ECOPHYSIOLOGY OF MARINE FISH RECRUITMENT: A CONCEPTUAL FRAMEWORK FOR UNDERSTANDING INTERANNUAL VARIABILITY

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ABSTRACT

Present data and our application of logic do not permit confident rejection of the null hypothesis: Interannual variation in recruitment of marine fishes (typified by certain flatfishes) is independent of ecophysiological factors. Our inability to reject this hypothesis reflects not its likely validity, but rather a lack of conceptual structure and appropriate data for realistic evaluation of alternative hypotheses. Therefore, in this paper, we set aside as presently intractable the problem of understanding in any generalizable way the specific effects of environment on interannual variation in marine fish recruitment. Instead, we return to a conceptual scheme first proposed almost 50 years ago by F.E.J. Fry for considering effects of environmental factors on the physiology of fishes. We first extend this scheme to population-level responses, including recruitment, and then even further, to community/ecosystem-level responses. Fry supposed that all of environment can be resolved into five classes of physiological effects—controlling (which set the pace of metabolism), limiting (which constrain maximum metabolism), lethal (which completely interdict metabolism), masking (which increase obligatory metabolic work), and directive (which release and unload metabolism by guiding enviroregulatory responses). We suggest that corresponding effects can be recognized at the levels both of population and community/ecosystem. The key analogy is that environment operates on individuals through metabolism, on populations through recruitment, and on communities/ecosystems through abiotic and biotic diversification. In the context of marine-fish populations, we propose that scope for population increase is the difference between maximum and maintenance recruitment to the spawning stock. Maintenance recruitment is the product of critical spawner density and spawner mortality rate; this product varies with environment as the resultant of controlling effects on the metabolism of individuals, and is increased by loading due to masking factors—e.g., predation—that increase one or both multiplicands. Maximum recruitment is limited by deficiencies of resources, primarily food, but also, potentially, by low spawner density. Population-level lethal factors cause extinction, by reducing population scope to sub-zero values for a time exceeding the generation interval. Directive factors distribute the population in space and time, influencing not only habitat use and zoogeographic range, but also providing context for genetic adaptation and speciation. Exploration of this conceptual scheme from the perspective of flatfish life-history strategies and population dynamics, leads to several testable ecophysiological hypotheses about recruitment.

1. INTRODUCTION

For the past 80 years, fisheries biologists have debated vigorously the causes of interannual variability in recruitment of marine fish stocks (for overviews of the debate, see May, 1984; Rothschild, 1986; Sinclair, 1988; MacCall, 1990; Hilborn & Walters, 1992). Some would contend that we are not much closer now than in Hjort's (1914) day, to resolving the issue of what regulates/assails recruitment—density-dependent or density-independent factors, or both. Perhaps, the problem is at least partly attributable to

a lack of proper perspective. As fishery scientists, we have tried to resolve the complexities of recruitment variation by an examination of evidence that is mostly circumstantial, frequently controversial, and almost always incomplete. We have tried, without much success, to distinguish between departures from the normal stock-recruit relationship and the system's correction for a previous departure. We have found proximal solutions to ultimate problems; then, we are dismayed and discouraged when those solutions fail the test of generalization. Hilborn & Walters (1992) have reminded us, that we 'must think about stock-

recruitment relationships rather than average curves'. We already knew that, but it is difficult advice to follow—because it is at odds with our experiential perspective.

In this paper, we offer, if not the proper perspective, then at least one that most students of the recruitment problem will find novel: We propose an elaboration and extension of F.E.J. Fry's (1947) 'physiological classification of environment' to population (and higher level) processes, among which recruitment is pivotal.

More explicitly, the objective of this paper is to probe the hypothesis that ecophysiological mechanisms do (are necessary to) or could (are sufficient to) account for the interannual variation regularly observed in recruitment of marine fishes such as flatfishes. Our approaches to resolution of the problem are 1. to review the ecophysiological mechanisms that logically underlie recruitment processes, and 2. to suggest and explore analogies between environmental responses of individuals and those of the population they comprise.

2. THE PROBLEM OF RECRUITMENT VARIABILITY

What, exactly, is the problem? In our view, the problem is not that recruitment is highly variable, but that the variability seems largely inexplicable, if not simply random. A case in point is that of the North Sea plaice (*Pleuronectes platessa*), for which we have a good record, extending back over 30 years (Fig. 1). In most of these years, recruitment of transformed plaice to the nursery grounds, predominately at Wadden Sea on the Dutch coast, varied between 300 x 10^6 and 700 x 10^6 individuals, but, in 1963 and 1985, plaice

recruitment reached values twice at high as 'normal'. Why? The most popular hypothesis seems to be that cold winters favour plaice recruitment to the Wadden Sea nursery, and that the critical Jan-Feb period both in 1963 and in 1985 was especially cold. Perhaps so—but, what about Jan-Feb of 1981, when plaice recruitment reached its second largest value ever? Water temperatures at Den Helder during that period averaged a relatively balmy 3.5°C (Fig. 2). To date, the 'why' of the 1981 value—and, thus, the 'how' of plaice recruitment, in general—remains an enigma. Recruitment in the stocks of most other marine fishes is even more obscure.

2.1. SOURCES OF CONFUSION ABOUT THE PROBLEM

In thinking about the issue of interannual variability of recruitment, we decided that at least part of the problem is the question of whether it is the strong or weak year classes that are 'normal'. The preponderance of weak year classes does not necessarily mean that such year classes are normal, except in the sense of typical as opposed to natural. We believe this issue is more than a matter of semantics, because if weak year classes are normal then we need to look for mechanisms by which the normal constraints are relaxed to permit an abnormally strong year class. On the other hand, if strong year classes are natural, then we must ask what factors usually assail eggs and larval fishes to produce the relatively small values of recruitment that are so typical.

In examining data bases for evidence about the normal state of things, it quickly becomes apparent that at least part of the uncertainty about what regu-
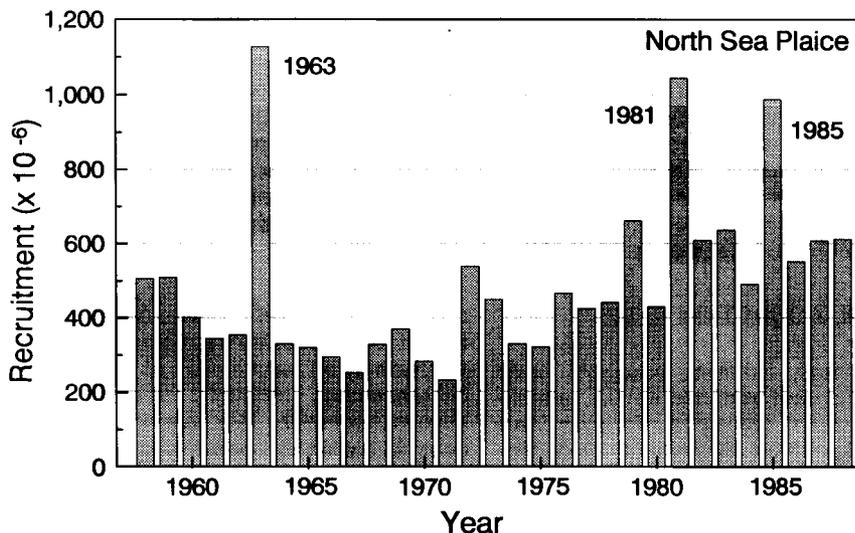

Fig. 1. Recruitment of North Sea plaice at age 1 during the years 1958-1988. Data after Rijnsdorp *et al.* (1991).
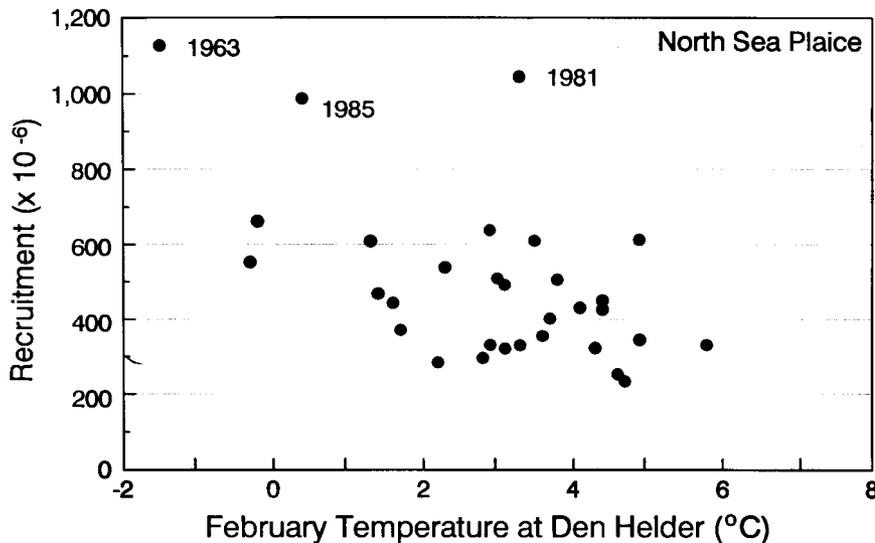
Fig. 2. Recruitment of North Sea plaice during the years 1958-1988 *versus* February water temperature at Den Helder, the Netherlands. Water temperature data from Van der Hoeven (1982) and NIOZ (unpublished). Recruitment data from Rijnsdorp *et al.* (1991).

lates recruitment is traceable to a dearth of relevant information, not only about the fish themselves, but also about the environment in which they live. Even for such well-studied species as plaice, we lack sufficient data on synoptic distributions of fish and environment with which even to formulate interesting hypotheses, much less test them. Yes, we have a 30+-year-long record of apparent recruitment of juvenile plaice to the Wadden Sea, and we have extensive concurrent data on temperature at various locations in the North Sea (*e.g.* Noordhinder and Den Helder). But, what of synoptic data on temperature *gradients*, dissolved oxygen profiles, the distribution of potential predators and competitors, *etc.*?

There is a tendency in all of ecology (not just fisheries) to believe that measurement of one or a few environmental variables (those most easily measured) can serve to characterize all of environment. To the contrary, it might be best in the general case to treat such measurements as class variables or labels—until we can be sure what and how components of environment are important to the fish. Such information is more effectively gleaned from conceptually relevant and well planned experiments—either in lab or field—than from exhaustive statistical analysis of survey data.

Added to the above 'sources of confusion' are some others that may be less substantive—but are no less real. First, there is a lack of uniformity in the way recruitment is defined and measured. Some authors use the word 'recruitment' to mean the processes whereby a specific cohort arrives at a specific time (age) or place, or enters the fishery. But those of us who speak of recruitment variability are using the word more loosely, to mean the outcome of recruitment processes, *i.e.* year-class or cohort strength. It is important to recognize that recruitment in this latter sense might be highly variable, yet devolve upon processes that are completely deterministic.

Second, investigators of the recruitment problem have not always been careful to distinguish between total recruitment and recruitment per unit spawning stock or per unit habitat (per year). Thus, a one-to-one relationship between total recruitment and size of spawning stock would imply strict *in*dependence between recruitment and spawner density (*i.e.*, that recruitment per unit spawning stock is constant). If condition or age structure, and, thus average fecundity, of the spawning stock depends on its density, the situation becomes more complex—and even more liable to confusion.

In this paper, we will use the word 'recruitment' to mean the outcome or result of recruitment processes; moreover, 'recruitment' without an appropriate qualifier will mean *total* recruitment (per year), in synonymy with year-class strength and total number of recruits.

2.2. TEMPORAL AND SPATIAL BOTTLENECKS TO RECRUITMENT: THE CRUX OF THE PROBLEM

The recruitment chain can be no stronger than its weakest temporal or spatial link. This is to say that recruitment must be a function of sequential events, each involving several essential elements with properly complementary spatial interrelations: Histories of
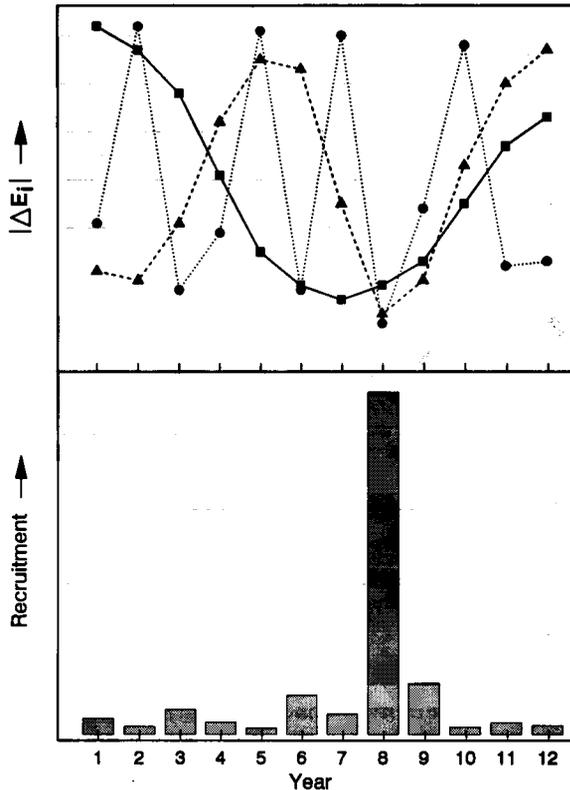
Fig. 3. Recruitment of some hypothetical fish under the 'rogue wave' model (see text). The upper panel shows time series of three quasi-periodic environmental factors, each as absolute deviations from the optimum value; the lower panel shows the corresponding time series of recruitment.
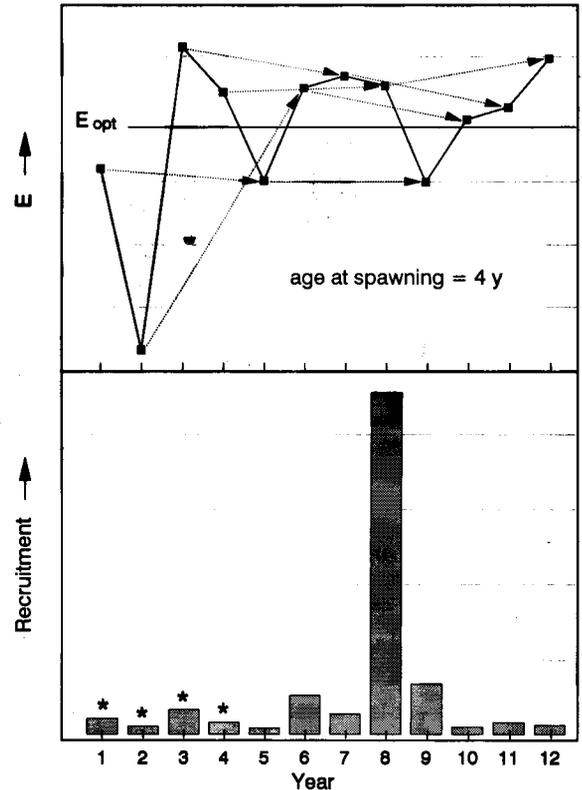
Fig. 4. Recruitment of some hypothetical fish under the 'irreversible nongenetic adaptation' model (see text). The upper panel shows the time series of some environmental factor relative to its optimum, and relative to its values 4 years earlier (arrows); the lower panel shows the corresponding time series of recruitment (with asterisks marking early years for which predictions cannot be made under this model).

spawning-stock and environment must converge in time and space in a small subset of ways (out of the infinitely many possible) for spawning and hatching of the new year class to be successful. For that success to be sustained to the point at which the new year class is deemed to have been 'recruited', there logically must be a continued succession of the proper time-space series of suitable abiotic environment (*e.g.*, temperature, dissolved oxygen, salinity, light/turbidity, orienting and transporting currents, *etc.*), sufficient quantity and quality of food, and tolerable levels of predation. Thus, recruitment must be viewed as some maximum potential value (perhaps, aggregate fecundity of the spawning stock, or, better, the maximum carrying capacity of the limiting habitat for pre-recruits) multiplied by many proportions or probabilities, only one of which needs be zero in order for the year class to fail completely! However, if the stock consists of independent sub-stocks, the year classes of all sub-stocks would have to fail completely in order for stock-wise recruitment to be zero for that year. This last consideration suggests a hypothesis to

account for the observation that year classes of some flatfish stocks (such as North Sea plaice; see Fig. 1) rarely if ever fail completely: Existence of an apparent recruitment 'floor' indicates that the stock consists of multiple sub-stocks, upon which recruitment processes operate independently.

Other contributors to this symposium (Bailey, 1994; Gibson, 1994; Leggett & DeBlois, 1994; Rijnsdorp, 1994; Van der Veer *et al.*, 1994) have discussed the relative roles of variation in growth and mortality as causal agents of recruitment variation. Here, it is appropriate to add that size of individual fish at recruitment can be considered a *sum* of mostly positive energy or biomass increments attributable to pre-recruitment growth; whereas, survival to recruitment is a *product* of the probabilities of surviving each time-increment prior to recruitment. Thus, it would seem to us that survival, not growth, is the emergent response of individuals that is proximal to their recruitment;

Erratum: In Fig. 4, the line labeled '*Eopt*' is positioned incorrectly. The correct position is at an elevation just below the year-6 value of E (about 5 mm higher than shown).

and, in this context, that growth *per se* is important primarily in its effect on probability of survival to recruitment. We hasten to add that extreme interannual variation in growth rate of a given age class—even with no variation in mortality rate—logically could cause a wave in subsequent recruitment to a particular size class (but, of course, no variation in recruitment to a subsequent age class). Still, we believe that times and places of high mortality constitute much more serious 'bottlenecks' to recruitment than do times and places of low or even zero growth, although the distinction between ultimate demographic effects of differential mortality *versus* growth rates may be less evident for early life stages, such as first-feeding larvae (Lasker, 1978; Houde, 1989).

3. SIMULATION APPROACHES TO THE RECRUITMENT PROBLEM

Simulation modelling offers an efficient way to probe for potential solutions to complex problems. However, it is important to keep in mind that reasonableness, or even realism, of simulation results can reveal only the sufficiency of a hypothesis, not its necessity. Once simulation suggests what *might be* (sufficiency), then only critical experiments can indicate what *is* (necessity). To demonstrate the use of simulation modelling to screen hypotheses about recruitment, we have erected and explored two that seem to make heuristic sense in that each can generate the kind (pattern) of interannual variation observed in flatfish recruitment.

The **rogue-wave hypothesis** was suggested by analogy with the well-known phenomenon in which ocean waves with differing periods, breaking on a shore, occasionally reach their peaks synchronously, thus generating a wave with unusually large amplitude. In the context of recruitment, the hypothesis is that the various environmental factors affecting recruitment vary in periodic or quasi-periodic fashion, but with differing periods; when these environmental cycles come into favourable harmony, a very large year class is produced. Suppose the ith of three environmental variables $E_{i,y}$ varies quasi-periodically about its optimum value $E_{i,opt}$, each E_i with a period different from the others, as suggested in the upper panel of Fig. 3. Then, recruitment of the yth year-class R_y will vary as a rogue wave (lower panel, Fig. 3) if it is inversely proportional to the product of the environmental factors' absolute deviations, each from its optimum value (provided none of the deviations quite goes to zero):

$$R_y \propto \frac{1}{\prod_i |E_{i,y} - E_{i,opt}|}$$

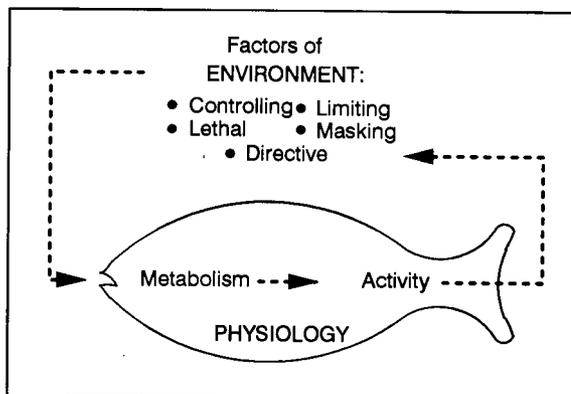The **irreversible nongenetic adaptation hypothesis** we owe to Kinne (1962), who concluded on the

Fig. 5. F.E.J. Fry's 'physiological classification of environment.' Environment operates on the animal's activity through its metabolism. Directive factors feed-back through distribution and anticipatory responses to modify the other effects of environment.

basis of salinity-adaptation experiments with *Cyprinodon macularius*, that certain ecophysiological optima might be 'set' in early development, in much the same way that meristic characters are fixed by temperature during the larval stage. Thus, Kinne (1962) suggested that each individual pupfish grows and otherwise performs better throughout its life at salinities near the salinity at which it passed its own critical developmental phase. If better performance extends to reproduction, then Kinne's scheme provides a simple mechanism for sub-stock or even race formation. In the context of recruitment, Kinne's hypothesis can be extended to interject a lag, equal to the time from hatching to reproductive maturity, into the recruitment time-series. Suppose recruitment of the yth year-class R_y is inversely proportional to the product of some environmental variable's absolute deviation from its optimum and that same variable's absolute deviation from its value n years earlier E_{y-n}, where n is age of the dominant spawners in the yth year (and neither of the deviations ever quite goes to zero):

$$R_y \propto \frac{1}{|E_y - E_{opt}| \cdot |E_y - E_{y-n}|}.$$

For a series of E varying about E_{opt} in a regular way, with n = 4 (upper panel, Fig. 4), R exhibits the familiar pattern of several small values, punctuated irregularly by a very large value (lower panel, Fig. 4).

Do available data on flatfish recruitment support either of these two hypotheses? No, they do not, except perhaps in the sense of pattern; certainly, the timing of strong year classes does not seem predictable under either model. The power spectra of the R series for neither plaice nor sole (*Solea solea*) in the

North Sea (Rijnsdorp *et al.*, 1991) over the past 35 years reveal any significant periodic component (at least for periods from 2 to 10 years). If any dominant period had been indicated, the challenge of identifying a probable environmental cause would remain—and temperature is really the only environmental factor for which the existing time-space series is sufficient for any sort of judgement. A direct test of the irreversible non-genetic adaptation hypothesis for recruitment of North Sea plaice *vs* temperature over the past 35 years yielded good agreement for pattern—but no correspondence whatsoever between predicted and observed time series of recruitment, for any supposed value of optimum temperature.

Simulation modelling offers an efficient way to probe for potential solutions to complex problems—provided there exists theory to guide the probing.

4. ECOPHYSIOLOGICAL MECHANISMS, ORGANIZED VIA FRY'S 'PHYSIOLOGICAL CLASSIFICATION OF ENVIRONMENT'

Our simulation effort convinced us of only one thing: there is no suitable conceptual framework within which to consider how and which combinations of environmental variables might affect recruitment or, for that matter, the dynamics of fish populations, in general. We suggest that Fry's 'physiological classification of environment' (Fry, 1947, 1971; Evans & Neill, 1990) provides an appropriate basis for development of such a framework.

4.1. OVERVIEW

Fry's (1947) classic monograph, 'Effects of the environment on animal activity,' crystallized numerous concepts fundamental to contemporary autecology. Fry's main thesis was that activities of the organism are distinct from metabolism and that the environment influences activity through metabolism. These insights formed the basis for his categorization of the environment into its controlling, lethal, limiting, masking, and directive effects on metabolism, and, thus, activity of the individual. Time has proven this physiological classification of environment to be one of remarkable utility and power.

Fry (1947, 1971) suggested that the complex of environment can be resolved into its physiological effects—controlling, lethal, limiting, masking, and directive. Controlling factors of environment regulate or dictate the intrinsic rates of the biophysical and biochemical processes that comprise metabolism. Purely lethal factors completely interdict metabolism. Insufficiencies of raw materials limit metabolism. Masking factors load metabolism, in that they mandate metabolic work for physiological regulation of internal environment. Finally, some environmental factors direct the organism's movements within the habitat or direct physiological adjustments that antici-
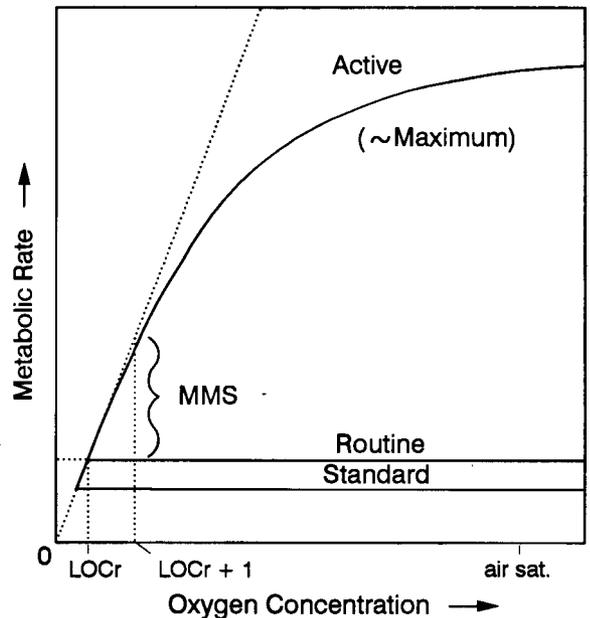

Fig. 6. Active, routine, and standard metabolic rates of an idealized fish as functions of dissolved oxygen concentration. The difference between active and standard rates is the metabolic scope (as traditionally defined). LOC = limiting oxygen concentration. LOC_r = LOC for routine metabolism. MMS = marginal metabolic scope.

pate future environment. Together, Fry's factors of environment define the total set of functional linkages between the individual fish and its surrounding world (Fig. 5).

The proximal effects of environment are on metabolism of the animal; metabolism, in turn, mediates the ultimate effects of environment on the animal's activity. Activity, in Fry's sense, includes all physiological work the animal does, not just that resulting in movement; in particular, activity includes growth and physiological regulation of internal environment.

Directive factors have a special place in Fry's scheme: through them, activity feeds back to control environment (Fig. 5). To the extent that directive factors permit exploitation of spatial and temporal heterogeneities of environment, fish and other animals can exercise individual control over the controlling, lethal, limiting, and masking effects of environment.

The factors of environment cannot be quantified independently of each other or independently of the individual animal's environmental history. This is because the various components of environment typically interact in their effects on metabolism, and because the physiological state of the animal represents an integral of those effects over time. Thus, 27°C (for instance) has fundamentally different physi-

ological meanings for two genetically identical fish—unless all other components of environment also are identical between fish, both in present and past time.

In nature (and in many laboratory situations) fish encounter environmental fluctuations that render their metabolism in a perpetually transient state. Knowledge of steady-state responses (activity) may have little value in predicting transient-state responses.

4.2. METABOLISM AND METABOLIC SCOPE IN THE CONTEXT OF FRY'S FACTORS

Metabolism can be considered the physiological engine that powers such activities as swimming, growth, and reproduction. The engine uses oxygen (together with nutrients from food) and produces wastes such as carbon dioxide and ammonia. Temperature (and, to a lesser extent, such variables as pressure, pH, and concentrations of certain ions—*e.g.*, calcium) controls the pace, or metabolic rate, of the engine. Restrictions in the supply of oxygen (or nutrients) limit the engine's capacity to perform metabolic work. Either a deficiency of oxygen itself or the presence of dissolved substances that interfere with oxygen uptake, transport, or use (*e.g.*, carbon diox-

ide, ammonia, detergents, metals, some organic biocides) can restrict oxygen supply to the engine. In water with non-optimal levels of certain dissolved solids (in aggregate, 'salinity'), the engine must do obligatory extra work to maintain proper internal concentrations of water and ions (ion-osmoregulation). This metabolic loading reduces or masks the engine's capacity for other work, such as swimming and growth. Many environmental variables, when they take on sufficiently extreme values, become lethal factors and cause the engine to fail—and, with that, the end of all activities that comprise life. Contrarily, the space/time distribution of many of these same environmental variables have directive effects, which feed back via activity to optimize performance of the engine.

In fishes, oxidation of food materials or stored energy reserves requires oxygen that generally must be acquired from the water via diffusion at the gills. Respiratory and circulatory systems of fish have evolved to function effectively over a range of dissolved oxygen concentration, from above air saturation, down to some concentration at which oxygen-demanding activities become constrained (Fig. 6). This limiting oxygen concentration (LOC) is increased
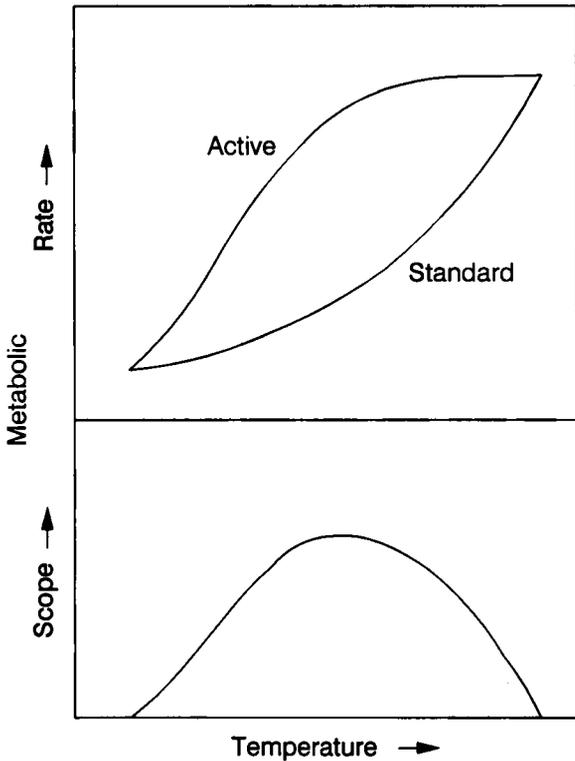

Fig. 7. Controlling effect of temperature on metabolic rates and scope of an idealized fish.
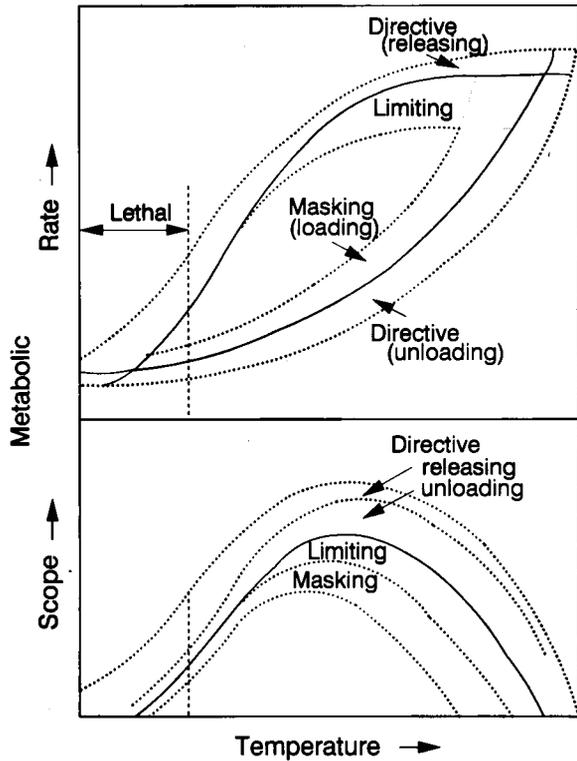

Fig. 8. Directive, limiting, masking, and lethal effects of environment, superimposed on the controlling effect of temperature shown in Fig. 7.
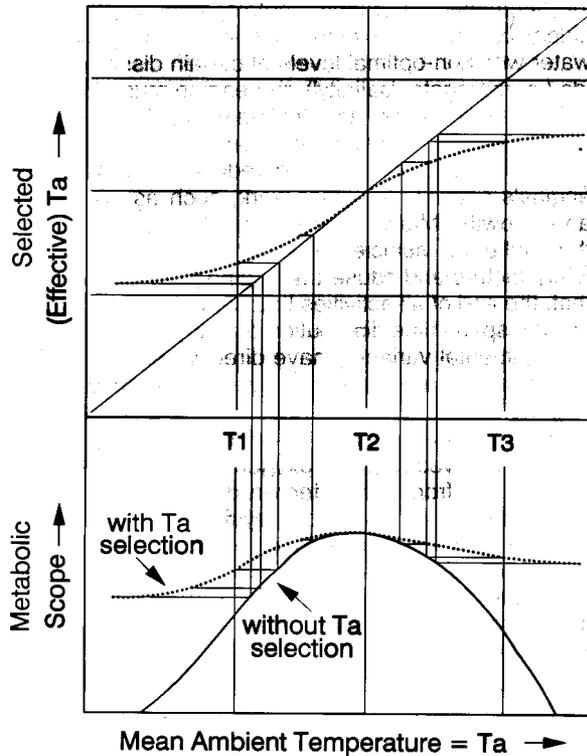
Fig. 9. Directive effect of temperature as modifier of temperature's controlling effect on metabolic scope. The upper panel indicates behavioural thermoregulation by which the fish achieves a selected temperature (thermal microhabitat) that is more moderate (nearer the preferred temperature) than the habitat's mean temperature; the lower panel shows the 'releasing' effects of such directive responses on metabolic scope.
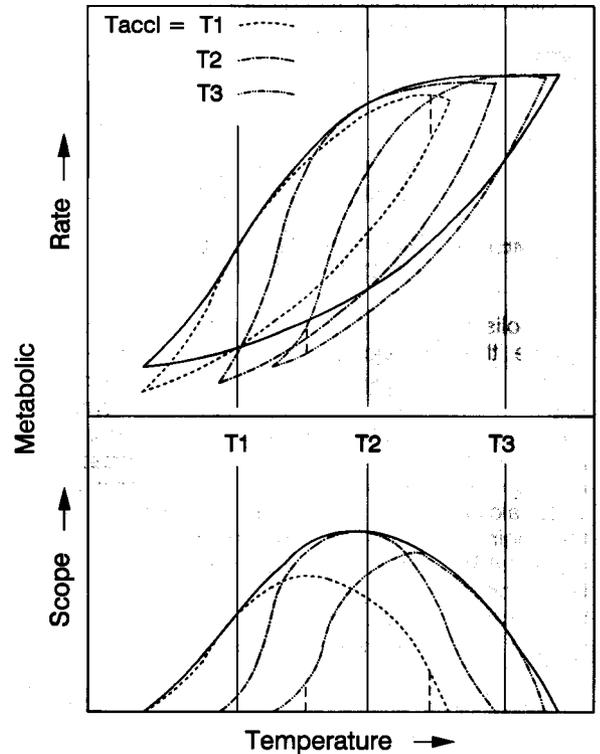
Fig. 10. Effect of thermal acclimation on metabolic rates and scope as functions of ambient temperature. Responses are indicated for three values of acclimation temperature (Taccl). From Neill & Bryan (1991).

by anything that increases total oxygen demand: *e.g.*, faster swimming, increased food processing, elevated temperature, and imposition of environmental stressors such as ammonia and non-optimum levels of salinity.

Consider a typical fish living in water with gradually declining oxygen concentration. Given no other cause for changing total activity, the fish maintains a relatively constant rate of oxygen uptake at all oxygen concentrations above LOC (Fig. 6). Such oxygen-independence typically is achieved by increasing gill ventilation (water flow) and perfusion (blood flow) as environmental oxygen declines. At LOC, these regulatory measures are exhausted and, as dissolved oxygen declines still farther, respiration becomes oxygen-dependent. If the fish had been engaged in instantaneously non-obligatory activities (swimming, digesting food, growing), those activities must now be curtailed. When the fish has been reduced to activities obligatory for continued existence (maintenance activities supported by 'standard metabolism'), the

fish must engage in anaerobic metabolism or die. Because most fish have very limited capacity for anaerobic metabolism, LOC for a fish metabolizing at the standard rate is, in effect, the incipient lethal oxygen concentration. To fish physiologists who strive to estimate LOC only for inactive, fasted fish, LOC is understood in this last, restricted sense. But, to those of us who are interested in the limits oxygen imposes on fish performance and production, LOC is a continuum. For fish that are forced to be maximally active (and, so, have 'active metabolism'), the continuum can extend from the standard LOC to an active LOC beyond air saturation. Fry (1947) called these end-points the 'level of no excess activity' and the 'incipient limiting level,' respectively. Others have identified various intermediate points, frequently calling them 'critical' oxygen concentrations (or tensions); perhaps, the commonest of these is the critical oxygen concentration for routine metabolism, which is the metabolism of an undisturbed, fasted fish engaged in voluntary swimming activity.

Values of LOC for a variety of fish species and activity levels have been compiled by Davis (1975) and Hughes (1981). At some risk of over-generalization, it may be said that standard LOC ranges from 1

TABLE 1

Fry's (1947) 'Physiological classification of environment', extended to the population and community/ecosystem levels of organization.

Fry's factors of environment	presumptive role, and representative identities, at organizational level of		
	individual	population	community
controlling	control metabolism by dictating rates of molecular activity and chemical reaction: temperature, pressure, pH	affect critical spawner density (including effects on reproductive potential) or spawner mortality rate, thereby governing recruitment rate required for maintenance of stock; affect 'intrinsic rate of increase'	affect immigration/establishment of pioneer and keystone species; other controlling effects of environment on metabolism of individuals, recruitment
limiting	constrain maximum metabolic rate: oxygen, micronutrients, certain metabolites and pollutants that interfere with oxygen transport	affect carrying capacity of habitat for pre-recruits, thereby constraining max. recruitment rate: factors that constrain relevant productivity of habitat, including 'density-dependent' factors	reduce habitat/ecosystem complexity and thus the number of niches: eutrophication, exclusionary land-use practices
masking	'load' metabolism (increasing min.): non-optimum salinity (osmoregulation); certain pollutants and other environmental stressors that increase obligatory metabolic work	load recruitment by increasing mortality or reducing growth of pre-recruits: joint effects of controlling, limiting, and lethal factors on individuals, especially predation (incl. cannibalism)	challenge habitat/ecosystem resiliency, homeostasis: overharvest of stocks, competitive land-use practices
lethal	completely interdict metabolism to cause death: supersaturated gases, toxins, predators	cause extinction: catastrophic consequences of controlling, limiting, masking, lethal factors on individuals, e.g. epidemic disease	cause failure of habitat/ecosystem integrity: indiscriminate catastrophe, e.g., a meteor strike
directive	'unload' metabolism, by putting animal in microhabitat or physiol. state where it is better (pre)adapted: temperature, light intensity and photoperiod, oxygen, other factors causing distributional, acclimatory, or anticipatory responses	cause shifts in spatial and temporal distribution: factors leading to migration, either active or passive; factors leading to genetic change and evolution	'channel' ecological succession and thus community structure over time: human intervention, changes in climate, continental drift, Gaia processes

to 3 ppm and that for 'normal' levels of activity LOC ranges upwards from 3 ppm, with a mean near 5 ppm.

The difference between active and standard metabolism is defined as metabolic scope (Fry, 1947). It increases monotonically with oxygen concentration, from zero at standard LOC, to a value 5-15 times standard metabolic rate at the active LOC corresponding with air saturation. Metabolic scope estimates the maximum rate at which oxygen can be supplied in support of swimming, growth, and other activities. Thus, metabolic scope provides a mechanistic basis for estimating the joint effects of environment on the capacity for fish performance.

Neill & Bryan (1991) showed that the derivative of metabolic scope, as it goes to zero at LOC for routine metabolism (Fig. 6), can be estimated via routine respirometry from the ratio of routine metabolic rate to LOC for that rate. This ratio (multiplied by 1 unit of oxygen concentration, to give the same units as metabolic scope) they called 'marginal metabolic scope' and offered as an easy-to-measure index of environmental suitability for fish performance.

The archetypal controlling factor of environment is temperature. Temperature sets the pace of metabolism by controlling molecular dynamics (diffusivity, solubility, fluidity) and biochemical reaction rates. The resulting patterns of metabolism and metabolic scope are generalized in Fig. 7. A resting, fasted fish's metabolic demand for oxygen (standard metabolism) generally increases exponentially with temperature, doubling or tripling for each 10°C rise (i.e., $2 < Q_{10} < 3$). However, the physiological capacity to supply this oxygen rises sigmoidally to a maximum at some high temperature (and then may decline precipitously as temperature increases farther). Thus, metabolic scope reaches a maximum at a species-specific optimum temperature, which is somewhat lower than the temperature permitting maximum supply. Under otherwise favourable conditions, the optimum temperatures for many 'cold-water' and 'warm-water' fishes are 14-18°C and 24-30°C, respectively (Magnuson et al., 1979; Jobling, 1981).

The controlling effect of temperature on metabolism (Fig. 7) provides a convenient template with which to consider the effects of the other factor
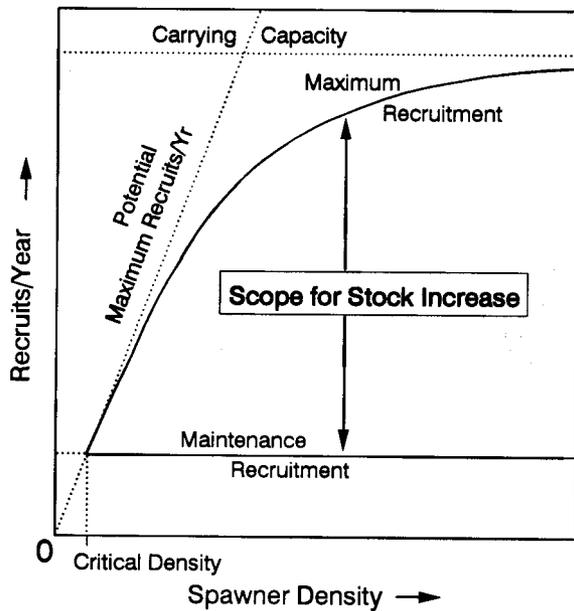
Fig. 11. Idealized (Beverton-Holt-like) spawner-recruit relationship, and emergence of scope for population growth. This presentation is designed to emphasize conceptual parallels with the oxygen-concentration/uptake relationship shown in Fig. 6.

Fig. 12. Controlling effect of temperature on recruitment rates and population scope.

classes (Fig. 8). Deficiencies of dissolved oxygen and other raw materials limit active metabolism progressively as temperature rises, and thus lower the optimum temperature. Other environmental stressors can both elevate obligatory demand for oxygen and reduce physiological capacity to supply it. These masking and limiting factors reduce metabolic scope at all temperatures and shift (in general, reduce) the optimum temperature for maximizing the surplus metabolic capacity that, in combination with adequate nutrition, leads to growth. Beyond certain extremes of environment, fish not only cannot grow, they cannot live—or they can live only for a limited time; the specific relationship depends on character of the lethal environmental factor, fish species (and perhaps size/age), past environmental experience and general condition of the individual, and levels of accessory lethal factors such as pH.

Just as limiting factors limit and masking factors load metabolism, directive factors can be considered to release and unload metabolism. The idea here is that distributional and anticipatory responses to directive factors serve to optimize the fish's state relative to environment's spatial and temporal heterogeneities, respectively. Appropriate distributional responses accomplish behavioural enviroregulation or habitat selection; appropriate anticipatory
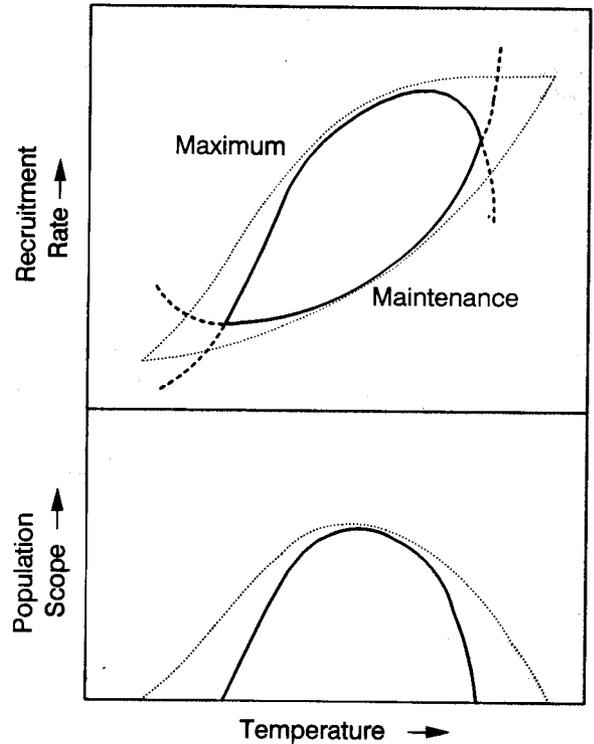
responses, in some cases mediated by the endocrine system, accomplish physiological (pre)adaptation via acclimation or acclimatization. Idealized consequences of behavioural thermoregulation and thermal acclimation on metabolic scope are illustrated in Figs 9 and 10, respectively.

5. EXTENSION OF FRY'S PHYSIOLOGICAL CLASSIFICATION OF ENVIRONMENT TO THE POPULATION AND COMMUNITY LEVELS

If environment acts on individual animals through their metabolism, then it is worth exploring how these ecophysiological effects might emerge at the levels of population and community. Just as environment controls, limits, masks, interdicts, and directs the metabolism of the individual, so, too, the equivalent effects can be recognized in the dynamics of populations and communities. A prospective scheme is outlined in Table 1.

5.1. RECRUITMENT AND POPULATION SCOPE

We suggest that recruitment is the population-level analogue of the individual's metabolism (Fig. 11). The analogue of standard metabolism is the maintenance level of recruitment, which is that necessary to sus-
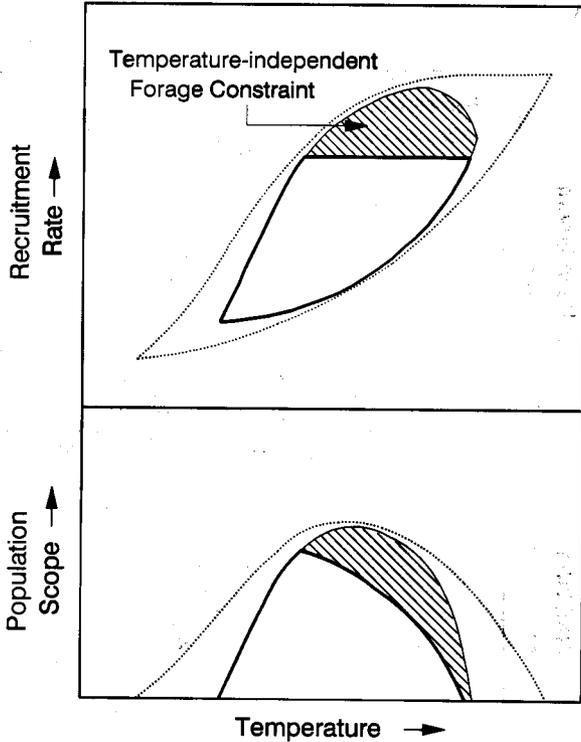
Fig. 13. Limiting effect of a temperature-independent forage constraint on maximum recruitment rate and consequent reduction in population scope, superimposed on the controlling effect of temperature shown in Fig. 12.
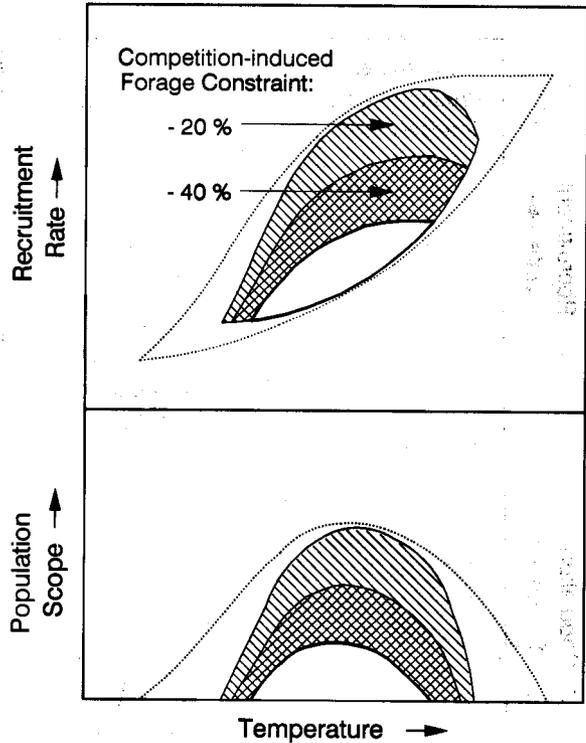
Fig. 14. Limiting effect of a competition-induced forage constraint on maximum recruitment rate, at two levels (20 and 40% reduction in maximum recruitment), and consequent reduction in population scope, superimposed on the controlling effect of temperature shown in Fig. 12.

tain the minimum breeding population. This recruitment rate is logically the product of critical (minimum) spawner density and the mortality rate of spawners, and ought to be independent of actual spawning-stock density at all levels above the critical value. The theoretical upper limit of recruitment is the intrinsic rate of increase, and is the product of spawning-stock density and fecundity (per average female spawner, assuming no effect of density on fecundity). Maximum actual recruitment is the analogue of active or maximum metabolic rate of the individual, and we presume it to follow a Beverton-Holt-like function of spawning-stock density (Beverton & Holt, 1957), with its asymptote determined by carrying capacity of the habitat for pre-recruits. The greater the age at which recruitment is registered, the lower the asymptotic value. The analogue of metabolic scope, then, is the scope for population increase. If scope for population increase is negative for a continuous run of years equal the age of the dominant spawners, the population must suffer the analogue of individual death, which is extinction. Even if population scope is positive, there is no guarantee that recruitment in a given year will actually exceed the maintenance rate; the

consequence of such a weak year class must be a dip in size of the post-recruit stock, unless there is density-dependent compensatory reduction in mortality of post-recruits.

5.2. EFFECTS OF ENVIRONMENT ON POPULATION SCOPE

There are several points at which environment might act on population scope. Controlling environmental factors such as temperature might affect fecundity, the spawning-stock density that is minimum for successful reproduction, and the mortality rate of post-recruits that comprise (or will comprise) the spawning stock. The net result would be a population scope 'envelope' similar to but more restrictive than the analogous envelope for metabolic scope (Fig. 12). The reason for the greater degree of environmental constraint in the population case is that population-level responses must be integrals over time, of the metabolic responses of individuals from moment to moment. Thus, the 'temperature' that appears on the abscissa of Fig. 12 must be thought of, not as a single instantaneous value of temperature, but as a temper-
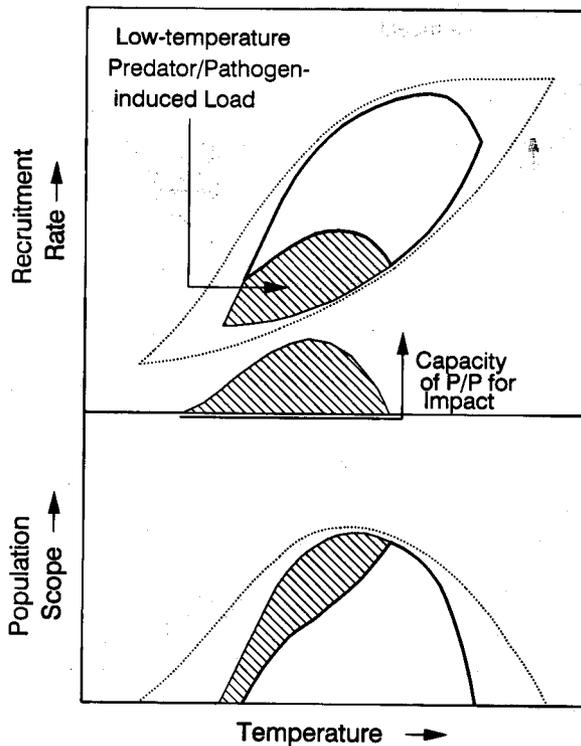
Fig. 15. Masking effect of predation or pathogenicity favoured by relatively *low* temperature (activity curve graphed beneath recruitment curves) on maintenance recruitment rate, and consequent reduction in population scope, superimposed on the controlling effect of temperature shown in Fig. 12.
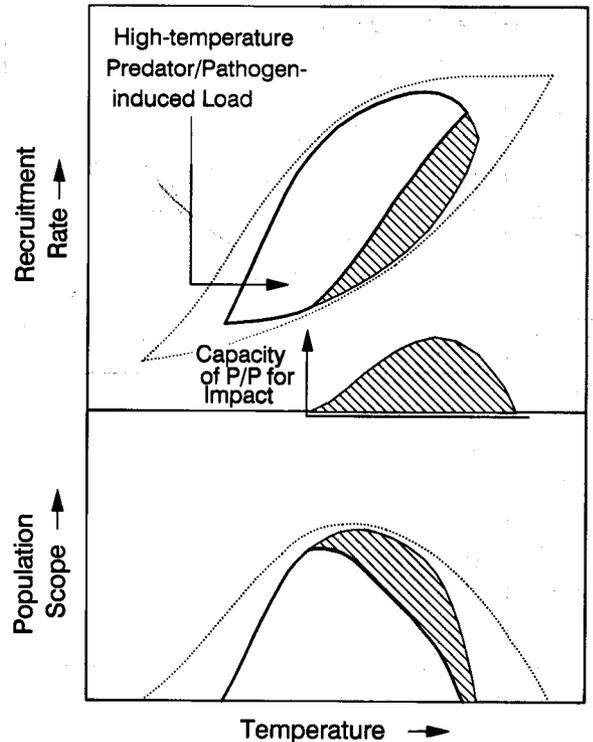
Fig. 16. Masking effect of predation or pathogenicity favoured by relatively *high* temperature (activity curve graphed beneath recruitment curves) on maintenance recruitment rate, and consequent reduction in population scope, superimposed on the controlling effect of temperature shown in Fig. 12.

ature that is in some consistent sense characteristic of the entire thermal regime under which a given year class has been or might be produced.

It seems likely to us that for wild fish in most marine systems, food, not oxygen, is the critical limiting factor at the population level (see Gibson, 1994). In the event that food limitation is independent of controlling variables (probably rare, except in some aquacultural situations), one would expect that population scope would be maximized where the joint distribution of controlling factors causes maintenance recruitment to be minimized. In the case of temperature, this would be at the lower end of the thermal spectrum (Fig. 13).

Doubtlessly, the more usual case of food limitation involves competition from conspecifics. Because conspecifics are identically subject to environmental controls, the expected effect of competition-induced food limitation on population scope is a reduction proportionate to maximum potential recruitment at all levels of the relevant controlling factors. In the case of temperature, for example, the thermal zone over which

population scope is positive, is reduced, and in fact the optimum temperature (that which maximizes population scope) is also reduced, because the maintenance-recruitment curve accelerates as temperature increases (Fig. 14). Whether food is limited because of competition or for some other reason (independent of controlling factors), some reduction in characteristic temperature should mean greater scope for population increase.

Predation, fishing, and other sources of mortality logically act to mask or load population scope; that is, anything that increases post-recruitment mortality should tend to increase the level of recruitment necessary to maintain the stock (assuming no compensatory shifts in mortality). If the imposed load varies with the joint level of relevant controlling factors, the impact on population scope is similar to that caused by interaction of limiting and controlling factors. In particular, low-temperature- and high-temperature-adapted predators will shift the thermal optimum for population scope of a prey species in opposite direc-
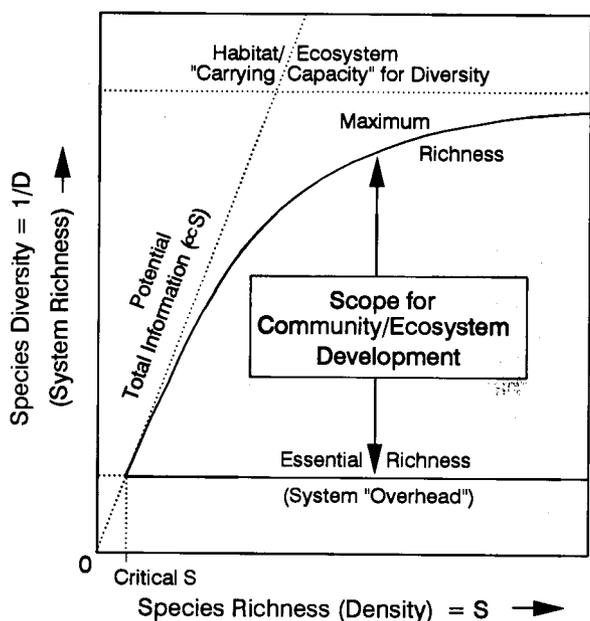
Fig. 17. Supposed relationship between species diversity and species richness, and emergence of scope for community/ecosystem development. This presentation is designed to emphasize conceptual parallels with the oxygen-concentration/uptake relationship shown in Fig. 6 and the spawner-recruit relationship shown in Fig. 11.

tions—to higher and lower values, respectively (cf. Figs 15 and 16). Predation by conspecifics (cannibalism) would be expected to cause reductions in population scope that are proportionate to maintenance recruitment at all levels of relevant controlling factors (provided there are no size/age-dependent changes in metabolic scope *versus* those controlling factors).

Directive factors logically must have a dominant, if not overwhelming, role in defining population scope of many marine fishes, including most of the commercially important flatfishes. At the population level, we would include among directive factors any that affect or effect distribution of the population in space and time. Thus, we would include among distributional responses to directive factors not only active migration but also passive drift and random dispersal. At the population level, the anticipatory response of main interest and importance is genetic adaptation, leading to evolution of the stock and, ultimately, to speciation.

We recognize that our extrapolation of Fry's physiological classification of environment from the level of the individual to the population, is a bit awkward. The reason is that we have tried to keep the emphasis on environment, when, in fact, recruitment and popula-

tion scope are one step removed from environment. To paraphrase Fry, we might say that the environment acts on the population through its individuals. The proximal identity of the 'joint level of relevant controlling (environmental) factors', in relation to population scope, is, in fact, realized metabolic scope of the individuals. There would tend to be a one-to-one relation between metabolic and population scope, if it were not for the time-scale mismatch (seconds to days for metabolism, years to generations for population dynamics) and the interacting effects of limiting (e.g., food, and, secondarily, competitors), masking (e.g., predators), and directing (e.g., spatial distribution of individuals, and genetic change) factors. Only when the joint impact of these interacting factors becomes so extreme as to drive spawning-stock density below the critical value, and thus put the population irreversibly on the path to extinction, can we say that the population-level analogue of Fry's lethal factor is at work. When a population-level lethal factor is operating, population scope simply becomes undefined (in the mathematical sense).

5.3. COMMUNITY/ECOSYSTEM-LEVEL RESPONSES

Fig. 17 offers a community/ecosystem-scope model, which is intended as a conceptual analogue of the population-scope model given in Fig. 11. We were motivated to try this extrapolation, not by any conviction of its intrinsic validity, but rather by the urge to challenge community/ecosystem ecologists to think about ecophysiological effects from the perspectives that Fry (1947) taught us.

We suggest as an appropriate practical basis for analysis of community/ecosystem-scope, the relation between species diversity and species richness, the former serving as proxy for community/ecosystem richness (Fig. 17). By species richness, we mean simply the spatial density of species (number per unit area or volume of habitat or ecosystem). As an appropriate measure of species diversity, we suggest the reciprocal of Simpson's index (Krebs, 1989):

$$\frac{1}{D} = \frac{1}{\Sigma\left(p_i^2\right)}$$

where p_i is the proportion of individuals or biomass in a sample, representing the ith species. Potential biotic information contained in the system (total per unit habitat or ecosystem) is presumed to increase linearly with species richness, with a slope dependent on average species' information value to the system. At low values of species richness, community/ecosystem richness is one-to-one with information; but, as species become ever more packed into a habitat/ecosystem of given complexity (niche variety), information becomes progressively more redundant—and community/ecosystem richness asymptotically approaches a maximum. The scope for biotic develop-

ment of the community/ecosystem is the difference between this maximum and some obligatory minimum of system richness required for functional integrity of the system. In our view, then, system richness becomes independent of species richness, in an acute sense, at large values of species richness. Thus, we envision habitat/ecosystem complexity as setting the upper limit on system richness—a limit which is approached only under conditions allowing sufficient species richness. But, over longer (system-specific) intervals of time, system and species richness must be interdependent, and ought to change together in response to system perturbations. Such system 'ascendancy' (Ulanowicz, 1986) should reach maximum values when the frequency of disturbance is intermediate (the definition of 'intermediate' being, again, system-specific). At both greater and lesser frequencies of disturbance, system productivity is channelled into proportionately larger biomasses of fewer species—opportunistic species in the case of frequently disturbed systems (Dobzhansky, 1950; MacArthur & Wilson, 1967), and more stenotopic, competitively superior species in the case of infrequently disturbed systems (Connell, 1978; Huston, 1979). Among flatfishes, generalists such as plaice dominate relatively depauperate bottom-fish communities in shallow subarctic and temperate waters characterized by highly variable and unpredictable environments—and, increasingly, by anthropogenic impacts such as exhaustive bottom-trawling; other, more specialized flatfishes, such as peacock flounder (*Bothus lunatus*), are regular members of the rich bottom-fish communities of shallow tropical seas like the Caribbean, where environment presumably is subject to intermediate disturbance and system ascendancy is greater.

The last column of Table 1 offers a summary exposition of Fry's factors of environment at the level of community/ecosystem. Among the central ideas are that controlling factors affect immigration/establishment of 'keystone' (Paine, 1966) and 'core' (Hanski, 1982) species; limiting factors reduce habitat/ecosystem complexity; masking factors challenge habitat/ecosystem resiliency; lethal factors destroy habitat/ecosystem integrity; and, directive factors give pattern to ecological succession. Given this paper's focus on population-level processes, it would be inappropriate to pursue community/ecosystem issues any further.

6. IMPLICATIONS FOR RECRUITMENT AND POPULATION DYNAMICS OF MARINE FISHES

6.1. LIFE-HISTORY STRATEGIES

For most commercially important marine fishes, maximization of population scope must, in a probabilistic sense, be tantamount to ecological and evolutionary success. Life-history strategies for maximizing population scope logically operate to maximize the ratio of maintenance recruitment to critical spawner density, which defines slope of the line labelled 'potential maximum recruits/year' in Fig. 11. By analogy with marginal metabolic scope (Fig. 6), this ratio might be called 'marginal population scope' (MPS). MPS should be one-to-one with fitness of the ecological system constituted by the fish population (given its structure in terms of age/size, acclimatory states, and genetics) in the context of total environment. For a fixed value of critical spawner density, MPS is maximized for combinations of stock and environment that maximize the tolerable rate of spawner mortality. For a fixed value of maintenance recruitment, MPS is maximized for combinations of stock and environment that minimize critical spawner density. In systems with variable and unpredictable environment, the fish's optimum strategy for maximizing MPS would seem to be maturation at an early age and high reproductive effort (fecundity), a view consistent with that of Winemiller & Rose (1992).

It follows, then, that fishes that have high fecundity and make little or no investment of parental care in their offspring (*e.g.*, flatfishes and most other commercially important marine fishes) are preadapted to exploit large-scale temporal and spatial heterogeneities of environment. Their evolutionary bet is not that each new year class will succeed everywhere and every time but that it will succeed somewhere, at least once in each generation. In the rare year when the factors of environment come together in harmony over much of the population's range, a 'rogue wave' of recruitment occurs, and the population realizes its maximum scope for increase. For highly fecund species such as most flatfishes, a large stock of spawners is not requisite to these very large year classes; in fact, for most flatfishes, there seems to be little spawner-recruit dependency. That is how it should be, if success in the current year is to be uncoupled from the relative success or failure of recruitment in previous years. Perhaps, this is as close as one can come, conceptually, to embracing the hypothesis that ecophysiological factors are important in marine fish recruitment.

6.2. LATITUDINAL LIMITS OF RANGE

Marine organisms at the latitudinal extremes of their geographic range are necessarily living closer to the environmental 'edge'—at least in a thermal sense—than are their more centrally distributed counterparts. At the northern and southern limits of geographic range, the population typically experiences thermal regimes that are shifted toward the tolerance limits, *i.e.* toward the values of effective temperature at which population scope goes to zero. At the thermal extremes, not only is population scope progressively reduced, but also—under the model presented in Fig. 12—scope decreases ever more steeply as tempera-

ture becomes more extreme. This set of relations implies that interannual variability in recruitment and other aspects of population dynamics should be greatest at the latitudinal limits of range. It also implies that directive factors assume even greater importance at these latitudinal extremes than nearer the centre of geographic distribution where variation in temperature and other physico-chemical factors about their presumed optima have smaller effects on population scope.

Why, then, should the population engage year after year in the gambles that comprise a test of the limits of latitudinal range? Within the conceptual framework of Fry's factors, the answer to this question is fairly obvious (and entirely consistent with niche theory): The dominant factors limiting and masking population scope are proximally biotic—competition-induced shortages of food, and predation, respectively—and these factors logically tend to have their greatest absolute impacts at the centre of the population's geographic range, not at its fringes (Fig. 14-16). Hall *et al.* (1992), following the reasoning of Ware (1982), have made a complementary point: environmentally-induced shifts in organismal energy balance cause populations to achieve greatest densities in parts of the geographic range where their genome permits maximization of bioenergetic profits in the form of successful reproduction (and subsequent recruitment). On average, this leads to highest population densities—and, thus, greatest potential for competition—near the centre of the range.

Therefore, anticipatory directive factors, at the population level, constantly drive the stock to extend its range; population-level directive factors of the distributional type constantly operate to implement these range extensions. More often than not, however, implementation fails, either because distributional mechanisms break down in an acute sense (*i.e.*, no or few members of the population ever arrive at the limits of range—see Sinclair, 1988) or because con-

trolling, limiting, masking, or even lethal effects of local environment are so extreme as to render population scope zero there—despite entirely appropriate directive responses on the part of the individual. But, on relatively rare occasions, the range-extension gamble pays off, and the population finds itself heavily invested at the margin(s) of distribution, and with a large return on investment (most of population scope realized) owing to transient lows (lags) in levels of limiting and masking factors. But the boom is short-lived—generally only one cohort in duration—and both geographic range and population scope return to more typical values.

Year-to-year adjustments in the marginal latitudinal distribution of spawning relative to weather variation may exacerbate interannual variation in recruitment. Probably most important are weather-associated changes in the timing or spatial distribution of spawning in relation to currents. Currents are especially critical to the successful transport of marine fish larvae to nursery areas (Miller *et al.*, 1984, 1985). In North Sea plaice it would seem that it is the distribution of spawning effort, not the spawners, that is displaced southward during relatively cold winters (Simpson, 1959). When unusually low winter temperatures allow North Sea plaice to spawn successfully as far south as the Southern Bight or even into the English Channel, prevailing easterly or northeasterly currents (Harden-Jones, 1980) then would tend to carry the larval fish, via such routes as the Marsdiep Channel, into the southern Wadden Sea, and a relatively strong year class should be recruited there. But during milder winters larval plaice drifting northeastward from more northerly spawning grounds should end up in Danish or Swedish estuaries—and the year class recruited to Wadden Sea should be weak. Such weak year classes may consist of larger-than-average individuals, both because higher temperatures favour more rapid growth and because these recruits, relative to those from a year class produced further south

TABLE 2

Emergent responses to Fry's (1947) factors of environment at the level of individual, population and community/ecosystem. The arrows are intended to emphasize the way that responses to limiting factors at a given level of organization tend to emerge as responses to controlling factors at the next higher level; similarly, responses to lethal factors at one level tend to merge as responses to masking factors at the next higher level.

factor	emergent response at the level of		
class	*individual*	*population*	*community/ecosystem*
controlling	critical DO, standard metabolism	critical spawner density, 'standard' recruitment	composition, organization
limiting	physiological performance (growth, swimming, fecundity)	maximum recruitment; intraspecific competition	diversity, richness; carrying capacity of habitat
masking	physiological stress	post-recruitment mortality	impoverishment; habitat degradation
lethal	lethal resistance, death	extinction	collapse
directive	enviroregulatory behaviour, physiological adaptation	distribution, genetic adaptation.	succession, Gaia processes

during a colder winter, may be older, having drifted a greater distance or perhaps via a less direct route from spawning grounds to nursery.

Weather-induced temporal variation in spawning might be no less important than spatial variation, as a contributor to recruitment variation near the latitudinal limits of range. Again using North Sea plaice as a convenient model, one might suppose that each winter the parent stock at a certain latitude would encounter a temporal dichotomy in the thermal regime, with optimum spawning temperatures occurring twice, once in early winter and again late in winter, separated by a mid-winter period of intense cold (Fig. 18). The result should be relatively early spawning (December), relatively late spawning (late February to early March), or both, giving rise to high intra- as well as interannual variability in age/size of larval fish available for recruitment to the nursery. Recent observations by Hovenkamp (1991) are consistent with this hypothesis, but a rigorous test would require considerably more data, particularly on temperature and currents over a period of years.

7. EMERGENT ECOPHYSIOLOGICAL HYPOTHESES

Ecophysiological considerations suggest several recruitment hypotheses that could be tested—assuming availability of appropriate data:

1. *Lack of an apparent stock-recruit relationship indicates that size of the spawning stock is 'healthy'; conversely, a strong stock-recruit relationship, especially when coupled with low variability in year-class strength, portends potential stock collapse owing to an approach to critical spawner density.*

2. *Critical spawner density should be directly proportional to the ratio of fecundity to instantaneous mortality rate of female spawners*, because maintenance recruitment is equal to critical spawner density multiplied by instantaneous mortality rate of spawners, and fecundity is one-to-one with maintenance recruitment rate at the critical spawner density (Fig. 11).

3. *If population scope is negative for a continuous run of years equal the age of the dominant spawners, the population must suffer the analogue of individual death, which is extinction.* Lethal factors for individuals amount to masking factors at the population level.

4. *Directive and controlling factors are likely to dominate recruitment at the latitudinal limits of range; whereas, limiting and masking factors are more likely to assume the dominant roles at the centre of geographic range.*

5. *Owing to the steepening of the population-scope curve at the thermal limits (Fig. 12), one would expect variation in temperature to cause more variation in recruitment at the edges, as opposed to the centre, of a species' latitudinal range.*

6. *Directive factors that involve active swimming, as opposed to passive or modulated drift, increase in rel-*
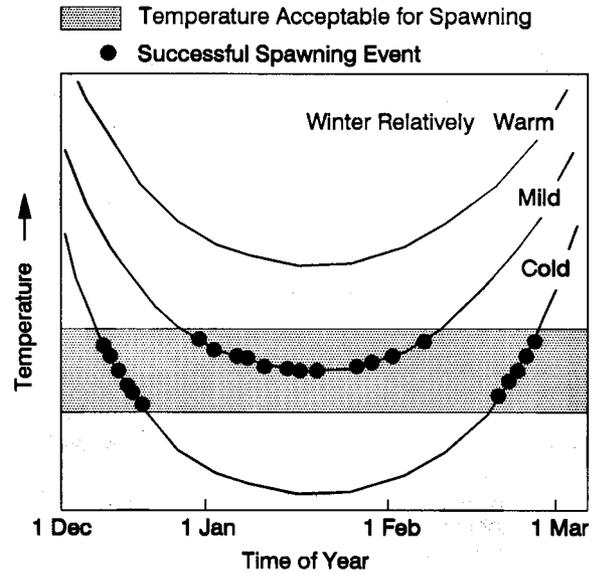

Fig. 18. Hypothesized episodes of plaice spawning in the southern North Sea during relatively warm, mild, and cold years. At the supposed location, plaice spawn not at all during the warm year, during the coldest part of winter in the mild year, and twice during the cold year—during early winter, and again during late winter.

ative importance with increasing age/size.

7. *Owing to the lower vagility of larvae and early juveniles, compared with older individuals, one would expect the impacts of ecophysiological factors to be greater the earlier the stage. Also, because variation in environmental factors has greater impacts on population scope near the latitudinal limits of range, environmental variation should produce a pattern whereby the closer to the limits of the range, the earlier the stage at which year-class strength is set.*

8. *Near the centre of geographic range, normally strong year classes should be punctuated by an occasional weak year class; whereas, near the edges of the range, normally weak year classes should be punctuated by an occasional strong one.* Because aberrant year classes reflect the overwhelming effects of ecophysiological factors in those years, the intrinsic character of the stock-recruit relationship must be sought in normal years—those in which year classes are large near the centre of the range, and small near the limits of the range.

Underlying these hypotheses is our premise that *evolution has favoured development of ecophysiological responses that maximize metabolic scope of individuals and population scope of stocks. Evolution may even have favoured the maximization of scope-for-development (and ascendancy?) of communities and ecosystems, to the extent that such systems*

maximize equitable distribution of resources among biological species, which are the fundamental units of information.

8. CONCLUSION AND RECOMMENDATIONS

Consideration of the recruitment-variability problem in the context of Fry's (1947) 'physiological classification of environment' has led us to the scheme presented in Table 1 and elaborated in the sections above. By way of summary, Table 2 provides a simplified exposition of emergent responses to Fry's factors of environment.

What we have tried to do in this paper, is to give logical structure to the search for biologically relevant (mechanistic) algorithms relating environmental variability and ecological variability, with particular attention to variability in recruitment of marine fishes. In extrapolating from the metabolism of individuals to recruitment of populations to diversification of communities and ecosystems, it has become profoundly evident that a distinction must be made between proximal and distal effects of environment. The ultimate source of all recruitment variability is the abiotic environment (and chance), whether it acts directly on the physiology of recruits or indirectly via their prey or predators. In any event, alternative recruitment hypotheses must acknowledge that physiological cold shock, low-temperature repulsion of predators, and ice-scouring of shallow bottoms are fundamentally different environmental effects, despite the fact that all are linked to low temperature. What Fry (1947) did, was to show that environmental effects fall into five functional classes, and that a proper analysis of these interacting effects is essential for understanding fish activities such as growth and locomotion. Only after Fry's scheme emerged, did it become feasible for fishery biologists to predict a fish's autecological responses to such environmental variables as temperature. It is our hope that this paper will encourage and facilitate similar development of predictive capability with regard to fishes' synecological responses.

More attention to conceptualization of the recruitment problem should relieve notoriously difficult logistics associated with research. At the very least, the 'one shot' per year that most recruitment situations afford would be maximally exploited, not just for data gathering, but also for hypothesis testing.

Undoubtedly, investigation of the recruitment problem (and the balance of fisheries research) would proceed more smoothly if scientists who study at different levels of organization—individuals, populations, communities—understood and respected each other's perspectives—or at least communicated openly with one another. To be maximally successful, population dynamicists must appreciate the biology of individual fish—and the way their populations interact with others to comprise communities. At the same time, autecologists who study individuals find fishery relevancy only in what their research can contribute to understanding the biology of fish populations.

It is our firm conviction that we who struggle with the recruitment problem ought to make more and better use of simulation modelling and related tools, both for efficient screening of hypotheses and for effective communication with each other (*i.e.*, for better planning and coordination of research). Recruitment variation is simply too complex an issue ever to be resolved only by regressing year-class strength on an endless series of single (or even multiple) variables—all the while, trying to keep the complexities 'in our heads.' Whether or not one subscribes to the specifics elaborated in this paper, it is obvious that biology and, to an even greater extent, ecology tend to integrate and damp some environmental variation, but to amplify other environmental variation via positive feed-back. Moreover, an analysis of ecological responses based solely on the biology of individuals must fail, owing to its neglect of responses that emerge only at the levels of population, community, and ecosystem; in particular, a proper analysis of ecological responses must acknowledge and account for feed-backs from the target organism to the abiotic and biotic environment in which it lives. The importance, complexity and hierarchical nature of the recruitment-variation problem demand a renewed research effort, organized around a working systems model with sufficient sophistication and power to suit the problem. Let's do it!

Dedication.—This paper is dedicated to the memory of Frederick Ernest Joseph Fry (1908-1989).

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