Understanding the role of turbulence on fisheries production during the first century of ICES

Brian R. MacKenzie

Since its inception, ICES has been concerned with the effect of hydrography on the abundance and distribution of fish and fish catches. One of the earliest and most significant oceanographic findings made by the ICES community was the influence of vertical mixing and turbulence on seasonal plankton production processes. This discovery, acquired over several decades of investigation, led to three major theories of fish population regulation and demonstrates the underlying impact that turbulence has on seasonal plankton and fish production. More recently, moderate levels of turbulence and upwelling have been shown to produce the highest recruitment among clupeid populations inhabiting major upwelling areas. The mechanism responsible for this pattern is a balance between the positive and negative effects of both turbulence and upwelling on plankton production, larval feeding, and advective processes. In one ICES upwelling zone (Bay of Biscay), recruitment of a local clupeid is related to some of these processes. This knowledge is contributing to the ICES assessment process for this stock. Frontal zones on continental shelves within the ICES Area are also moderately turbulent environments, may also have an impact on fish recruitment, and have received particular attention by colleagues within the ICES community. In future, an understanding of how turbulence affects fish and plankton production at upwelling and frontal zones and during storms could help justify including additional environmental and ecosystem information in recruitment and catch prediction models.

Keywords: fish production, fronts, ICES, spring bloom, storms, turbulence, upwelling.

Introduction

But the great fisheries of temperate seas probably depend upon the start of production in turbulent waters. - D. H. Cushing (1989).

Turbulence is an oceanic property which has a major influence on life in the sea. Phytoplankton species composition (Margalef, 1978), production rates (Lewis et al., 1984), plankton foodweb structure (Kiørboe, 1993), feeding rates (Dower et al., 1997; Kiørboe, 1997), and distributions (Lasker, 1975; Mackas et al., 1985; Serner et al., 1999) have all been shown to co-vary with turbulent intensity. Since turbulence is generated or suppressed by many different kinds of physical processes (e.g., tides, winds, buoyancy inputs, convection), the structure and functioning of aquatic ecosystems are commonly being perturbed by turbulent water motion of various intensities and scales.

In this paper, I describe how this turbulence affects fish and fish production and how this understanding has developed during the first 100 years of ICES. To be consistent with the theme of this session of the Symposium ("Variability at all scales and its effect on the ecosystem"), I will consider processes covering both large and small scales.

Large-scale influences (decadal–century; whole basin)

Arguably one of the most important influences of turbulence on fisheries production is its role in vertical mixing and seasonal plankton production cycles in temperate-boreal waters. In particular, turbulence generated by winds, tides, and convection is responsible for the replenishment of nutrients during the winter that allows phytoplankton blooms to occur in the following spring (Cushing, 1975, 1989; Mann and Lazier, 1996). The initiation of these blooms depends partly on a relaxation of turbulent mixing so that phytoplankton remain longer in
the photic zone. The blooms lead to the seasonal increase in zooplankton production and biomass which becomes an important food source for fish larvae and juveniles, as well as for adult zooplanktivores (e.g., herring, sprat; Cushing, 1975).

The role of turbulence on the timing (i.e., initiation, delay, duration) of the spring plankton bloom in temperate-boreal waters is central. Specifically, the reduction in water column turbulence during the transition from winter to summer (e.g., due to reduced wind speeds and increasing temperatures) is critical for determining when the onset of rapid phytoplankton growth occurs after nutrients have been re-mineralized and re-supplied to the surface layer during the autumn-winter mixing period (Mann and Lazier, 1996; Huisman et al., 1999). Excessive turbulence in the spring will delay the initiation of the phytoplankton bloom because phytoplankton cells will be mixed below the photic zone where light-limitation will suppress growth rates. As a result, a sequence of turbulence "events" (i.e., strong followed by calm) is necessary to initiate the spring plankton bloom.

This sequence of events (re-mineralization and strong winter mixing that replenishes nutrients followed by greatly reduced spring mixing that allows phytoplankton to remain in the photic zone) is a highly regular and predictable feature of temperate-boreal habitats. As a result, these environments are characterized by strong seasonal pulses in plankton production, although their exact timing, magnitude, and duration can vary greatly from year to year. Nevertheless, at decadal–century time scales and over large areas of the sea, they are consistent features that provide important environmental signals to other biota in the ecosystem.

The role of ICES in defining these links between turbulence, plankton production, and fisheries production has been enormous. In fact, a century ago, many of the same workers who laid the organizational foundations for ICES were also instrumental in demonstrating that a seasonal plankton production pattern existed, that the seasonality itself depended on the availability, via vertical mixing and turbulence, of nutrients for phytoplankton growth, and that the seasonality also depended on phytoplankton becoming exposed in the spring to proper light and nutrient conditions. The fundamental observations of phytoplankton abundance and distribution were made by scientists working in the late 1800s and early 1900s (Mills, 1989). These scientists included Hensen, Brandt, and Lohman in Kiel, Gran and Braarud in Oslo and St. Andrews (Canada), Whipple in Boston, Riley in Woods Hole, and Sverdrup in Norway.

One of the key roles that ICES played after its inception was the development of standardized techniques for measuring nutrient concentrations (Mills, 1989). These techniques were spread among colleagues by meetings and courses arranged by ICES and, for the first time, enabled comparisons of phytoplankton abundance/distribution with nutrient concentrations (Mills, 1989). Based on the empirical field observations, it was possible to demonstrate that phytoplankton abundance was associated with some of the variations in nutrient concentrations. These observations were key to demonstrating that the spring bloom was related to vertical mixing and stabilization processes (e.g., Gran and Braarud, 1935; Riley, 1942; Sverdrup, 1953).

Notably one of the motivations to develop an international body for marine science investigations was the desire to improve the possibility for predicting fluctuations in the important fish stocks of northern European waters. It was understood at the time that hydrographic variability was part of the cause of such variations (e.g.,

Figure 1. Schematic representation of Cushing's match–mismatch hypothesis (see Cushing, 1990). The peaks illustrate the seasonality of the abundance of fish eggs, larvae, and larval food. The striped area indicates temporal overlap between larvae and prey.
Hjort, 1914), but the mechanisms were only vaguely known and not quantified (e.g., owing to changes in timing and location of migration routes, effects on egg and larval mortality rates). However, as more knowledge of the spring plankton bloom became available, attention began to focus on the role of this event in fish growth and survival.

Cushing (1975, 1990) observed that many of the most abundant fish species in temperate-boreal waters (e.g., cod, haddock, herring) spawned in the spring during or shortly after the spring plankton production peak and that spawning times were relatively stable compared with the temporal variability in onset of the spring plankton bloom. He and others before him (notably Hjort, 1914) also noted that the larvae produced by these fish were poor swimmers, yet needed to find sufficient food to grow and survive when their yolk reserves became depleted. Cushing suggested that one of the conditions for a strong year class was therefore overlap in time and space of larvae with their prey, and this theory came to be known as the "match-mismatch" theory (Cushing, 1990; Figure 1).

This theory has since formed the basis of numerous fisheries research programmes throughout the North Atlantic and farther abroad. Unfortunately it has proven extremely difficult to verify because of various sampling problems, measurement error (Heath, 1992; Leggett and deBlois, 1994; Cushing, 1995a), and the possibility that larvae and juveniles may not be food-limited (Sinclair, 1988). In particular, and perhaps somewhat surprisingly, there are relatively few studies which have directly compared plankton production, growth or condition of larvae or 0-group juveniles, and recruitment time-series. Thresher et al. (1989) appear to have conducted one of the few investigations to demonstrate that fish recruitment was strongly correlated with phytoplankton production peaks following storm-induced mixing (Figure 2). Other colleagues have observed relationships between larval/0-group growth and recruitment (Campana, 1996; Ottersen and Loeng, 2000), but it is unclear to what extent the growth rates were driven by variations in temperature or food supply.

Nevertheless, the influence of turbulence on seasonal plankton production and fish ecology is great. It seems obvious that large parts of continental shelf regions would be considerably less productive if turbulence during winter were too weak to remix the water column and resupply the photic zone with nutrients. In such a case, the productivity and fish biomass of these regions would probably decrease to much lower levels.

Alternatively, perhaps better evidence for the match–mismatch theory could be found at the much longer scale of life history adaptation (decades–centuries) in terms of spawning time and location. Few species in temperate-boreal latitudes spawn in winter when phyto- and zooplankton concentrations are low, whereas most spawn later in the spring or summer when food concentrations are higher. However, even at this scale, there are other explanations (e.g., the member-/vagrant theory of population maintenance; Sinclair, 1988) for the timing of spawning in fish populations.

**Interannual influences**

Turbulence has major effects on fish production in upwelling areas (Bakun, 1996). First, Lasker (1975, 1978) has shown that storms inhibit formation of phytoplankton patches required by first-feeding anchovy larvae. This observation has led to the development of the
"stable-ocean" theory of recruitment variability. Second, Peterman and Bradford (1987) have shown that storm frequency directly affects larval anchovy mortality rates (Figure 3). Third, Cury, Roy, and Bakun have shown that recruitment of pelagic clupeids in several of the world's major upwelling zones is optimal at intermediate levels of upwelling and turbulence intensity (Cury and Roy, 1989; Bakun, 1996; Figure 4). In many of the systems studied, the turbulence and upwelling are strongly correlated (Cury and Roy, 1989) because both are estimated indirectly from windspeed.

The role of upwelling and turbulence in these systems is believed to be related to general principles of biological (plankton) production in marine ecosystems (Cury and Roy, 1989; Bakun, 1996). Years with low upwelling and turbulence have low phytoplankton production because nutrients are not mixed into the surface layer at high rates. As a result, the base of the foodweb is smaller, and there is less food for zooplankton whose production rates remain low. Moreover, we now know that in low turbulence situations, pelagic foodwebs will be dominated by smaller phytoplankton species (Margalef, 1978; Kiørboe et al., 1988) and have more trophic links due to the microbial food web (Kiørboe, 1993, 1997). This means that the foodweb is less efficient at transferring energy from phytoplankton to zooplankton (Cushing, 1989; Legendre, 1990; Kiørboe, 1993), and that zooplankton production rates and abundances will be lower. As a result, it is assumed that larvae will have lower feeding, growth, and survival rates during these years.

In comparison, when upwelling intensity and turbulence are too strong, the phytoplankton will be light-limited owing to excessive vertical mixing. Zooplankton concentrations will still be low, and zooplankton distributions will be more homogeneous than in calmer conditions. Fish larvae will, therefore, have difficulty finding high concentrations of prey required for high growth and survival rates (Lasker, 1975, 1978). Moreover, the high upwelling intensity favours advection of eggs and larvae away from the coastal area and hence loss of offspring from the population (Roy, 1998). Both the low and high turbulence/upwelling regimes are, therefore, predicted to result in low recruitment.

In contrast, an intermediate level of turbulence and upwelling appears to produce the oceanographic conditions that lead to highest recruitment (Figure 4). Intermediate intensities of turbulence and upwelling result in moderately high growth rates of phytoplankton because the cells experience optimal light and nutrient conditions. The higher mixing intensity results in a simpler foodweb with a higher proportion of diatoms than in the calmer situation. The simpler foodweb and higher concentration of phytoplankton stimulates zooplankton production rates, which in turn increase zooplankton concentrations. Since the turbulence intensity is moderate, some of the phytoplankton and zooplankton can remain aggregated in patches, thereby providing larvae and juveniles with relatively high concentrations of prey. The moderate upwelling intensity will help to retain eggs and larvae in coastal areas where survival is probably higher (Roy, 1998). Lastly, the moderate turbulence regime is also highly advantageous for the feeding of individual larvae on their prey (see below).

Much of this work has been conducted outside the geographical framework of ICES because most of the ecosystems lie beyond the North Atlantic. However, the biological oceanographic basis (e.g., vertical mixing and plankton production, role of patchiness in larval feeding success, advection) for the statistical analyses have been discussed and presented in various ICES fora (e.g., Lasker, 1978; Parsons et al., 1978).
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There are few upwelling zones within the ICES Area and, therefore, the influence of these findings on fish production and management there may be limited to an improved general understanding of how hydrographic conditions might influence fish stocks. However, in one of the larger ICES upwelling zones (Bay of Biscay), it has recently been shown that recruitment to the anchovy stock is strongly related to windspeed and upwelling intensity in ways consistent with the patterns seen by Bakun and colleagues (Borja et al., 1998; ICES, 2000). Notably for the Biscay anchovy stock, this environmental information was used to provide inputs to the short-term catch predictions and to justify a reduction in fishing effort in 2000 to conserve the stock (ICES, 2000).

This step indicates that knowledge of oceanographic processes affecting the stock may have important practical benefits for fisheries management. It also suggests that ICES has improved its understanding of how hydrography and, in particular, upwelling and turbulence affects fish production in at least one of its stocks.

Turbulence also affects plankton, and probably also fish, production in other ways at interannual time scales. For example, frontal zones (Simpson and Hunter, 1974; LeFevre, 1986) appear to have some (but certainly not all) of the same turbulence and plankton production characteristics of upwelling zones (Cushing, 1995b; MacKenzie, 2000). These areas often have more larvae and 0-group juveniles than neighbouring areas (Buckley and Lough, 1987; Munk et al., 1995, 1999). Their importance for both plankton production and aggregation, and as young fish nursery areas, has received much attention among scientists within and outside the ICES community (Kiorboe et al., 1988; Munk et al., 1995, 1999; Nakata et al., 1995; St. John and Lund, 1996; MacKenzie and Werner, 1997) and also within its Cod and Climate Change Programme (ICES, 1994). As a result, many researchers have presented findings at ICES Statutory Meetings and Annual Science Conferences on how frontal processes affect the distribution and production of both fish and plankton (e.g., Christensen et al., 1985; Kiorboe and Johansen, 1986; Munk et al., 1986; Richardson et al., 1986). However, the influence of fronts on fish recruitment is still undetermined, but since their formation, intensity, location, and duration are partly climatically determined (LeFevre, 1986; Bowers and Simpson, 1987), it is possible that the mixing and turbulence associated with fronts could contribute to fish production. The issue remains unresolved. Consistent with this possibility, however, are statistical analyses of the influence of various environmental factors on fish recruitment. These studies frequently show that turbulence-related variables (e.g., windspeeds, stratification, freshwater run-off, salinity) can have significant impacts on recruitment in ICES fish stocks (Shepherd et al., 1984; Svendsen et al., 1995).
Small-scale (individual-level) influences

In recent years, the influence of small-scale turbulence on plankton has become a research focus. One part of this focus has been the role of turbulence on feeding rates between planktonic predators and prey. Rothschild and Osborn (1988) developed a theory for encounter rates between predators and prey which demonstrated that turbulent water motion at small scales (cm-mm) can increase the apparent prey concentration perceived by planktonic predators. This result means that encounter rates are higher in turbulent water than in calm water, if other factors (especially food concentration) remain unchanged.

These findings relate particularly well to fish larvae. The typical size of fish larvae (ca. 3–20 mm) places them in a size range where the small eddies of decaying turbulence still have sufficient energy to affect relative velocities between two separated particles (e.g., a larva and its prey). Notably, at very small size scales (i.e., below the Kolmogorov scale; Sanford, 1997), turbulent motion is greatly reduced owing to viscosity (Sanford, 1997), and little effect on encounter rate is expected.

Turbulent dissipation in the upper layer of the sea is mainly related to windspeed (Oakey and Elliott, 1982; MacKenzie and Leggett, 1993) and in shallow areas also to tidal currents (Simpson and Hunter, 1974; Simpson et al., 1996). Fish larvae encounter rates with prey as predicted from models can be several-fold higher than in calm situations (Dower et al., 1997). Direct laboratory observation of cod larvae feeding on live copepods showed that these predictions agree well with the observations (MacKenzie and Kiorboe, 1995). However, encounter is only one part of the complete predation sequence; predators must also pursue and capture their encountered prey. Models that estimate the success of pursuit in turbulent conditions show that pursuit success deteriorates with increases in turbulence (Matsushita, 1991; MacKenzie et al., 1994; Kiorboe and Saiz, 1995). One of these models has been validated with experimental observations which showed that pursuit success decreased with increasing turbulence (MacKenzie and Kiorboe, 2000; Figure 5), consistent with model predictions.

In the field, these theories are difficult to evaluate because of sampling errors (MacKenzie, 2000). However, Sundby and Fossum (1990) and Sundby et al. (1994) have shown that gut contents of cod larvae increase significantly with windspeed up to ca. 10 m s⁻¹. This suggests that turbulence may also affect feeding rates in nature. However, a large compilation of field studies which considered various biological responses to turbulence (i.e., gut contents, RNA/DNA ratios, otolith growth rates) showed that there was no overall pattern in how turbulence affected these responses (MacKenzie, 2000). Reasons for the inconsistencies (especially sampling deficiencies), and potential ways to overcome them, are detailed in full elsewhere (MacKenzie, 2000). More work at small scales (cm–m) is needed in situ (e.g., direct behavioural observations, improved understanding of the dynamics of patchiness under changing turbulence conditions) to resolve some of these issues.

These relatively new findings of the roles of turbulence at small scales in fish ecology can contribute to the oceanographic basis of statistical relationships between turbulence-related variables and fish recruitment or growth. For example, the overall ingestion rate response of larval fish to changes in turbulence is dome shaped (MacKenzie et al., 1994). This response shape is
Figure 7. Number of citations per year for seven papers investigating how turbulence affects plankton and fish. Citations are from the ISI Science Citation Index database covering more than 3500 scholarly journals.
similar to the dome-shaped response of recruitment in sardine and anchovies to turbulence and upwelling in their habitats (Bakun, 1996). The influence of turbulence on feeding of individual fish larvae is probably a factor that contributes to these statistical patterns along with the plankton production and advection mechanisms outlined above.

Interestingly, copepods appear to live at the border between the viscous and inertial worlds, as defined by the Reynolds number (Naganuma, 1996). Copepods feed mainly in the viscous regime (Re <1), but when attacked by predators, they can escape at velocities in the inertial regime (Re >1). Hence, copepods are one of the few taxa which live at the border of the viscous-inertial worlds, and this may be a reason why they are so abundant in the ocean (Nanaguma, 1996). Copepods also live in the transition regime between laminar and turbulent flow (Re = 1–2000). This Reynolds range is occupied by fish larvae (e.g., a 5-mm larva swimming at 1 body length s⁻¹ has Re = 25). Hence, predation of copepods by fish larvae represents a link between lower and higher trophic levels, and between photosynthetic and fisheries production (Naganuma, 1996). These links are possible because copepods live at the border of important fluid dynamic regimes and because fish larvae themselves begin life at the laminar-turbulent regime (Re ~25), but grow into the turbulent regime (Re >2000) during ontogeny.

Many of the investigations of small-scale turbulence have been motivated by ICES findings, presentations (e.g., Parsons et al., 1978; Roy, 1993), and study groups. Since variations in the intensity of turbulence are partly related to climatic factors, the investigations are relevant to the ICES/GLOBEC Working Group on Cod and Climate Change and to the Working Group on Recruitment Processes. They may also help to interpret environmentally based models of recruitment (Bakun, 1996).

Impact of turbulence-related studies on the marine science community

Several papers showing how turbulence affects fish, fish production, and pelagic ecosystems have had major impacts on the fisheries/biological oceanographic communities. One measure of this impact is how frequently the studies have been cited by subsequent workers. I have conducted a citation analysis of some of these papers to evaluate their total number of citations and annual citation rates. The citation data are compiled from the Institute for Scientific Information’s Science Citation Index, and the analysis includes data until the end of 1999. According to SCI (http://www.isinet.com/products/citation/citsci.html), the index covers 3500 of the world’s leading scholarly journals.

I have chosen seven papers for the analysis. The choice no doubt reflects the personal bias of the author, and apologies go to those whose papers are excluded. Nevertheless, the citation data show that these papers have been widely read and used by many other colleagues (Figures 6 and 7). In particular, the papers by Lasker (1975), Rothschild and Osborn (1988), Cushing (1989), and Curry and Roy (1989) are notable because they deal explicitly with fish and fisheries, whereas the other papers consider hydrography or lower trophic levels. Nearly all of the papers have been cited on average about 10 times per year (Figure 7).

A future role for ICES in evaluating how turbulence affects fish and fish production?

ICES has been very supportive of studies investigating biological-physical interactions and how these interactions might influence fish populations (e.g., the Baltimore Symposium on Recruitment Dynamics of Exploited Marine Populations: Physical-Biological Interactions in 1997, Cod and Climate Programme, Working Group on Recruitment Processes). A large amount of work remains to be done to fully understand how fish and pelagic ecosystems respond to turbulence (see, for example, reviews by Kierboe, 1991; Bakun, 1996; Dower et al., 1997; Marrasé et al., 1997; Sanford, 1997; MacKenzie, 2000) and to identify which of the many oceanographic processes that turbulence influences have the most impact on fish growth and survival. More work is needed, and continued support from ICES for combined biological-physical oceanographic investigations is needed.

It is still too early, in many cases, to link the consequences of changes in turbulence or other environmental variables to entire fish populations. However, as such links become available, it may become desirable for ICES to assist with the incorporation of this information into new fish population and assessment models. One role for ICES in future could be to assist with the development of more ecologically based models. Notably, some encouraging steps in this direction are being taken (e.g., Study Group on Incorporation of Environmental Processes into Assessment Models).

Conclusions

The most important role that ICES has had in understanding how turbulence affects fish production was in identifying the existence of the spring plankton production bloom and the factors controlling it. This was done in the earliest decades of ICES' existence and set the stage for developing at least three major theories of recruitment and population dynamics: the match-mismatch theory, the member/vagrant theory, and the stable-ocean theory. ICES has also supported research programmes on other topics more or less directly related to
turbulence and fisheries by generally encouraging studies of biological-physical interactions. These studies have identified several of the major production characteristics of upwellings, frontal zones, and storms, and their potential importance to fish production.

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