

Fluctuations in marine fish populations: physical processes and numerical modelling

Francisco E. Werner and John A. Quinlan

Werner, F. E., and Quinlan, J. A. 2002. Fluctuations in marine fish populations: physical processes and numerical modelling. – ICES Marine Science Symposia, 215: 264–278.

The question of whether variability in hydrodynamics can explain variability in fish recruitment is one that has been pondered for more than 100 years, ever since Pettersson, Helland-Hansen, Hjort, and others, in the early days of ICES, identified the importance of oceanic physical processes to understanding fluctuations in fish populations. In this paper, we outline our present-day understanding of some of these processes. We find that significant progress has been achieved in the past two decades in certain areas, such as in the description of the dynamics of continental shelf regions and in the coupling of hydrodynamics and fish early life stages – including effects at the level of individual larvae. With the advent of sophisticated numerical or computational modelling tools that are now relatively reliable and available to the research community, quantitative descriptions of the transport and dispersal of larvae and changes in their feeding environment are not uncommon. At the same time, we note that we are not yet able to consider regional studies for more than seasonal time scales, and we have not yet considered basin-scale spatial and temporal processes and their connection and effect on the coastal/shelf regions. These extensions will be necessary as we begin to consider variability on decadal time scales and the synchronicity of the populations' fluctuations across the ocean basins.

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Introduction

The question of whether variability in hydrodynamics can explain variability in recruitment is a question that has been pondered for more than 100 years, ever since O. Pettersson, B. Helland-Hansen, J. Hjort, and others, in the early days of ICES, identified the importance of physical processes to understanding fluctuations in fish populations. The studies of the causes of fisheries fluctuations included not only the role of biotic variables, but recognized and sought to identify links between physical and biological conditions as key components in determining the observed fluctuations, e.g., Helland-Hansen and Nansen (1909):

It is to be expected that variations in the sea have great influence upon the biological conditions of the various species of fishes living in the sea, and it might be therefore expected that such variations are the primary cause of the great and hitherto unaccountable fluctuations in the fisheries. It is therefore obvious that it would be of great importance, not only scientifically, but also practically, if the relation between

variations in the physical conditions of the sea and the variations in the biological conditions of the various food fishes could be discovered.

Initially, fluctuations in fish catch were thought to be due to migrations of adults to and from coastal areas, with a poor year occurring when the fish failed to visit their usual grounds. It was thought that fish of a given species constituted a single integrated group throughout their distributional range and that the interannual variability in catches was caused by the interannual differences in oceanic-scale migration patterns of the particular species (see discussion in Sinclair, 1988). In the case of Norwegian herring, the variability was believed to be related to their annual migration to the Arctic (see discussion provided by Hjort, 1914; pp. 3–5). Physical conditions of the sea, temperature, salinity, currents, etc. were believed to be of extraordinary importance for the migrations of these fishes, but the precise nature of the connection was not known (Hoek, 1905). An example of an early attempt at linking the fluctuations in fish populations and physical oceanographic conditions was suggested by Pettersson's observed periodicity in the fluctu-

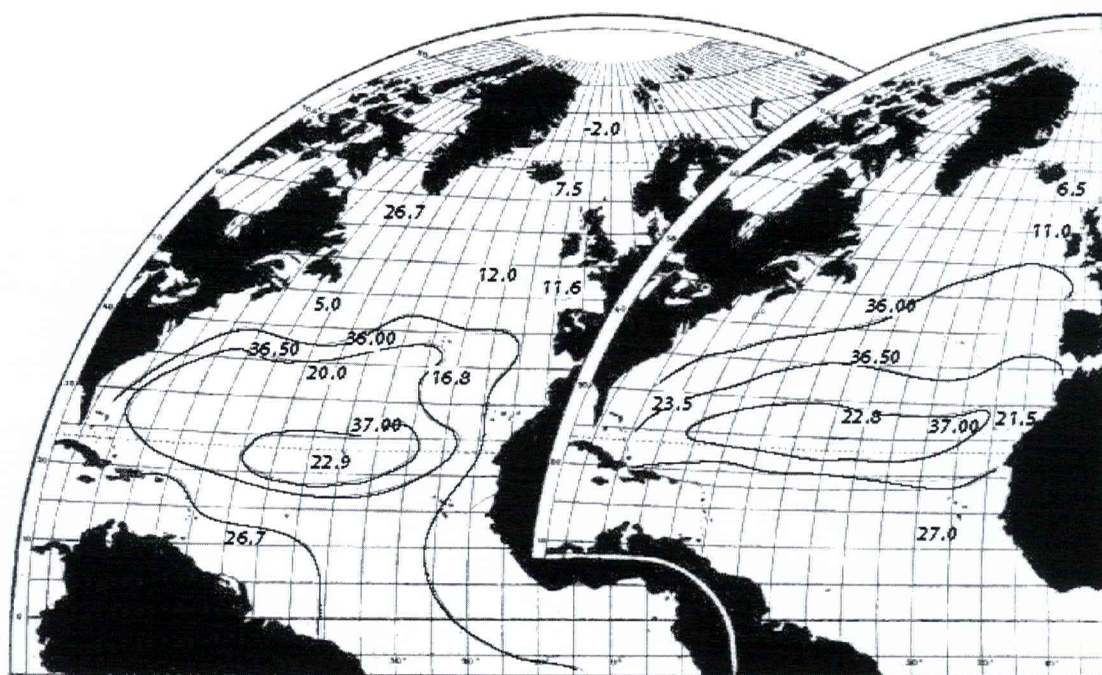


Figure 1. Variations in Gulf Stream circulation (temperature and salinity values are indicated); from Pettersson (1905).

tuations of the Atlantic Stream (Figure 1) and their connection with meteorological and biological phenomena, especially the migration of the fishes (Hoek, 1905).

With the introduction of ageing techniques (through the use of growth rings on fish scales), the idea of population variability being related to variation in year-class size was established (Hjort, 1914). Using age information, length frequency distributions revealed that the catch was often dominated by a single large year class. Hjort suggested that adult migrations would be limited by hydrographic conditions (temperature), and that spawning adults and eggs were found in relatively limited areas around banks. This meant that rather than a continuous smooth resupply of new individuals to the fishable population, the recruitment mechanism seemed to be "highly irregular" related to factors including larval drift, mortality associated with dispersal into unfavorable regions, e.g., low food concentration, thermal stresses, etc. Hence, interannual variability in landings was related to recruitment and year-class strength variability in age-structured populations. This shift in approach defined a new set of questions concerning the causes of the differences in recruitment and year-class strength.

Today, these ideas continue to be an integral component of national and international research efforts studying population regulation of marine species, e.g., through programs like GLOBEC (Global Ocean Eco-

system Dynamics), SPACC (Small Pelagics and Climate Change), CCC (Cod and Climate Change), CCCC (Carrying Capacity and Climate Change), among others. This paper addresses two aspects of our understanding of the relationship between physical processes and recruitment. First, a review is provided of physical processes that may contribute to fluctuations in fish populations, and second, we discuss the role of mathematical models in unraveling this relationship. While our discussion focuses on physical processes affecting early life history stages, the matter of year-class strength being set during larval stages (e.g., Hjort, 1914) or post-larval stages is unresolved (e.g., Leggett and DeBlois, 1994).

Hydrodynamic processes affecting fish populations

Most studies between the 1920s and 1970s on the links between physical variability and fluctuations in fish populations were qualitative. Difficulties from the physical oceanographic standpoint in making them more quantitative included the inability to make long-term synoptic observations, the development of theoretical underpinnings of the governing geophysical fluid dynamic principles, and the absence of significant com-

putational capabilities. The work conducted by physical oceanographers and hydrographers focused on understanding the dynamics of open-ocean circulation, e.g., western boundary currents, oceanic gyres, equatorial circulation, and changes in their patterns. It is perhaps safe to say that the coupling of physical oceanography with biological processes was correlative for most of this time period, with only a few clear examples of mechanistic understanding. One notable exception was the notion of "critical depth" described by Sverdrup (1953), where the relationship between stability of the water column, vertical mixing, and light penetration enabled the prediction of the onset of the spring phytoplankton bloom in the North Atlantic. This may be the first instance where variability in physical processes and the ensuing biological response were so clearly and elegantly linked.

In the 1970s, a rapid increase occurred in the ability to relate our understanding of physical process and their effect on marine populations. The Simpson and Hunter (1974) criterion, which predicts the timing and occurrence of tidal fronts, had a profound impact on the study of the regulation of population variability as related to the coupled physical-biological processes. Since fronts are regions of aggregation, retention, and enhanced growth, the research community's newly found ability to predict their occurrence and their variability set the stage for paradigms such as Cushing's match-mismatch hypothesis on the effect of the timing of the fronts' presence and the growth of the first feeding larvae, and Sinclair's member-vagrant hypothesis in relation to frontal circulation features (discussed below).

In the decades that followed, there was an explosion of studies and understanding of the link between physical oceanographic processes and their effect on biological variability. This is a result of advances in our abilities to collect data on the appropriate scales, a better understanding of the relevant ocean dynamics, and the ability to implement numerical models in desktop computing environments. In the sections that follow, which are based on, among others, Wroblewski and Hofmann (1989), Heath (1992), and Werner *et al.* (1997), we identify physical processes that characterize coastal and shallow seas and their effect on transport, turbulence, temperature, etc., as well as on the feeding environment of the target species. A summary is provided in Table 1. We focus on coastal and shelf regions as it is there that many of the critical stages of larval and juvenile marine fish are found; however, basin-scale variability and forcing must be included in any complete description of key processes (e.g., see Beamish, 1995; Mullin, 1993; Bakun, 1996).

Outer shelf

This is the region at the seaward edge of the continental shelf, near the shelf break, where the physics of offshore

(deep ocean) current systems is dominant and where the spawning area exists for many fish species (e.g., Boehlert and Mundy, 1988a). There are significant differences in the hydrodynamics depending on whether the location of interest is near an oceanic western boundary current 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.

Western boundary current systems

Driven by basin-scale wind systems, these systems are characterized 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 (e.g., 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 neighboring continental shelf or coastal sea (e.g., Hare and Cowen, 1996). Instabilities of western boundary currents also affect neighboring embayments and shelf regions. Meanders can be a source of different water masses, they may advect larvae on or off the shelf (e.g., Flierl and Wroblewski, 1985), or they can provide nutrients for phytoplankton and zooplankton populations (Hofmann and Ambler, 1988).

Eastern boundary current systems

These systems are also driven by large-scale windfields, but are weaker than western boundary currents, with currents flowing equatorward off western continental margins. Summer conditions are typically upwelling-like with equatorward surface jets and high biological productivity. These regions are known for their large fisheries off the west coasts of the United States, South America, and Africa. In the Benguela system, variability in alongshore currents and transport of anchovy eggs and larvae in frontal systems have been suggested by Shelton and Hutchings (1982). Off California, Sinclair *et al.* (1985) suggest that, during El Niño years, reduced offshore transport can result in reduced losses offshore of certain larvae and hence increased survival. Variability in squirts, jets, and filaments are likely to affect the on- and offshore transport of pelagic larvae, suggesting that behavioral 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).

Table 1. Physical processes on the continental shelf, sources of variability, and their effect on pelagic stages of marine species. Adapted from Werner *et al.* (1997).

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 Cowan (1996); Hofmann and Ambler (1988); Stegmann and Yoder (1996); Checkley <i>et al.</i> (1988)
Eastern Boundary Currents	Instabilities, jets, squirts, winds	Cross-shelf transport, nutrient supply	Hofmann <i>et al.</i> (1991); Botsford <i>et al.</i> (1994); Parrish <i>et al.</i> (1981); Sinclair <i>et al.</i> (1985)
Others (Shelf-edge fronts and upwelling)	Winds, rings, tidal turbulence, internal tides	Cross-front exchange, transport, expatriation, nutrient supply, prey aggregation	Hare and Cowan (1991); Heaps (1980); Munk <i>et al.</i> (1995); Shelton and Hutchings (1982); Heath (1999)
<i>Mid-shelf and shallow seas</i>			
Wind-driven flows	Wind direction and intensity, storm frequency	Transport, turbulence intensity (encounter rates)	Bartsch <i>et al.</i> (1989); Hermann <i>et al.</i> (1996); Sundby and Fossum (1990); Lasker (1975); Heath and Gallego (1998); Quinlan (1999)
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, interannual variability	Absolute temperature, growth, spawning location, stratification, internal wave transport	Brander (1995); Frank <i>et al.</i> (1990); Denman and Gargett (1995); Shanks (1983); Marsh <i>et al.</i> (1999)
Tides	Spring-neap cycle, nodal cycles	Intensity of residuals, frontal location, turbulence, transport	Garrett and Loder (1981); Parker <i>et al.</i> (1995); Metcalfe <i>et al.</i> (1993)
<i>Inner shelf</i>			
Wind-driven flows	Wind direction and intensity	Transport, upwelling/nutrient supply	Boehlert and Mundy (1988b); Nielsen <i>et al.</i> (1998); Leggett <i>et al.</i> (1984); Werner <i>et al.</i> (1999a)
Buoyancy-driven flows	Freshwater discharge	Transport, retention, chemical cues	Ruddick <i>et al.</i> (1995); Creutzberg (1961)
Tides	Spring-neap cycle, nodal cycles	Intensity of residuals, formation of fronts, turbulence, transport	Loder and Garrett (1978); Rothlisberg <i>et al.</i> (1983); Metcalfe <i>et al.</i> (1990)
<i>Near inlet</i>			
Windforcing	Wind direction and magnitude	Transport	Wang (1988); Epifanio <i>et al.</i> (1989)
Tides	Spring-neap cycle, lunar phase, shifting bathymetry	Transport, residuals	Ridderinkhof and Zimmerman (1990); Roessler and Rehner (1971); Rijnsdorp <i>et al.</i> (1985)
Buoyancy-driven flows	Freshwater discharge	Plumes, fronts, two-layer gravitational flow	Kapolnai <i>et al.</i> (1996); Wheless and Valle-Levinson (1996)
<i>Banks</i>			
Tides	Spring-neap cycle, nodal cycle, internal tides	Intensity of residuals, turbulence, transport	Loder <i>et al.</i> (1988); Werner <i>et al.</i> (1993, 1996); Perry <i>et al.</i> (1993)
Fronts	Winds, heating, tidal mixing	Transport, retention, prey aggregation	Naimie (1996); Incze <i>et al.</i> (1996)
Neighboring currents and remote forcing	Upstream inflow, deep ocean currents	Transport, retention	Flierl and Wroblewski (1985); Polachek <i>et al.</i> (1992)
Windforcing	Wind direction and intensity, storms	Transport, retention, prey supply	Lough <i>et al.</i> (1994); Lewis <i>et al.</i> (1994); Hannah <i>et al.</i> (1997)

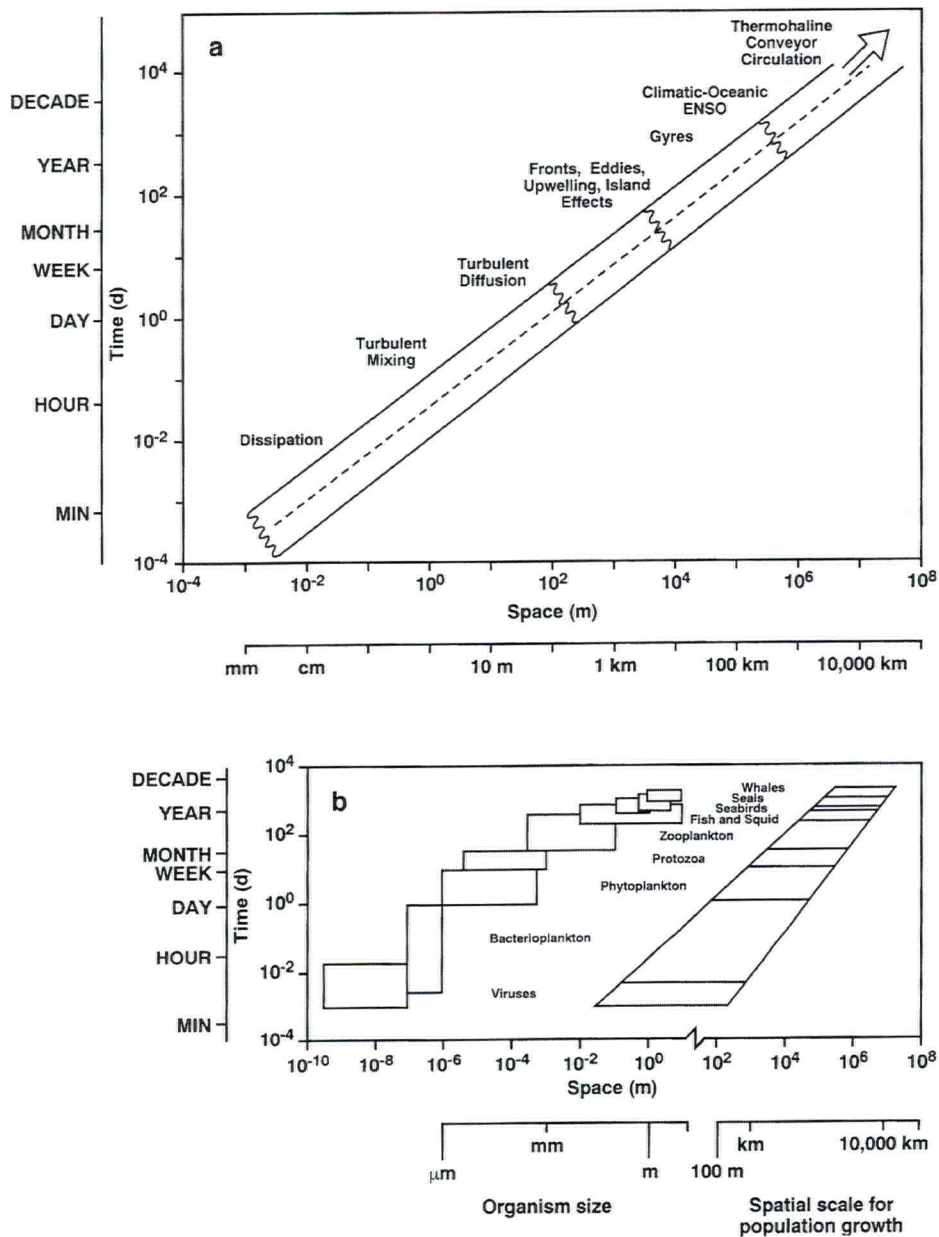


Figure 2. Schematic showing the dominant space and time scales in the ocean for (a) physical motions and (b) biological populations (from Hofmann and Powell, 1998).

Other shelf-edge regions

Shelf-edge domains such as the Middle Atlantic Bight off the east coast of the United States and the European continental shelf edge are not part of either an eastern or western boundary current system. These are usually hydrodynamically complex regions, owing to the abrupt topography of the shelf break and the disparity in scales found at the juncture between continental shelf dynam-

ics and that of the deep ocean. There is typically a persistent density front between the deep ocean and shelf water masses which will generate (unstable) flows and internal waves resulting in exchanges (losses and gains) between the shelf and the offshore regions (see Pingree and Mardell, 1981). Shelf-break upwelling (e.g., Heaps, 1980) and shelf-break fronts can result in regions of increased prey aggregation (Munk *et al.*, 1995) favorable to larval growth and survival.

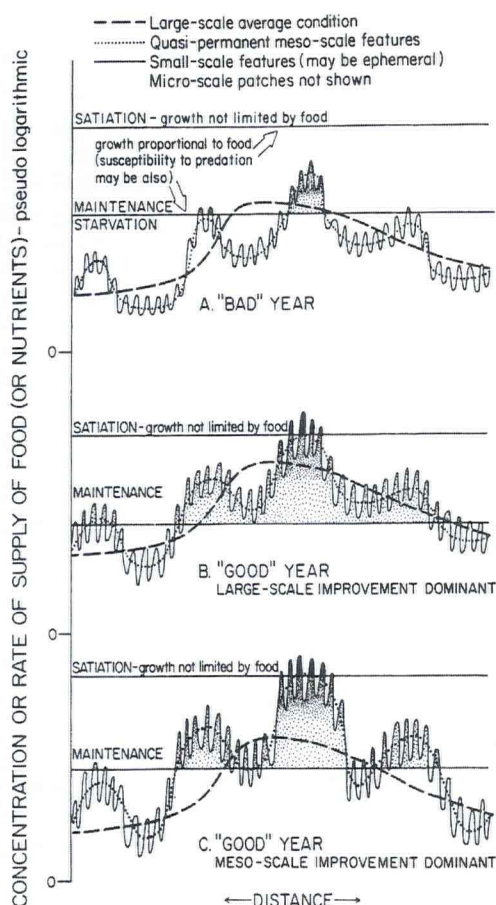


Figure 3. Conceptual sketch of potential range of a population in one year of poor food supply and two years of abundant food (relative to the amount necessary to sustain the population) (from Mullin, 1993). Instead of food supply, the variability could also represent changes in other environmental or physical parameters.

Mid-shelf and shallow seas

These regions are seaward of the 20-m isobath, but not within the direct or continuous influence of deep-ocean current systems. Typical depths range between 20 and 150 m. 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 and set the local turbulence levels in the water column. Local topographic features modify this flow, determine the location of fronts (Simpson and Hunter, 1974), and generate tidal residuals (Loder, 1980). The physical oceanography of mid-shelf regions is perhaps the most studied component of the continental shelf (see Brink and Robinson, 1998).

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 on- and offshore Ekman transport and the resulting convergence or divergence of mass at the coast. The SABRE program examined variations in wind-driven, alongshore transport and their effect on changes in the recruitment of certain estuarine-dependent species (e.g., Quinlan, 1999; Werner *et al.*, 1999a).

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, e.g., the equatorward flow component in branches of the Greenland and Labrador currents along the western North Atlantic shelf (Loder *et al.*, 1996). 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. Marsh *et al.* (1999) related the tilefish kill of 1882 to a cold-water intrusion triggered by the North Atlantic Oscillation. 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). 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).

Inner shelf

We define the inner shelf as regions inside the 20-m isobath. Owing to the proximity to freshwater (buoyant) discharges, the inner shelf is often characterized by the presence of plumes and coastal fronts (Blanton, 1986; Simpson and James, 1986). Tidal currents and mixing tend to be strong and, in this region, behaviors 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 on account of ontogenetic changes in larval behavior.

Integration of physical and biological scales leading to recruitment

Recruitment to a population may be a function of a single or an integrated set of the processes and effects outlined in Table 1. Although these studies show relationships between environmental variability and the sur-

vival, dispersal, or transport of larvae, they focus on small windows of the life cycle and/or on small subsets of the population. To date, no study has truly 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.

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 from spawning grounds to the nursery areas. 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. The poorest recruitment may be from either a catastrophic event (e.g., extreme cold affecting eggs at spawning sites) or a combination of adverse factors in a given year, such as washout events and unfavorable winds.

Our understanding of the relationships between variations in hydrodynamics or physical forcing and marine populations can be synthesized in the form of space-time diagrams such as Figure 2. These diagrams (Haury *et al.*, 1978; Denman, 1989; Hofmann and Powell, 1998) show the overlaps in scales between physical processes and populations. At the smallest scales, the ability of organisms to encounter their prey is affected by turbulent processes that occur at the scale of the individuals. Intermediate scales, such as the seasonal presence or absence of fronts or the strength of upwelling structures, may affect the regional distribution and maybe the type of populations at selected locations over scales of hundreds of kilometers. Interannual fluctuations, such as El Niño or the North Atlantic Oscillation, may affect the basin-scale variation of populations on the order of thousands of kilometers and introduce possible synchronicities or asynchronicities across oceanic basins. At the largest scales, global variations play a role, such as global warming or the thermohaline ocean conveyor-belt circulation.

One of the issues to keep in mind when interpreting diagrams such as Figure 2 is that although the discussion and presentation of the processes and scales are discrete, the scales are not independent (Hofmann and Powell, 1998). Changes at one scale are generally coupled, at least, to those at neighboring scales. Storms affect mixing which, in turn, affects stratification, nutrient availability, and primary production. Ensuing trophic interactions will cascade upward and affect secondary producers (zooplankton), larval fish, and eventually fish stocks. Figure 3 is a sketch illustrating this concept in terms of processes occurring at different scales that may lead, through their interactions, to high or low food concentrations and thus variations in growth rates for par-

ticular species. The top panel (Year A) is generally poor. The middle panel (Year B) corresponds to a generally "good" year as a result of favorable conditions at the largest scales. The bottom panel is also a "good" year, but attributable to enrichment at the mesoscales.

Despite the realization that all scales may, at some point, be important in the quantitative description of the observed variability of fish populations, the approach to studying these fluctuations has been, by necessity, focused on subsets of these scales – either as subsets of trophic scales, environmental scales, or both. Returning to Figure 3, it is easy to see why this approach may fail in the long run to explain and predict the state of target populations. A study that quantitatively captures the variability at intermediate scales, e.g., the onset and strength of tidal front, stratification, and associated circulation on submerged banks, may still be an inadequate predictor of the overall state of target populations if it misses a larger-scale change in circulation that provides a source of prey or temperature and its impact on growth rates.

Hydrodynamics and fisheries fluctuations: concepts and paradigms

Four main paradigms have been proposed 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 summarize these in Table 2.

Hydrographic containment

A combination of Harden Jones' (1968) migration triangle and Cushing's (1974) match-mismatch hypotheses, this hypothesis recognizes 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 (for additional discussion see Cushing, 1995).

Stable ocean

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

Table 2. Paradigms explaining population pattern, abundance, or variability. Adapted from Sinclair and Page (1995) and Werner *et al.* (1997).

Hypothesis	Population pattern Individual stocks kept distinct by	Abundance Mean population level set by	Variability Fluctuations in abundance due to
Hydrographic containment (migration triangle match–mismatch)	Presence of tidal current stream- lines 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 mix- ing such that prey aggregations at the pycnocline are disrupted
Encounter rate	(Not explained)	(Not explained)	Influence of small-scale turbu- lence on relative motion between predator and prey
Member/vagrant	Retentive hydrographic struc- tures which result in limited dis- persal of early life history stages	Size of the hydrographic structure associated with spawning location	Foodweb and physical loss from appropriate habitat are both pos- sible

these layers was related to (weak) local windstress through (reduced) turbulent mixing.

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; MacKenzie and Kjørboe, 2000). This hypothesis is counter to the stable-ocean hypothesis, although both may be favorable for recruitment depending on the larval fishes' life stage or on the species (Leggett and DeBlois, 1994), e.g., younger larvae may do better in lower turbulence regimes than older larvae, or cod may thrive in turbulent conditions that may be detrimental to anchovies.

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 behaviors, 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.

Modelling approaches

Hydrodynamic models

The study of marine ecosystems requires that models of different systems be coupled to properly capture biological, geochemical, and hydrodynamic interactions across a wide range of temporal and spatial scales. As discussed above, important biological processes are affected by transport mechanisms that can occur over hundreds of kilometers as well as turbulent mixing events that can occur on scales of meters or less. Hydrodynamic circulation models have now achieved a level of sophistication and realism where new and significant opportunities for scientific progress in studying coupled physical–biological simulations are within reach (e.g., Blumberg and Mellor, 1987; Backhaus, 1989; Haidvogel *et al.*, 1991; Lynch *et al.*, 1996; and review by Haidvogel and Beckmann, 1998).

One of the earliest examples using a three-dimensional (3-D) hydrodynamic model to study larval advection is that of Bartsch *et al.* (1989). These investigators 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 during the 1987/1988 recruitment season using a 3-D model which included tidal forcing, baroclinicity, surface windstress, atmospheric pressure fields, and 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 the loss of a portion of the year class in the Norwegian coastal current and therefore to have contributed to fluctuations in recruitment.

Spatially and temporally explicit models of the coastal physical environment, including the specifica-

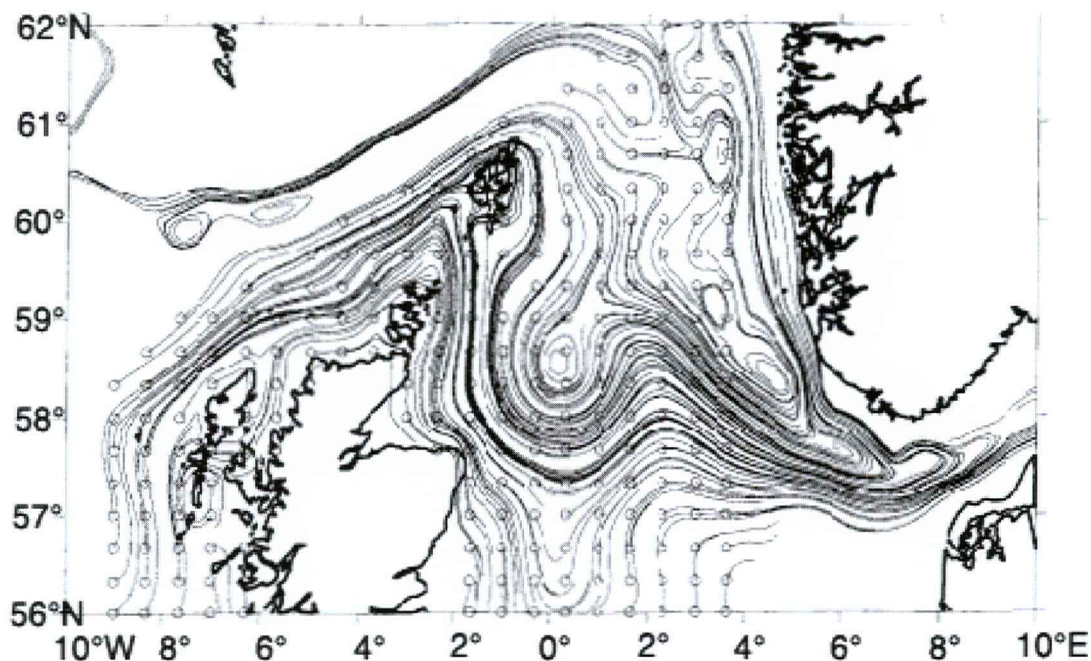


Figure 4. Trajectories of particles from release location on the North Sea continental shelf (from Heath and Gallego, 1997).

tion of velocity, hydrography, and turbulent fields, continue to improve on scales relevant to biological processes. As such, the investigation of ecosystem-level questions involving the role of hydrodynamics in determining the variability and regulation of planktonic and fish populations are now being attempted. There are now many case studies that have coupled the growth and feeding environment of planktonic and larval fish species with coastal circulation models. Examples include the study of retention, survival, and dispersal of larval cod, haddock, and their prey in the Northwest Atlantic and North Sea (Werner *et al.*, 1996, 2001a; Heath and Gallego, 1997, 1998); the transport of estuarine-dependent fish from offshore coastal spawning regions to estuarine nursery habitats on the eastern coast of the United States (Stegmann *et al.*, 1999); and the interannual recruitment variability of pollock in the Gulf of Alaska (Hermann *et al.*, 1996).

The hydrodynamic models used to explore (relatively successfully) the different regions of the shelf 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 neighboring 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., Robinson *et al.*, In press). 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.

Biological models

Biological models attempt to relate abundance, distributions, fluctuations, and production of living organisms to variations in the abiotic environment, food condition, and predation (Carlotti *et al.*, 2000). These models can be simple or they can be complex representations of the marine foodweb, and they can have various objectives, including the estimation of the energy and/or matter through an ecological entity (be it an organism or a community), the estimation of the survival and persistence of populations in response to the factors that regulate their variability, and the study of behavioral traits. Details of the modelling approach are defined by the objectives of each modelling study, including what are appropriate simplifications, e.g., can state variables be lumped and modelled as $dQ/dt = \alpha Q$, where Q is biomass with α (generally) assumed constant, or does size

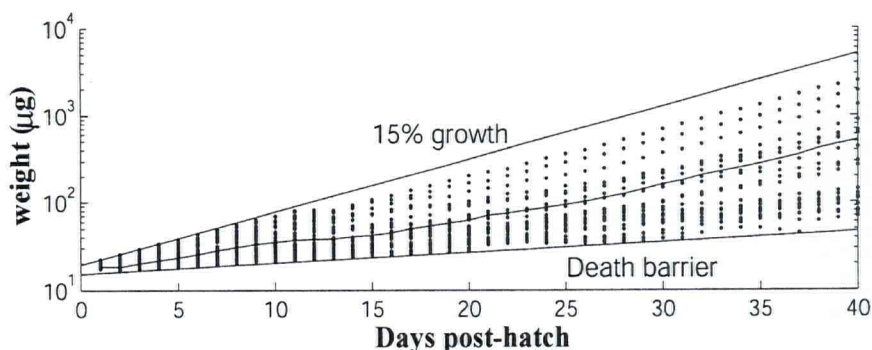


Figure 5. Size distribution of modelled cod larvae during the 40 days post-hatch (from Werner *et al.*, 1996). The distribution of weights is a result of individual model larvae sampling different feeding environments of the domain (Georges Bank). The upper growth limit is 15% per day; larvae that fall below the death barrier are considered starved. The mean weight is indicated by the line through the scatter of points. The property (mean weight) of the population is determined by the variability in the individual larvae.

and age structure need to be explicitly considered? In other words, the currency of the model may vary from lumped units of carbon to address budget questions, e.g., mass balances, to increasingly detailed representations of size and class to address questions of community structure, where the currency may be numbers of individuals or density if population abundance is the target.

Individual-based models

The basic idea of individual-based models (IBMs) is that properties of ecological systems can be derived by considering properties of the individuals constituting them (as opposed to the average/aggregate of the individuals; see review of Werner *et al.*, 2001b). Individual differences may be physiological or behavioral or may arise from interactions among individuals. The end result is unique life histories which, when considered as a whole, give rise to growth/size distributions that provide a measure of the state of the population. Recent advances in ocean (hydrodynamic) circulation models that include realistic temporal and spatial variation of currents, turbulence, light, prey, etc. have enabled IBMs (mainly developed for planktonic and/or early life stages) to be embedded in model flow fields and for unique (possibly behaviorally modified) Lagrangian trajectories to be computed (e.g., Werner *et al.*, 1993; Hermann *et al.*, 1996; Heath and Gallego, 1998). The explicit consideration of realistic spatial heterogeneity provides an additional factor that contributes to the differentiation among individuals, to variances in population structure, and ultimately to the recruitment process. This is particularly important in marine environments

where fronts, boundary layers, pycnoclines, gyres, and other smaller spatial features have been hypothesized to play a significant role in determining vital rates and population structure.

An example of the intersection of large- and small-scale physics affecting recruitment is given in Werner *et al.* (2001a), in which the effect of the feeding environment – modified by turbulence at the smallest scales – on larval growth and survival was examined. They found that regions of larval survival (with growth rates comparable to field values) coincided with the hydrodynamically retentive subsurface regions of Georges Bank. However, these retentive regions were a subset of those defined by Werner *et al.* (1993). 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.

During the past decade, the use of spatially explicit IBMs in the study of marine systems has proven to be quite successful on a number of fronts. Coupled with spatially and temporally realistic descriptions of the physical environment, IBMs provide a tool to explore the factors that contribute to the individuals' unique time histories and thus the ability to extract information about the population based on the variance among the individuals (see Figures 4 and 5).

Linking spatially explicit IBMs where full hydrodynamics and full population dynamics co-occur will likely be attempted in the next five years. This will allow exploration of ideas such as Cushing's match-mismatch hypothesis where spawning strategies are related to timing of food availability and consequently the observed variability of certain marine populations. One reason

these studies have not yet taken place is that, to date, the population dynamics of prey (e.g., copepods) have been studied separately from those of the predators (e.g., fish larvae). These studies are now at a point where we are beginning to see the first attempts at integrating these approaches (e.g., Hermann *et al.*, 2001).

The added complexity of more realistic prey distribution will invite advances in approaches to determine behavior. Externally imposed (and/or passive) behaviors may not make sense in view of the added detail of the feeding environment and will likely be replaced by model-derived behaviors that include components maximizing some biological characteristic such as reproductive value (Giske *et al.*, 1994; Fiksen and Giske, 1995; Fiksen *et al.*, 1995). Dynamic programming methods allow organisms to "find" optimal habitats by balancing risks of predation, growth, and advective loss.

Concluding remarks

Environmental effects and physical forcings play a significant role in the fluctuation of marine populations. Unfortunately, covariation in environmental forcings makes unambiguous identification of the causes of recruitment variability a difficult task. Programs such as the ICES Cod and Climate Change, GLOBEC, and others are attempting to deal with this difficulty through intensive, organized, field and modelling efforts. This is admittedly non-trivial, given the geographic and time scales involved. However, advances in understanding and modelling biological and physical processes may provide inroads into disentangling environmental (and biological) signals.

Recently, the confounding effect of fishing/anthropogenic pressure has made the disentanglement more difficult. Attempts to consider environmental forcings (in the absence of anthropogenic stresses or at least in times of reduced stresses) took place during the ICES Backward-Facing Workshops. These workshops sought to explain past "events" of fish populations, e.g., the 1882 tilefish kill (Marsh *et al.*, 1999), the large fluctuations in the gadoid populations in the Northwest Atlantic and the North Sea in the 1960s and 1970s (Werner *et al.*, 1999b), and the gadoid outburst in the North Sea during roughly the same time period (Heath and Brander, 2001). While it was suggested that the tilefish kill was related to a large-scale response to the North Atlantic Oscillation in the form of a cold-water intrusion off the east coast of the United States, no such mechanism was identified to explain the 1960s and 1970s gadoid population fluctuations.

Over the past decades, we have made considerable advances in our ability to examine the coupling of physics and biology in the field and in the laboratory. We have also begun to use the detail provided by available numerical models to explore the couplings of behavior and abiotic factors in realistic settings. These

developments are encouraging, and the answer to the initial question whether or not physical variability can explain fluctuations in marine populations is affirmative in that physical processes directly or indirectly affect populations, as suggested by the present review. As such, physical variability is part of the answer. However, quantitatively stating how much of the fluctuation is caused by a particular forcing or forcings is made difficult by the above-mentioned covariation of signals, the mediation or masking by biological processes including predation (and fishing), and the inability to isolate a particular process.

It should also be reiterated that recent advances in modelling physical and biological processes, while impressive, have been, for the most part, regional or of short duration. The studies have focused largely on shelf regions, submerged banks, and rarely for more than a season at a time. Clearly, one of the more important challenges we face is to develop our ability to consider larger, e.g., basin-scale phenomena, as many of the observed fluctuations in marine populations are correlated either over large distances (whether synchronously or asynchronously, as shown by studies such as by Luch-Belda *et al.*, 1992), or occurring "suddenly" as large-scale regime shifts in environmental variables and marine populations (Francis and Hare, 1994). Physical/circulation models will need to couple with climatic/atmospheric signals (the North Atlantic Oscillation, the Pacific Decadal Oscillation, etc.), possibly including feedbacks between the atmosphere and ocean. Modelling of biological processes will require more complete descriptions of the target species' life cycles, as well as of their prey and their predators.

Acknowledgements

We wish to thank Emory Anderson, the Convener of the ICES History Symposium, Mike Sinclair and Bob Dickson for their invitation to prepare this paper, and Katherine Richardson for providing very helpful comments. We also wish to express thanks for the support from the US GLOBEC Program, funded by NOAA and NSF. This is Contribution No. 212 of the US GLOBEC Program.

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