ECOPHYSIOLOGY OF MARINE FISH RECRUITMENT:

A CONCEPTUAL FRAMEWORK FOR UNDERSTANDING

PATTERNS IN TIME AND SPACE

WILLIAM H. NEILL
Department of Wildlife and Fisheries Sciences, Texas A&M University System,
College Station, TX 77843-2258, USA
phone (409) 845-5777; fax (409) 845-3786

JOHN M. MILLER[1], HENK W. VAN DER VEER[2], and KIRK O. WINEMILLER[3]
[1]Department of Zoology, Box 7617, North Carolina State University,
Raleigh, NC 27695, USA
[2]Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg,
Texel, The Netherlands
[3]Department of Wildlife and Fisheries Sciences, Texas A&M University System,
College Station, TX 77843-2258, USA

In search of a better basis for understanding variation in marine fish recruitment, we have returned 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 have extended this scheme to population-level responses, including recruitment...and even have attempted an extrapolation to community/ecosystem-level responses (Table 1).

Fry (1947) 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 (Figure 1). 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 patterns in time and space. Perhaps most intriguing are these three: 1) Directive and controlling factors are likely to

Table 1. F.E.J. Fry's "physiological classification of environment" (Fry 1947), extended to the population and community/ecosystem levels of organization. From Neill et al. (1994).

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 recruit. rate required for maintenance of stock; affect "intrinsic rate of increase"	affect immigration/ establishment of pioneer and keystone species; other controlling effects of environ. on metab. 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 (incr. min.): non-opt. salinity (osmoreg.); certain pollutants and other envir. stressors that increase obligatory metabolic work	load recruitment by incr. mortality or reducing growth of pre-recruits: joint effects of controlling, limiting, and lethal factors on individ., esp. predation (incl. cannibalism)	challenge habitat/ecosystem resiliency, homeostasis: overharvest of stocks, competitive land-use practices
Lethal	completely interdict metab. 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 catastrophy, e.g., a meteor strike
Directive	"unload" metab., 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

dominate recruitment at the latitudinal limits of range; whereas, limiting and masking factors are more likely to assume the dominant roles at the center of geographic range. 2) Near the center 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. 3) 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.

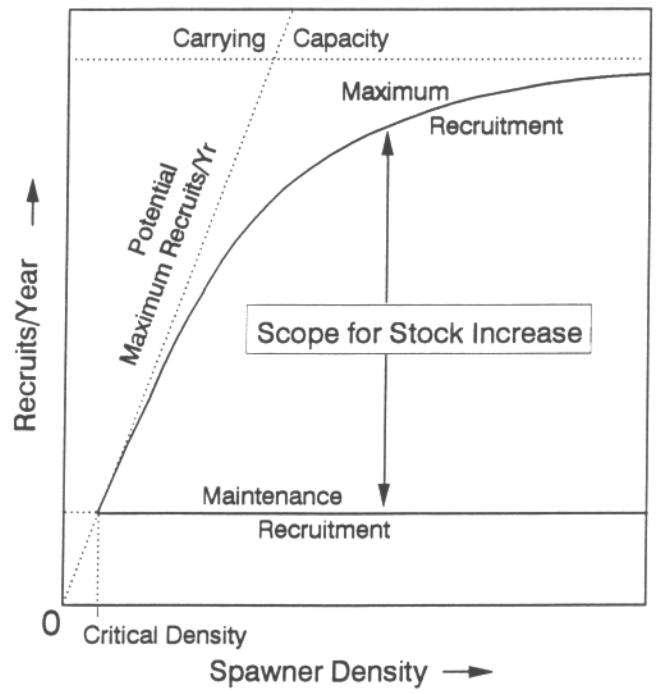

Figure 1. Idealized (Beverton-Holt-like) spawner-recruit relationship, and emergence of scope for population growth. From Neill et al. (1994).

The ideas introduced here are treated more fully in a paper being published elsewhere (Neill et al., 1994).

References

Fry, F.E.J. 1947. Effects of the environment on animal activity. University of Toronto Studies, Biological Series 55:1-62.

Neill, W.H., J.M. Miller, H.W. Van Der Veer, and K.O. Winemiller. 1994. Ecophysiology of marine fish recruitment: A conceptual framework for understanding interannual variability. Netherlands Journal of Sea Research.