

# Turbulence, larval fish ecology and fisheries recruitment: a review of field studies

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**Abstract** – Fish recruitment varies widely between years but much of this variability cannot be explained by most models of fish population dynamics. In this review, I examine the role of environmental variability on fish recruitment, and in particular how turbulence affects feeding and growth of larval fish, and recruitment in entire populations. One of the main findings is that field studies show contrasting effects of turbulence on feeding, growth and mortality rates in nature and on recruitment. Coincident and multiple variations in ecosystem processes, lack of understanding of how some of these processes (e.g. larval diet composition, feeding behaviour, growth rates, prey patchiness) respond to turbulence, and unavoidable sampling artifacts are mainly responsible for this result. Upwelling as well as frontal processes appear important for larval fish growth and survival, and turbulence levels vary both within and across these features. Process-oriented studies of some of these interactions could provide more definitive links between turbulence and biological responses in future. © 2000 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

**turbulence / larval fish / recruitment / upwelling / front**

**Résumé** – **Turbulence, écologie des larves de poissons et recrutement des pêcheries : synthèse des études de terrain.** Le recrutement des poissons est très variable d'une année à l'autre, mais sa variabilité reste inexpliquée dans la plupart des modèles de dynamique des populations. Le présent travail porte sur le rôle de la variabilité environnementale dans le recrutement du poisson, en particulier l'effet de la turbulence sur l'alimentation et la croissance des larves, et sur le recrutement des populations. Les études de terrain montrent que la turbulence a des effets contrastés sur l'alimentation, sur les taux de croissance et de mortalité dans la nature, ainsi que sur le recrutement. Ce résultat est attribué à des variations concomitantes et multiples dans les mécanismes de l'écosystème, à notre mauvaise connaissance de la manière dont ces processus (composition de l'alimentation larvaire, mode d'alimentation, taux de croissance, dispersion des proies) répondent à la turbulence, et aux artefacts inévitables de l'échantillonnage. L'upwelling et les phénomènes frontaux semblent importants pour la croissance et la survie des larves de poissons, et l'intensité de la turbulence varie à la fois à l'intérieur et au-delà de ces zones. Des études consacrées au mécanisme de certaines de ces interactions devraient conduire à des relations plus générales entre la turbulence et les réponses biologiques. © 2000 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

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## 1. INTRODUCTION

Turbulence in the sea is an important agent of ecosystem variability and has received increasing attention from the oceanographic community in the last 20–30 years. This attention has resulted from numerous

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field, laboratory and theoretical studies that have demonstrated how turbulent mixing can influence biological and physical processes in the ocean. Many of these studies have reported changes in primary and secondary plankton production, plankton patchiness, and pelagic food web structure as a consequence of variability in the intensity of turbulent mixing [2, 32, 68, 89, 90, 135]. Since the intensity of turbulence in the ocean is coupled to climatic and hydrographic processes such as storms, tides, upwellings, and buoyancy inputs (e.g. solar heating, freshwater runoff; [139]), variations in weather and climate will have direct and indirect effects on biological processes [6, 61].

Many fisheries' oceanography studies have addressed how feeding and growth rates in larval fish vary in relation to different physical processes and in different types of hydrographic environments [28, 52, 77]. These processes and environments presumably have different levels of turbulent dissipation and frequencies of input of kinetic energy. A large number of other studies have compared the population dynamics of entire fish populations to turbulence-related variables such as wind speed [29, 112, 136]. This report will summarize the literature concerning responses of fish at the individual and population level to turbulence in natural environments.

## 2. METHODS

### 2.1. Literature compilation

The published, refereed fisheries oceanographic literature was examined for papers describing larval fish feeding, growth, mortality and recruitment in relation to estimated turbulence (e.g. wind- or tidal-induced mixing) in the sea. Modelling and laboratory studies of these processes have been excluded, except in cases where they may help interpret the field observations. In order to synthesize the findings, the overall relationship of the biological response to variations in turbulence was recorded from each study. In most cases, studies reported biological responses via multivariate statistical analyses that accounted for influences of other important variables such as food concentration (for feeding and growth responses) or spawning stock biomass (recruitment responses).

Responses to turbulence were categorized according to the type of relationship observed: positive, negative, dome-shaped (increasing response at low-intermediate turbulence and decreasing response at intermediate-high turbulence) and independent (no differences in biological responses at different turbulent dissipation rates).

### 2.2. Definition of turbulence

It is appropriate to specify how the term turbulence will be used in this review. Turbulence represents those motions which transfer kinetic energy on a large scale (e.g. up to tens of metres, as in the case of tidally mixed water columns) to a small scale (e.g. centimetres–millimetres). At the smaller scales, viscosity dampens the mechanical motions and the remaining kinetic energy is dissipated as heat [135]. The resulting motion at small scales can be induced by many different physical processes, including surface and internal wave-breaking, convective mixing and interactions of currents with bottom topography (e.g. tides). Hence the processes that generate mixing and turbulence differ greatly, but the characteristics of turbulent motion itself (i.e. the consequence of the physical forcing) are universally described by theory [135, 149]. Since processes such as upwelling, storms and frontal circulations all generate turbulent motion in the water column, this review will address how these processes affect young fish stages and fish recruitment.

## 3. RESULTS

### 3.1. General

The studies that have been used in this literature survey are listed together with the biological responses in *table I* (e.g. feeding, growth) and *table II* (recruitment). In *table I*, the studies are grouped according to the complexity of the biological response to turbulence: gut content analyses as indicators of recent feeding activity; nucleic acid studies as indicators of recent somatic growth; otolith growth and abundance and mortality (survival) indices.

**Table I.** Effects of turbulence on larval fish captured in the sea. Note that in many studies, turbulence was directly or inversely proportional to in situ prey concentrations, and that in other studies, prey concentrations were not measured. For these reasons, the table must be interpreted cautiously. All turbulence estimates are based on indirect estimates (e.g. from wind speed), except for [36] which are based on ADCP-derived Richardson numbers, and [46] which is based on both wind-based and direct measurements of turbulent dissipation rate. Table entries reflect increasing complexity of the biological process related to turbulence. For studies near tidal fronts, turbulence is assumed to increase with hydrographic situation from stratified to frontal to mixed [56, 138, 139].

Authors	Species	Prey Relationship to Turbulence	Feeding/Growth Relationship Investigated	Response to Turbulence	Site
<i>Gut contents studies:</i>					
Lasker [75]	Northern anchovy	Decreased following storm	Gut contents before/after storm	decreased	California Current
Owen et al. [119]	Northern anchovy	More prey at calm stations than turbulent stations	Gut contents at calm and turbulent stations	=	California Current
Sundby and Fossum [145]	Cod	Varied between stations. Accounted for in analyses.	Gut contents (no. of prey) and wind speed 2–6 m s <sup>-1</sup>	+	Lofoten, Norway
Sundby et al. [144]	Cod	Varied between stations. Accounted for in analyses.	Gut contents (no. of prey) and wind speed 2–10+ m s <sup>-1</sup>	+	Lofoten, Norway
Bailey et al. [4]	Walleye pollock	Prey concentrations lower during/after storms	Larval feeding and storms	–	Shelikof Strait, Gulf of Alaska
Lough and Mountain [82]	Cod	Varied between stations. Accounted for in analyses.	Gut contents and wind/tidal turbulence	– (weak)	Georges Bank
Lough and Mountain [82]	Haddock	Varied between stations. Accounted for in analyses.	Gut contents and wind/tidal turbulence	– (weak)	Georges Bank
McLaren et al. [95]	Cod	Varied between stations. Accounted for in analyses.	Gut contents (no. of prey) and wind speed	– (weak)	Scotian Shelf, Canada
Conway et al. [20]	Anchovy	Prey concentration decreased after storm.	Gut contents before/after storm	=	No. Adriatic
Dower et al. [36]	Radiated shanny	Varied between stations. Accounted for in analyses.	Biovolume and prey size of gut contents and turbulence	+, +	Newfoundland, Canada
Cox et al. [23]	Herring	Stable within sampling periods.	Gut contents at different points in tidal cycle.	=	Blackwater Estuary, UK
<i>Somatic growth rate studies:</i>					
Buckley and Lough [14]	Haddock	Prey higher at stratified site than mixed site	RNA/DNA content in stratified and mixed water	–	Georges Bank
Munk [104]	Sprat	More zooplankton at stratified and frontal stations than mixed.	Growth rates highest in mixed and frontal water.	+	Se. North Sea
Bailey et al. [4]	Walleye pollock	Prey concentrations lower during/after storms	RNA content and storms	–	Shelikof Strait, Gulf of Alaska
Nakata et al. [113]	Sardine	Higher in front than offshore stratified area.	RNA/DNA content in frontal and offshore stratified zone.	Higher in front	Kuroshio region, central Japan.
Lough et al. [81]	Cod	Prey concentration approx. Same before and after storm.	RNA/DNA before vs. after storm	=	Georges Bank
Clemmesen et al. [19]	Anchovy	Prey highest in front, lower in mixed and stratified water	RNA/DNA highest in stratified water	–	Argentinian shelf
Lough et al. [81]	Haddock	Prey concentration approx. Same before and after storm.	RNA/DNA before vs. after storm	increased	Georges Bank
Chicharo et al. [18]	Sardine	Prey concentration unrelated to wind speed.	RNA/DNA and wind speed	+	So. Portugal

**Table I.** (Continued)

Authors	Species	Prey Relationship to Turbulence	Feeding/Growth Relationship Investigated	Response to Turbulence	Site
<i>Otolith growth studies:</i>					
Maillet et al. [88]	Atlantic menhaden	Not described.	Otolith growth and storms	—	Mid-Atlantic Bight, USA
Gallego et al. [47]	Herring	Varied between stations. No effect on growth.	Otolith growth and wind speed	Dome	W. of Scotland
Gallego et al. [46]	Haddock	Varied between stations. No effect on growth.	Otolith growth and wind speed	=	No. North Sea
<i>Abundance &amp; mortality studies:</i>					
Peterman and Bradford [121]	Northern anchovy	Not described	Larval mortality rate and storm frequency	+	California Current
Butler [15]	Sardine	Not described	Larval mortality rate and wind-based water column stability ("Lasker events")	=	California Current
Bailey and Macklin [5]	Walleye pollock	Not described	Larval mortality rate and storms	+	Shelikof Strait, Gulf of Alaska
Bailey et al. [4]	Walleye pollock	Prey concentrations lower during/after storms	Larval survival rate and storms	—	Shelikof Strait, Gulf of Alaska
Cury et al. [26]	Northern anchovy	Not described	Larval abundance and upwelling	Dome	California Current

### 3.2. Feeding and growth

There were a total of 22 studies that compared feeding ( $N = 11$ ) and growth ( $N = 11$ ) to variations in turbulence. The responses to turbulence are diverse (positive, negative, dome-shaped, no effect) for both variables (*table I*). Food concentrations in many cases co-varied with variations in turbulence or among the different hydrographic situations. What is perhaps surprising is that some of the studies investigating gut contents as measures of feeding activity [82, 95, 144, 145] have used similar species (cod, haddock larvae) and similar sampling and larval analysis (gut contents) methods but have not produced consistent results.

### 3.3. Mortality

Four out of six studies showed that larval mortality rates appear to be highest in windy conditions, which are partly related to turbulent dissipation rates. However this pattern must be treated cautiously because three of the four studies with this relationship involve one species in one region: several years of intensive study in the Gulf of Alaska have shown that walleye pollock mortality rates are higher in windier years or following windy periods than in calm years [4, 5].

One other study showed that larval mortality rates were higher in years with strong winds (northern anchovy: [121]) and one study found no relationship between larval mortality rates and a wind-based stability index (larval sardine mortality and Lasker events; [15]).

### 3.4. Recruitment

Recruitment studies typically used wind speed as a proxy indicator of the amount of turbulence in the surface mixing layer. One of the more consistent responses involved clupeids in upwelling regions. Nearly all of these populations responded to turbulence in a dome-shaped fashion (see also [7] for review; *table II*). Relationships of populations in other types of ecosystems to wind estimates of turbulence were much more variable (*table II*).

## 4. DISCUSSION

### 4.1. General

Biological responses of individual fish larvae and fish

populations to variations in turbulence are inconsistent, especially when results from many studies are compiled and analysed together. All four types of turbulence relationship are evident both for process-oriented field studies of larval ecology and for the statistical studies investigating recruitment dynamics

of entire populations. These observations suggest that in some studies other processes affecting these responses vary by larger amounts and have bigger impacts on the responses than the variations in turbulent dissipation rates. In addition, strong covariation in some variables (e.g. patchiness and turbulent

**Table II.** Effects of wind speed (e.g. expressed as indices of turbulence, upwelling, storms) on fish recruitment. Note that in some cases the statistical analyses have not adjusted the recruitment series for interannual differences in spawning stock biomass which can cause trends in recruitment [112].

Authors	Species	Spawning Stock Biomass Considered in Analysis?	Wind Index	Relationship	Site
Cury and Roy [25]	Anchoveta	yes	wind-based turbulence estimate	Dome	Peru
Cury and Roy [25]	Sardine	yes	upwelling	Dome	Peru-California
Cury and Roy [25]	Sardine	no	wind-based turbulence estimate	Dome	Morocco
Butler [15]	Sardine	yes	wind-based water column stability (“Lasker events”)	=	California
Ware and Thomson [156]	Sardine	yes	wind speed	Dome	West coast, N. America
Roy et al. [129]	Northern anchovy	no	upwelling	Dome	California
Roy et al. [129]	Sardine	yes	upwelling	Dome	Current Morocco
Ottersen and Sundby [117]	Cod	yes	turbulence (wind speed <sup>3</sup> )	=	Artco-Norwegian cod
Megrey et al. [97]	Walleye pollock	yes	wind speed (age 0 recruits)	=	Shelikof Strait, Gulf of Alaska
Svendsen et al. [147]	Whiting	no	wind speed <sup>3</sup>	–	North Sea
Svendsen et al. [147]	Herring	no	wind speed <sup>3</sup>	+	North Sea
Svendsen et al. [147]	Haddock	no	wind speed <sup>3</sup>	=	North Sea
Svendsen et al. [147]	Cod	no	wind speed <sup>3</sup>	+	North Sea
Svendsen et al. [147]	Saithe	no	wind speed <sup>3</sup>	+	North Sea
Svendsen et al. [147]	Sandeel	no	wind speed <sup>3</sup>	=	North Sea
Borja et al. [12]	Anchovy	no	wind speed	+	Bay of Biscay
Hutchings [59]	Anchovy	no	wind-based upwelling estimate	–	S. Benguela Current
Nielsen et al. [114]	Plaice	no	wind speed (age 0 recruits)	+	Kattegat
Daskalov [29]	Sprat	yes	wind speed	+	Black Sea
Daskalov [29]	Anchovy	yes	wind speed	dome	Black Sea
Daskalov [29]	Horse mackerel	yes	wind speed <sup>3</sup>	+	Black Sea
Daskalov [29]	Whiting	yes	wind speed	+	Black Sea

dissipation rates; advection and wind mixing) and various sampling and measurement errors (to be described below) will also contribute to the observed variability between studies. The biological response to variations in turbulence within a study may therefore represent the response to the given state of the entire ecosystem (e.g. prey distribution, zooplankton community composition) rather than the response to a single component process (e.g. food availability) within the ecosystem. Lastly the aggregate findings described here are also partly due to the effects of combining studies conducted at different ranges of variables (e.g. prey concentrations, turbulent dissipation rates). Some of these factors will be discussed in more detail below.

The next two sections use two of the findings by Dower et al. [35] as starting point: there is no direct evidence of increased encounter rates between larvae and prey in field settings (p. 200); and there is no field evidence which shows increased growth of larval fish resulting from the effects of turbulence [35]. It will be suggested below that many studies that have been used to evaluate these ideas and processes in the field may not and could not be designed to address these issues with high statistical power, and new alternative studies could increase our process-based understanding of how turbulence affects larval fish feeding and growth.

## 4.2. Factors contributing to inconsistent feeding, growth and mortality relationships to turbulence

### 4.2.1. Gut contents as a measure of larva–prey encounter rate

Several of the studies which investigated encounter and feeding rate responses to turbulence relied almost exclusively on analyses of the contents of larval guts. However gut contents may not always be an accurate index of larval–prey encounter rates. The prey contained within a gut represents the endproduct of several previous behavioural events (e.g. encounter, pursuit, attack), all of which must be successful in order for the prey to be ingested. If some of these components are unsuccessful then the assumption that gut contents represent encounter probability is no longer valid. For example, pursuit and attack success vary with larval and prey behaviour [53, 57, 103, 105, 107]. Both theory [64, 71, 87, 93] and experiments [85] show that pursuits are unlikely to be as successful in turbulent water as

in calm water. Evaluation of encounter rates due to variations in turbulence probably requires direct behavioural observations [57, 84, 105].

### 4.2.2. Wind conditions only provide approximations of turbulent dissipation rates or turbulent velocities

A second factor that contributes to the inconsistent nature of the findings in *table I* is that almost without exception no study listed in *table I* has directly measured turbulent dissipation rates using microstructure profilers [33]. Only one group of investigators [46] has included direct dissipation rate measurements using these methods in their sampling program. These measurements were then used to develop a site- and cruise-specific relationship between turbulent dissipation rate, wind speed and depth that was applied in otolith growth rate analyses. Turbulent dissipation rates in most of the remaining studies have been estimated from general relationships to wind speed, which provide a reasonable estimate of turbulent dissipation rate in parts of the surface mixing layer [86, 115]. However such estimates are much less certain than direct measurements [48, 86, 115] and in any case cannot provide reliable estimates of the turbulent dissipation rates at and below pycnoclines [48, 82] where some larvae may feed [75, 82]. Improved sampling and modelling [48] could reduce uncertainties associated with wind-based turbulence estimates.

### 4.2.3. Estimated prey concentrations do not always represent those experienced by fish larvae

Estimating the true concentration and taxonomic/size composition of zooplankton experienced by fish larvae during feeding periods is problematic due to sampling limitations. Most of the studies in *table I* must employ various assumptions about the prey field which may not be valid. These assumptions include: i) all zooplankton species and sizes within a given size range are suitable prey; ii) concentrations of all species and sizes within the depth layer where zooplankton concentrations are measured are homogeneous [152]; iii) larvae actively feed within this same depth layer and not elsewhere in the water column where food, light and turbulence conditions might be different.

It is unlikely that these assumptions are fully valid during most field studies. Regarding the first assumption, larval diets are often composed of taxa which differ significantly from those present in the water

column [37, 41, 65, 107, 132]. Some taxa or size groups are therefore more vulnerable to larval fish predation than others [53].

The second assumption that zooplankton distributions in the sea are homogeneous is also unlikely, given that zooplankton are patchily distributed at small scales ( $< 1\text{--}2\text{ m}$ ) even in moderately turbulent environments [31, 45, 118]. If larvae encounter and can exploit such patches, then the depth-averaged concentration will underestimate the concentration experienced by larvae during feeding periods. In general the role of patchiness on larval feeding rates is unclear, with some authors demonstrating important effects for some species [75], and other authors showing that other species can feed and grow at low food concentrations [10, 40, 42, 43, 84, 100, 101, 103, 105, 108]. Other evidence shows that feeding and growth rates in fish larvae in nature are frequently food-limited [17, 19, 81, 113, 141, 144, 146, 150]. Feeding rates in these studies may have been higher if larvae were able to locate higher concentrations of prey. Some suggestions for clarifying the role of patchiness on larval fish feeding will be discussed below.

Moreover, and related to the third assumption stated above, the depth layers within the photic zone within which larvae feed are not known, but probably depend on local food concentration [75], light conditions [39, 50] and turbulence [55]. Larval vertical distributions vary with all three of these variables [55, 109, 116]; during vertical movements larvae may encounter zooplankton patches and taxonomic/size compositions of prey which differ from the depth-averaged conditions within the depth layer used to estimate food concentrations. Measured feeding responses may therefore reflect gut fillings at layers other than those at which food concentration and turbulent dissipation rates were measured. This will also contribute to the variability observed in *table I*.

Considerations such as these suggest that few studies have accurately measured the true prey field experienced by feeding fish larvae.

#### *4.2.4. Larval growth rates may not show the same response to turbulent dissipation rates as larval feeding behaviour*

The effects of turbulence on growth may not be identical to their effects on encounter, pursuit or

ingestion [35]. Levels of turbulent dissipation that yield optimal growth may be at different magnitudes than those which optimise ingestion rate and the increase (or decrease) in growth due to variations in turbulence (for a given prey concentration) may be different from the amplitude of variation in feeding-related processes (e.g. encounter, ingestion). Differences in the responses of growth and ingestion to turbulence will depend on how assimilation and metabolic rates are influenced by turbulence, which is partly related to activity levels (see also [35]). Both fish larvae and other taxa display different activity levels in calm and turbulent water [84, 134] so it is reasonable to assume that metabolic rates and growth rates will display different functional responses to turbulence than encounter or ingestion rates. These issues have not been addressed but should be investigated further.

#### *4.2.5. Food concentrations may not have limited ingestion or growth rates*

In some of the studies in *table I*, it is possible that prey concentrations were high enough to ensure high feeding and growth rates. In these cases turbulence will not have a positive effect on ingestion rates even though encounter rates are promoted by turbulence [127]. Turbulence will in these cases have an insignificant, or a negative, influence on ingestion rates due to reduced pursuit success [85, 127].

### **4.3. Suggestions for future studies**

#### *4.3.1. Influence of turbulence on larval activity and growth rates*

Resolving how larval fish growth rates vary with exposure to turbulence may be a suitable topic for both experimental and field evaluation. Definition of such relationships could lead to a better understanding of how survival probability might be affected by climatic and hydrographic variability [127]. Stated differently, are the surviving individuals of a cohort a subset of offspring which have experienced some optimal level of turbulence that enabled high growth or survival rates? These hypotheses could perhaps be evaluated from otolith studies of survivors' hatch-dates [21, 96, 99] and daily growth rates, particularly

if the relationship between otolith and somatic growth rates can be defined and modelled accurately [102, 159].

Changes in larval and juvenile (e.g. 0-group) prey search behaviour could also affect the functional response of growth rates to turbulence. For example in some moderately turbulent situations, it may be bioenergetically more efficient for cruise-searching larvae or juveniles to greatly reduce their swimming speeds while searching or even behave as pause-travel or ambush predators. This strategy would reduce metabolic costs due to lower swimming activity [11, 74], while allowing the mechanical energy of turbulent motion to advect prey within visual range [84, 143]. The net result could be higher growth rates and efficiencies than if the fish maintained an active cruise behaviour.

Habitats that might be suitable for employing an adaptive search strategy would have to be moderately energetic (e.g. tidally mixed regions, other areas where bottom flow interacts with bathymetry). One example of fish using such a strategy appears to be coral reef fish occupying the windward and highly turbulent side of coral reefs [51]. Fish along parts of the Great Barrier Reef effectively form a “wall of mouths” by orienting upstream against the main orientation of wind- and tidally-driven currents and feeding on drifting zooplankton as they are advected onto the reef [51]. The hypothesis that larval and juvenile fish actively adjust their search behaviour (and reduce foraging costs) when feeding in turbulent or other flow situations where advection increases prey encounter rates could be investigated by direct in situ observations and video-recording of larval and juvenile behaviour [66, 78, 79].

#### 4.3.2. Larval diet composition

The difficulty in understanding variations in larval diets limits progress in linking feeding and growth rates to food availability. Without improved knowledge a precise definition of ‘food’ or ‘prey’ is not possible. Food concentration variables in many cases therefore cannot be configured accurately (regarding species or sizes) in statistical analyses. The factors controlling diet composition depend on behavioural traits of both predator and prey [36, 53, 72, 107], and small scale water motion [36, 72, 153]. However this knowledge is still insufficient to allow accurate gener-

alisations and predictions of dietary taxonomic and size composition in many wild larvae when exposed to different species mixtures and concentrations [52, 120]. This situation could perhaps be overcome in future if behavioural studies (experimental, field, theory) of predator–prey interactions at the individual level could resolve how dietary composition depends on factors such as larval-prey behaviours and small scale water motion [72, 73, 153].

#### 4.3.3. Importance of small scale (1–2 m) prey patches for fish larvae

The ability of larvae to locate and respond to patches has not received much experimental investigation, and field approaches to resolve the issue are not yet able to sample fish larvae and their prey simultaneously at the small scales of larval search and feeding behaviour. Given that patches do occur in both turbulent and other environments, it is possible that larvae might encounter a patch due to turbulent motion in a manner analogous to that described for the role of turbulence on encounter rates between individual planktonic prey and predators [127] and between individual microzooplankton and patches of bacteria feeding on microclouds of dissolved organic matter [126]. Encounter rates of fish larvae with patches could be quite high because the relative velocity due to turbulence will be much larger at the spatial scale of these patches (e.g. 50–100 cm) than at the spatial scale of larvae encountering a single prey (ca. 1 reactive distance or 1 body length [38, 154]).

The contribution of patchiness to feeding and growth rates in nature remains therefore unclear, but could perhaps be clarified experimentally following the approaches of Hunter and Thomas [58] and Price [123]. These two studies created patches of phytoplankton in respectively small aquaria and large mesocosms and then recorded the search behaviour of predators (anchovy larvae and euphausiids) in and near the patches. In both cases, when the predators located the patches, the search behaviour changed to maintain proximity to the patch. Notably the role of patchiness on feeding and growth in fish larvae has been investigated frequently using models [9, 30, 160], but many of the findings of these models still require testing.

One experimental approach that could be used to test the hypothesis that larvae can locate and ingest prey

in patches in situ would be to conduct similar experiments to those of Hunter and Thomas [58] and Price [123] in the field with wild larvae and zooplankton, and record the behaviours with modern video-recording camera-ROV technology [66, 151] or by divers' records [78, 79]. In particular, Kils [66] has recorded and described quantitatively direct feeding by wild 0-group herring in a dense patch of zooplankton in Kiel Bay. Leis and colleagues have shown that it is possible to capture and release wild fish larvae, and to follow and record undisturbed swimming behaviour of such larvae sufficiently long to produce quantifiable and statistically significant results. Applying these techniques to feeding behaviour studies is a promising and as yet essentially untried way to investigate whether larvae can exploit small patches of zooplankton prey in field situations. Similar methods could also be used to test other aspects of larval feeding behaviour (reactive distances, encounter, pursuit, attack) which are usually only investigated in laboratory aquaria [84, 85, 103].

#### *4.3.4. Roles of swimming behaviour and turbulent dissipation on zooplankton patch formation and dispersion*

A major gap in the zooplankton patchiness literature which is potentially relevant to larval fish feeding is the interaction between turbulence and zooplankton swimming behaviour in producing and maintaining patches, especially at spatial scales which are most relevant to larval fish search behaviour (i.e.  $< 50$ – $100$  m). Few field studies have yet considered in three dimensions the dynamics of patch dispersion or formation at scales  $< 100$  m that occurs during major changes in turbulent dissipation rates (e.g. storm passage, diel tidal cycles). Strongly swimming zooplankton should be able to maintain themselves in patches or swarms under higher turbulent dissipation rates than weaker swimmers; expressed alternatively, aggregations of strong swimming zooplankton should have greater persistence against dispersion (assuming a stimulus to remain aggregated) than aggregations of weak swimmers. While the potential importance of behaviour on patchiness has been acknowledged for many years [1, 83, 118, 122, 142], swimming behaviour has, with few exceptions [30, 44], not been quantitatively included in recent models of zooplankton patchiness [1, 122]. Investigation of non-equilibrium situations in the field at smaller scales than in

the past will probably add considerable insight into patch dynamics and their utilization by fish larvae.

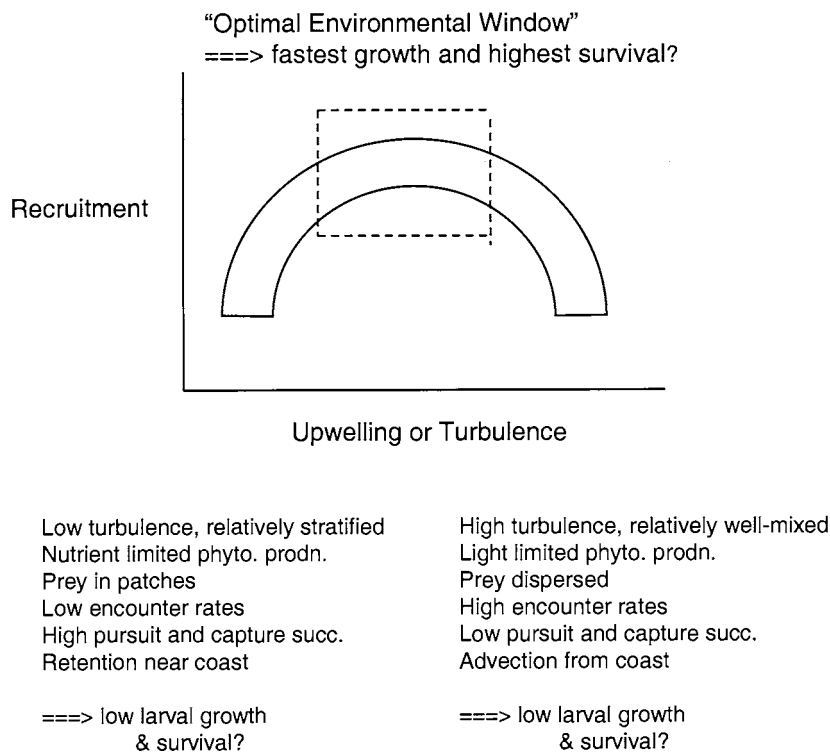
Studies to address this topic could include transect acoustic or particle counting studies [24, 31, 45, 83, 158] in which patch characteristics (e.g. size and shape of patches; concentration of prey inside and outside patches) are directly related by statistical analyses or modelling to organism swimming ability/buoyancy and water motion variables (e.g. turbulent dissipation rates, shear, relative velocities). Additional approaches could include laboratory behavioural investigations of patch formation/dispersion during different regimes of turbulent dissipation and using zooplankton species that are key larval fish dietary components (e.g. copepod nauplii and copepodites). These studies could contribute to a size- (or swimming behaviour-) based modelling framework that could enable one to describe and predict zooplankton distributions in nature under varying combinations of swimming behaviour and turbulent dissipation. Such a framework is presently lacking.

#### **4.4. Fisheries recruitment and interannual variations in turbulent mixing**

##### *4.4.1. Upwelling zones*

Some of the strongest evidence for the influence of wind-forcing (and consequently turbulence) on fish is at the population level. Bakun, Cury, Roy and colleagues have shown that recruitment in sardine and anchovy populations in nearly all the major upwelling systems around the world is related to wind-based upwelling or turbulence indices in a dome-shaped fashion (*table II*). This result is rather surprising given the wide range of effects turbulence has on plankton production and ecosystem structure and functioning. Nevertheless in nearly all cases, maximal recruitment is obtained at a seasonally or annually averaged wind speed of ca.  $6 \text{ m s}^{-1}$ . In addition analyses by other colleagues investigating fish recruitment in upwelling areas have identified similar patterns (Pacific sardine [156]; Bay of Biscay anchovy [12]).

The oceanographic mechanisms responsible for these results involve the production of plankton in the spawning and nursery areas [25]. The mechanisms are



**Figure 1.** Schematic relationship between recruitment and upwelling and turbulence for pelagic clupeoids in major upwelling systems around the world. Below the figure are oceanographic processes associated with limiting or excessive upwelling and turbulence which may affect growth and survival of larvae and pelagic 0-groups. Modified after Cury and Roy [25].

based on some general principles of plankton production and distribution in the sea (nutrient/light limitation of phytoplankton production, patchiness of phyto- and zooplankton). These earlier ideas may now have to be extended to include more recent interpretations of the roles of upwelling circulation on advection/retention of eggs and larvae [128] and of turbulence on larval feeding behaviour [7, 84, 85, 127, 145].

The strong relationship between upwelling intensity and recruitment in the various clupeid stocks, and the inferred oceanographic mechanisms responsible for these patterns suggests that conditions for growth and survival of the larvae are the key to above-average recruitment in these stocks. Since it is believed that faster-growing larvae are probably the ones most likely to survive to recruitment [54, 96], and since some but not all studies [3, 21] have found positive links between growth or condition during the first few months of life and subsequent recruitment [16], one might hypothesize that condition, growth

and survival rates of clupeid larvae and 0-groups might also have a dome-shaped relationship to upwelling/turbulence (*figure 1*). Few time-series are presently available to test this hypothesis but new time-series of larval growth or condition in relation to upwelling and turbulent mixing could support the mechanisms believed responsible for statistical correlations between recruitment and upwelling/turbulence.

The consistent influence of upwelling on clupeid recruitment in different ecosystems suggests that upwelling and turbulence in these regions may have similar effects on other local fish species (e.g. hakes, jack mackerel, rock- and flatfishes). To the author's knowledge a multi-species comparison of recruitment [34, 147] for non-clupeid species within individual upwelling systems or among different systems has not yet been conducted. In contrast, conditions which are suboptimal for clupeid recruitment occur frequently [25]. This type of environment may be favourable for some species whose life history may be adapted to

years when turbulent mixing and upwelling are too weak or too strong for optimal clupeid recruitment.

#### 4.4.2. Shelf ecosystems

There are some other examples of wind conditions affecting recruitment (*table II*). In a comprehensive statistical study of several species in the North Sea, significant positive relationships between recruitment and the cube of wind speed were found for herring, cod and saithe in the North Sea, but no effect of wind speed on recruitment was found for haddock or sandeel; whiting recruitment was negatively related to wind speed [147]. Wind speed was also shown to influence recruitment in several fish species in the Black Sea (sprat, anchovy, hake, horse mackerel; [29]). In both sets of analyses, wind speeds were measured during the months when eggs and larvae were in the water column and the relationships obtained are believed to represent impacts on survival during the early life history stages [29, 147].

Few studies have directly considered the influence of tidal mixing on fish recruitment, although the size of herring stocks in the northwest Atlantic is positively correlated to size of the larval nursery areas which are located in tidally mixed regions [62]. Tidal mixing itself however is unlikely to influence interannual variations in recruitment because tidal mixing is a highly predictable environmental signal to which fish life histories have presumably evolved [140]. However, tides do affect stratification of the water column, and in years having different buoyancy inputs (e.g. heat, freshwater runoff), the onset of stratification and frontal positions will vary from long-term mean dates and locations [13]. This variation will affect plankton production processes and potentially also recruitment.

The empirical evidence for such couplings is weak but can be addressed with field work (e.g. comparisons of larval and 0-group growth and survival in years having different buoyancy inputs). Notably the statistical analyses [29, 34, 136, 147] obtained significant correlations between recruitment and stratification-related variables (e.g. heat content, stability, water temperature, river runoff). Lastly, ocean stability and its effects on lower trophic level production may also be the key mechanism controlling decadal-scale fluctuations in North Pacific salmon stocks [8, 49].

#### 4.4.3. Role of juvenile mortality on environment-recruitment relationships

The hypothesis that fish recruitment is related to turbulent mixing assumes that turbulence affects the survival probability of the larval and early juvenile stages, and that recruitment trends are independent of processes during the late juvenile or benthic stages. In many fish populations this latter assumption is not valid because juvenile mortality can be so high and variable that it can obscure time trends in larval mortality [98]. In these cases environmental variables that affect larval mortality rates will not explain significant amounts of variation in recruitment. The inconsistent responses of recruitment to turbulence observed in *table II* may reflect varying degrees of juvenile mortality between and within studies.

#### 4.4.4. Summary

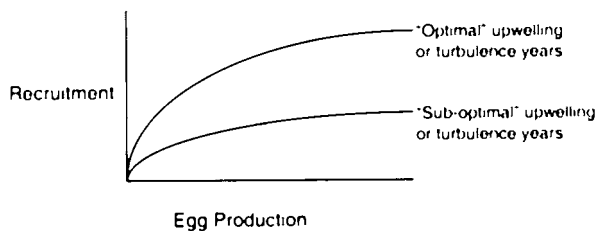
Aside from the clupeids residing in upwelling areas, there is little evidence that recruitment depends on wind speed or turbulence in a consistent manner across species or geographic regions. The remaining studies were all from temperate-boreal shelf ecosystems where interactions between oceanographic processes and fish recruitment still remain unclear [28, 52] and appropriate environmental variables cannot be scaled properly [8]. Relationships in these areas were positive, negative or insignificant, and some did not account for interannual differences in egg production or spawning biomass which can contribute to time trends in recruitment [92, 112].

### 4.5. Similarities between frontal zones and upwelling regions

The results of Cury and Roy [25] and Roy et al. [129] indicate that environmental factors associated with wind (i.e. turbulent mixing, upwelling intensity, transport, lower trophic level production) and the spawning stock have significant impacts on fish recruitment. This relationship means that different levels of recruitment can be produced per unit spawning biomass (*figure 2*), depending on the ability of the environment to produce new fish (i.e. carrying capacity). No other comparable effect of an environmental variable has yet been detected for any other fish species complex in widely separated ecosystems. In this way, the clupeid recruitment-upwelling relationship is unique at the present time.

In this context it is relevant to ask whether there are other similar dominant production-related processes that might affect recruitment in temperate-boreal ecosystems in the way that upwelling systems do for clupeids. Three such processes seem obvious candidates. First, the spring and autumn diatom blooms have long been considered to be key features around which most fish species in temperate-boreal systems have evolved to reproduce [27, 28]. Some evidence of such a linkage is available [131] but in general the relationship between spring primary or secondary production and recruitment is uncertain [67, 77, 130]. As a result, recruitment models used in stock assessment do not include this or generally any other environmental variable [112].

A second phenomenon which might be related to recruitment in some temperate-boreal species could involve frontal zones [28]. Frontal zones occur around banks, on continental shelves where tidal mixing is strong, and at continental shelf breaks [76]. In the case of tidal fronts, hydrographic processes result in a balance between mixing (winds, tides) and stratification processes (heating, freshwater runoff from land masses; [139]). These processes have been parameterized into predictive models that describe the locations and seasonal durations of the presence of tidally-generated fronts in shelf seas [13, 139]. Tidal fronts represent areas of intermediate mixing intensity [56, 138] and are transition zones between fully mixed and stratified water masses [139]. For example, direct measurements of turbulent dissipation rate at the front and mixing zones on Georges Bank showed that dissipations in the frontal zone were ca. 10-fold less than those in the mixed area [56] and ADCP current measurements revealed large variability across a frontal zone in the North Sea [106].



**Figure 2.** Schematic of how population egg production and environmental processes might interact to determine recruitment in clupeoid populations in upwelling ecosystems. As depicted, carrying capacity for recruit production depends on variations in upwelling or turbulence.

The oceanographic and production characteristics of many frontal zones [76] bear some similarities with those of upwelling zones. In particular, frontal circulations mix nutrients into the photic zone which stimulates primary production by large phytoplankters. Higher rates of primary production and higher phytoplankton abundance stimulate production at secondary trophic levels so that concentrations of consumers (e.g. copepods) increase [70, 113]. In addition, circulation near the frontal zone can advect and retain plankton to the front [44, 76]. Hence some patchiness of plankton can be expected, encounter rates between trophic levels will be increased due to turbulence, and pursuit success of encountered prey will still be higher than in fully mixed water masses. In these ways, frontal regions share many key plankton production features with upwelling areas.

Frontal areas are also important larval and juvenile fish habitats. A large number of studies have shown that larval fish in temperate-boreal ecosystems are more abundant in such zones than surrounding water masses [22, 104, 110, 111, 124, 133, 141, 148]. The mechanism by which larvae accumulate at such regions is unclear. Nevertheless, the nutritional condition of larvae and pelagic 0-groups captured in frontal zones is often significantly higher [19, 113, 141] or more variable [80] than in larvae captured in neighbouring water masses. The improved condition of these larvae may give them a survival advantage in times of food limitation and is believed to be related to the generally higher levels of plankton abundance and production found in frontal regions [69, 70, 76, 113, 148]. Persistence of both the frontal feature and larvae in its vicinity appear to enable the larvae to feed and grow at faster rates. However, in situations where frontal zones are ephemeral the coupling of larval distributions or growth/condition to frontal plankton production and abundance may be less evident or manifested as increased variability [80].

The enhanced abundance of fish larvae in frontal regions, coincident with both relatively high levels of prey and moderate turbulence, suggests that frontal regions may be important nursery areas for the production of new recruits [60, 110, 111]. Given that frontal formation and positions depend on climatic variables (e.g. heating, freshwater input), their impact on larval fish growth and survival could vary between years. If this is true, differences in recruit production

at frontal zones may be a factor determining recruitment in some temperate-boreal species [60, 110, 141, 148]. This hypothesis remains to be formally tested for most species occupying frontal areas. Given the potential similarities between frontal and upwelling types of plankton production, and the documented influence of upwelling intensity on clupeid recruitment [7], this hypothesis may well be supported by empirical data for some species. The type of data needed to test this hypothesis could include time-series of recruitment, plankton and larval abundances at the frontal zone, characteristics (e.g. turbulent dissipation rates, geographic size, seasonal duration, nutrient fluxes) of the frontal zone, and temporal and spatial variability in larval growth rates or condition indices.

However, there are areas (Baltic Sea, Newfoundland shelf, Scotian Shelf) where fish stocks are (were) successful but which appear to have no major persistent frontal structures (*sensu* [139]) around which early life-history stages of fishes and their prey (and predators?) aggregate. In these cases, other mechanisms of recruit production must be available. One of these might involve a greater reliance of fish on vertical gradients in plankton production, particularly in the vicinity of pycnoclines [125]. These can be productive, prey-rich and moderately turbulent regions [63], and occupy large horizontal areas of stratified seas. As such, they may represent another important habitat responsible for recruit production and survival among species inhabiting shelf regions of temperate-boreal seas.

Interestingly, many sardine and anchovy populations (e.g. Japan, Mediterranean, Black Sea, southwest Atlantic shelf) reproduce in shelf or shelf-break areas [7, 29, 113, 157] and estuaries [94] in addition to upwelling areas. Recent investigations of Black Sea anchovy [29], Argentinian-Brazilian anchovy [19, 137] and Japanese sardine [113, 155, 157] indicate that these populations are sensitive to environmental variability. The fact that these species and genera reproduce in upwelling, shelf-tidal and estuarine regions suggests that there are some fundamental similarities in the structure and functioning of the ecosystems to which adults of these species expose their offspring. This observation supports the possibility that frontal zones and/or pycnoclines may serve functionally sim-

ilar roles for larval growth and survival as the major upwelling zones, at least in terms of pelagic food web interactions. A comparative analysis of sardine/anchovy recruitment variability in relation to environmental variables (e.g. winds, tides, thermoclines, fronts, and turbulence), reproductive biology and spawning biomass could be useful for understanding how these stocks survive in different habitats (upwelling vs. shelf-tidal regions), and how other species living in shelf areas might be influenced by wind and turbulence conditions.

## 5. SYNTHESIS AND CONCLUSIONS

One of the main findings from this review is that there is no clear relationship across systems between turbulent mixing and field estimates of larval fish feeding, growth and mortality, and fish recruitment. The diversity of the response to turbulence that has been observed so far makes it difficult to infer how larval fish and fish populations might respond to turbulence in nature. Reasons for this finding include a failure to sample directly the processes of interest (i.e. those directly responsible for variations in growth or mortality), and the covariation of many ecosystem processes as water columns become more (less) turbulent [91, 135].

It is evident that the field studies surveyed here have mainly investigated population-level responses (e.g. changes in growth rates by entire populations; recruitment) to turbulence, or more accurately, to mixing-induced differences in the state of entire pelagic ecosystems (e.g. their food web structure, prey distribution, zooplankton community compositions, etc.). The observed response within each study represents an integrated response to the effect of turbulence on the structure and functioning of the local pelagic ecosystem. The roles of component processes (e.g. changes in prey abundance due to increased turbulence) on a biological response (e.g. recruitment) are not precisely known in a functional or mechanistic sense, are difficult to resolve and perhaps may not be the critical issue in some contexts [7]. What is perhaps most critical in these cases, at least for understanding causes of fluctuations in fish biomass, is the population-level response to the overall effect of turbulence on the ecosystem.

It is also evident that these same field studies are unlikely to increase our understanding of how processes (e.g. encounter rate, patch utilization, predator activity levels and metabolic rates) related to feeding or growth of individuals might vary with turbulence. This type of individual-based process information could nevertheless be useful in interpreting feeding and growth rates, diets and distributions of fish in the field. Investigations of individual-based processes require different approaches from those used in most field studies considered here. These approaches must include methods where the responses and forcing variables (e.g. dissipation rate, prey concentration and type) of interest are not influenced by other processes and where they can be reliably measured and quantified.

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