

Emerging from Hjort's Shadow

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Abstract

Early in the 20th century, Johan Hjort developed compelling arguments and hypotheses to explain recruitment variability that became dominant for more than 75 years. A cautious emergence from Hjort's shadow began late in the 20th century. Hjort's "Critical Period" hypothesis, *i.e.*, failure of first-feeding larvae to find food, and a second hypothesis, "Aberrant Drift" of eggs and larvae, were proposed to explain causes of recruitment variability. Tests of the Critical Period hypothesis became an obsession, although support for it was inconsistent and equivocal. Single-minded research on the Critical Period hypothesis gave way to realization that recruitment variability was the outcome of complex trophodynamic and physical processes acting over many temporal and spatial scales and throughout pre-recruit life. A complex mix of main effects and interacting factors can easily generate order-of-magnitude variability in recruitment *via* small effects on mortality and growth rates during the abundant egg and larval stages, or *via* cumulative effects during the pre-recruit juvenile stage. New considerations of compensatory mechanisms that can dampen variability and stabilize recruitment emerged. A little density dependence, especially in the relatively long juvenile stage, can regulate recruitment. Multidisciplinary programs instituted in the 1990s and successful development of statistical models and coupled bio-physical models, offered new insights into mechanisms generating recruitment variability. Despite progress, forecasting recruitment remains a formidable challenge. "Solving the recruitment problem" is no longer the Holy Grail of fishery science. Appreciating recruitment variability, explaining its probable causes, considering implications for management, and understanding it in the context of broader variability in marine ecosystems, are all worthy goals.

Key words: advances in understanding, Johan Hjort, recruitment variability

Introduction

Fluctuations in abundance of fish stocks have captured the attention of fishers, fishery managers, and fishery scientists since the late 19th century (Hjort, 1914) and shaped the foundation for research on recruitment variability. A century ago, the International Council for the Exploration of the Sea (ICES) sought to identify causes of variability, and focused its attention on two primary mechanisms of fish migrations and effects of fishing. ICES Committee A, the Migration Committee, was chaired by a leading scientist of the day, Johan Hjort. The Committee, and especially Hjort, discovered that fluctuations in abundance were caused not so much by variability in migratory pathways as by variability in reproductive success, *i.e.*, recruitment variability (Sinclair,

1997). The extraordinary 1904 year class of Norwegian herring and its persisting dominance in the fishery laid the foundation for Hjort's famous "Critical Period Hypothesis" (Hjort, 1914, 1926). This hypothesis and its corollaries were a focus of research on recruitment variability in the 20th century.

In essence, the Critical Period hypothesis proposes that fates of year classes are determined in the early larval stage, shortly after yolk absorption when larvae must find suitable amounts and types of planktonic prey. Failing to find those feeding conditions would lead to massive mortality and order-of-magnitude losses of larvae in a short span of time (Fig. 1). The hypothesis has appeal, is seemingly testable, and became the emphasis of recruitment research. Despite decades of research, there

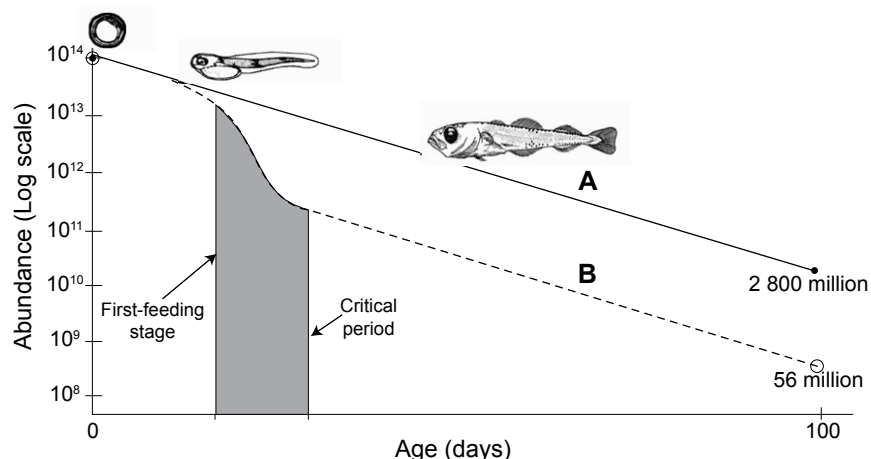


Fig. 1. Illustration of the “Critical Period” as hypothesized by Hjort (1914, 1926). Failing to find suitable prey in sufficient quantity, >90% mortality occurs soon after larvae absorb their yolk and initiate feeding (cohort B). In this example, the daily mortality rate, except for the critical period, is $M = 0.1$. Recruitment at 100 days post-hatch differs by 50-fold in cohort B experiencing a critical period and in cohort A not experiencing a critical period. (Modified from Houde, 2002, Fig. 3.4).

has been mixed and equivocal support for the hypothesis, at least as presented by Hjort (May, 1974; Lasker, 1987; Anderson, 1988; Leggett and Deblois, 1994; Cowan and Shaw, 2002). In retrospect, the hypothesis has merit and was insightful in identifying larval nutrition and starvation (trophodynamics) as probable sources of variability in early-life survival. However, its narrow focus on first-feeding larvae and its single-mindedness with respect to starvation as the cause of recruitment variability were misleading.

Hjort (1914) offered a second hypothesis to explain variability in year-class success. He proposed that dispersal of early-life stages by unfavorable currents to areas beyond where juveniles could return to recruit might generate variability, at least in availability of fish to fisheries. This hydrodynamics or “Aberrant Drift” hypothesis also has considerable appeal but was tested less than the Critical Period hypothesis until late in the 20th century. Together, Hjort’s two hypotheses laid the groundwork for subsequent theory and hypotheses to explain recruitment variability. Moreover, mechanisms associated with the two Hjort hypotheses (trophodynamics and hydrodynamics) may act together. New understanding of recruitment variability gained in the past 25 years has largely confirmed the importance of the combined action and interaction of biological and physical processes.

Moving Outside the Shadow

Moving beyond the fringes of Hjort’s shadow was slow initially, but has gained momentum. Emergence

was a consequence of new technologies as well as development of theory, new hypotheses or corollaries. In this essay I review recruitment research and discoveries that led to new understanding of variability and its causes. I conclude that recruitment variability can result from numerous processes operating on different time and space scales, and represents an integrated process acting throughout pre-recruit life.

Discoveries

Perhaps the single most important breakthrough advancing research on larval fish ecology and dynamics was the discovery that daily increments are laid down in otoliths (Pannella, 1971). This technological advance provided ability to confidently and accurately age fish larvae, estimate growth rates and, most importantly, estimate survival and mortality patterns during early life. Furthermore, chemistry of the otolith, combined with microstructure analysis, preserves a record of water quality and habitat experienced by early-life stages. Chemical signatures recorded in otoliths during the larval stage offer the potential to define stock structure and origins, retrospectively evaluate habitat use by early-life stages, and identify cohort-specific contributions to recruitment (Gunn *et al.*, 1992; Campana, 1999; Thresher, 1999).

Notable advances evolved from better measurements and modeling of hydrodynamic processes in the sea. It became possible to observe, analyze, and model dispersal patterns or aggregations of fish larvae with respect to water masses, frontal zones, transport processes,

and hydrography. Sophisticated, coupled bio-physical models were developed (Heath and Gallego, 1998; Hermann *et al.*, 2001; Werner *et al.*, 2001; North *et al.*, in press). Moreover, computing power and software able to support bio-physical coupled modeling became widely available in late decades of the 20th century.

Recruitment Hypotheses

Links and Roots

Research on recruitment variability intensified in the 1960s. Much of it aimed at testing or supporting Hjort's Critical Period hypothesis. A family of recruitment hypotheses evolved (Fig. 2), many clearly linked to the Critical Period hypothesis. The most prominent is Cushing's (1974, 1990) "Match-Mismatch" hypothesis in which a match in timing of fish spawning and larval production with the spring zooplankton bloom, *i.e.*, larval prey, is hypothesized to be critical. Hjort (1914, p. 205; 1926, p. 33) laid out the kernel of the Match-Mismatch idea, indicating his awareness of its possible importance. The Match-Mismatch hypothesis is intuitively appealing and has received considerable support in investigations of seasonally-spawning, high-latitude fishes, *e.g.*, Atlantic cod (*Gadus morhua*) (Ellertsen *et al.*, 1989). The Match-Mismatch idea emphasizes larval fish nutrition and prey production within an overlapping time window; it is an important extension of Hjort's hypothesis.

Lasker's (1978, 1981) "Stable Ocean" hypothesis proposes that occurrence and frequency of calm periods in upwelling ecosystems (sometimes called "Lasker events") induce temporary vertical stratification of the water column, with attendant aggregation of fish larvae and prey at strata interfaces that supports high feeding, survival, and recruitment. For northern anchovy (*Engraulis mordax*) high survival of larvae occurs when the frequency of calm periods increases, but there is little relationship to recruitment levels recorded many months later (Peterman and Bradford, 1987). In an extension of the Stable Ocean hypothesis, Cury and Roy (1989) and Roy *et al.* (1992) developed a conceptual model ("Optimum Environmental Window") whose major elements included wind stress and associated micro-turbulence. They hypothesized that recruitment level in upwelling ecosystems is dome-shaped and most successful under moderate wind stress that controls both advective losses and foraging success (*via* micro-turbulence) by larvae. Recruitments of pelagic sardines and anchovies in Ekman-type upwelling areas provide evidence supporting the hypothesis.

A hypothesis with roots in Hjort's Aberrant Drift hypothesis was proposed by Iles and Sinclair (1982) and (Sinclair, 1988). They hypothesized that physical retention, *i.e.*, "Larval Retention/Membership-Vagrancy" of early-life stages, not levels of available prey, is critical in the recruitment process, and is dependent on adult

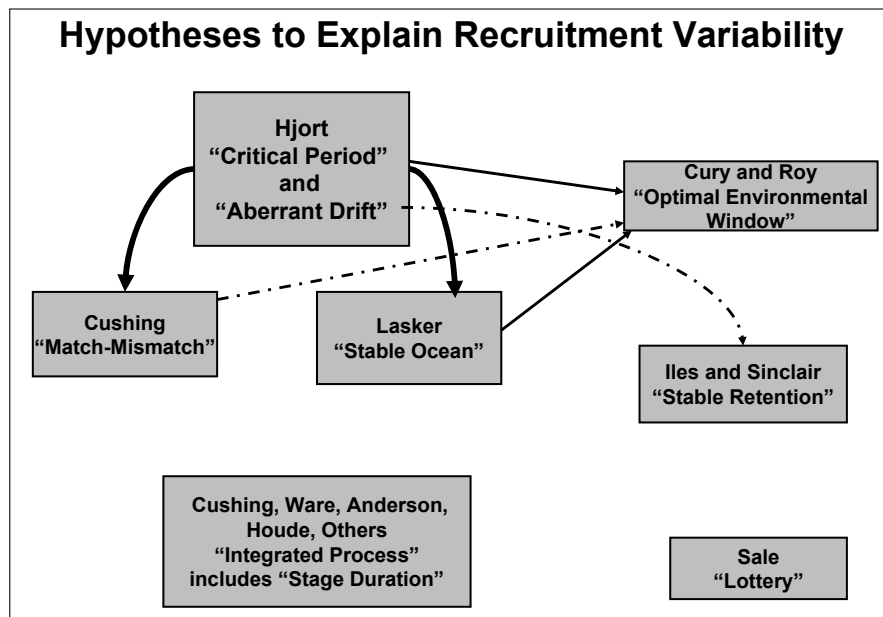


Fig. 2. Hypotheses to explain recruitment variability. Linkages to Hjort's Critical Period and Aberrant Drift hypotheses are indicated. Solid arrows indicate direct, and broken arrows indirect, derivations from Hjort's hypotheses. Thickness of arrows indicates strength of relationship.

fishes spawning in appropriate places when conditions are conducive for retention of eggs or larvae. In support, Iles and Sinclair cited Atlantic herring (*Clupea harengus*). One or more stocks of herring spawn on specific grounds in every month of the year. In the herring, spawning apparently is not keyed to plankton productivity but to physical features associated with retention. Sinclair (1988) emphasized that processes of retention within physically defined systems contributed to pattern, richness, and abundance of populations as well as contributing to recruitment variability.

In the tropics, especially in coral-reef ecosystems, extensive recruitment research, at least initially differed notably from approaches derived from Hjort's hypothesis. In the 1970s Sale (1978, 1991) proposed that recruitment of tropical reef fishes depended strongly on delivery potential to the reef of settlers and that post-settlement processes ("Lottery Hypothesis") could control recruitment levels. In recent years, thinking (and evidence) has converged such that pre- and post-settlement processes in reef-fish dynamics are considered important in determining recruitment variability (Doherty and McB. Williams, 1988; Jones, 1991; Doherty, 2002). Additionally, "self-recruitment" mechanisms, dependent on physical circulation patterns and larval behavior have been demonstrated to be surprisingly important in island-reef ecosystems (Jones *et al.*, 1999; Cowen *et al.*, 2000; Cowen, 2002) and probably important in other ecosystems.

We now generally acknowledge that no single process, mechanism or factor is responsible for recruitment variability, but that many processes may act together over the entire egg to pre-recruit juvenile period. In this context, both growth and survival processes are important determinants of recruitment success (Cushing, 1975; Houde, 1987, 1997b, in press; Anderson, 1988; Cowan and Shaw, 2002). Large size and/or fast growth, shortened life-stage durations, and processes supporting those attributes, are associated with high recruitment. Even the seemingly contrasting Match-Mismatch and Larval Retention/Member-Vagrant hypotheses are, in many cases, complementary when plankton blooms and retention act together to nourish larvae while insuring retention in the nursery area.

Five Dominant Mechanisms

Early-life stages of fishes live in a trophodynamics arena defined by physics and hydrographic features. Predation generally is the agent of mortality. But, its effect is modulated not only by predator abundance but by temperature and the nutritional state and growth rates of lar-

vae, which are themselves governed by prey availability, the diversity and sizes of the predators and larvae, and other environmental factors.

Temperature

For many taxa a substantial fraction of variability in recruitment can be explained by temperature (*e.g.*, Francis, 1993, 1994; Houde, in press). Temperature acts directly or indirectly to control biological processes. It acts across the spectrum of biologically relevant space and time scales, *e.g.*, at the micro-scale it continuously controls activities of individual cells, while at ocean-basin scales it exercises decadal to century-scale control over productivity of ecosystems. Considered with Hjort's hypotheses in mind, it is probable that in many instances temperature exercises stronger control over early-life dynamics than prey availability. Physiology and metabolic activity, behavior, and growth of early-life stages of fishes are responsive to temperature (Blaxter, 1992). Growth is strongly responsive (Fig. 3). In cross-taxa meta-analyses, Houde (1989) and Pepin (1991) documented predictable relationships between temperature and mortality rates, growth rates, and stage durations of larval fishes (Fig. 4). Such relationships are broadly predictable, and effects on larval stage duration, across marine invertebrate and vertebrate taxa appear to be universal (O'Connor *et al.*, 2007).

Physical Processes and Features

The physical arena in which recruitment processes act is more complex than Hjort envisaged. In the 1970s, Cushing (1975) proposed a modification of the Harden-Jones (1968) "triangle of migration" to explain how recruitment is contained within circulation features of an ecosystem. The conceptual model depends not only on circulation patterns, but also on adult migratory behaviors and spawning sites, and especially on larval denantant drift patterns. This model helped to focus research on early-life history and highlighted the importance of physical boundaries, processes and features. Importantly, it includes all life stages in the recruitment process. The "triangle" model has affinities with the "retention" hypothesis of Iles and Sinclair (1982) and (Sinclair, 1988). In each case, it is the primacy of physical processes defining larval drift pathways and retention areas that determines recruitment, in addition to maintaining stock integrity (*i.e.*, Member-Vagrant hypothesis).

Hjort (1914, 1926) recognized the risk of advective loss imposed on eggs and larvae during the larval drift. While explicit in recognizing risk, Hjort also believed that larvae having been dispersed far from traditional

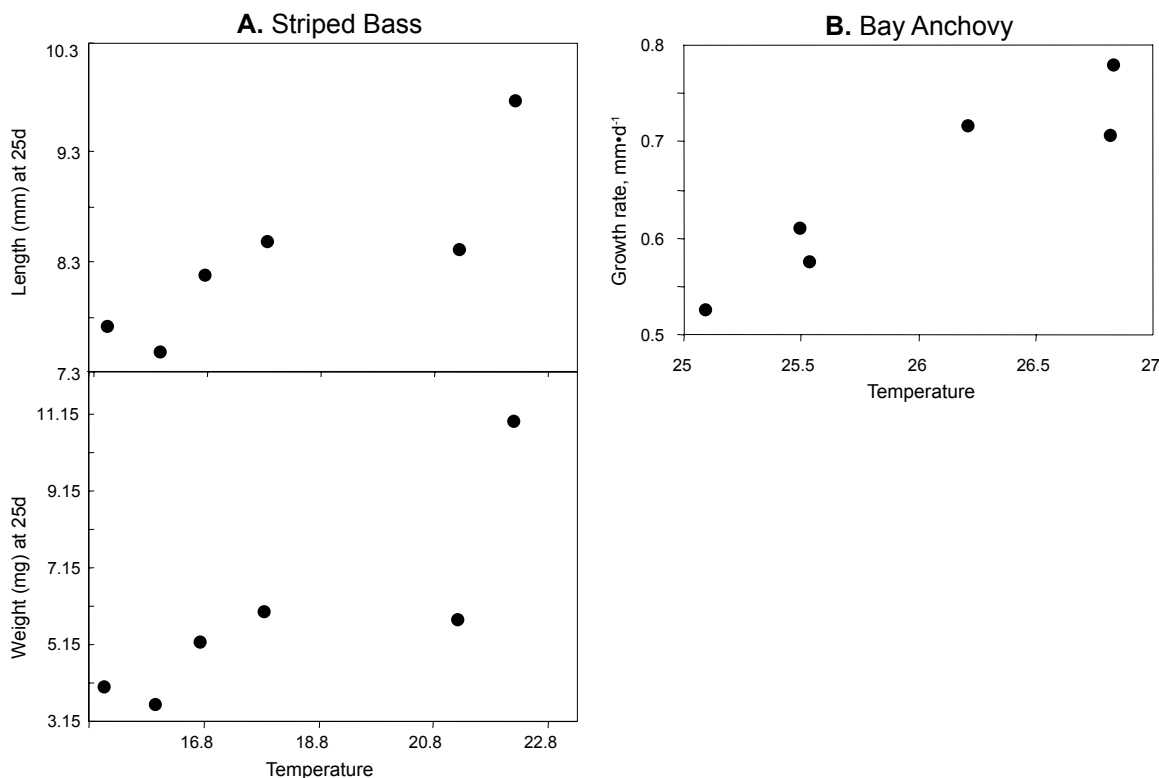


Fig. 3. Temperature effects on growth of fish larvae. **A.** Mean lengths and wet weights of striped bass larval cohorts at 25 days post-hatch in relation to average temperature experienced during larval life (modified from Secor and Houde, 1995, Fig. 8). **B.** Growth rates ($\text{mm}\cdot\text{d}^{-1}$) of bay anchovy larval cohorts in relation to temperature (modified from Rilling and Houde, 1999, Fig. 8).

nurseries by aberrant drift still had potential to return to shelf areas and recruit, although the probability was small. Hjort's frame of reference was cod larvae that, under unfavorable conditions, might be advected into the Norwegian Sea from which, he believed, some might return to settle in coastal nurseries, although generally too late in the season to survive and contribute to recruitment.

Research in the late 20th century documented the importance of circulation, frontal features, and hydrographic variability that act to contain, retain, or transport early-life stages. There was recognition that physics and the environment were coupled to biological processes, including behavior of fish larvae and dynamics of predators and prey. For example, in well-studied walleye pollock (*Theragra chalcogramma*) trends and patterns in recruitment and population structure are described well by statistical modeling that demonstrates the importance of high-frequency "activating" and low-frequency "constraining" factors (Bailey *et al.*, 2005). Complex coupled bio-physical models (CBPMs), which link hydrodynamic

models to biological models of ocean productivity (*e.g.*, NPZ) and larval dynamics (*e.g.*, often Individual-Based Models) emerged and demonstrated how variability in recruitment could be generated (Hinckley *et al.*, 1996, 2001; Heath and Gallego, 1998; Brickman *et al.*, 2001; Hermann *et al.*, 2001; Werner *et al.*, 2001; Mullon *et al.*, 2002; Bartsch and Coombs, 2004). These models often explain a substantial fraction of observed variability in distributions, growth, and mortality of early-life stages. There is a need to further improve CBPM models (*e.g.*, North *et al.*, in press). Behavior of early-life stages usually is poorly represented in CBPMs and in other modeling approaches although it is clear that including behavior (swimming, vertical migration, diurnal, foraging, predator avoidance) has important consequences for growth and survival.

Prey

Hjort correctly inferred that amounts and types of prey were important to support production of larval and pre-recruit fish. Better survival and growth of fish larvae

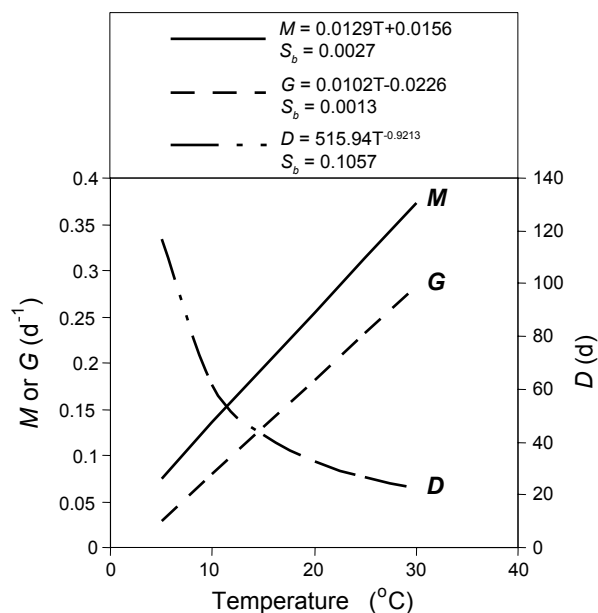


Fig. 4. Summary figure of daily Mortality (M), weight-specific Growth (G), and a power model regression for Larval Stage Duration (D), based on meta-analysis of marine fish larvae in relation to temperature, derived from relationships in Houde (1989). Lines are the fitted linear regressions for G , M and D . S_b = standard error of the regression coefficient. (modified from Houde, in press, Fig. 8).

generally are associated with high prey levels (Rilling and Houde, 1999; Zenitani *et al.*, 2007). Nevertheless, prey levels once thought essential for larvae to initiate feeding and support nutritional needs (*e.g.*, Hunter, 1981) probably were over-estimated. Based largely on laboratory experiments, prey (often rotifers, copepods, or *Artemia* spp. nauplii) at levels $>10^6 \text{ m}^{-3}$ were thought necessary for fish larvae to feed successfully. Such levels far exceed average levels in the sea, providing indirect support (or at least sympathy) for Hjort's hypothesis. Furthermore, initial feeding success in most taxa of fish larvae is low, with $<25\%$ of feeding attempts resulting in prey capture (Hunter, 1981). Prey patchiness and mechanisms promoting prey aggregation were invoked to explain how larvae could find sufficient prey. Later, Rothschild and Osborn (1988) hypothesized that micro-turbulence could substantially elevate encounter rates between larvae and relatively rare prey. Adding micro-turbulence to a foraging model, they demonstrated surprisingly large increases in feeding potential. Subsequent field observations (*e.g.*, Sundby and Fossum, 1990) and modeling research (*e.g.*, MacKenzie *et al.*, 1994) lent strong support to micro-turbulence as a mechanism that improves larval feeding success at low prey concentrations.

Experiments on feeding by fish larvae in the 1960–1980s led to estimates of required prey levels that were too high. The experiments had not accounted for prey patchiness or effects of micro-turbulence, and also were biased by artifacts imposed by small or stressful experimental systems. Despite low feeding success rates, larvae are capable of high consumption, even at low prey levels (Houde, in press). Larvae forage more effectively than initially thought but this is not strong or sufficient evidence to reject Hjort's Critical Period hypothesis. Under some circumstances, starvation of a substantial fraction of larvae may occur in the sea. Additionally, low prey levels may limit larval growth, lead to poor nutritional condition, and increase susceptibility to predation.

Predators

Hjort (1914, 1926) did not explicitly specify predation as a mechanism controlling recruitment. In aquatic ecosystems, size-based/size-selective predation is recognized as an agent responsible for structuring biological communities. We now acknowledge that predation controls or regulates recruitment levels (Bailey and Houde, 1989), but explicit hypotheses are seldom tested. Observation and theory indicate that mortality rates of marine organisms are inversely related to size (Peterson and Wroblewski, 1984; McGurk, 1986), in accord with size-spectrum theory (Kerr and Dickie, 2001). Theory and observation support the hypothesis that mortality of fish early-life stages generally is size-specific and primarily a consequence of predation (Bailey and Houde, 1989).

If predation is the primary agent of mortality, the rapid decline in mortality rate with increasing size in early-life stages (Fig. 5) indicates reduced predation pressure with growth and ontogeny (McGurk, 1986; Bailey and Houde, 1989; Houde, 1997b). A diverse assemblage of fishes and invertebrates preys on early-life stages (Houde, 2002) although the levels, size-selectivity, and variability in mortality attributable to particular predators are only rarely directly quantified (Paradis *et al.*, 1996). It appears that large size, on average, confers a degree of protection. Some experiments that failed to detect size-specific predation on eggs and larvae were constrained by small experimental systems that could affect behavior, and by a limited scope in sizes and taxa of both prey (fish early-life stages) and predators.

Bigger and Faster

Mortality from nutritional deficiencies and predation may not act independently. Slow-growing and small fish larvae remain relatively vulnerable to predation for a longer duration. This is the foundation of the "Stage-Duration" hypothesis, which implies that large

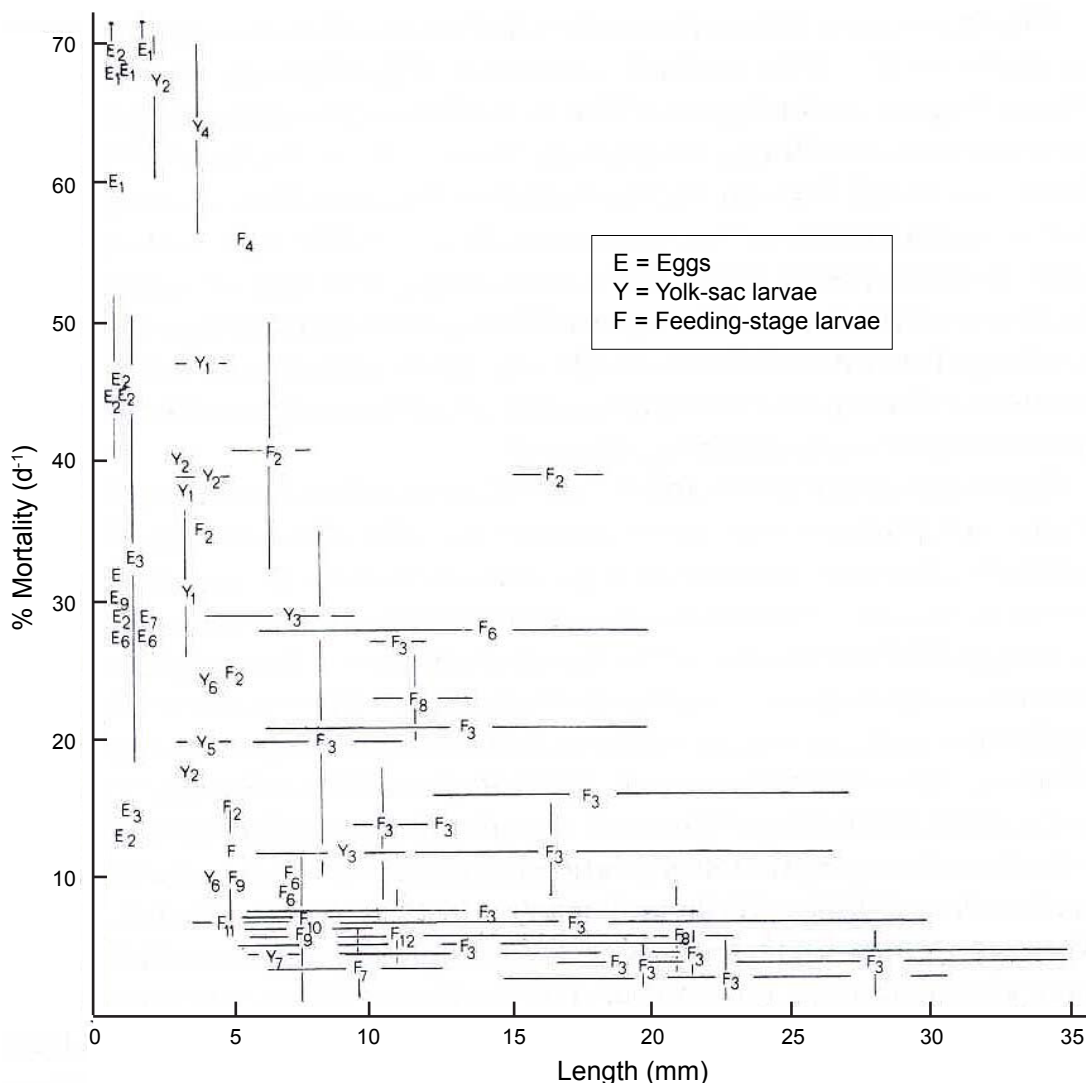


Fig. 5. Mortality of early-life stages of marine fishes declines rapidly as size increases. Summary from literature surveyed by Bailey and Houde (1989, Fig. 1). The exponent in the power model describing the relationship between instantaneous mortality and length is ~ -0.70 .

size (“bigger is better”) and fast growth improve survival potential (Houde, 1987; Anderson, 1988). Size-selective and/or growth-rate-selective predation often is hypothesized or observed to drive this process (Meekan and Fortier, 1996; Vigliola and Meekan, 2002; Takasuka *et al.*, 2003, 2004; Vigliola *et al.*, 2007). There is reasonably strong evidence supporting the relationship between fast growth of early-life stages and recruitment success, although there are notable exceptions (*e.g.*, Nishimura *et al.*, 2007). In some circumstances, high recruitments are associated with cohorts experiencing fast growth, but environmental factors other than size-selective predation may be the cause (Robert *et al.*, 2007). Regardless, cohorts of fast-growing larvae that reach large size early in life (*i.e.*, short stage durations) experience lower

cumulative, stage-specific mortality and have higher probability to recruit.

Climate

The reality of long-term, global climate change and accumulating knowledge of periodic shifts in ocean conditions (*e.g.*, ecosystem regime shifts) caused by oscillations in the earth’s atmospheric pressure fields (*e.g.* NAO, PDO), have drawn attention and concern to climate as a factor generating inter-annual, decadal, and longer-term variability in recruitments (*e.g.*, Ottersen *et al.*, 2001, 2004; Stenseth *et al.*, 2002; Brander and Mohn, 2004; Sullivan *et al.*, 2005; Brunel and Boucher, 2006). Shifts in community composition and dominance may

be driven by shifting climate regimes, as in Japanese sardine (*Sardinops melanostictus*) and Japanese anchovy (*Engraulis japonicus*) (Takasuka *et al.*, 2007). Hjort and his contemporaries were cognizant of inter-annual variability in climate-weather patterns and their potential to affect abundance of fish stocks. However, they could not have foreseen how important climate might be, nor have understood its long-term consequences for stocks, their distributions, and overall recruitment success.

Stock Sizes and Maternal Influence

Adult stock abundance plays a role in controlling and regulating recruitment through stock fecundity, egg quality, and *via* density-dependent effects. Hjort (1914) knew that high recruitment was not always derived from abundant adult stock, thus implicating the ocean environment as the primary factor generating recruitment variability. It is notable that Hjort (1914) recognized adult nutritional condition to be a contributing factor to quality and quantity of eggs, and he discussed the probable importance of variability in fat content of herring and in liver weights of cod with respect to wellbeing of stocks. Liver weight in many fishes, including Atlantic cod, has been demonstrated to be a good indicator of adult condition and fecundity (Marshall *et al.*, 2000; Yaragina and Marshall, 2000).

Meta-analyses on stock and recruitment conducted in the 1980s confirmed what was intuitive, but had been obscured by highly variable data and short time series; the probability of high recruitments did, on average, depend on numbers, biomass and fecundity of adults, especially in depleted stocks (Myers, 2001; Myers and Barrowman, 1996). In Hjort's time, few fished stocks were severely depleted and his observation that strong recruitment often emanated from moderately-low stock levels was correct in the early 20th century. Subsequently, heavy fishing reduced stock biomasses to low levels and many depleted stocks have experienced diminished or failed recruitment.

Beyond Stock and Recruitment

Recently, the role of maternal and, sometimes, paternal effects has been investigated to define how they contribute to variability in numbers, sizes, and quality of embryos and larvae. Young, small females in many stocks produce eggs and larvae that are smaller and inferior to those from older, larger females. There is evidence that such effects can reduce potential for survival of early-life stages and recruitment success (Trippel *et al.*, 1997; Marteinsdottir and Steinarnsson, 1998; Marshall *et al.*, 2003; Berkeley *et al.*, 2004; Rideout *et al.*, 2004).

Fishing shifts age structure of spawning stocks toward a predominance of younger, smaller females and can increase relative variability in recruitment by depleting stocks to levels where recruitment success is low on average, but relatively variable under a "recruitment overfishing" scenario. Truncation of age structure in adult stocks can lead to shifts in growth potential, size- or age-at-maturity, spawning times, and other stock traits. The shifts may be phenotypic and presumably reversible or genotypic with long-term consequences for stocks, although the two modes of response are difficult to distinguish (Conover *et al.*, 2005; Kraak, 2007; Morita and Fukuwaka, 2007). Presence of older spawners and age-diversity in the spawning stock may improve recruitment success (Figs. 6 and 7), especially at low stock levels, presumably because quality of eggs and larvae is enhanced. A diverse age structure that contains a high proportion of older spawners may be essential to assure long-term sustainability and resilience in marine fish stocks (*e.g.*, Longhurst, 2002).

An Integrated Process

Hjort (1926, p. 35) appreciated the potential for recruitment variability to result from complex, interacting factors, stating, "...the simultaneous investigation

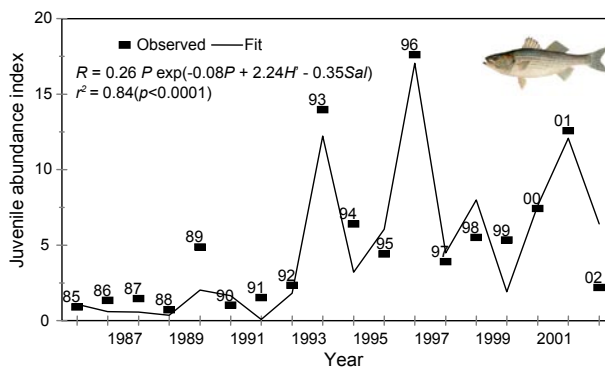


Fig. 6. Modified Ricker Stock-Recruitment model for Chesapeake Bay striped bass, 1985–2002. Observed and modeled young-of-the-year recruitment. R : Recruitment indices from Maryland Department of Natural Resources (MD DNR) juvenile seine index data; P : spawning stock biomass, from spring gillnet surveys by MD DNR; H : age diversity of female spawners \geq age-5 based on Shannon-Wiener diversity index; Sal : mean surface salinity in mid-Chesapeake Bay for April–October. P , H and Sal all contributed significantly to the modeled recruitment. Recruitment success depends on a substantial contribution to spawning by age-8 – age-12 females (Modeled by Houde and Jung; presentation, American Association for Advancement of Science Meeting, Washington, D.C., February 2005).

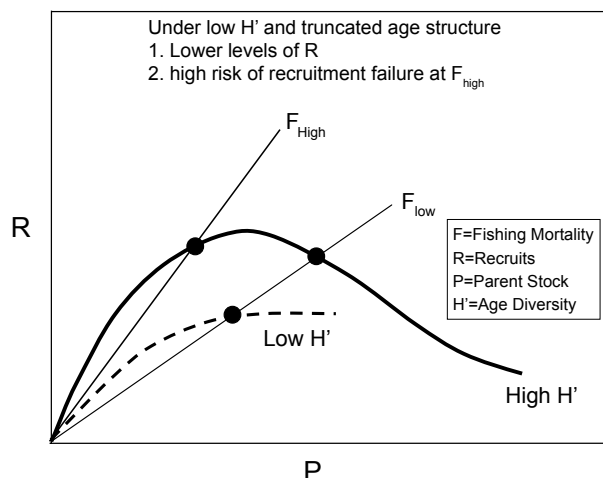


Fig. 7. Conceptual model of hypothesized effects of fishing on a stock-recruitment relationship under conditions where age structure and age diversity are maintained (solid line) and where these attributes are truncated and eroded (dotted line) from heavy exploitation. Resilience and sustainability of a stock are hypothesized to be at risk when age structure and diversity are diminished. The solid circles (●) indicate points of stable equilibria on the stock-recruitment relationship; there is no equilibrium for the case of heavy fishing with low age diversity and truncated age structure.

of meteorology, hydrography and biology seems the only way to a deeper understanding of the conditions in which the destiny of the spawned ova is being decided.” Contributions by Hjort and contemporaries early in the 20th century played an important role in fostering development of “recruitment fisheries oceanography” as a multidisciplinary science to investigate the spectrum of oceanographic processes controlling recruitment (Kendall and Duker, 1998). Before mid-20th century, Sette (1943) produced a remarkably detailed conceptual model of processes affecting recruitment in Pacific sardine (*Sardinops caerulea*), indicating recognition of the multiple factors affecting recruitment, if not the ability to conduct research on them.

Integrated approaches to investigate recruitment variability were lacking until the last quarter of the 20th century when several multi- and interdisciplinary oceanography programs were instituted to address questions on causes of variability in biological production, including fish recruitment variability (e.g., Fisheries-Oceanography Coordinated Investigations (FOCI) and GLOBAL Ocean ECosystems Dynamics Program GLOBEC)). The ability to conduct such integrated research emerged in large part from newly developed technologies and instrumentation that allowed better measurements (e.g., CTDs, ADCPs, satellite remote sensing, MOCNESS-

type plankton samplers) and availability of computing power to manage large databases and run complex numerical models.

Growth, Mortality and Stage Durations

Growth and mortality are linked processes. Variability in either during early life will be expressed in variable sizes-at-age, stage durations, and stage-specific cumulative mortality (Houde, in press). Cushing (1975) referred to effects of this linkage as the “single process.” The biomass dynamics of cohorts during early life depend on relative values of rates of instantaneous mortality (M) and weight-specific growth (G). Successful cohorts generally experience a rapid decline in M with ontogeny and growth (Houde, 1997b), while maintaining high or relatively slowly declining G . Cohorts of most marine fishes initially lose biomass, often rapidly, during the early larval stages (i.e., $M/G > 1$) before a transition and subsequent accumulation of biomass (i.e., $M/G < 1$). The age or size at transition indicates a cohort’s potential for recruitment success (Houde, 1997a,b). Cohorts making the transition at small size or young age have higher potential to recruit (Houde, in press).

At What Life Stage is Recruitment Fixed?

The question is not easily answered and is not equivalent to asking “At what life stage can recruitment be successfully predicted?” Answering that question is relatively easy by correlating abundances-at-age with subsequent recruitment. In general, prediction success is higher the closer one gets to the stage at which recruitment occurs (e.g., Bradford, 1992). For some taxa, however, there are high correlations between abundance of either eggs or early larval stages and recruitment (e.g., eggs, plaice (*Pleuronectes platessa*); larvae, striped bass (*Morone saxatilis*)), although such relationships seldom are sufficiently strong to confidently support management forecasts.

Hjort believed that recruitment was fixed during the earliest life stages, indeed within the first few days of larval life as larvae encountered either acceptable or poor conditions to feed, and experienced hydrographic conditions and ocean circulation that served to maintain larvae on nursery grounds or advect them into unfavorable environments. While this supposition may be true for some fishes in some years, the generalization must be rejected based on evidence now in hand. In plaice, levels of recruitment may be coarsely fixed at the embryo or earliest larval stages (Zijlstra and Witte, 1985; Van der Veer and Witte, 1999; Van der Veer *et al.*, 2000), although substantial adjustments in abundance at recruitment occur, attributable to variable mortality in the

post-settlement, juvenile stage. In other taxa, for example pelagic clupeoids, recruitment levels in most years may be set during the late-larval stage or in the long pre-recruit, juvenile stage (e.g., Watanabe, 2002; Nash and Dickey-Collas, 2005). In the Baltic Sea, recruitments of cod and sprat (*Sprattus sprattus*) are fixed in the egg-larval and late larval-juvenile stages, respectively (Köster *et al.*, 2003). Environmental factors, adult spawning behaviors, and predator-prey interactions between sprat and cod account for the differences in dynamics leading to recruitment in the two species. The primary factor determining life stage at which recruitment is set is the stage-specific level of cumulative mortality ($M \cdot t$) and its variability. Variability in cumulative mortality during a long juvenile stage (often >1 yr) can determine recruitment success or failure (Sissenwine, 1984; Bradford and Cabana, 1997). In some circumstances, for example during an ecosystem regime shift, the life stage at which recruitment is controlled can switch as was observed for walleye pollock in the 1990s when control switched from the larval to the juvenile stage (Bailey, 2000; Bailey *et al.*, 2005).

Density-Independent and Density-Dependent Processes

Variability in recruitment mostly results from variable survival in response to environmental conditions acting on early-life stages. Such controls are primarily density-independent and account for most of the high and variable mortality in early life (Houde, in press). However, strong evidence has emerged in the past three decades on the role of density-dependent regulation in setting or adjusting recruitment levels for many taxa.

Density dependence in early life can result from competition for prey acting on growth rates, leading to increased vulnerability of eggs and larvae to predators, or a combination of nutrition- and predation-related factors. Density-dependent growth or survival could have substantial impact on recruitment, if acting at any early-life stage (Rothschild, 1986). However, with a few exceptions (e.g., Jenkins *et al.*, 1991; Duffy-Anderson *et al.*, 2002), there is relatively little observational evidence of strong density dependence in the egg and larval stages. In contrast, there is strong evidence for it in the early juvenile stage (Myers and Cadigan, 1993; Cowan *et al.*, 2000; Kimmerer *et al.*, 2000; Doherty, 2002; Hixon and Webster, 2002; Shoji and Tanaka, 2007). For example, in Chesapeake Bay striped bass, recruitment variability is largely generated in the first month of life during the larval stage and is density-independent (Rutherford *et al.*, 2003), but substantial density dependence in growth and survival of juveniles (Fig. 8) reduces the >30-fold interannual variability in abundance of young-of-the-

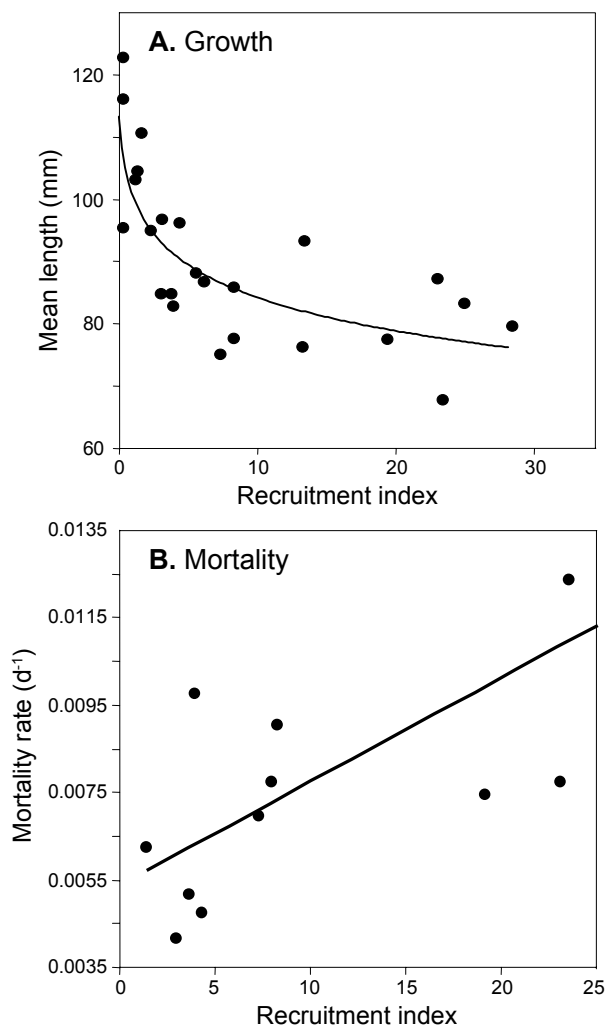


Fig. 8. Density-dependent growth (1980–2003) and survival (1993–2003) in young-of-the-year Chesapeake Bay striped bass. **A.** Mean lengths in September in relation to abundance (catch-per-unit effort, Maryland Department of Natural Resources seine-survey data). Mean lengths at ~120 days posthatch vary inter-annually by ~50 mm. **B.** Instantaneous daily mortality from September to the following August in relation to abundance (cpue, MDNR seine-survey data). Mortality rates vary >2-fold inter-annually with respect to abundance. (Figure modified from Martino and Houde, 2004, Figs. 14 and 15).

year juveniles to <5-fold variability in recruitment at age-3 (Martino and Houde, 2004).

State of Knowledge

Hjort's insights and hypotheses provided a foundation for research that has generated broad understanding of causes of variability in recruitment. Hjort's influence is enduring. We now are confident that variability in

recruitment can result from many sources acting throughout pre-recruit life. While Hjort's Critical Period hypothesis was too restrictive in defining a critical life stage, this does not diminish its importance as a foundation for theory and development of recruitment science. There is ample evidence that nutritional deprivation, which lies at the heart of the Critical Period hypothesis, is responsible for substantial and variable mortality of early-life stages, although it need not act only on first-feeding larvae or act directly by causing starvation. Hjort also recognized the potential for advective losses to cause recruitment failure. Surely, Hjort must have contemplated the potential for predation on early-life stages to be a significant and variable source of mortality and contributor to recruitment fluctuations, although he is surprisingly silent on it in his two seminal papers.

As noted earlier, Hjort's influence played a key role in founding the discipline of fisheries oceanography and specifically "recruitment fisheries oceanography". Kendall and Duker (1998) and Govoni (2005) discussed this important contribution. Prior to insights by Hjort and colleagues on the ICES Committee A (Migration Committee), many scientists had attributed apparent fluctuations in abundance of fish, as reflected in variable landings, to shifting migration pathways and variable availability to fisheries (Sinclair, 1997). Hjort and Committee A demonstrated that fluctuations were attributable to stock-specific variability in recruitment success. This advance in understanding represented a major paradigm shift (Sinclair, 1997).

Synopsis of Major Advances

Investigations of causes of recruitment variability advanced slowly until the 1970s. Some significant discoveries or breakthroughs are highlighted here.

- *Otoliths*: Chief among discoveries that pushed us to the fringe of Hjort's shadow was recognition that otoliths deposited daily increments (Pannella, 1971) and could serve as chronometers from which hatch dates, growth rates, and mortality rates could be estimated. More recently, otoliths were discovered to be storehouses of chemical information that provided a means to discriminate stock structure, conduct field experiments, or to judge how early-life stages utilized their environment and made transitions during ontogeny (Kalish, 1990; Gunn *et al.*, 1992; Secor *et al.*, 1995; Campana, 1999; Thresher, 1999; Thorrold and Hare, 2002).
- *Predation is the chief agent of mortality*: Hjort did not single out predation as a major factor controlling early-life survival, but it is now evident that high and variable predation is the principal, proximal agent of mortality (Bailey and Houde, 1989). Nutrition, as it affects condition, growth rate, and stage durations, modulates susceptibility of young fish to predation. Predation mortality often is size-specific and growth-rate dependent.
- *Nutritional condition can be evaluated*: Morphological and biochemical indices can define nutritional condition of early-life stages, including detection of starvation or slow-growth. Of the numerous condition indices, RNA/DNA analysis, alone or evaluated with other variables, *e.g.*, temperature, perhaps is best able to delineate nutritional state and growth potential (Buckley, 1984; Buckley *et al.*, 1999; Clemmesen, 1996; Caldarone *et al.*, 2003). When RNA/DNA analysis has been conducted, in most (but not all) cases larvae were judged to not be in starving condition. However, if starving larvae are removed rapidly from the population, either directly by starvation or selectively *via* predation, relatively high RNA/DNA values in survivors could be misleading.
- *No single life stage controls or regulates recruitment*: Recruitment levels are not determined at a particular ontogenetic stage. Levels may be set at a very early stage, *e.g.*, egg-larval stages in plaice (Bannister *et al.*, 1974; Harding, 1974), or in the late larval-juvenile stage, *e.g.*, Japanese sardine (*Sardinops melanosticta*) (Watanabe, 2002). The stage at which recruitment is fixed can vary from year to year, depending on environmental conditions, *e.g.*, North Sea herring (Nash and Dickey-Collas, 2005) or can shift at decadal scales as observed in wall-eye pollock under ecosystem regime shifts (Bailey, 2000). Regulation *via* density-dependent growth and mortality, usually in the juvenile stage, can tune and adjust recruitment levels in many species (*e.g.*, gadids, Myers and Cadigan, 1993; plaice, Van der Veer *et al.*, 2000).
- *The "Single Process"*: Cushing (1975) argued that control and regulation of recruitment resulted from combined variability in growth (G) and mortality (M) in early life. Cushing proposed that the ratio G/M , its level and variability, was an index of recruitment potential, emphasizing the importance of fast growth in controlling cohort production. The inverse ratio, M/G , sometimes termed "physiological mortality" (Beyer, 1989; Houde, 1997b, *in press*) may be preferred as an index of cohort-specific survival potential and responsiveness to environmental or biological variables. Low values of M/G in early

life, a fast decline in its level, and transition to values of $M/G < 1$ at young ages are associated with high recruitment.

- *Physical and biological processes are important across many spatial scales:* Hjort probably understood that processes operating at many scales contribute to variability in recruitment. In the Critical Period hypothesis, feeding behavior, environmental and trophodynamic processes, and physics operating from regional productivity scales to the micro-scale at which individual larvae feed contribute to the nutritional state of larvae. In his Aberrant Drift hypothesis, Hjort invoked regional and meso-scale physics as mechanisms leading to possible loss of larval cohorts. Recent evidence of climate change and ecosystem regime shifts calls attention to processes operating at ocean-basin scales that affect variability in fish recruitment. Despite advances in seagoing research, few projects address oceanographic or trophodynamic processes at the fine spatio-temporal scales perceived by an individual larval fish (Pepin, 2004).
- *Models and Modeling:* Numerical modeling is now an essential component of research to explore and evaluate mechanisms, and to provide new insights into recruitment variability. Large, multi-disciplinary programs conducted in the last two decades of the 20th century fostered development of improved coupled biological-physical models to explain recruitment variability (Miller, 2007). Statistical modeling, applied to long-term datasets that are increasingly available in recent decades, also has advanced our understanding of how the environment affects survival, growth, and recruitment of marine fish stocks.
- *Adults count:* Hjort and contemporaries thought that shifting migration patterns of recruited fish could cause variability in fishery landings. At the time of his seminal papers Hjort was not much concerned with stock-recruitment relationships and the potential for low adult stock to control recruitments, in part because the stock concept was only vaguely developed at the time. Beginning near the mid-20th century, stock-recruitment (S-R) models became prominent (Ricker, 1954; Beverton and Holt, 1957). Although fundamentals of S-R models were understood, it was not until the 1980s that highly variable S-R relationships gained appreciation for their potential to explain recruitment variability. The change in perception in the 1980s and 1990s was strongly influenced by meta-analyses of S-R relationships (Myers and Barrowman, 1996; Myers, 2001) that demonstrated the importance of adult numbers,

biomass and fecundity, and the propensity for low recruitments in depleted stocks subjected to heavy fishing. Moreover, the quality of adult stock (*e.g.*, age structure, condition) came to be recognized as an important factor affecting recruitment potential (Marshall *et al.*, 2003).

- *Do We Lack Unifying Theory?:* In the 1970s, it was popular to invoke lack of underpinning theory as the major impediment to progress in understanding causes of recruitment variability and ability to predict recruitments. In retrospect, there was a reasonable, hypothesis-based, theoretical framework to advance recruitment research, grounded on the fundamental hypotheses of Hjort and supplemented by later emergent hypotheses (Fig. 2). However, there was insufficient technology, computing power, knowledge of oceanography, time series of recruitments, and models of ocean dynamics (physical and biological). Still, the argument that unifying theory was lacking was a strong selling point in generating badly needed science programs (*e.g.*, GLOBEC) that led to major advances in understanding causes of recruitment variability.

What Are Critical Research Needs?

- *Implementing or continuing long-term surveys on early-life stages:* Long time series are essential to define conditions that control and regulate recruitment. Except for a few economically and ecologically important stocks (*e.g.*, some Atlantic cod stocks, Atlantic herring, plaice, California sardine, northern anchovy, walleye pollock, Japanese sardine, S. African anchovy), there are few observational time series that span decades to identify and analyze trends in abundance and recruitment variability, and to link variability to environmental factors, including changing climate.
- *Better understanding of larval behavior:* Larval fishes are not passive particles. Behavior and cues that trigger it in early-life stages are poorly known. Behavior plays a key role in many aspects of early-life biology and dynamics, *e.g.*, swimming, vertical migrations, foraging, predator avoidance, dispersal/retention, habitat selection (Forward and Tankersley, 2001; Leis, 2006; Woodson and Mcmanus, 2007) but often is insufficient or lacking in recruitment research. Incorporating behavior into models of early-life dynamics and recruitment processes is a particular need.
- *New and improved coupled biological-physical models (CBPMs):* Sampling the sea at appropriate frequency, and at time and space scales required to

evaluate mechanisms controlling recruitment variability, presents formidable financial, technical, and logistical challenges. The CBPM approach has had notable success in helping to explain mechanisms that generate recruitment variability but much remains to be done (North *et al.*, in press). Most CBPMs have been developed as explanatory or inferential tools (Miller, 2007) and relatively few as tools to test hypotheses, although the biggest contribution to understanding recruitment variability ultimately may come from that approach.

- *Research that transcends life stages:* Research and models on recruitment variability should broadly include all life stages. There is growing recognition that recruitment success can depend on variability in survival during all pre-recruit life stages (*e.g.*, Rothschild, 2000) and that abundance and condition of adults also serve to control and regulate recruitment.
- *Understanding effects of climate change:* Global climate change is upon us. Its implications for recruitment in fish stocks, while likely to be substantial, are not understood. Distributions of stocks and stock structure, reproductive seasons and locations, and a host of questions related to shifts in habitat and ecosystem properties must be addressed to evaluate climate change, ecosystem regime shifts, and effects on fish reproduction. This knowledge will be critical for future fisheries management.

Understanding and Predicting: Needs of Science and Management

Most recruitment-related science has at least an implicit goal of predicting and forecasting. This was true in Hjort's time and remains true today. Describing processes, determining probable effects on recruitment, and hindcasting recruitment are valuable undertakings, but fall short of predicting. Without constant and intensive monitoring of early-life stages and variables that affect recruitment, accurate prediction will remain an elusive goal, except for a few economically valuable species. If forecasts could be made from information on early-life stages, developing even modest ability to predict recruitments or its trends, *e.g.*, high, medium, low, has value in management planning. Additionally, forecasting at that level of confidence has utility in predicting probable responses in reproductive success of stocks to climate change or other major perturbations in ecosystems.

Although numerous statistical, descriptive models effectively hindcast recruitment, forecasting, with a few exceptions, has a history of failure, sometimes preceded

by years of success before failure. Simple correlations of environmental variables with recruitment success don't hold up over time because ecosystems change and forces controlling recruitment also change. Successful forecasting and predictive science depend on long-term observations, time-series analysis of recruitment and oceanographic variability, development of models to define and quantify oceanographic processes, and evaluation of stock-recruitment relationships and maternal effects.

Is There a Recruitment Problem?

Solving the "Recruitment Problem" was the Holy Grail of fishery science in the late 20th century. In retrospect, casting recruitment variability as a problem waiting to be solved was misleading. Variability in recruitment owes to variability in numerous factors operating on early-life and recruited stages of fish. It no longer surprises us that variability in the environment, even if causing only small variability in survival or growth rates of abundant pre-recruit fish, can generate extraordinary variability in recruit abundances. Understanding causes of recruitment variability is a desirable goal; "solving the problem" may be an unrealistic goal.

Why Isn't Recruitment Even More Variable Than Observed?

Recruitment typically varies 10-fold inter-annually and 100-fold variability is observed. But, given the extraordinary abundances of eggs and larvae and the high and variable mortality they experience, many of us are surprised that variability isn't higher yet. More than 100-fold variability is in fact observed rather commonly in some fishes, *e.g.*, haddock (*Melanogrammus aeglefinus*), and on occasion in many species. Regulation is an expression of compensatory ability (density dependence) that generally reduces variability and tends to stabilize or dampen recruitment variability. Much of the compensation may occur in the juvenile stage. Even a small amount of compensation during early life can have a substantial stabilizing effect.

Moving Forward

Appreciating recruitment variability, explaining its causes, considering implications for management, and understanding it in the context of broader variability in marine ecosystems are worthy goals. Hjort made immense contributions to our fundamental appreciation of why fish stocks vary in abundance. While we are now emerging from Hjort's imposing shadow, we acknowledge his enduring influence. There is little to be gained from continued testing of the Critical Period hypothesis as Hjort proposed it. Our knowledge of early-life

dynamics and processes generating recruitment variability has progressed beyond Hjort's narrow view. The recruitment process and mechanisms generating variability cut across life stages and operate on many spatio-temporal scales. We now have a strong foundation and knowledge base for understanding recruitment variability and a challenge to reliably forecast it.

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