70 m isobath is indicated by the solid line, the 100 m isobath by the dot-dash line and the 200 m isobath by the dashed line. Each full shaft on the wind vector corresponds to a stress of 0.04 Pa; the axes are in km. Taken from Lough et al. (1994).

and survival was examined. They found that regions of larval survival (with growth rates comparable to field values) coincided with the hydrodynamically retentive subsurface (deeper than 25 m) regions of Georges Bank. However, these retentive regions were a subset (Fig. 6) of those defined by Werner et al. (1993b) and Lough et al. (1994). The increase in larval survival in these smaller areas was due to an enhancement of contact rates and effective prey concentrations by turbulence within the tidal bottom boundary layer (Fig. 7).

## 6. Discussion

It has been argued that covariation in environmental forcings may make identification of the causes of recruitment variability a difficult, if not impossible task (Fogarty, 1993). Programs with regional focus

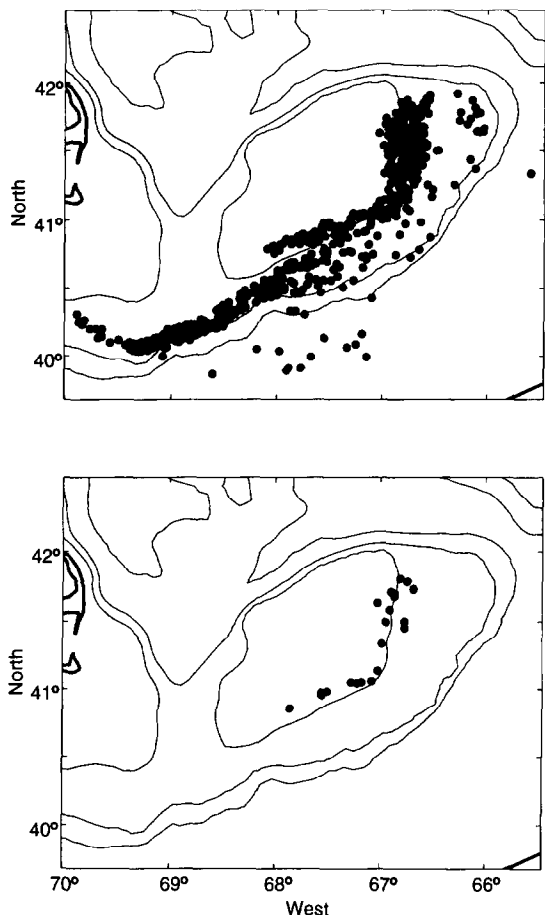


Fig. 6. Locations of Georges Bank larval cod at day 60 post-spawn during late-winter/early spring. Spawning location is as in Fig. 5. Top panel shows particle locations with no feeding, growth or mortality; bottom panel shows surviving larvae after the inclusion of feeding, growth and mortality. Surviving larvae straddle the 60 m isobath with the average depth of the larvae approximately 50 m. Contours are the 60, 100 and 200 m isobaths. Adapted from Werner et al. (1996).

(such as GLOBEC, SABRE, Mare Cognitum, etc.) are attempting to deal with this difficulty through intensive field and modelling efforts. This is admittedly a non-trivial task given the geographic and time scales involved. However, recent advances in understanding and modelling biological and physical processes may provide inroads into disentangling environmental (and biological) signals.

One approach showing promise is coupling individual-based models (IBMs; DeAngelis and Gross,

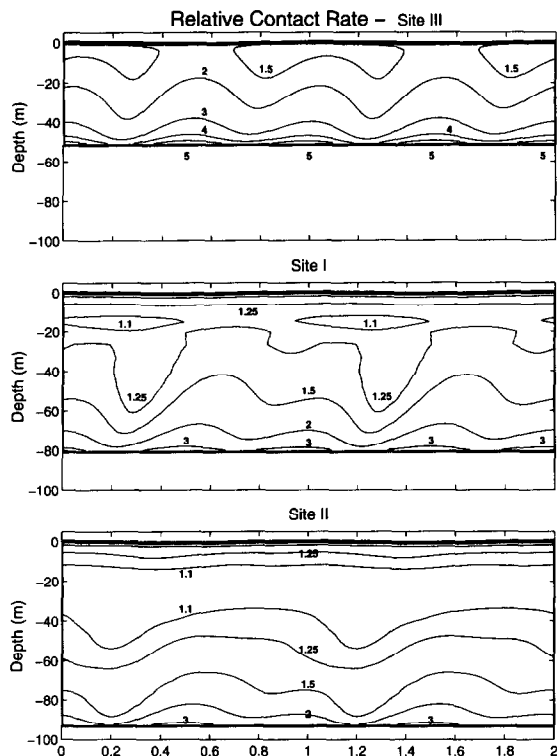


Fig. 7. Dimensionless predator-prey contact rates (turbulence-enhanced/no turbulence) as a function of depth during two tidal cycles on the southern flank of Georges Bank at three sites: a shallow site (*Site III*), an intermediate depth site (*Site I*) and a deep site (*Site II*). The inclusion of turbulence in feeding processes increases larval-prey contact rates at depth (due to tidal turbulence) by a factor of 2–5 over the no-turbulence case at each site. From Werner et al. (1996).

1992) and three-dimensional hydrodynamic models. IBMs attempt to reconstruct the variance in populations by modelling processes at the individual organism level (Houston et al., 1988; Crowder et al., 1992; Cowan et al., 1996). The importance of fully three-dimensional representations of physical processes has been noted in a number of different studies (e.g., Wroblewski and Hofmann, 1989). Progress in IBMs can be seen in Rose et al. (1996), who modelled the complete life cycle of winter flounder by coupling an early life history IBM with an adult age-structured model. Similar progress has been shown in the development of spatially explicit IBMs incorporating three-dimensional environmental variability in the study of early life stages of marine fishes (Hermann et al., 1996; Werner et al., 1996). A combination

of these two model approaches, full life-cycle modelling and spatially explicit IBMs, along with a ‘sensitivity analysis’ approach, would allow examination of the population-level implications of variation in hydrodynamics as well as variations in any other modelled process or variable. This type of analysis would also provide the ability to rank processes in terms of the impact on recruit strength. Similar approaches have been the basis for many insights into important processes in the life histories of a number of different species (Crouse et al., 1987; Lande, 1988; Quinlan, 1996).

### 6.1. Issues and future work in hydrodynamic modelling

Hydrodynamic numerical models have become de facto tools in the study of environmental fluctuations and their effect on marine fish populations. There are several numerical models for shelf circulation that have reached similar levels of sophistication and which have been used in interdisciplinary studies (e.g., Blumberg and Mellor, 1987; Backhaus, 1989; Haidvogel et al., 1991; Lynch et al., 1996). While they all have been used to explore (successfully) the different regions of the shelf, they are not ‘finished products’ and share similar challenges.

First, to carry out long-term simulations it is necessary to include appropriate boundary conditions to account for exchanges of limited area domains with neighbouring regions, e.g., effects of remotely forced flows, ‘upstream’ inflows, etc. One approach still at the research stage is to use data assimilation techniques (e.g., Aikman et al., 1996). These simulations even if successful, can be costly and require continuous input of data that may be difficult to acquire.

The second challenge is coupling across dynamically distinct regions: the shelf-edge (where oceanic and shelf regions meet), the continental shelf proper, and the nearshore (where shelf and inner-shelf dynamics merge). Again, computational costs will be high if the entire range of scales is to be captured in a single simulation. And finally, there are mathematical challenges to the formulation of the models themselves. For example, the long-term behaviour of nonlinearities in these simulations is not understood and neither is their behaviour at small scales. Both of

these are subjects of continued study by numerical analysts.

### 6.2. Relationship to management

Hilborn and Walters (1992) state that “fisheries management involves the use of statistical and mathematical calculations to make quantitative predictions about the reactions of fish populations to alternative management choices.” They were stressing the fact that management attempts to make quantitative predictions about an intrinsically variable process and that no single decision is always the correct one. The acuteness of this uncertainty was laid out in a consideration of human population and economic growth and the responses (regime shifts) already seen in some fisheries (Beamish, 1995). The difficulty that management faces, in some cases, is one of increasing resource utilisation and potentially nonreversible ecosystem shifts.

A watershed event in fisheries management was the development of the stock–recruit curve (S–R curve) which related spawner biomass to recruits under a set of assumptions concerning the mechanisms of mortality in the population (see Larkin, 1989). S–R curves require few parameters to be estimated and provide a handy tool for managers, but the large variance around these curves is well known. This variance, like ‘diffusion’ in hydrodynamic models, arises from unresolved processes — the model simply does not account for enough of the dynamic. To account for this lack-of-fit, correlations between different environmental variables and recruitment have been sought for quite some time (see Beamish and McFarlane, 1989; and Beamish, 1995, for a number of recent examples). These correlations often identify linkages between particular environmental variables and recruitment — sometimes recruitment in a number of stocks simultaneously. When a relationship is found, an attempt is made to modify the S–R curve to generate a better model-to-data fit (Ricker, 1958; Tang et al., 1989).

Larkin (1989) noted that fisheries research had taken two routes after the development of the S–R curve. One direction involved the development of further stock assessment models, while the other involved exploration of mechanisms behind the variation in recruitment. Hydrodynamic models, or more

specifically, linked physical–biological models fall into the mechanistic class of research. These models are somewhat different from most of those discussed by Larkin (1989) (e.g., correlative studies, multi-species models, etc.) in that we can explicitly explore the interactions between physics and biology.

Megrey et al. (1996) provide an example of how regionally focused programs can contribute to recruitment forecasts. Certain key processes impacting recruitment success were identified through field and modelling efforts. Indices, roughly describing these processes, were then used as input into a stochastic switch model of the recruitment process. Each input index in effect modified the mortality experienced by the cohorts in a year class. For example, wind stress was found to influence mortality, with weak winds resulting in lower mortality than strong winds. A simulation would therefore classify the wind stress during the year and then adjust mortality accordingly. This technique does not yet provide quantitative recruitment forecasts, but Megrey et al. (1996) found that they produced statistically similar time series to those observed in the field.

### 6.3. Concluding remarks

Over the past decade we have made considerable advances in our ability to examine the coupling of physics and biology in the field and the laboratory. We have also begun to use the detail provided by available models to explore the couplings of behaviour and abiotic factors in realistic settings. These developments are very encouraging, but the initial question was whether or not physical variability can explain recruitment variability. The answer is yes in that physical processes directly or indirectly affect populations as suggested by studies reviewed above. As such, physical variability must be part of the answer. However, quantitatively stating how much recruitment variability is caused by a particular forcing or forcings is made difficult by covarying environmental signals, mediating or masking biological processes including predation (e.g., Sissenwine, 1984; Leggett and DeBlois, 1994), and the inability to isolate a particular process. Unravelling these signals is the goal of a number of efforts currently underway (e.g., Wiebe et al., 1996).

Two paradigms outlined in Section 2, hydro-

graphic containment (combining match/mismatch and migration triangle) and member/vagrant provide frameworks within which answers to this question should be sought. The member/vagrant hypothesis explains population pattern, abundance and variability using physically based arguments, while the hydrographic containment hypothesis uses a combination of biological and physical processes to explain those same three characteristics. Acceptance of one hypothesis over the other would result in a different management strategy, i.e., if physics alone can explain fluctuations in populations an important consequence is that an ecosystem management approach may not be warranted (Sinclair and Page, 1995). It is clear, therefore, that we need to seek answers to the next level of questions: how do we test existing paradigms and provide better information for use in management decisions?

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