Chapter 4
Recruitment

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4.1 The recruitment problem: why do fish populations vary?

It may be hard for today's student of fishery science to believe, but consideration of the population dynamics of the early life stages of fishes in studies of recruitment variability has not always been the norm. Indeed, for its first 100 years fishery science focused on the population dynamics and effects of fishing on adults to advance our understanding of population regulation. During these early years, important concepts began to emerge in the fishery literature that recognized the existence of distinct populations within a species' range, the role of density dependence in long term population stability, and how environmental variability influences short term changes in abundance. As our ability to estimate population size improved, however, so did our appreciation for the degree to which year-class success in fishes varies from year to year. This was quickly followed by recognition of the importance of this variability to fishery management as inconsistent year classes recruited to fishable age. Today, we recognize that order-of-magnitude variation in year-class success is the norm.

It was apparent to early fishery scientists that prior understanding of stock dynamics and vital rates of adult fishes (growth rates, death rates, and egg production) were unable to fully explain observed variability in stock size. Thus in 1914 the Norwegian fishery scientist Johan Hjort, while working on his own studies of North Sea herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Figure 1.3m, p, n), and synthesizing work by colleagues of his day,* proposed that variable "year-class success" (he actually coined this term) was most likely determined during early life in marine fishes. He arrived at this conclusion by observing that fish eggs and larvae experienced extremely high mortality rates *in situ*, suggesting that year classes could be reduced dramatically if mortality was nearly total. Thus the notion was born that variability in recruitment – defined here as the survival of an annual cohort to the end of the first year of life – is determined by variability in vital rates of newly hatched fishes, a premise that has guided much research in the intervening years. In the remainder of this chapter, we develop a brief history of the major recruitment hypotheses that followed from Hjort's classic work, emphasizing those that focus on the contribution of early life stages. We end with a discussion of the progress of, and prognosis for, recruitment prediction.

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* More details of the historical context for Hjort's work are discussed in Section 9.2.

4.2 Predicting recruitment: need and implications

Since Hjort's time our understanding of population dynamics and the consequences of density dependence and environmental variability (even on the global scale) as they affect early life stages and subsequent recruitment variability, has improved dramatically. For example, Canadian fishery scientist Ransom Myers and colleagues have focused on environmental factors and the wide scale correlative nature of recruitment variability in many stocks, as well as the role of density-dependent vs. density-independent controls of recruitment dynamics. Moreover, the long-recognized and powerful stock–recruitment relationship is becoming better understood for many stocks as long time-series data become increasingly available.

Still, our ability to predict recruitment success in any year remains poor, while the need for prediction remains high given the dismal state of many fisheries. Knowledge of processes that strongly affect larval survival would provide early evidence of the abundance of the emerging year class. Despite our inability to accurately forecast recruitment, the focus of recruitment studies on early life stages of fishes is steadfast, although the life stage of emphasis has changed through the years. Combined empirical evidence for when year-class success is determined in marine fishes can be visualized by showing the relative correlation between estimates of successive life-stage-specific abundances (Figure 4.1). By the time the juvenile stage is reached, population or cohort-specific mortality rates generally are lower than for earlier life stages (Figure 3.2), and correlations between abundances of successively older stages are high, supporting the notion that year-class success is determined prior to the juvenile stage.

More precisely, by comparing growth (G') and mortality (M) rates as well as energetics properties of marine and freshwater fish larvae, fishery scientist Edward Houde predicted that recruitment levels and variability of marine fishes will be determined more by larval stage dynamics than juvenile stage dynamics, but that the reverse will be true for freshwater species. This suggests a high potential for environmental variability to drive recruitment variability during the larval stage of marine fishes relative to freshwater fishes. Nevertheless,

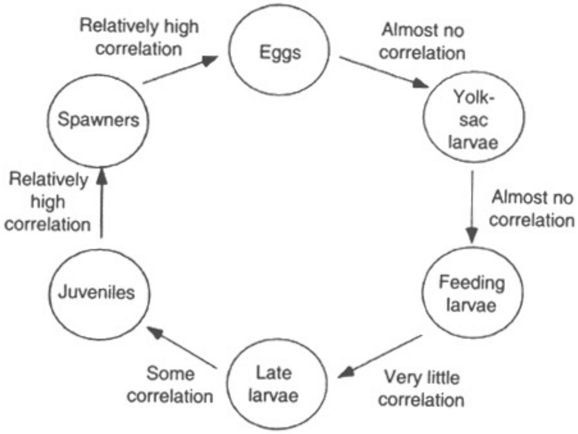

Figure 4.1 The relative correlations between estimates of successive life-stage abundances.

despite some differences in stage-specific characteristics and dynamics (for example, size, growth rate, and starvation potential), the fundamental processes that determine survival of fish eggs and larvae are similar in both lakes and oceans and occur over similar spatial scales. The similarity in processes affecting survival is remarkable given the fundamental differences in the degree of spatial connectivity of marine and freshwater ecosystems. Clearly, the depth of our understanding of the causes of recruitment variability has grown, and it will continue to broaden.

4.3 Hjort's hypotheses: in the beginning

Hjort's discussion of possible causes of inter-annual differences in mortality during early life offered two clearly stated hypotheses. The first suggests that differential mortality between years is a result of variation in food availability at a critical stage during larval fish development. The second hypothesis stresses the influence of transport of eggs and larvae away from appropriate nursery areas due to inter-annual differences in ocean circulation. As will be seen in the following sections, work initially focused on Hjort's first hypothesis but eventually both hypotheses have been addressed in early life-history studies.

4.4 Hjort's Critical Period Hypothesis

Hjort was the first to explicitly link feeding, larval survival, and subsequent recruitment to food abundance during the transition of larvae from endogenous (yolk) to exogenous (plankton) feeding. He proposed what became known as the Critical Period Hypothesis, which stated that when food was limiting during this critical transition, many larvae would die from starvation, but when food was high, survival would be high (Figure 4.2; see also Figure 3.4). He further proposed that these variations in survival owing to starvation could generate recruitment variability and hence explain the variability in year-class strength that he observed in

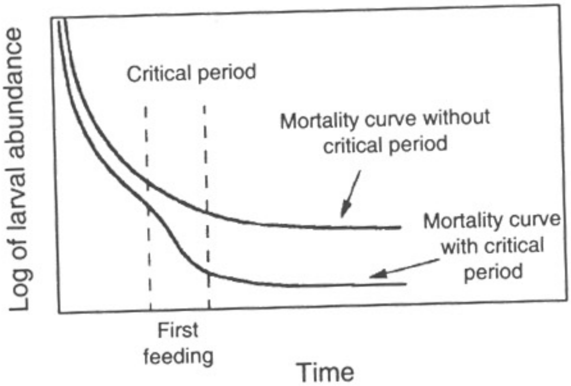

Figure 4.2 Schematic representation of Hjort's Critical Period Hypothesis illustrating the link between survival at the time of first feeding and subsequent year-class success (from Leggett & Deblois 1994 with permission from Elsevier Science).

North Sea fishes. The case study of Japanese sardine described in Chapter 11 includes empirical tests of the Critical Period Hypothesis.

Following Hjort's hypothesis many researchers set out to determine what and how much fish larvae eat, and whether sufficient food was indeed available in the sea. Since the 1960s, an extensive literature based upon laboratory studies has developed on the relationship between food type, concentrations, size, and quality at the time of first feeding, and the subsequent survival of larvae following varying intervals of starvation. In general, laboratory studies have demonstrated that larvae at first feeding and soon thereafter are indeed vulnerable to starvation due to very high weight-specific prey-consumption rates, but that food concentrations in the sea can, at times, be sufficient to support good larval growth and survival. More importantly, strong evidence of a relationship between food abundance and/or quality at the time of first feeding and either larval survival or year-class success has been elusive, as has strong evidence for the existence of high numbers of starving larvae in the wild.

Thus, a feeding paradox appears to exist. Despite very high *in situ* feeding rates, perhaps even higher than predicted in laboratory feeding studies, fish larvae in the sea apparently are able to feed at or near satiation levels, largely independent of food concentrations, even when food concentrations appear to be too low. Several factors may contribute to this apparent paradox, but they can be concisely collapsed into two main issues, both related to difficulties of sampling organisms the size of larval fish prey in the wild. Firstly, traditional estimates of prey abundance, when integrated over large spatial scales, are generally believed to underestimate the effective concentrations of prey available to fish larvae, if larvae have the ability to detect and exploit food patches. Secondly, prey abundance estimates may underestimate prey availability if they neglect the production of new prey biomass, which can be high in coastal ecosystems for prey in the size range generally required by larval fishes. Nevertheless, the feeding paradox exists because prey concentrations, on average, seem low when compared to demand by fish larvae. Several of the recruitment hypotheses that have followed Hjort's contributions have attempted to address this feeding paradox in one way or another.

4.5 Hjort's first hypothesis extended

4.5.1 Cushing's Match/Mismatch Hypothesis

Almost 60 years following Hjort's publication, the English fishery scientist David Cushing extended our thinking about the role of early life stages in recruitment variability in his Match/Mismatch Hypothesis. In essence, Cushing collapsed Hjort's original two hypotheses into a single hypothesis which suggested that fish spawn in relation to the particular timing of spring and autumn plankton blooms in the geographic area of inferred larval drift from spawning grounds to nursery areas. He hypothesized that a fixed time of spawning coupled with a variable time of plankton blooms generates variable larval fish survival and, hence, variable recruitment. While the mechanism of larval mortality is again starvation, what Cushing added was the consequences of critical depth (or compensation level in freshwater systems). Critical depth is defined as the depth at which total photosynthesis is balanced by total plant respiration, which must be deeper than the mixed layer (usually above the thermocline)

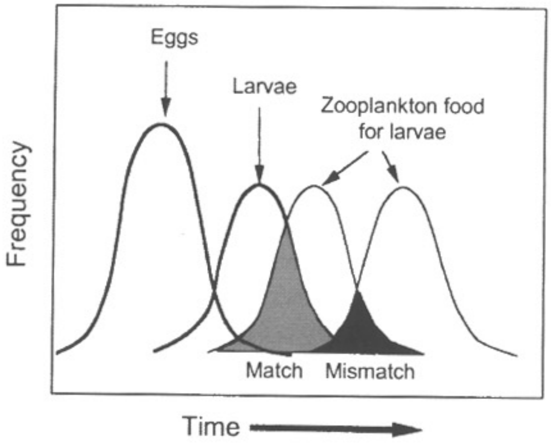

Figure 4.3 Schematic representation of Cushing's Match/Mismatch Hypothesis illustrating variability in the degree of overlap between the timing of a seasonal peak in the production of planktonic food for larvae and the co-occurrence of fish eggs and larvae. The stippled area is a match representing high overlap and the darkened area is a mismatch representing low overlap (redrawn from Leggett & Deblois 1994).

if the plankton are to stay up in the well lit water column. Cushing's modification highlights the dependence of secondary production cycles (production of prey for larval fishes) on variation in the development of water-column stratification/destratification and primary production in the spring and autumn. This generates variability in the magnitude of temporal overlap between the production of larvae (spawning) and the production of larval fish food through the development of appropriate food webs (Figure 4.3). The Match/Mismatch Hypothesis removed the restriction that food-mediated mortality leading to recruitment variability is limited to a particular critical developmental period. Rather, food limitation during any part of the larval period could be a major contributor to recruitment variability, and abiotic factors that regulate water-column destratification and the timing and intensity of seasonal production cycles may be involved.

In the years since Cushing published his ideas, many studies have attempted to test the Match/Mismatch Hypothesis in marine, estuarine, and freshwater environments. Much of the available evidence is broadly consistent with the existence of the hypothesized relationship between overlap in the development of seasonal food production and larval abundance and survival, although the link to recruitment is less well established.

4.5.2 Lasker's Stable Ocean Hypothesis

Reuben Lasker and his colleagues, working with northern anchovy (*Engraulis mordax*, similar to Figure 1.31) off the California coast, developed an extension of Hjort's hypotheses. Lasker accepted the initial premise that food for first feeding larvae may be limited, but suggested that there are times and places in the sea where food aggregations occur, upon which larval fish survival depends. Based upon laboratory and field studies, he established the existence of minimum thresholds of prey concentrations for larval feeding and that first feeding larvae could detect good feeding areas in the sea. In a series of cruises in the

California Current in 1974 and 1975, he further showed that maintenance of "threshold-for-feeding" concentrations of food were associated with chlorophyll maximum layers in a stratified water column formed during calm and stable ocean conditions, hence the Stable Ocean Hypothesis. Thus, he hypothesized that poor recruitment would occur in stormy or windy years when too few calm periods (later called "Lasker events") occurred. Lasker suggested that measures of wind effects on water such as the cube-of-the-wind-speed, upwelling, and wind-curl indices could be correlated with larval mortality, larval food distributions, and subsequent year-class success. Indeed, relatively stormy conditions in 1975 off California produced one of the worst northern anchovy year classes previously recorded.

In the years since Lasker formulated the Stable Ocean Hypothesis, other researchers working off California in highly productive upwelling environments have shown good correlations between year-class success in Pacific mackerel (*Scomber japonicus*) and upwelling and wind-curl indices. Similarly, others have related mortality rate in larval northern anchovy to wind activity, presumably through its effect on food concentration. Strong correlations between larval mortality rates and subsequent recruitment to the juvenile stage, however, have been more elusive. It may be that stable ocean conditions are more important to larva feeding success in upwelling areas than in other locations in the sea.

4.5.3 Rothschild and Osborn's Plankton Contact Hypothesis

In a novel attempt to explain the aforementioned feeding paradox (see Section 4.4), the American fishery scientist Brian Rothschild and his colleague Thomas Osborn hypothesized that fish larvae can survive in the sea at lower prey densities than expected, if encounter rates between larval fishes and their prey increase as a function of small scale, wind-driven turbulence. This small scale turbulence should not be confused with Lasker's large scale vertical and horizontal mixing events. In the absence of turbulence, encounter rates between larvae and their prey result primarily from the combined swimming speeds of both. Turbulence at scales relevant to predator–prey interactions (centimeters to meters) increases effective swimming speeds, and thus relative motion, thereby increasing the potential for contact between larval fishes and their prey (hence the Plankton Contact Hypothesis). This is especially true when prey density is low. In periods or years when wind speeds are relatively low, it follows that larval fish feeding rates would decrease, reducing larval survival and subsequent recruitment.

Others have used Rothschild and Osborn's theoretical constructs to develop turbulence–encounter rate models to predict encounter rates that could be expected under natural levels of both wind-driven turbulence and plankton and larval fish densities. Failure to consider the effects of small scale turbulence when prey densities are low could result in greater than a 10-fold under-estimation of encounter rates under natural conditions typical of continental shelf waters in summer. In one study, it was demonstrated that under-estimates of up to 112% are possible for larvae at a depth of 20 m during turbulence that is generated by wind velocities of $5\,\mathrm{m\,s^{-1}}$ (Figure 4.4). The magnitude of under-estimation increases as prey density declines and when prey are distributed in patches. It also has been suggested that turbulence may slow the rate of starvation in larvae because weakened, slowly swimming individuals are more likely to benefit from the effect of turbulence than healthy larvae.

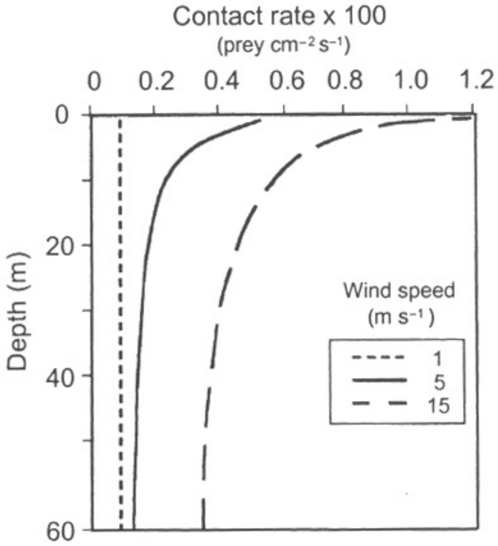

Figure 4.4 Effect of turbulence on encounter rates between larval fishes and their zooplankton prey. The relationship is for 6-mm larvae feeding at a prey density of 5 nauplii dynamic m^{-3} (reproduced from Mackenzie & Leggett 1991 with permission of Inter-Research).

This is not to say that increased turbulence always has a positive effect on larval feeding rates. Recent research has shown that when turbulent velocities become too high, the ability of larvae to capture prey declines. Perhaps this also contributes to low recruitment in stormy years, as first described by Lasker. It is probable that wind speeds greatly in excess of 10 m s^{-1} are no longer beneficial to fish larvae feeding in surface waters. In 1990 Norwegian fishery scientists showed that gut fullness for Arcto-Norwegian cod in the field increased in relation to wind speed, reaching a maximum when wind speed exceeded 6 m s^{-1}. No direct tests of the Plankton Contact Hypothesis as it relates to recruitment variability have been made to date, however.

Upwelling systems such as those studied by Lasker and colleagues also generate small scale turbulence that is consistent with the velocities described above. While wind-generated upwelling generally is believed to enhance biomass production via persistent nutrient enrichment to surface waters, a dome-shaped relationship between upwelling and recruitment of pelagic fishes has been observed. In populations of such fishes as Peruvian anchoveta (*Engraulis ringens*) and Pacific sardine (*Sardinops sagax*), maximum recruitment occurs in periods of intermediate upwelling velocities of 5–6 m s^{-1} (Figure 4.5). It is not clear, however, whether the increased recruitment reported for these fishes is related to enhanced feeding success due to more food production, to turbulence-enhanced feeding associated with upwelling, or to the occurrence of more Lasker events (wind speeds <10 m s^{-1} for four or more days) in years of moderate upwelling-producing winds.

4.5.4 Freshwater discharge and riverine plumes: prey concentrations increase

In addition to the cases already discussed, there are places in the sea where concentrations of prey-sized organisms for larval fishes are consistently high, thereby diminishing the

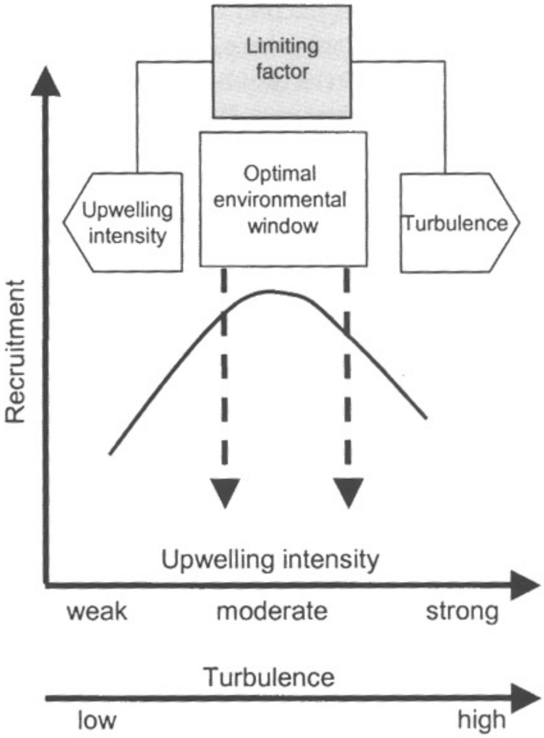

Figure 4.5 Theoretical relationship between recruitment and environmental factors in upwelling areas (redrawn from Cury & Roy 1989).

feeding paradox. It is generally recognized that hydrographic density fronts or discontinuities and riverine/estuarine plumes are important sites for energy transfer and intense biological activity, potentially supporting large phytoplankton and zooplankton standing stocks. Larval fish aggregations also are common in areas of concentrated nutrients and chlorophyll found in oceanic fronts and plumes, such as the Columbia and Mississippi Rivers, the Frisian Front in the North Sea, and the Amazon River plume. These small scale elevated gradients or patches of microzooplankton food are relevant to larval fish searching behavior and may enhance survival. Recruitment may be enhanced at such sites, where physical processes generally insure that biological conditions are favorable for survival and are stable over time.

Simple linear food chains and trophic cascades

Correlations between fishery production and nutrient input from river runoff often have suggested a "bottom-up" linear food chain. Simply stated, freshwater discharge increases the nutrient pool available to primary producers, which increases primary production, which can stimulate zooplankton production, resulting in increased ichthyoplankton survival and fishery production. Estuaries may work this way, as we will discuss later. In some freshwater systems, the strength of trophic linkages apparently is great, whereby one trophic level (usually a consumer), can control the biomass of its prey (zooplankton), which in turn releases predation pressure on the prey's prey (phytoplankton). Fishery scientists Steven Carpenter and James Kitchell labeled this phenomenon a trophic cascade, such that recruitment and production dynamics can also be controlled from the "top down," especially when the abundance of the planktivorous fishes also is controlled by predation. Most field observations from marine systems indicate that the direct linear food chain argument – that is, either a bottom-up or top-down trophic cascade – works only up through primary producers and the smallest zooplankton; cascading effects do not always appear to extend to higher trophic levels such as larger zooplankton and fishes. Reasons for apparent differences in degree of susceptibility to cascading trophic effects among riverine, lacustrine, estuarine, and marine systems are still debated. Some investigators have suggested that the cumulative effects of consumption on one trophic level by another are likely to be more profound in small, closed systems, such as ponds and lakes, and less obvious in larger, more open marine systems. It also has been suggested that marine communities, with many omnivorous taxa and high levels of food-web redundancy, may be less susceptible to cascading trophic effects than more simple freshwater communities.

Another alternative hypothesis for the failure of the linear food chain is that for higher trophic levels, physical processes dominate in open marine systems. These processes are exemplified by local frontal convergences (places where water masses come together), which accumulate buoyant objects, or large scale circulation features, which can determine current directions and velocities that influence transport or retention of eggs and larvae within the appropriate geographic area for the population.

An interesting feature of riverine plumes, fronts, gyres, and their associated convergences, however, is that they are often ephemeral in space and/or time. They frequently meander, migrate, form, strengthen, relax, and dissipate on daily or seasonal time scales, being influenced by tides, winds, and seasonal changes in hydrology (river discharge) and meteorology. The point along this ephemeral development–decay continuum that a larval fish encounters a convergence zone influences what it may encounter, since it affects how long the convergence may have been actively accumulating buoyant particles such as prey or potential predators. In addition, predators have been known to actively seek out discontinuities or gradients in salinity, turbidity, temperature, and food, and to actively maintain contact with such gradients once encountered. Thus, any feeding advantage for larval fishes gained at frontal convergences may be counteracted by increased potential for predation mortality resulting from co-occurrence with increased concentrations of active predators, including cannibals and cruising or ambush predators such as other fishes and jellyfishes.

The Mississippi River discharge plume

One specific example of the type of environment described above is the Mississippi River, which has a great influence on fisheries in the Gulf of Mexico. This large riverine plume is characterized by a buoyant, shallow lens of low salinity, nutrient-rich, and turbid surface water that flows out of the delta's distributaries and expands over the high salinity (more dense) oligotrophic (nutrient limited) Gulf of Mexico shelf waters (see Box 10.4 for more information). A third water mass is formed between the plume and shelf waters called the frontal zone, which consists of a broad zone, 6–8 km wide, containing one or more turbidity fronts and having intermediate temperature and salinity signatures. This frontal zone is characterized by high primary productivity resulting from phytoplankton in the nutrient-rich waters being no longer light limited by the river plume's high sediment load. The frontal zone is believed to be the accumulated effect or sum ("memory") of repeated formations and dissipations of individual convergence zones generated by the horizontal density gradients between the plume and shelf water.

Definitive evidence of the role of the Mississippi River plume on recruitment in the northern Gulf of Mexico has been elusive. In some studies, larval fishes associated with the plume and frontal waters have exhibited a clear feeding and growth-rate advantage over those that were outside of the plume, while in other studies, differences are less clear. Similar results have been reported for mortality rates. In no study has a direct relationship between plume/front dynamics and year-class success been demonstrated, despite the aforementioned general correlation between recruitment and freshwater discharge.

Nevertheless, the magnitude of large continental shelf fronts and gyres associated with oceanic circulation systems is sufficient to influence the survivorship of a larger number of recruits, thereby influencing the adult stock or population. Other fronts may have spatial and temporal scales that only influence the local dynamics of small portions of the population. Yet, at the level of the individual larvae they may still be important.

4.6 Hjort's second hypothesis extended

4.6.1 Larval transport, larval retention, and recruitment

Nursery areas of fishes are often distant from oceanic or coastal spawning grounds. In order to reach nursery areas at the proper time, size, and condition, fish larvae require appropriate currents and sufficient and suitable food during transit (see Chapter 7 for more details). Reproductive activity, however, generally occurs at selected sites or only within a relatively small portion of a species' total range. Spawning aggregations for migratory species are often concentrated in geographic areas that historically provide conditions for reproductive success, that is, areas of relatively long term hydrographic stability but not necessarily consistent year-to-year predictability. Fishes with pelagic eggs often reproduce in gyres and fronts, thus making areas of upwelling and boundary currents among the most productive sites of fisheries in the world. Environmental variation, however, is always a factor, necessitating adaptable life-history characteristics. Some coastal species have increased their reproductive potential with multiple spawning sites, extended spawning seasons, or high fecundities to counteract mortalities associated with unpredictable environments. Yet, other species appear to simply maximize larval survival by taking advantage of normal oceanographic conditions. There are relatively few kinds of current systems, and these influence transport of young fishes in predictable ways. Therefore, as Hjort first hypothesized, displacement of spawning grounds or spawning products can have an adverse effect on recruitment. A one-time transport loss involving a fraction of the cohort and occurring early in its existence may not be as detrimental, however, as the cumulative and long term exposure to high daily mortality rates. If these two sources of mortality act in concert, the prognosis for cohort survival may be poor. Therefore, anomalous physical and biological conditions can either enhance or inhibit survival and, ultimately, recruitment success.

4.6.2 Migration Triangle Hypotheses

In the late 1960s and early 1970s, after the flurry of research activity related to the Critical Period Hypothesis, some recruitment hypotheses specifically advocated the importance of the migratory life-history circuit. This concept recognized that spawning grounds often are located within a residual circulation system that transports eggs and larvae to favorable downstream nursery grounds, with the pre-adults migrating back to adult areas (for example, the Amazon catfish described in Section 2.3.3). The circuit is usually completed by eventual upstream migration to spawning grounds. While it has been difficult to test Migration Triangle Hypotheses in the field, they can best be exemplified in concept by the following two cases.

Townsend's coastal conveyor belt

Biologically productive areas can occur where thermally stratified and tidally mixed coastal waters meet and are mixed by strong tides such as those found in the Gulf of Maine, where tidal ranges are from 2 to 6 m, because deeper nutrient-rich waters are brought toward the surface and stimulate productivity. This is the case off Grand Manan Island in northeastern Maine, a known spawning area for Atlantic herring. Herring usually spawn in tidally well mixed waters from late summer through the autumn. They have an extended larval stage and complete metamorphosis when 5–8 months old.

A portion of the larvae spawned at the mouth of the tidally energetic Bay of Fundy are transported to the southwest within the eastern Maine coastal current. As the herring larvae drift further away from the high energy, vertically well mixed area, the nutrient-rich coastal water column begins to stratify. This leads first to increased phytoplankton production and biomass, soon followed by zooplankton production. Hence, the larvae find themselves in an environment of elevated food as they begin exogenous feeding after yolk absorption. This residency in the downstream coastal current can provide a more favorable feeding environment than if the larvae were retained in their spawning area, which has lower production because the phytoplankton are light-limited due to tidal mixing (that is, the phytoplankton are often mixed below the critical depth). David Townsend coined the phrase "coastal conveyer belt" to describe this phenomenon where larvae develop while drifting along with their developing food supply. He also pointed out that this conveyer belt had the advantage of taking the larvae past numerous estuarine and coastal nursery areas before turning offshore to become part of the Gulf of Maine's Jordan Basin cyclonic gyre (Figure 4.6). Entry into the basin gyre may also serve as a retention mechanism for keeping herring larvae within the inner portion of the Gulf of Maine, which may have ramifications for helping to maintain stock integrity.

Larval Retention or Member/Vagrant Hypothesis

As mentioned above, spawning often consistently occurs at fixed locations for many species. This consistency not only fixes the initial position of larval drift but also determines the position of the nursery grounds when the current regime is relatively predictable. A given stock, therefore, may be determined by the constancy of, or be contained within, a migratory

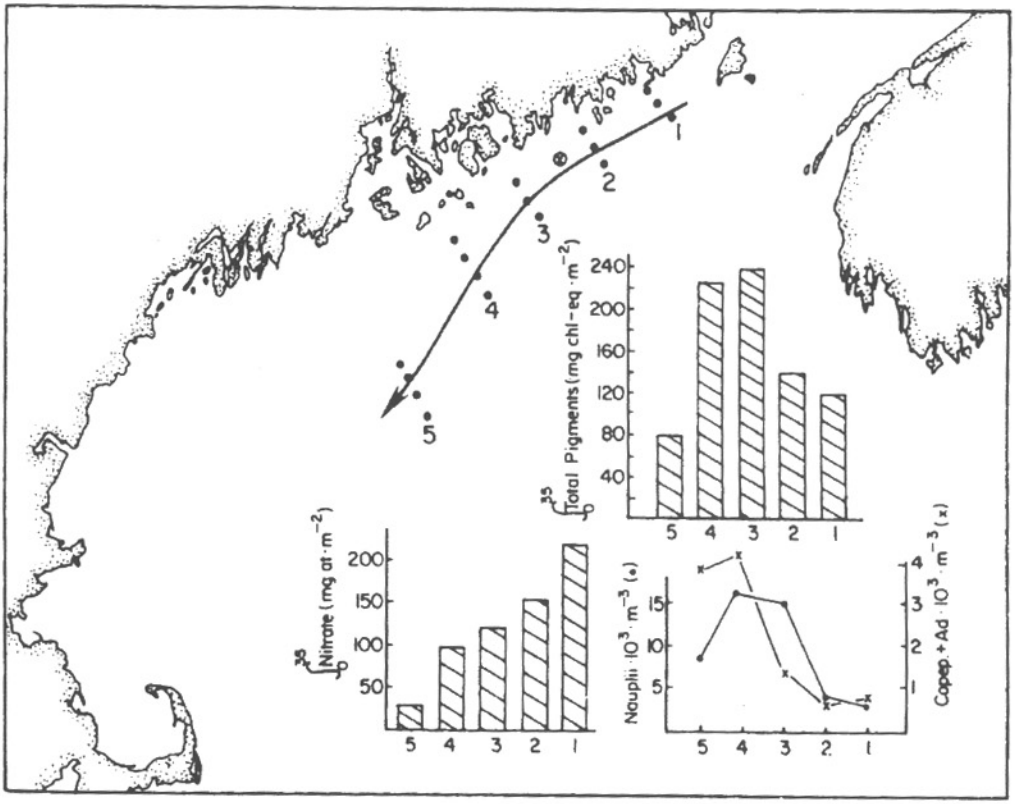

Figure 4.6 Summary plot of the changes in nitrate, chlorophyll, and naupliar and copepodid stages of copepods along the eastern Maine coastal current/plume system for July 1985, used here to illustrate the coastal conveyor belt. The nitrate and chlorophyll histograms are the averages of the vertically integrated (to 35 m depth) values at the stations shown for each of the five transects. The arrow is a streamline of the geostrophic current (reproduced from Townsend 1992 with permission of Oxford University Press).

circuit. The resultant larval drift pattern, when combined with the return migration of adults to the upstream spawning grounds, would then form the geographic base for the stock. In the North Atlantic, the number of genetically distinct herring stocks may be a direct result of the number of oceanographic, larval retention areas. Overwintering larval distributions indicate little stock mixing during the larval phase. Such distinct larval distribution patterns are associated with hydrographic features that show a remarkable degree of year-to-year consistency within the same geographic areas. The physical retention mechanisms for segregating the young of individual stocks appear to be counter-clockwise gyres, which are tidally induced.

Because of the existence of retention areas, fishery scientists Michael Sinclair and T. Derrick Iles further extended Hjort's second hypothesis in an idea that has been referred to as the Larval Retention or Member/Vagrant Hypothesis. It states that through the years species tend to spawn at specific times and places within predictable and distinct circulation features. This selection process enhances the retention or residence time of its "members" within these features by limiting dispersal of passive eggs and weakly swimming larvae until they are able to develop the ability to control their own distribution. In this way, retention helps to maintain the distinctiveness of the population's geographic distribution. In fact, they proposed that population size can also be regulated in this fashion. A density-dependent mechanism may be activated when the population size increases to the point that a portion of the expanding spawning population is displaced to less favorable spawning grounds. These less favorable areas have a lower capability to retain larvae near the spawning and nursery grounds where residence times within the circulation feature are shorter. This eventually will lead to individuals being lost from the local spawning population ("vagrants"). The process of vagrancy, therefore, is the increase in loss rate of eggs and larvae as the size of the spawning stock increases and spawning grounds expand outside of the population's favorable retention area (see also Box 7.3). This density-dependent process could limit population size independently of any previously defined, density-dependent food-chain mechanisms.

4.6.3 Further relationships between hydrography and recruitment

The apparent dependence of pelagic spawning success and recruitment upon drift conditions suggests that anomalies in drift patterns or movement of spawning grounds could be one of the major sources of the widespread variation in recruitment success in marine fishes. When population habitat boundaries shift, there is generally an effective change in potential habitat available to larvae, which can then influence reproductive success and recruitment variability. We offer a few more examples.

Upwelling environments

In the northern hemisphere when wind blows over the surface of water, the resultant current flows to the right of the wind direction (or to the left in the southern hemisphere). This is known as Ekman transport. Where such wind-induced transport is offshore (Ekman divergence), displaced inshore surface waters are replaced by cold, nutrient-rich waters upwelled from below. Persistent upwelling generally occurs along western continental margins and is associated with prevailing winds blowing toward the equator. Well known examples include the Peruvian and the North African Mauritanian upwelling systems. Upwelling also takes place to a lesser degree along the eastern coast of continents, where it is induced by winds blowing toward the poles. Continental shelf or oceanic fish larvae will benefit from increased productivity associated with upwelling, while larvae needing estuarine or coastal nursery areas will benefit from onshore transport in the deeper waters. If the upwelling system decays or disappears, both groups of larvae may experience increased mortality. Recall the role of upwelling environments in the Stable Ocean Hypothesis (Section 4.5.2).

Estuaries

Estuaries are important because many fish species are considered to be estuarine dependent, whereby they must utilize the estuary during some portion of their life. This generally occurs during early life, as estuaries are believed to be enriched in nutrients from freshwater runoff and hence richer in food for larvae and juveniles, thus providing important nursery habitat for young fishes. Estuarine dependency implies that recruitment success may be determined for some species by the degree to which fish eggs and larvae are transported to, and retained within, the estuary. There is a tremendous body of literature on this subject, but indications of direct relationships between estuarine residency and recruitment variability, again, are difficult to find.

Estuarine circulation is influenced by tide, river flow, local wind, topographically induced circulation, and non-tidal forcing from the coastal ocean. Estuarine circulation can also be altered by short term meteorological events and by seasonal or annual river discharge variability. Wind-induced transport toward coastlines (often eastern continental margins) – known as Ekman convergence, coastal setup, or downwelling – can produce significant non-tidal variation in sea level, which can directly affect estuarine currents because the estuary tends to fill with more water. Several of the world's coastlines have such seasonal, non-tidal changes, which can result in seasonal or short term net coastal flows into estuaries. In addition Ekman divergence or convergence can change the density structure of the coastal water column, thereby altering the gravitational circulation and exchange between estuary and ocean.

There are fundamentally two types of estuaries: positive estuaries, in which river discharge and local precipitation exceed evaporation, and negative estuaries, where evaporation dominates (for example, lagoons). The normal exchange pattern for a positive estuary is a residual downstream movement of fresh water at the surface, a level of no net motion at mid-depth, and a net, non-tidal upstream counter current of denser, saltier water at the bottom. This exchange pattern facilitates the passive upstream transport of fish eggs and larvae (or any other neutrally or negatively buoyant planktonic organism) in the estuarine bottom layer with varying degrees of success due to turbulent-mixing-induced downstream losses. The vertical position of an organism in the water column over time can determine the direction of its transport.

Space-limited environments

There are species of marine and freshwater fishes for which recruitment may be limited by the availability of space when pre-recruits settle from the three-dimensional planktonic environment to an essentially two-dimensional benthic habitat. Most notable are the coral reef fishes whose larvae are pelagic, but whose juveniles and adults are associated with a reef. We mention this here, however, because there continues to be debate among fishery scientists as to whether recruitment by these species is indeed limited by post-settlement processes or is limited by the supply of larvae transported to, and retained upon, the reef. Post-settlement processes include reductions in growth rate due to intraspecific competition for food and increased mortality due to a lack of shelter, among others. Similar arguments have been made for the flatfishes, another group whose larvae (Figure 1.3t) are pelagic before settling to the bottom to assume a benthic existence. Like coral reef fishes, post-settlement mortality in flatfishes and other demersal species may be mediated by predation, if the supply of larval pre-recruits is not limiting. Pre-settlement processes include all of those related to egg and larval stage dynamics as discussed elsewhere in this chapter.

Space also can be limiting for freshwater species that spawn in streams, as adults compete for spawning sites and young of the year must compete for a finite number of optimal locations for growth and survival within the complex habitats of streams. In this scenario, currents again play a role because optimal locations often are defined by the balance between flow rates that are not too energetically demanding for young fishes struggling to maintain their position in the stream and flow rates that are high enough to deliver enough drifting food.

4.6.4 Relationships between hydrography and recruitment: examples

Haddock

The Gulf of Maine was an early testing ground for relating plankton distributions to circulation patterns. The normal cyclonic circulation pattern over Georges Bank can cause the loss of haddock eggs and larvae (Figure 1.3n) to the deep waters, since near-surface currents on the bank are generally southerly and offshore, except for short periods in the summer. Transport off the bank can result in mortality due to removal of eggs and larvae from feeding areas and to transport to depths too great for settlement of larvae.

Walleye pollock

Walleye pollock spawn in the Gulf of Alaska mostly along the Shelikof Straits, where eggs and larvae (Figure 1.3o) drift within a southwesterly current along the Alaska Peninsula and enter fjords where their first summer is spent. This current system has abundant food resources, which favor larval survival during transit. Several oceanographic fronts in the Bering Sea separate characteristic water masses that support distinct zooplankton populations with varying food quality. Recruitment of walleye pollock, therefore, is likely to be affected by these oceanographic systems, which can influence the distribution of concentrations of their eggs, larvae, and food supply. We will discuss this example further in Section 4.8.2.

Capelin

The survival of larvae can also be influenced by winds, since winds can alter local conditions by exchanging or replacing water masses. For example, onshore winds along coastal Newfoundland can exchange the local water mass, which normally has a high concentration of predators, for one that has fewer predators and higher densities of prey for larval fishes. The characteristics of this new water mass trigger the emergence of larval capelin from demersal eggs buried within the sand of the intertidal zone. Capelin larvae, therefore, may initiate their drift and first feeding in a "safe-site" that is mediated by the wind. If there is a survival advantage to such a water-mass exchange and transport event, then any synchrony with the time of hatching could be positively reinforced. Other examples of safe sites may exist, but it remains to be seen whether the oceanographic features or the physical processes producing them, and their subsequent impact on larval survival and recruitment success, can be sufficiently documented over time.

4.6.5 Some large scale examples

In recent years, fishery scientists have begun to discover even larger scale links between recruitment variability, oceanography, and climatology. For example, the periodic phenomenon known as the El Niño–Southern Oscillation (ENSO) has been shown to dramatically alter sea surface temperatures in the eastern Pacific, rainfall patterns and sea surface temperatures in the Atlantic, and the frequency of Atlantic tropical storms. All of these changes have been implicated as factors that affect recruitment dynamics to some degree, especially in the upwelling environments of the eastern Pacific. Also in the Pacific basin, large scale and persistent changes in patterns of atmospheric high and low pressure systems result in oceanographic regime shifts in the North Pacific Ocean that have been implicated in the recruitment variability of many species there, especially Pacific salmons.

A somewhat similar atmospheric–oceanic coupled system, albeit much less studied, exists within the North Atlantic (the North Atlantic Oscillation, NAO). That climatic system, however, involves a north–south dipole (low-frequency atmospheric pressure anomalies between the Icelandic/Greenland low pressure and the Azores high pressure systems) rather than an equatorial, east–west dipole as in the Pacific. The NAO, however, may also prove to have some degree of coherence with the tropical North Atlantic Ocean by way of the Mauritanian upwelling system off northwest Africa (such as, correlations with its coastal upwelling index) and perhaps the Caribbean Sea.

Also in the North Atlantic basin, a change in the circulation pattern of the North Sea resulted in a dramatic increase in the abundance of cods and haddocks and declines in Atlantic herring, which persisted for many years but has since reversed. Herring stocks are now increasing. Cod stocks in the North Atlantic Ocean exhibit positive correlations in year-class strength across broad spatial scales (that is, patterns of strong and weak year classes are correlated among stocks), implying a link to climate.

Finally, in oceans worldwide, anchovy and sardine* stocks synchronously alternate in abundance, one replacing the other at a location for long periods of time. Fishery scientists suspect that this periodic alternation is driven by large scale climatic and oceanographic variability, although the mechanisms remain unknown. As our ability to measure synoptic ocean and atmospheric conditions improves as a result of technological advances such as high altitude and satellite remote sensing, coupled with recent dramatic improvements in weather forecasting and ocean circulation computer models, our ability to unravel these large scale links will undoubtedly improve. Such advances will become increasingly important to fishery science in the face of global warming. We will discuss other technological advances in a later section.

4.7 Predation mortality and the paradigm shift

Recently, a dramatic shift in thinking about the causes of recruitment variability has emerged, potentially making the work of fishery scientists more difficult. As described above, most of the previous recruitment hypotheses elaborated on one or the other of Hjort's original two

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*A detailed analysis of population fluctuations in Japanese sardine, resulting from variable recruitment, is summarized in Chapter 11.

hypotheses and described mechanisms that generally resulted in episodic year-class successes or failures – sort of an all or nothing proposition. Since the mid- to late-1970s, however, it has become increasingly clear that predation is a (perhaps *the*) major source of egg and larval mortality in fishes (see Chapter 3). Although largely forgotten in today's literature on the subject, David Cushing was perhaps the first to recognize the potential importance of predation as a recruitment regulator in his 1975 Single Process Concept. He suggested that as the length of time that eggs or larvae remain vulnerable to predators increases, so will cumulative mortality rate increase. More specifically, larvae that experience favorable feeding conditions and grow more quickly will complete metamorphosis at earlier ages and thereby experience lower cumulative predation mortality during the larval stage, the time when mortality rates are known to be high. More importantly, it suggests a mechanism by which episodic processes are not the only means by which a year class can succeed or fail.

4.7.1 Houde's subtleties and episodes: Cushing's Single Process rediscovered

In several important papers in the late 1980s, Edward Houde revived Cushing's Single Process concept by showing that relatively subtle changes in larval growth and mortality rates potentially could result in strong or weak year classes. In these papers, Houde argued that rate changes, the magnitude of which would be difficult to detect in the field, were sufficient in exponential decline models to generate more than 100-fold variability in the numbers of larvae surviving to the juvenile stage (Table 4.1). Other researchers later called this argument the Stage Duration Hypothesis. Houde furthered argued that predation was the likely source of most egg and larva mortality.

4.7.2 The Stage Duration Hypothesis

Unlike the other recruitment hypotheses that we have discussed, the Stage Duration Hypothesis is important because it represents a different way of thinking about the recruitment problem. And if correct, it may be more difficult to predict recruitment success because of the difficulties in understanding all of the environmental factors that can contribute to subtle changes in larval growth and mortality rates. This may best be understood by viewing Figure 3.5, which shows the magnitude of decline in numbers typical of many marine and freshwater fish species, and the many biotic and abiotic factors that can

Table 4.1 Hypothetical recruitment of young fish under one "good" and three possible "bad" conditions, the latter represented by 25% changes in mortality or growth rates (as age at metamorphosis). Recruitment is defined here as the number of survivors at the end of the larval stage (data from Houde 1987).

Condition	Initial number in cohort	Instantaneous mortality (Z, day^{-1})	Age at metamorphosis (day)	Number of recruits
Good	1×10^6	0.100	45.0	11 109
Bad-1	1×10^6	0.125	45.0	3607
Bad-2	1×10^6	0.100	56.2	3625
Bad-3	1×10^6	0.125	56.2	889

contribute to recruitment success or failure, including density-dependent (or compensatory) feedbacks that arise when numbers in a population become too high or too low (see Section 3.1.4). The extremely high mortality rates implicit in Figure 3.5 also imply that the average fish egg or larva in the sea is destined to perish. Such high mortality has led many investigators to search for characteristics among the relatively few survivors that distinguish them from their departed siblings, especially with respect to their ability to avoid predation. Interestingly, some marine and many freshwater species, those employing the equilibrium or *K* reproductive strategy discussed in Chapter 1, have greatly reduced recruitment variability associated with egg and larval stage dynamics because they invest more energy in parental care, mainly by building and subsequently guarding nests. In these species, many of which are found in resource-limited environments, high fecundity is traded for large eggs and large, well developed larvae upon hatching. The result is the production of a more constant, but low number of new recruits. Space, again, can limit recruitment for these species because adults compete for the best territories.

4.7.3 The fate of the average fish larva

Because the average fish larva dies soon after hatching, and predation is now believed to be the major source of larval mortality, it follows that survivors from cohorts exposed to predators may be exceptional individuals with respect to characteristics that shape predation vulnerability. This notion led many fisheries scientists in the late 1980s and early 1990s to search for simple conceptual models that could offer a better understanding of how predation works. These conceptual models ultimately focused on the empirically derived relationship between increased larva size (or in the degree of ontogenetic development) and decreased probability of being captured by any of a host of different types of predators (Figure 4.7) as a means to simplify our thinking. Some in the fishery literature later referred

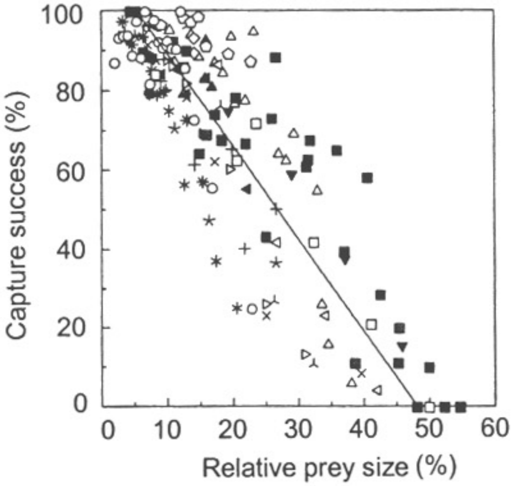

Figure 4.7 Capture success as a function of prey to predator length ratio for different combinations of fish species as predators (12 species) and prey (nine species). Each symbol identifies a different combination of predator species, prey species, and temperature (reproduced from Fuiman 1994 with permission of Academic Press).

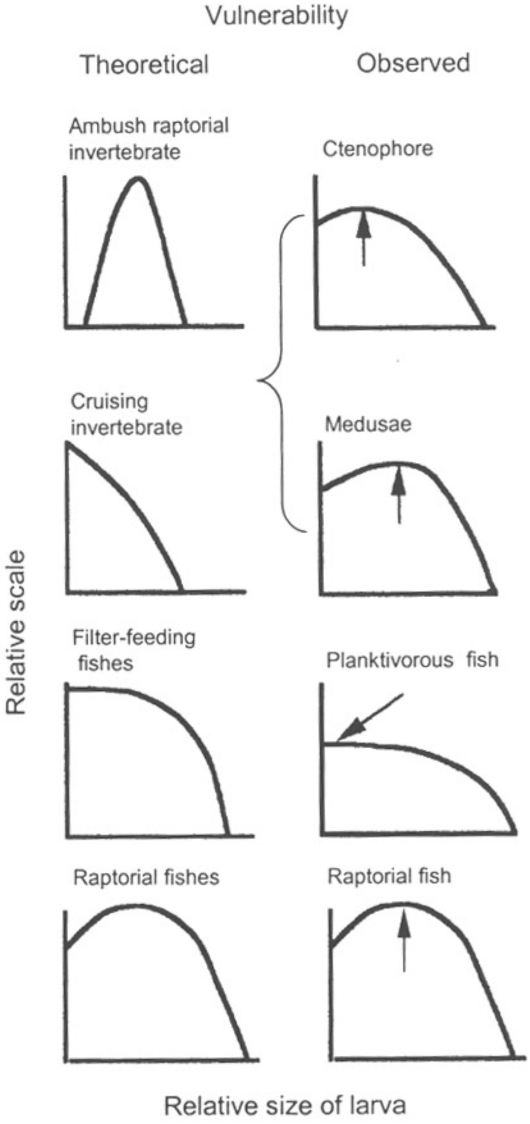

Figure 4.8 Vulnerability of fish larvae to different types of predators. Theoretical relationships are the same as those shown in Figure 3.6 (from Bailey & Houde 1989). Observed relationships were derived from mesoscosm experiments with larval fish and their predators. Arrows indicate the relative size of maximum vulnerability to the predators. Note that ctenophores and medusae did not behave as true cruising invertebrates nor as ambush predators, but were somewhere in between (modified from Cowan *et al.* 1996 with permission of Academic Press).

to this notion as the Bigger-is-Better Hypothesis. This parsimonious view, in our opinion, initially led to an oversimplification or misinterpretation of the mechanics of predation, resulting in the elevation of connate ideas such as bigger is better and stage duration to the level of contradictory hypotheses.

We now know that these mechanics are far too complex to be easily described by simple models that relate vulnerability to any one larval characteristic. As we learned in Chapter 3, empirically derived vulnerability curves are often dome-shaped as predicted by theory (Figure 4.8), but these curves can be generated by very different properties inherent to specific predator–prey interactions. Moreover, because it is likely that members of most cohorts of larvae *in situ* are exposed to a continuously changing gauntlet of predators during early life, where the mix of predator types and sizes is highly variable, it seems unlikely that any simple conceptual model could apply, nor does it appear likely that survivors are indeed inherently exceptional individuals. In fact, it has been suggested that characteristics of individual larval survivors may be more influenced by attributes of the predators to which they were exposed in early life than by their initial sizes within the cohort and their potential individual growth rate.

What does seem clear, based on results of numerous experimental and modeling studies, is that it is likely that survivors are derived from faster growing cohorts of larvae because they spend less time in the stage vulnerable to predators, as Cushing stated so well in his definition of the Single Process. It is less likely, however, that large size or other single attributes of an individual within a cohort will afford it a clear advantage for survival over others. More importantly, faster growing cohorts appear to experience considerably lower cumulative mortality rates regardless of the types of predators to which they are exposed, suggesting the importance of relationships between cohort mean growth rate (not body size *per se*), predation, and recruitment success. Thus, while is has been difficult to directly test the Stage Duration Hypothesis *in situ* by virtue of the mechanisms proposed in the hypothesis itself (that is, subtle changes), its logic and implications are clear.

4.7.4 Peril of the unfit or the unfortunate?

Even while considering the arguments made in the previous section, we believe that the jury is still out regarding the attributes that may make individual fish larvae more or less vulnerable to predation because larval size and growth rate are not the only attributes that need to be considered. Toward this end, fishery scientists Lee Fuiman and James Cowan are currently (as of 2002) asking the following question in a combined laboratory, modeling, and field study. Is there a subset of individuals in a cohort that have a suite of physiological or behavioral characteristics that confer greater fitness in predator–prey situations, leaving less fit individuals to succumb to predators? Preliminary results indicate that larval "athletes" – individuals that consistently see and hear better, swim faster, and respond more quickly and more vigorously when exposed to a threat – appear to exist. These larval athletes are less frequently consumed by predators in the laboratory. It remains to be determined whether these differences are important in a field setting.

4.8 Predicting recruitment: progress and prognosis

It should be clear that larval fish distribution, abundance, and survival is controlled by both biotic and abiotic factors. Biotic factors include: adult spawning condition, behavior, and abundance; environmental optima and tolerances; *in situ* concentrations of suitable food and potential predators; and larval behavior. Physical factors include patterns or cycles in the climatology, hydrography, and oceanography of the area (that is, water temperature and salinity; vertical and horizontal gradients in water density; turbidity; and water current speeds, directions, and anomalies). Moreover, it should be apparent that the processes underlying the recruitment hypotheses we have discussed may represent endpoints in a continuum of processes that shape the recruitment function. In other words, processes emphasized in specific hypotheses may work simultaneously or sequentially to determine year-class success, both through episodic losses of eggs and larvae in some situations and through subtle but cumulative changes in vital rates in others. In this light, the ultimate goal of recruitment prediction seems daunting. Yet, progress is being made through a series of technological innovations fashioned in the past decade that have provided new insights on, and increased detectability of, the recruitment variability problem. Some of these include: otolith aging and chemical analysis of skeletal material (see Chapters 2 and 6 and Section 12.6); new methods of mass marking of eggs and larvae for use in experiments (see Section 12.9); molecular genetic approaches to stock identification (see Chapter 6); new acoustic and video abundance measurement methods (see Section 12.2); new statistical and time-series analysis methods; incorporation of stochasticity (variability, random and otherwise) into population models; assembly of large data bases; and individual-based modeling (see Section 12.8). We will briefly discuss some of these in more detail, ending with an example fishery to which many of these innovations have been applied.

4.8.1 Technological innovations

The following information about technological advances was taken largely from a review paper on compensation by fishery scientist Kenneth Rose and colleagues. Because many of these innovations also have bearing on the future of recruitment prediction, some of the information is repeated here. This list is not meant to be comprehensive, but rather to illustrate that we are at a point where diverse technical advances are providing an opportunity for a major leap in our understanding of recruitment. The growing emphasis on synthetic and comparative analyses, coupled with advances in measurement, statistical, and population modeling methods, is encouraging and absolutely critical for progress in understanding recruitment dynamics and in the effective management of fish populations.

Mass marking of eggs and larvae

The traditional mark–recapture approach to estimating mortality and movement has been greatly expanded by the use of chemicals for mass marking of eggs and larvae, tags that permit information on individual fish to be retained and stored, and by the use of ultrasonic telemetry that allows continuous tracking of marked individuals.

Acoustic and video measurements of abundance

Video and acoustic technologies are two examples of new abundance measurement methods that have recently become available. Video and acoustic methods have been used to augment and calibrate traditional sampling gear, and to permit sampling in situations where traditional gear cannot. They have also been used to simultaneously monitor biological and environmental variables on the scale of meters or less, as well as over large areas, and for recording detailed behavioral interactions between individuals.

New statistical data analysis

New statistical methods are available that are well suited for analyzing fish population-dynamics data. Statistical analysis in ecology in general has been moving from hypothesis testing and linear models to multiple hypothesis evaluation (such as, maximum likelihood) and non-linear models. New methods, such as generalized additive models, non-linear time series, neural networks, fuzzy mathematics, classification and regressions trees, geostatistical methods, and methods that explicitly account for sampling and measurement error, are being applied to fishery-related data. Recent advances also allow for much greater flexibility in time-series model formulation. A promising trend is the focus on the interaction between environmental stochasticity and density dependence, and how they combine to control the long term dynamics of populations. Bayesian approaches using maximum likelihood methods are being used to robustly estimate the many unknown parameters in population dynamics and stock-assessment models. Synthetic analyses involving diverse studies can now be rigorously analyzed statistically using meta-analysis methods.

Explicit treatment of stochasticity in population models has increased realism. Population modeling has moved from deterministic models of simple equilibrium to non-equilibrium approaches that explicitly include stochasticity and uncertainty. The definition of a regulated population has been expanded from simple statements about equilibrium densities to more encompassing definitions appropriate for highly stochastic populations, such as a bounded variance of population densities and a long term stationary probability distribution of population densities. Embracing the stochasticity that is characteristic of almost all fish populations, rather than using models that attempt to average the variability away and produce precise but inaccurate predictions, will increase model credibility.

Individual-based models

Individual-based modeling offers a promising approach for understanding population and community dynamics, and has features that should help in quantifying recruitment variability of fish populations. Representing local interactions in space, size-based interactions, episodic effects, movement, and stochasticity, all of which are important to realistically simulating fish population dynamics and recruitment, is relatively easy in individual-based models. Intuitively, if one can realistically represent how individuals grow, survive, reproduce, and move, then realistic estimates of population-level phenomena such as recruitment can be obtained by simply summing over all of the individuals in the model.

4.8.2 *FOCI and walleye pollack: the state of the art*

The Bering Sea supports some of the most productive fisheries in the North Pacific Ocean, and the walleye pollock is the most abundant of the species harvested there, accounting for more than 65% of the total groundfish biomass. During the 1980s total pollock biomass in the Bering Sea was estimated to exceed 20 million tonnes and was harvested in the exclusive economic zones of both Russia and the United States. The annual United States catch of pollock in recent years has averaged 1.3 million tonnes, with an ex-vessel value of $210 million. Besides their economic importance, pollock are important to the Bering Sea ecosystem, providing most of the food for the extensive marine mammal and bird populations found there.

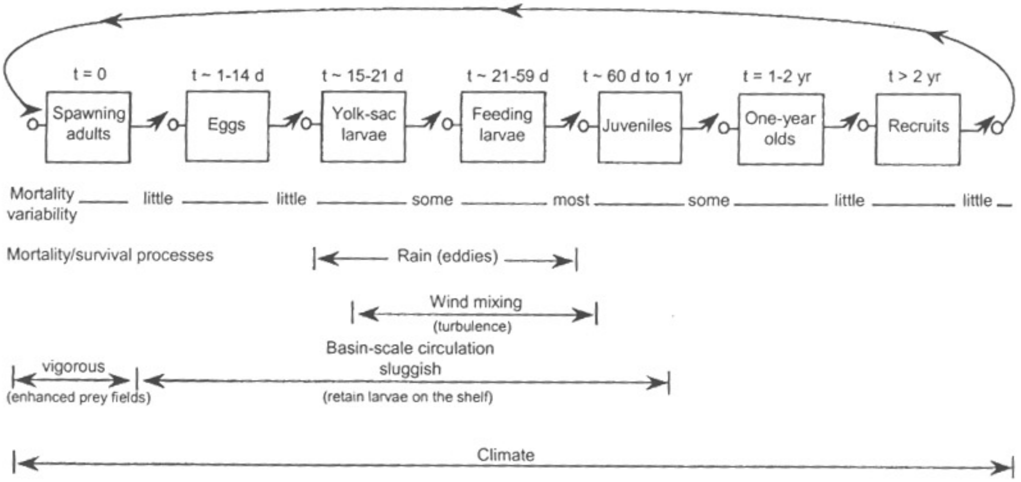

Figure 4.9 Conceptual model of Gulf of Alaska walleye pollock survival at different life stages. Relative mortality, important environmental processes, and the life stages they affect are indicated. Note the similarity to Figure 4.1 under Mortality Variability (redrawn from Megrey *et al.* 1996).

As for most marine fish species, Bering Sea walleye pollock experience large inter-annual variations in recruitment and these determine population size and thus fishery quotas and harvest levels. Recruitment is thought to be largely set during its first year of life. The need for early prediction of year-class success for this ecologically and economically important species is self evident. Thus, to develop an understanding of stock structure and recruitment variation in Bering Sea walleye pollock, the United States National Oceanic and Atmospheric Administration established in 1992 the Bering Sea Fisheries Oceanography Coordinated Investigations (FOCI) program, the most ambitious program to date devoted to the subject of recruitment. This program of study included a major emphasis on the dominant physical oceanographic features that could directly or indirectly influence survival of pollock larvae, through modulation of larval food production. As a result of this effort, more than 400 papers have appeared in the published fisheries literature and most of the technological innovations that we listed earlier have been employed and further developed. More importantly, this effort has led to the ability to predict, although coarsely, walleye pollock recruitment. FOCI scientists now can review a series of biological and physical inputs and provide fishery managers predictions of recruitment that can distinguish between strong and weak year classes. Prediction is based upon model-generated relative mortalities of early life stages, including eggs, yolk-sac larvae, feeding larvae, juveniles, 1-year olds, and recruits, and the environmental processes that drive their population dynamics (Figure 4.9). While this level of prediction may seem crude, it represents the state of the art in fishery science and fishery managers are extremely happy to get it.

4.8.3 Epilogue

The following paragraphs are taken almost verbatim from a paper describing the history of recruitment fishery science in the United States written by Arthur Kendall and Gary Duker. It eloquently summarizes where we are today.

Although much information has been gathered and analyzed, and numerous publications completed, understanding of the mechanisms that drive recruitment remains an elusive goal. Some have suggested, as Hjort himself did to the newly formed International Council for the Exploration of the Sea, that understanding recruitment processes is not worth the effort; managers merely need relative estimates of recruitment strength. We disagree with this admonition and further suggest that just correlating year-class strength with environmental variables is not enough; a true understanding of the processes involved in variations in survival of young stages, as Spencer Fullerton Baird (the first Commissioner of the United States Bureau of Fisheries) advocated, is required.

> *"Since the 1920's, correlations of the strength of year classes with environmental factors ... began to take a certain melancholy consistency. Initial data might suggest a high correlation ... but eventually the correlation would fail."*

Could the founders of recruitment fishery science have anticipated the complexity of the recruitment process when they first advocated an ecological approach to the study of fluctuations in fish populations? Even with increased awareness of the importance of fish recruitment to management and recent technological and conceptual advances, many of the questions and hypotheses remain unanswered and untested.

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