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Chapter 12

Perspectives on Larval Fish Ecology and Recruitment Processes

Probing the Scales of Relationships

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Abstract

The scale of the test in larval fish ecology research must match the scale of the hypothesis. This chapter illustrates the importance of resolving significant scales of variation by drawing on published studies, unpublished data, and theoretical modeling. Aliasing a cyclic variation in egg abundance is used to show how various sampling frequencies can result in an apparent increase, decrease, or near-random pattern in abundance estimates. Egg, larval, and postlarval mortality estimates may be biased in a time-dependent manner by assumptions concerning constant production or immigration and emigration, the spatial distribution of the target population, and the exponential decay model. A theoretical model is used to illustrate how misleading interpretations can be drawn from the relationship between larval mortality and instantaneous measures of larval predator and prey abundances that are biased by different rate processes having different scales of operation. The results of an extensive field program are used to illustrate how water-mass dynamics and the characteristic fauna associated with them can produce asynchronous patterns of coupled predator/prey oscillation that have no biological basis. Identifying the actual relationships is shown to be achieved only by resolving the biological processes at and below the scales of the physically driven processes. Finally, we will illustrate how localized small-scale, high-resolution approaches to hypothesis testing can be scaled upward and tested at the scale of large marine ecosystems (LMEs).

Introduction

Robust predictions of recruitment variation among freshwater, anadromous, catadromous, or marine fish stocks inhabiting relatively small "closed" inland lakes and seas or more "open" large marine ecosystems have proven to be unobtainable after more than a century of fairly intensive efforts.

We suggest that two principal reasons exist for the present lack of predictive capability. First, there is no general theoretical framework acceptable to all researchers within which to place the hypothetical-deductive scientific method. Second, and perhaps most important, is our collective failure to test hypotheses (within or outside of what loose theoretical framework that does exist) correctly scaled to the relationships thought to exist. In brief, we emphasize that the scale of the test must match the scale of the hypothesis, an approach championed by Harper (1977) in the field of terrestrial plant ecology.

In this chapter we stress the importance of resolving the significant temporal and spatial scales of variation by drawing on published studies, unpublished data, and some theoretical modeling. We show how localized, small-scale, high-resolution approaches to hypothesis testing can be scaled upward and tested at the scale of LMEs. Some solutions are suggested to improve the predictive capabilities of environmentally based models of recruitment variation.

Scale and the Scientific Method

Logistics often dictate the scale of data acquisition in ichthyoplankton studies (Smith, 1978). Sampling is spaced on the order of tens of km covering areas of hundreds to thousands of km^2 over time scales of weeks to months. However, the greatest rate changes and variations in growth, mortality, dispersion, and reaggregation (schooling) apparently occur during the egg, larval, and early postlarval stages, and at scales below those most commonly employed for sampling. This could explain in part the general failure of hypotheses related to the early life history to be rejected (or supported) simply because of inappropriately scaled sampling. This can lead to a situation where the sampling scale employed distorts our perception of the significant time and space scales.

The scientific method proceeds more or less as follows (Andrewartha, 1957): from existing observations and data, a conceptual model is formulated by deduction. Using mathematically supported logic, the model is made operational and restated as a testable hypothesis. The empirical test requires measurable independent variables (Peters, 1980). The test can result in either (i) rejection or the inability to reject the hypothesis; (ii) suggestions that the operational model is flawed due to unsound logic; (iii) suggestions of a flawed model because of erroneous or insufficient empirical knowledge and/or a faulty interpretation of the knowledge, or (iv) statistically indefensible rejection of the hypothesis because of insufficiently rigorous data collection and analysis. We suggest that the latter two results are the most critical in fisheries research, because scale-related problems easily result in biased data and analyses that can form the basis for new models supported by untested assumptions.

Recruitment Variation and the Environment

Explanations of recruitment variation range from the belief that recruitment is some function of stock size or biomass, to the idea that it is solely dependent on variations in the environment. Neither is really exclusive of the other (Rothschild, 1986), yet it is undeniable that the environment exerts a major influence on recruitment variation in marine finfish and shellfish populations. Many published studies (see, for example, Cushing and Dickson, 1976; Hempel, 1978; Lasker, 1978; Bakun and Parish, 1980; Bardach and Santerre, 1981; Bakun *et al.*, 1982; Shepherd *et al.*, 1984; Sissenwine, 1984; Kawasaki, 1985; Frank *et al.*, 1988) have reviewed the vast body of literature reporting relationships between recruitment (or some proxy thereof) and some physical-environmental factor(s). In spite of this ever-increasing body of correlative evidence, the fisheries scientific community is far from agreement on the significance of these studies for the following reasons: poor predictive power due to statistical problems related to sample size; post publication failure; a posteriori approaches where several variables are tested but their number and the lags employed (in time-series data) are not reported (distorted statistical significance); autocorrelative problems in both the recruitment data and the techniques used to generate them, and in the environmental data (Bradford and Peterman, 1989; Thompson and Page, 1989); and the limitations of the environmental data that are available (see also Gulland, 1952, 1965; Bell and Pruter, 1958; Walters and Ludwig, 1981; Sissenwine, 1984).

Such criticisms are indeed valid. Most environment-recruitment correlation studies are based on the premise that year-class strength is established during the early life history. If correct, then it can be argued that most of these studies have used inappropriate time and space scales for measuring and comparing the biological and physical variables. A fundamental requirement in the analysis of the influence of environmental effects on the growth and survival of the early life stages is measurement at appropriate time and space scales. Failure to meet this requirement can have profound effects on the data and subsequent analysis and interpretation. Even when hypotheses determine the sampling strategy, this does not ensure their proper evaluation. Scaling is a multifaceted problem. It ranges from simple aliasing to the use of sampling gear. We now highlight some scale-related problems and their association with theory and hypothesis testing.

Aliasing

Aliasing is simply the problem that exists when a significant amount of variation in a process is not resolved due to an observational scale (spatial or temporal) that is too large. The biasing effect of the phenomenon is most critical to resolving cyclic processes. We present a hypothetical example in Figure 12.1, which shows that the abundance of eggs in a water column is a function of tidal velocity (eggs are resuspended or advected to the sampling area during each tidal cycle). Egg sampling conducted with a fixed daily periodicity would not reflect the true cyclic nature of abundance variation. Instead, it would present an apparent decay in abundance (if sampling ended after a few days) that could be misinterpreted as mortality or hatching (Figure 12.1, line A). Shifting the fixed daily sampling by approximately six hours would result in an apparent increase in abundance (Figure 12.1, line B). If, in either case, sampling continued for several days, the apparent cyclic behavior would still bear no relationship to reality. If the daily sampling time was not fixed, but varied by a few hours among days, then a more-or-less random pattern would be apparent (Figure 12.1, line C). Although in this example the variation in the biological phenomenon is physically driven (tidal), this fact is not readily apparent from any of the three sampling strategies employed. It is clear that aliasing effects easily distort the estimates of statistical parameters (e.g., mean, variance) that are frequently the basis for hypothesis testing. This phenomenon can occur at all scales due to physical (tides, storms, seasons, etc.) and biological (diel migrations, serial spawning, etc.) processes that have characteristic periodicities.

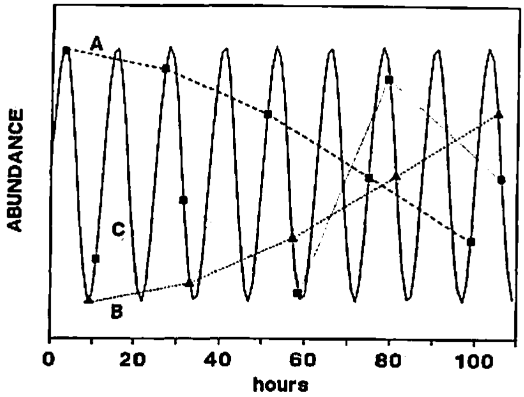

Figure 12.1. An example of aliasing the abundance of eggs (solid line), that vary as a function of tidal velocity, by sampling with different but fixed daily periodicities (lines A and B) and with a slightly varying (± a few hours) daily periodicity (line C).

Scale Effects on Mortality Estimates and Assumptions

High mortality estimates appear typical for marine fish eggs and larvae. However, few estimates are based on replicate samples, and their range and variability reflect both natural variation and sampling biases that stem from the gear type, sampling frequency, and the spatial and temporal resolution employed to assess mortality (Taggart and Leggett, 1987a,b). Sampling frequency typically ranges from once every 4–14 days (d) for yolk-sac larvae (Dahlberg, 1979), to as long as 100 d for post larvae (Graham and Townsend, 1985). In most studies, changes in abundance due to immigration and emigration (diffusion and advection) are not considered. While field sampling is typically large-scale, it is assumed that (i) the target population is adequately sampled, (ii) dispersion does not bias the mortality estimates, and (iii) immigration or production of new individuals is nil, or positive but constant (Taggart and Leggett, 1987b). Furthermore, it is generally assumed that the best estimate of mortality is defined by the exponential decay model fitted to abundance estimates over a series of sampling intervals. The implicit assumption is that deviations from the fitted exponential reflect "sampling error" and not variation due to immigration, emigration, or mortality.

Mortality and sampling intervals: An empirical relationship

In reviewing the literature on the mortality estimates (M) of marine fish eggs and larvae (Table 12.1), we noted that studies reporting high mortality rates (Dragesund and Nakken, 1971; Fortier and Leggett, 1985; Hewitt *et al.*, 1985; Taggart and Leggett, 1987b) were those that were designed to directly measure mortality over short intervals (0.5 to 3 d). They were also studies that corrected for immigration and emigration to and from the target populations. In the data summarized in Table 12.1, we also noted an apparent relationship between the estimates of daily mortality and the length of the interval between sampling surveys that were used to estimate abundance and subsequently derive the mortality estimates using the exponential decay model. Linear regression analyses were used to examine the relationship between estimates of daily mortality (% d^{-1}) and the sampling intervals (d) used to derive the estimates. The data were normalized with the arcsin-square root and logarithmic transformations.

Daily mortality decayed exponentially for all developmental stages with increasing duration of the sampling interval (Figure 12.2). The equation describing the relationship (Table 12.2) was highly significant (r^2=0.68). The mortality estimates for different stages also showed an exponential decay in mortality with sampling interval (Figure 12.2). Each was statistically significant, though the strength of the relationships weakened with increasing development. It is unlikely that the developmental stage is solely responsible for the phenomenon, as an analysis of covariance showed that the slopes of the egg, larval, and postlarval relationships were homogeneous ($F = 0.31$, $p = 0.731$, $n = 58$). Clearly, our argument would be stronger using a species-specific approach, but insufficient data forced us to use a composite.

Mortality and sampling intervals: Theoretical relationships

Modeling results (Figure 12.3) show the expected relationships between the daily mor-

Table 12.1. Data sources from the published literature giving the number of daily mortality estimates of marine fish eggs, larvae, and postlarvae. These data were used to determined the relationship illustrated in Figure 12.2.

Source	Eggs	Larvae	Postlarvae	Comments
Dahlberg, 1979	11	12	13	Numerous species; numerous references
Graham & Townsend, 1985	—	—	17	Atlantic herring; 7 different cohorts
Frank & Leggett, 1986; and unpublished data	—	18	—	Capelin; 8-11 d enclosure experiments
Fortier & Leggett, 1985	—	1	—	Capelin; 48 h drift study
Taggart & Leggett, 1987b	—	40	—	Capelin; multiple short-term estimates
Ware & Lambert, 1985	—	1	—	Atlantic mackerel; average estimates
Munk *et al.*, 1986	—	2	—	Atlantic herring; 1984 yr-class, 2nd cohort

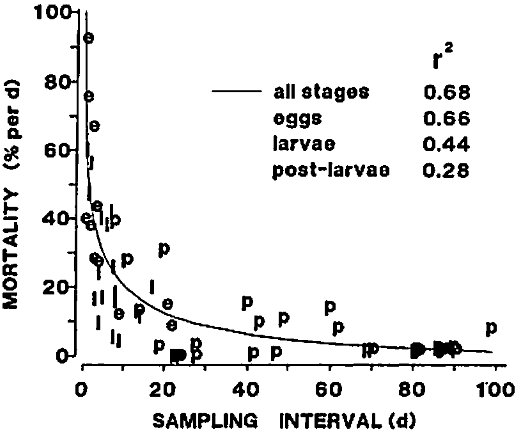

Figure 12.2. The relationship between estimated daily mortality (%/d) and the time interval over which the estimate was derived for marine fish eggs (e), larvae (l), and post larvae (p) from the sources listed in Table 12.1.

tality estimated for a series of increasing sampling intervals (maximum 18 d) using the exponential decay model and the interval between the abundance estimates used to calculate z (instantaneous mortality) and M for various theoretical changes in z over time. Not surprisingly, the relationship is flat and linear when z is constant and therefore independent of the sampling interval. When z declines linearly with time, there is a monotonic decay in apparent mortality with the interval. However, when z declines exponentially with time, so does the relationship between apparent mortality and the interval, in a manner similar to the empirically defined relationship (Figure 12.2). The addition of an immigration term to the population model (Figure 12.3) results in a more rapid decay in the estimated mortality with increasing sampling intervals, a decay rate that further approaches the relationship in Figure 12.2. However, it can be easily shown that the estimated decay in a population over time using z (estimated at the end of a given interval) is only correct when z is constant. The estimated decay in population size increasingly deviates from the actual decay when z declines either linearly or exponentially with time and as the interval used to estimate z increases.

Table 12.2. Regression statistics for the relationship between the arcsin square-root of daily mortality in all stages, eggs, larvae, and postlarvae of marine fish species (see Table 12.1 and Figure 12.2.), and the natural logarithm of the interval between sampling surveys used to derive the mortality estimates. All relationships are significant ($p < 0.01$).

Development stage	n	Slope	Intercept	r^2
All stages	58	− 9.01066	47.47616	0.678
Eggs	11	−12.32164	54.54774	0.660
Larvae	17	−10.33155	46.63857	0.441
Postlarvae	30	− 6.70334	39.28084	0.278

Mortality and sampling intervals: Possible explanations

Based on the outcome of these simulations, the empirical relationship (Figure 12.2) has at least two possible explanations. First, daily mortality (Table 12.1) was poorly described by a simple exponential decay model, and a two-parameter model is required to account for mortality during the earliest developmental period (e.g., size- or age-dependent mortality; see, for example, Peterson and Wroblewski, 1984). If true, a simple exponential model fitted to the same data would yield accurate estimates only when the data were obtained over very short intervals concentrated near the beginning of the developmental stage affected. Longer intervals would yield biased mortality estimates in the absence of constant mortality. Second, a simple exponential decay model is representative of mortality, but the abundance variation is unrelated to mortality, and the effect on apparent mortality increases with the measurement interval. Variation in immigration and/or emigration rates, size-(age-) dependent changes in catchability (gear-related), and changes in contagiousness would all produce such an effect. McGurk (1986) touched on the potential for bias in mortality estimates caused by changes in larval patchiness with time, but

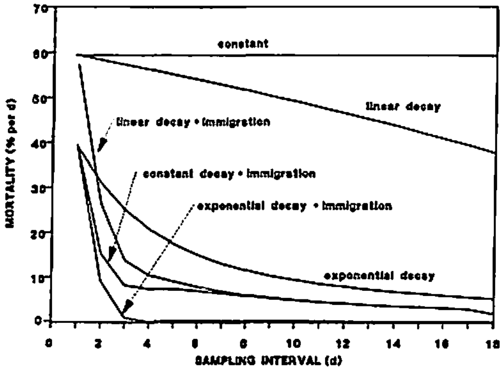

Figure 12.3. The expected relationship between daily mortality estimated using the simple exponential decay model at increasing sampling intervals when actual mortality is constant or decays linearly or exponentially with and without an immigration term.

he invoked predation to explain the relationship between patchiness and mortality. Our analysis suggests that temporal scale effects related to sampling design alone will artificially bias the mortality estimates.

The effect of increasing population losses through either increased sampler avoidance or emigration (diffusion and/or advection) would not account for the relationship and may be demonstrated by the relationship between larval and postlarval herring mortality estimates and sampling intervals taken from Graham and Townsend (1985). Their data show that the mortality estimates of several larval herring cohorts increased linearly with increasing survey intervals (Figure 12.4) and indicates that either time- (age- or size-) dependent sampler avoidance or advective losses were responsible. Graham and Townsend (1985) assumed that advective losses were insignificant, whereas the relationship in Figure 12.4 indicates that such losses may have significantly biased the mortality estimates.

Mortality and sampling intervals: Possible implications

The effect of eliminating mortality-independent population losses and gains on the relationship between daily mortality and sampling interval is well illustrated by the daily mortality estimates provided by Frank and Leggett (1986, and unpublished data). In their study of mortality in capelin larvae in large, in situ enclosures, the biasing effects of diffusion, advection, and larval production were eliminated. Their data show that there is a very slight decline in the mortality rate of larvae in different rearing conditions when evaluated against increasing sampling intervals (Figure 12.5). This relationship is consistent with the idea that z is constant (Figure 12.3).

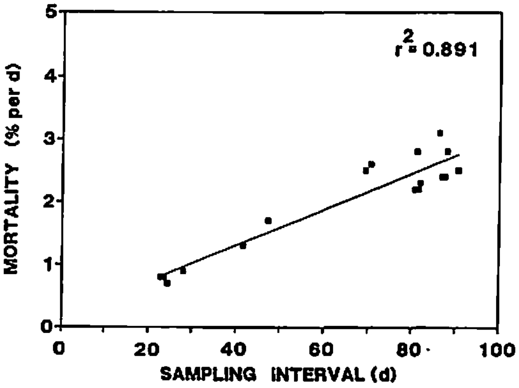

Figure 12.4. The relationship between larval and post larval herring mortality and the length of the sampling interval calculated from Graham and Townsend (1985).

Taggart and Leggett (1987b) determined 40 different field estimates of short-term daily mortality in sequentially emerging populations (here defined as cohorts) of capelin larvae. There was no relationship be-

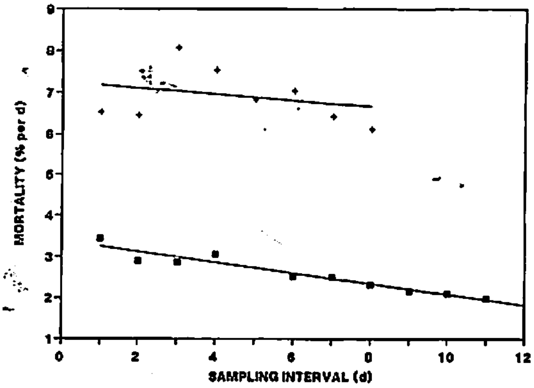

Figure 12.5. The relationship between mortality in enclosed larval capelin populations and the length of sampling intervals calculated from Frank and Leggett (1986, and unpublished data).

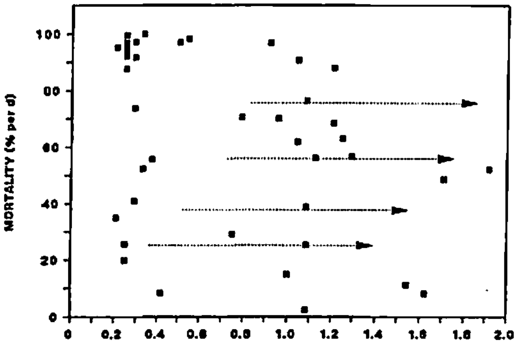

Figure 12.6. The relationship between 40 different field estimates of larval capelin mortality and the length of sampling intervals calculated from Taggart and Leggett (1987c). Arrows depict the hypothetical mortality trajectory among different cohorts if mortality within cohorts was constant.

tween the mortality estimate and the duration of the sampling interval (Figure 12.6). However, immigration (hatching and emergence) and emigration (through advection) were considered when calculating the estimates. Immigration alone contributed considerable bias to the mortality estimates. If mortality was constant within any given cohort, but varied among cohorts as in Figure 12.5, then the hypothesis that mortality was more or less constant within cohorts but varied among cohorts is feasible (Figure 12.6). This implies that those cohorts with the low mortality rates will persist longer relative to those with high mortality rates. Such a suggestion is consistent with Lambert's (1984) hypothesis that relatively few of many cohorts may be responsible for year-class strength.

The relationships presented here, and the demonstrated influence of immigration and advection on mortality estimates (Taggart and Leggett, 1987b), indicate that mortality estimates are easily biased by assumptions concerning (i) constant production or immigration and emigration, (ii) the spatial distribution of the target population, and (iii) the validity of the simple exponential decay model. Failure to consider these constraints can lead to biases in mortality estimates that seemingly accelerate with time. McGurk (1989) has reached a similar conclusion and has called for the development of an analytical advection-diffusion-mortality model that incorporates a time-varying z.

Predator-Prey Relationships: A Simulation Example

Some of the leading hypotheses to explain recruitment variation deal with starvation and predation. Each of these can be physically mediated. Recently, arguments have been made supporting the predation hypothesis over the food limitation hypothesis due to lack of supporting evidence (e.g., Sissenwine, 1984). Therefore, one might expect to find that larval mortality or abundance and predator abundance are correlated in some way. In fact, such arguments can form the basis of support for the predation hypothesis over the starvation hypothesis. The implication is that predation exerts a major effect on mortality, and therefore recruitment. Predation may be affected by the condition of the larvae. However, the scales of predation and starvation processes and the scales of sampling can easily distort the true nature of relationships. This point was made by Taggart and Leggett (1987c) when they warned that misleading inferences can be drawn from data that are collected near instantaneously and used to test competing hypotheses that pertain to near-instantaneous processes (predation) and to those whose effect is cumulative over a relatively longer period (starvation).

To illustrate this phenomenon, we simulated a larval population simultaneously purposely subjected to high daily mortality directly related to food abundance and relatively low predation mortality directly related to predator abundance. In the model, predator and food abundances (Figure 12.7) were drawn randomly from rectangular distributions (predator mean = 0.333; food mean = 0.5). Predator-(P) related larval mortality operated instantaneously at time t(d) and was directly proportional to predator abundance at t. Food-(F) related mortality at t was proportional to the average

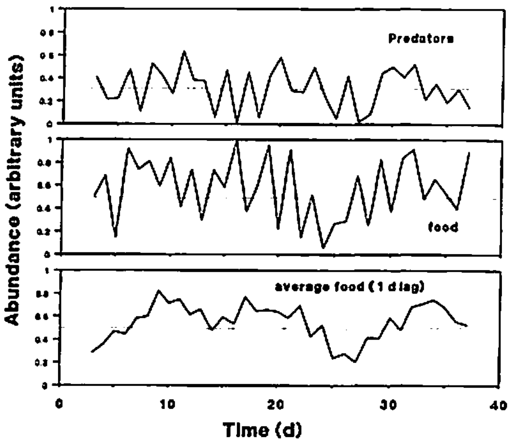

Figure 12.7. Simulation trial of daily predator and daily food abundance and 3 d averaged food abundance lagged by 1 d (average abundances are indicated by the dotted line). The predator and the lagged average food abundance estimates were used to drive the population decay (predator and food related mortality) illustrated in Figure 12.8.

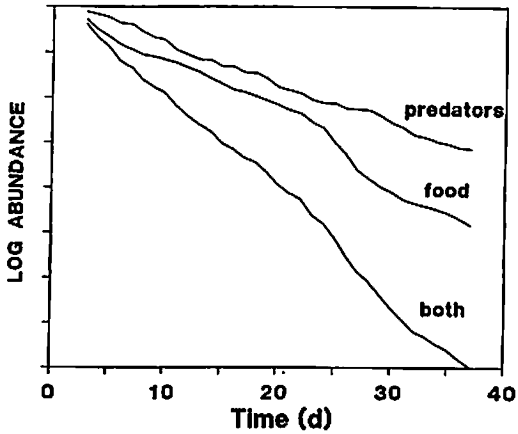

Figure 12.8. Simulation trial of larval population decay resulting from daily predator related mortality only, lagged average food related mortality only (see Figure 12.7), and by both mortality factors.

food abundance over the previous three intervals $F_{ta} = [(F_{t-3} + F_{t-2} + F_{t-1})/3]$ to simulate starvation (Figure 12.7).

The effect of these two processes on the simulated population yielded time-dependent exponential decay in numbers of larvae and illustrated the greater impact of food limitation relative to predator-induced mortality (Figure 12.8). The population surviving both mortality processes was used to determine the daily mortality estimates, which were subsequently compared with the instantaneously "sampled" predator (P_t) and food (F_t) abundances. Perhaps not surprisingly, there was no significant relation between mortality and instantaneous measures of food abundance (Figure 12.9). In contrast, there was a significant relationship between mortality and predator abundance (Figure 12.10). If F_{ta}, the lagged average food abundance (not easily measured in the field), is used as the independent variable, a significant relationship with mortality is evident (Figure 12.11). Replicate trials with this model show these results to be repeatable (Figure 12.12).

In spite of the simplicity of the model and the imbedded assumptions, it serves to illustrate that the analysis of instantaneous state measures, directly related to rate processes that have distinctly different scales of operation, can lead to misleading interpretations and conclusions. Frequently, the importance of a given factor is assigned on the basis of the significance level of the chosen statistic. For example, Taggart and Leggett (1987c) were guided by this erroneous principle and assigned more significance to predator abundance than was warranted. Nevertheless, they viewed such interpretations with caution.

Predator-Prey Relationships: A Field Example

Several field studies have suggested predator-dominated control of larval fish populations based on inverse correlations between predator and prey abundances (see review in Frank and Leggett, 1985). However, such inverse correlations are often suspect due to failure to consider the influence of the physical structure and dynamics of the environment where the predator and prey populations are found (Frank and Leggett, 1985).

Several potential predators of marine fish larvae are confined to subpycnocline waters and occur in large quantities in the

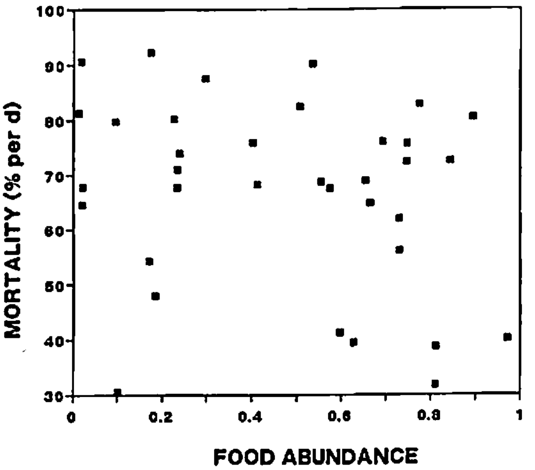

Figure 12.9. The relationship between simulated mortality calculated daily from the population ("both") illustrated in Figure 12.8 and "food" illustrated in Figure 12.7.

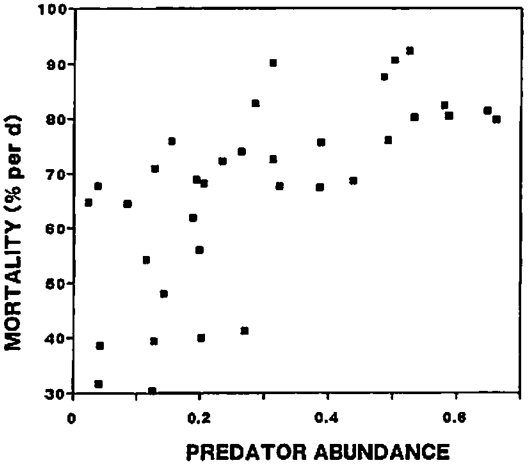

Figure 12.10. The relationship between simulated mortality calculated daily from the population ("both") illustrated in Figure 12.8 and "predators" illustrated in Figure 12.7.

nearshore during the upwelling of cold water masses. Upwelling favorable winds (SW) are the prevailing winds in summer in eastern Newfoundland, and large quantities of chaetognaths, jellyfish, and ctenophores (known from laboratory and field studies to consume significant quantities of fish larvae; e.g., deLafontaine and Leggett, 1988) occur in the nearshore during the course of wind-driven upwelling. Their occurrence and daily variation in abundance is a function of the wind field, with greatest abundances occurring during SW winds (Frank and Leggett, 1982a; 1985). Capelin spawning occurs on beaches in this area during June, and the mass emergence of larvae from the beach sediments is timed to periods of warm surface water mass intrusions driven by NE winds (Frank and Leggett, 1981a; Taggart and Leggett, 1987a). Winds from the NE sector are associated with low pressure systems passing across eastern Newfoundland with an approximate 5 d periodicity. Warm water intrusions in the nearshore are coupled with increased wave turbulence, and together they facilitate the emergence of capelin larvae from the beach sediments.

Warm surface waters are characterized by a prey size spectrum in the optimum size range for first feeding larvae and a depauperate predator community (Frank and Leggett, 1986). Conversely, cold water upwelling in the nearshore during SW winds inhibits larval emergence through a temperature-related reduction in larval activity and the absence of wave turbulence. The survival potential of larvae would be considerably lower in the upwelling water mass due to an unfavorably large prey size spectrum coupled with the abundant predator suite. Selective occupation of the warm surface water mass through episodic mass emergences greatly improves the growth and survival potential of capelin larvae. The characteristic fauna associated with each of these water masses produces an asynchronous temporal pattern of occurrence in the nearshore resembling a coupled predator/prey oscillation that has no biological basis whatsoever (Frank and Leggett, 1985). The actual relationship between the larvae, their predators, and their prey was identified only by resolving the biological processes at and below the scales of the physically driven hydrological processes. High-resolution approaches of this kind can reveal fairly precise larval fish, predator, and zooplankton community structures that are clearly related to

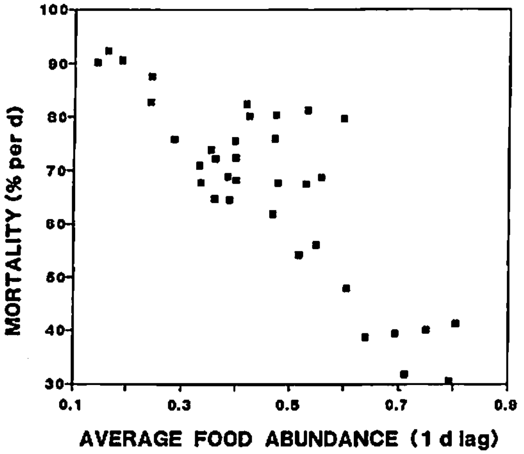

Figure 12.11. The relationship between simulated mortality calculated daily from the population ("both") illustrated in Figure 12.8 and "average food (1 d lag)" illustrated in Figure 12.7.

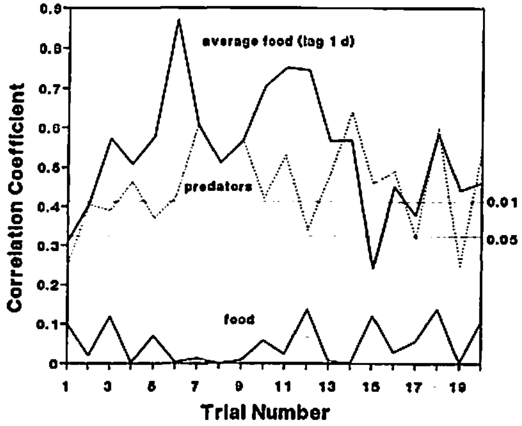

Figure 12.12. Variation in the correlation coefficients between daily mortality and food, predators, and lagged average food. Each series was calculated from 20 different trials (60 trials in all). Each trial was similar to those illustrated in Figures 12.7 through 12.11. Significance levels (p = 0.01 and 0.05) are noted.

the physical characteristics of dynamic water masses (Taggart *et al.*, 1989).

Scaling Upward to Large Marine Ecosystems

Capelin spawn on beaches having a similar orientation throughout their distributional range in eastern Newfoundland (hundreds of km), and the wind field driving the nearshore water mass dynamics occurs on an equivalent or larger scale. Therefore, any one spawning beach can be used to monitor the growth and survival patterns of the early life stages of capelin. This has, in fact, been confirmed and has culminated in a robust recruitment model for capelin (Leggett *et al.*, 1983, 1984). The physical/biological coupling observed at different trophic levels in eastern Newfoundland has also led to accurate predictions of both net-fouling conditions and catch variation in the inshore cod fishery (Taggart and Frank, 1987), as well as the distribution of humpback whales in eastern Newfoundland (Whitehead and Carscadden, 1985). A similar approach was taken to the problem of predicting catch variation in cod along the north shore of the Gulf of St. Lawrence (Rose and Leggett, 1988), where variation in onshore movements and inshore catch rates of cod are associated with wind-driven upwelling along the coast.

Nikolsky (1965) stated that "every adaptation is at the same time a limitation" to an organism, and this philosophy underlies the capelin recruitment model alluded to previously. When the interval between onshore winds exceeds the long-term average, thereby prolonging the residence of capelin larvae in the beach gravel, the energy reserves of the larvae are depleted, their physical condition is reduced, and postemergent swimming ability is seriously impaired (Frank and Leggett, 1981a, 1982b). The conclusion was that the duration of beach residence, itself a direct function of the interval between meteorological events that trigger emergence, was a major regulator of early larval survival of capelin. In addition, the capelin recruitment model required knowing when median hatching occurred each year to define the relevant period to assess the wind field. This was possible only with the knowledge of spawning times and locations, and incubation temperatures in the beach gravel. Empirical models were then devised for the latter by using the appropriate meteorological and hydrographic factors as independent variables (Frank and Leggett, 1981b). The recruitment model for the Northwest Atlantic Fisheries Organization Subarea 2J3K stock explained greater than 70% of the interannual variation in the abundance of two-year-old capelin by incorporating the effects of wind and water temperature (Leggett *et al.*, 1983), a remarkable result considering that the study began in an isolated embayment in Conception Bay, Newfoundland. Collectively, these findings suggested that abiotic factors operating at critical periods in larval development may be more important than spawning stock biomass as regulators of year-class strength. Critical periods must be identified and quantified at time scales relevant to individual larvae if reliable forecasting of year class strength is to be achieved, and the large spatial scale of the effects suggests that the space scale of individual larvae is of less importance in such analyses. This implies that long-term averages (e.g., annual) of abiotic factors will not be sufficient to explain variations in biological processes that are event-driven.

Analysis of age-composition data has revealed parallelism in strong year classes in the beach-spawning stock of capelin and a separate, offshore stock of capelin on the Southeast Shoal of the Grand Bank, some 350 km from the nearest spawning beach and a region where capelin annually spawn during June/July on the bottom at depths averaging 50 m (Carscadden, 1983). Recent field studies have been based on the working hypothesis that the same environmental factors operating during the immediate post hatching period are responsible for strong year classes in both stocks of capelin (Frank and Carscadden, 1989). During field studies in 1986 on the Southeast Shoal, the dominant cohort of larval capelin was produced during the passage of a major meteorological low pressure system (tropical storm Charley) that coincided with sharp increases in bottom temperature and currents over the spawning grounds. This sequence of changes in the water column structure appeared to reflect an episode of destratification due to in situ mixing. The passage of the tropical storm near the study area was not an unusual event considering that the annual occurrence of tropical cyclones during the period 1969–1986 was between three and 12 (Neumann *et al.*, 1978). Between one and five of these storms pass over the southern Grand Bank annually, primarily during August and September of the 18-year period, and August is the principal hatching period for capelin in this region (Frank and Carscadden, 1989). It was hypothesized that emergence, timed to periods of destratification, is beneficial to larval survival due to the rapid ascent of larvae from the bottom waters. During the initial stages of larval drift associated with the passage of storms the normally high predator densities that occur during stratified conditions are diluted, and feeding conditions are enhanced (Frank and Carscadden, 1989). Once again it appears that the temporal scale of variability is dominant, and storms serve an important role in this respect, acting to obliterate any predispersal spatial variability and to establish a common starting condition (both in terms of the physical and biological state of the water mass) in the early stages of larval dispersal in capelin.

Species whose life-stage transitions depend on such temporal events during the early life history should be more amenable to development of robust recruitment models. Recent examples in the literature support this view. Red drum *(Sciaenops ocellatus)* spawning coincides with the hurricane season in the Gulf of Mexico, with the result that the timing of hurricanes can influence the numbers and/or survival of juvenile red drum advected into nearshore nursery areas from offshore spawning sites (Matlock, 1987). The above-average, nearshore-directed larval transport to nutrient-rich estuarine nurseries that occurs during hurricanes appears to result in strong year classes of red drum (Matlock, 1987). Atlantic menhaden *(Brevoortia tyrannus)* also appear to have evolved a reproductive strategy to optimize the survival and shoreward transport of eggs and larvae. Schooling adults located along the western edge of the Gulf

Stream and south of Cape Hatteras time their offshore spawning to the occurrence of winter storms (Checkley *et al.*, 1988). These winter storms result in upwelling induced spawning and buoyancy-driven shoreward transport of menhaden eggs and larvae to estuarine nursery areas. It has been hypothesized that variation in these physical conditions may explain interannual variation in menhaden recruitment and, possibly, recruitment in other species that spawn shoreward of warm boundary currents during winter months (Checkley *et al.*, 1988). Finally, Myers and Drinkwater (1989) have shown that warm-core ring activity has the potential of reducing recruitment in 15 of 17 groundfish stocks (six species, including cod, pollock, redfish, yellowtail flounder, and silver hake) spawning on the continental shelf from the mid-Atlantic Bight to the Grand Bank.

Summary

We hope that this chapter will serve a useful purpose in warning researchers of the various pitfalls of inappropriate scaling when dealing with estimates of mortality during the early life of fishes. Sampling limitation, whether avoidable or not, underlies our collective inability to decide among several competing hypotheses concerning the growth and mortality of fishes. The implications of inappropriate scaling and the actual errors that might be incurred with regard to recruitment predictions for species in large marine ecosystems remains to be explored explicitly.

We recognize that there are several limitations to what we have presented and that our chapter can be criticized on several grounds. The literature used to support our arguments is not as broad as is perhaps possible. For example, McGurk (1989) has examined similar scale-related problems in the early life-stage dynamics of Pacific herring (*Clupea harengus*) from a different perspective, but he reached a strikingly similar conclusion (although we were unable to extract the simple measures and parameters to incorporate into our analyses.) It was also necessary to develop the relationship in Figure 12.2 by combining data for different species and different studies. The argument proposed would have been much stronger if examined on a species-by-species basis, but the data are limited. With more data, relationships such as that in Figure 12.4 (herring) may prove their utility and allow a prediction of biases in mortality estimates.

The collective experiences of many researchers (some cited herein) attempting to estimate in situ mortality and abundance has provoked some new approaches to recruitment determination. In the past, the majority of research into recruitment problems has focused almost exclusively on determining the abundance and mortality of eggs and larvae, of which the overwhelming majority never recruit to the fishery. We propose that the new insights needed to predict recruitment variations will come from the alternative approaches of studying the phenological, genetic, phenotypic, biochemical, and physiological traits of those individuals that survive and eventually recruit. This new emphasis on the characteristics of the survivors represents a unique departure from traditional thinking. The opportunity to embark in this new direction now exists as part of a Canadian National Sciences of Engineering Research Council (NSERC) multi-institutional and interdisciplinary programme called the Ocean Production Enhancement Network (OPEN).

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BOOK REVIEW

LARGE MARINE ECOSYSTEMS: PATTERNS, PROCESSES AND YIELDS

K. Sherman, L.M. Alexander, and B.D. Gold

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This book is the third in a series of AAAS volumes resulting from symposia on large marine ecosystems. The first two were published in 1986 and 1989 and both were edited by Sherman and Alexander.

Large marine ecosystems (LMEs) are defined by Sherman and Gold in the introduction as "relatively large regions of the global EEZs, generally on the order of $> 200,000\ k^2$, characterized by unique bathymetry, hydrography, and productivity, within which marine populations have adopted reproductive, growth and feeding strategies." The objective of the three AAAS symposia and the corresponding volumes that resulted was to make the case for the adoption of LMEs as regional units for the conservation and management of marine resources.

The present volume is divided into three sections. The first (Perturbations and Yields of Large Marine Ecosystems) presents case studies of the state of knowledge of six LMEs ranging from the high polar Weddell Sea to the tropical Banda Sea. The second presents a series of chapters on the mysterious new concept of biodynamics, an approach to the study of the sea which integrates physics and biology at meaningful scales. I think what all of this means is an attempt to link the different time and space scales upon which causal physical and resultant biological processes occur. Certainly, mathematics and mathematical modeling will play an extremely important role in this development. The final section (Theory and Management of Large Marine Ecosystems) takes a number of holistic views of LMEs in terms of processes and patterns, and yields and management.

In my view, three of the 18 chapters really stand out as being first-class contributions and of particular interest to the natural resource modeler. All three chapters deal with the issue of scale. Christopher Taggart and Kenneth Frank (Chapter 12, Perspectives on Larval Fish Ecology and Recruitment Processes: Probing the Scales of Relationships) discuss reasons for the present inability of the fisheries scientists to robustly predict recruitment variation in both "closed" freshwater and more "open" marine ecosystems. Their point is that seldom do the scales (time-space) of experiment match those at which recruitment processes occur. They emphasize a reorientation of our focus on characteristics of survivors of critical early-life history stages rather than on trying to quantify mortality.

Robert Ricklefs (Chapter 13, Scaling Patterns and Process in Marine Ecosystems) defines scale as "the characteristic distance or time associated with variation in natural systems" and proceeds to give a fascinating exposition of why the problem of appropriate scale is so important to understanding the dynamics of (marine) ecosystems. He shows how scale changes as signals propagate through systems, particularly as they move from physical to biological components of a system. He goes on to postulate that linkages of system patterns and processes that occur on different scales, once we discover them, may help define ecosystems boundaries.

Finally, Simon Levin (Chapter 14, Physical and Biological Scales and the Modeling of Predator-Prey Interactions in Large Marine Ecosystems) discusses why he thinks that modeling provides the necessary linkages between natural experiments conducted over relatively small scales and large ecosystem processes. He goes on to challenge modelers to integrate physics and biology when he states that "a modeling framework is strongest when it can relate phenomena on different scales, providing 'mechanistic' bases underlying observed patterns." He proposes a protocol of sequence of steps for developing an understanding of the complex dynamics of large marine ecosystems—(1) statistical analysis of observed patterns, (2) construction of competing models of critical processes, (3) investigation of competing models through experimental and theoretical studies of component systems, and (4) integration of validated component models.

The above-mentioned three chapters are jewels and make this book a worthwhile reading experience for anyone interested in the dynamics of marine ecosystems. In my view, the remaining 15 chapters make a well-padded carrying case for these jewels.

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