

Life history strategies, population regulation, and implications for fisheries management¹

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Abstract: Life history theories attempt to explain the evolution of organism traits as adaptations to environmental variation. A model involving three primary life history strategies (endpoints on a triangular surface) describes general patterns of variation more comprehensively than schemes that examine single traits or merely contrast fast versus slow life histories. It provides a general means to predict a priori the types of populations with high or low demographic resilience, production potential, and conformity to density-dependent regulation. Periodic (long-lived, high fecundity, high recruitment variation) and opportunistic (small, short-lived, high reproductive effort, high demographic resilience) strategies should conform poorly to models that assume density-dependent recruitment. Periodic-type species reveal greatest recruitment variation and compensatory reserve, but with poor conformity to stock–recruitment models. Equilibrium-type populations (low fecundity, large egg size, parental care) should conform better to assumptions of density-dependent recruitment, but have lower demographic resilience. The model's predictions are explored relative to sustainable harvest, endangered species conservation, supplemental stocking, and transferability of ecological indices. When detailed information is lacking, species ordination according to the triangular model provides qualitative guidance for management and development of more detailed predictive models.

Résumé : Les théories démographiques cherchent à expliquer l'évolution des caractéristiques des organismes comme des adaptations à la variation du milieu. Un modèle qui comprend trois stratégies démographiques primaires (les points extrêmes d'une surface triangulaire) décrit les patrons généraux de variation de façon plus complète que les méthodes qui examinent des caractéristiques individuelles ou qui se limitent à classifier les cycles biologiques en « rapides » et « lents »; il fournit une méthodologie générale pour prédire a priori les types de populations qui possèdent des degrés faibles ou élevés de résilience démographique, de potentiel de production et de conformité au contrôle lié à la densité. Les stratégies périodiques (forte longévité, fécondité élevée, importante variation du recrutement) et opportunistes (petite taille, vie courte, effort reproductif élevé, grande résilience démographique) devraient mal s'accommoder des modèles qui présupposent un recrutement relié à la densité. Les espèces de type périodique possèdent la variation de recrutement et la réserve de compensation les plus grandes, mais elles s'ajustent mal aux modèles de stock–recrutement. Les populations de type équilibré (fécondité basse, oeufs de grande taille, soins parentaux) devraient s'ajuster mieux aux présuppositions de recrutement relié à la densité, mais elles ont une résilience démographique plus faible. Les prédictions du modèle sont examinées en ce qui a trait à la récolte soutenable, la conservation des espèces menacées, le stockage d'appoint et la transférabilité des indices écologiques. Quand il manque de renseignements précis, une ordination des espèces d'après le modèle triangulaire fournit un guide qualitatif pour la gestion et la mise au point de modèles prédictifs plus détaillés.

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Introduction

Life history theories seek to explain the evolution of organism traits as adaptive responses to environmental variation and differential mortality or resource allocation to life

stages (Roff 1992; Stearns 1992). Life history theories also examine how traits are intercorrelated and constrained by ecological factors. Reproductive effort varies in relation to mortality schedules (Cole 1954; Murphy 1968; Benton and Grant 1999), and reproductive allocation to optimize off-

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spring size versus numbers is influenced by the scale of environmental variation (Southwood 1988), availability of resources for early life stages (Pianka 1970), or the degree of environmental stress (Grime 1977). Life history theories also predict demographic response to disturbances at variable spatial and temporal scales. For example, organisms may adopt strategies of iteroparity or migration to maximize reproductive success in variable environments (Murphy 1968; Roff 1988; Orzack and Tuljapurkar 1989).

Life history theories have been invoked to predict relative influences of density-dependent versus density-independent ecological influences on life stages and age classes (Reznick et al. 2002). The most notable example is the theory of r - and K -selection (MacArthur and Wilson 1967; Pianka 1970), in which populations possessing the K -selected suite of attributes (delayed reproduction, low fecundity, large parental investment in individual offspring, long life-span) are expected to have higher fitness under density-dependent influences (competition, predation) than species having the opposite suite of r -selected traits. Interactions among species traits, ecological influences, and population dynamics can be simulated by manipulating organism traits and ecological variables using matrix-based (e.g., Orzack and Tuljapurkar 1989; Grant and Benton 2000; Van Tienderen 2000) and individual-based models (e.g., Van Winkle et al. 1993). A limitation of these models is that variables generally are manipulated independently without knowledge of the nature of functional constraints among suites of life history traits. Species life history attributes have been examined in relation to diverse fisheries management challenges, including environmental assessment (Schlosser 1990), extinction risk (Parent and Schriml 1995; Jennings et al. 1999b; Reynolds et al. 2005), and resilience to harvest and other human-induced sources of mortality (Beverton 1992; Van Winkle et al. 1993; Rochet et al. 2000). My objective here is to explore fisheries management implications of a triangular model of life history evolution that identifies adaptive suites of attributes by taking into account functional constraints (Winemiller 1989, 1992; Winemiller and Rose 1992).

A model of primary life history strategies

Several models ordinate species according to patterns of life history variation. Perhaps the best known is the r - K selection model. Tests of this model seem to have yielded as much negative as positive evidence (Stearns 1992). Some of these experimental tests proposed that K -selection should select for larger population carrying capacity (K). Yet, the original K -selection model (Pianka 1970) merely proposed that selection in chronically resource-limited and (or) predator-rich habitats should favor certain traits, such as parental care and higher juvenile and adult survival, attained at the expense of early investment in reproductive effort and large clutches of small offspring. Another problem is that the r - K continuum fails to recognize additional axes of variation required to describe patterns of interspecific variation in nature (Winemiller 1992; Reznick et al. 2002). Several two-dimensional, triangular models of life history evolution have been proposed. Grime (1977) proposed a model for plants that contrasted ruderal (r -selected with high reproductive allocation), competitive (K -selected with greater investment in

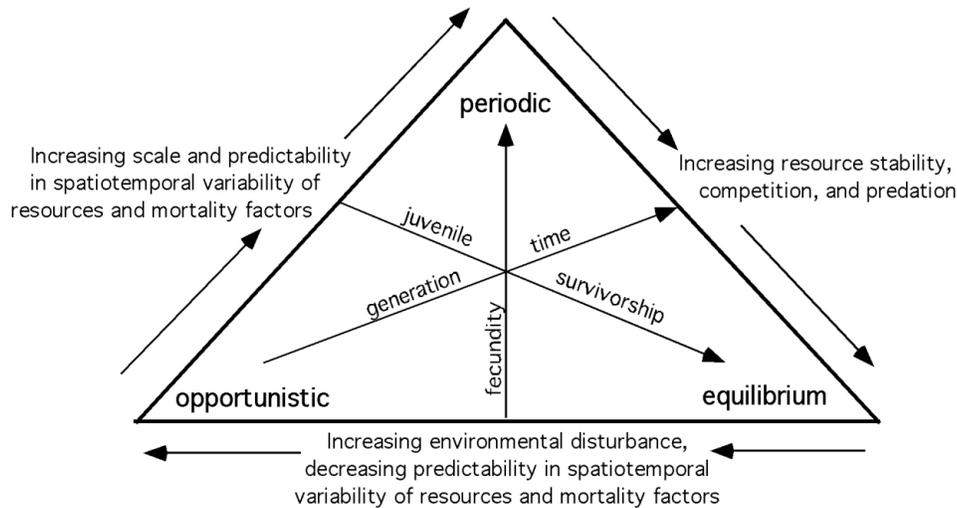
soma), and stress-resistant species (plants with traits of adults and (or) seeds that enhance fitness in harsh habitats). Attributes of stress-resistant species essentially are more extreme expressions of those defining the competitive strategy. Based largely on evidence from insects, Southwood (1977, 1988) and Greenslade (1983) proposed a triangular model of adversity selection that shares many features of the Grime model. In these models, environmental gradients of productivity and disturbance influence resource availability and stress.

Based on evidence from Pacific fishes, Kawasaki (1980) proposed a triangular model of fish life history strategies that contrasts small, early maturing species having high reproductive effort, and low batch fecundity (Type IA) with larger species possessing later maturation, longer life-spans, and high fecundity (Type II). The third strategy (Type IB) possesses attributes that are essentially intermediate. According to Kawasaki (1980), Type IA species are favored when environmental variation is "irregular" (i.e., variable in the short term), with recruitment dynamics also being irregular. Type IB species are favored when environmental variation occurs over longer periods, and Type II species are favored when environmental variation is low and predictable.

Based on patterns of life history variation in tropical freshwater fishes (Winemiller 1989) and North American freshwater and marine fishes (Winemiller and Rose 1992), a triangular model of life history evolution was proposed to explain adaptive response to environmental variation in terms of its predictability and scale relative to generation time. The Winemiller and Rose (W&R) model recognizes three endpoint strategies: (i) opportunistic (short generation time, high reproductive effort, small body size, low batch fecundity, and low investment per offspring), (ii) periodic (long generation time, moderate reproductive effort, large body size, high batch fecundity, and low investment per offspring), and (iii) equilibrium (moderate to long generation time, low reproductive effort, variable body size, low batch fecundity, and high investment per offspring). This model appears superficially similar to Kawasaki's (1980) model; however there are major differences. Kawasaki's Type IA blends attributes of opportunistic (short life-span, high reproductive effort, high r) and equilibrium (slow growth rate, large eggs, parental care) endpoint strategies. Kawasaki's Type IB strategy is a mixture of equilibrium (intermediate age of maturity, low fecundity, low r) and periodic (long life-span, high growth rate) endpoints. Kawasaki's Type II strategy corresponds to the periodic strategy, but his model proposes that stable and predictable habitats select for this suite of attributes, whereas the W&R model proposes adaptation in response to large-scale periodic variation in space or time.

Each endpoint strategy in the W&R model can be viewed as an adaptive suite of attributes associated with maximizing the per capita rate of population increase, r , according to the demographic relationship $r \approx \ln(\sum l_x m_x)/T$, where l_x is age-specific survivorship, m_x is age-specific fecundity, and T is generation time. This relationship actually defines a set of life history trade-offs (Laughlin 1965; Southwood et al. 1974; Kawasaki 1980). Relative investment in tissues-activities that increases survivorship also reduces lifetime fecundity (greater allocation to soma and maintenance functions reduces alloca-

Fig. 1. Triangular life history model illustrating environmental gradients selecting for endpoint strategies defined by optimization of demographic parameters generation time (T), age-specific survivorship (l_x), or age-specific fecundity (m_x) (from Winemiller 1995).



tion to gametes and associated reproductive tissues and functions) and increases generation time (greater investment in somatic growth prior to maturation increases the interval to maturation). Larger reproductive allocation in the form of greater fecundity would reduce survivorship (given lower relative investment in soma and maintenance processes) and would increase generation time (high fecundity can be achieved only by delaying reproduction until a sufficiently large size has been attained). Reduction in generation time as a means to increase r would reduce both survivorship (because reproduction takes place sooner with less investment in soma and maintenance) and fecundity (because earlier maturing organisms are smaller with less biomass and energy available to produce large clutches of eggs). The result of these functional trade-offs is a species ordination according to suites of life history traits that defines an adaptive surface within the space defined by juvenile l_x , m_x , and T (Winemiller 1992; Winemiller and Rose 1992).

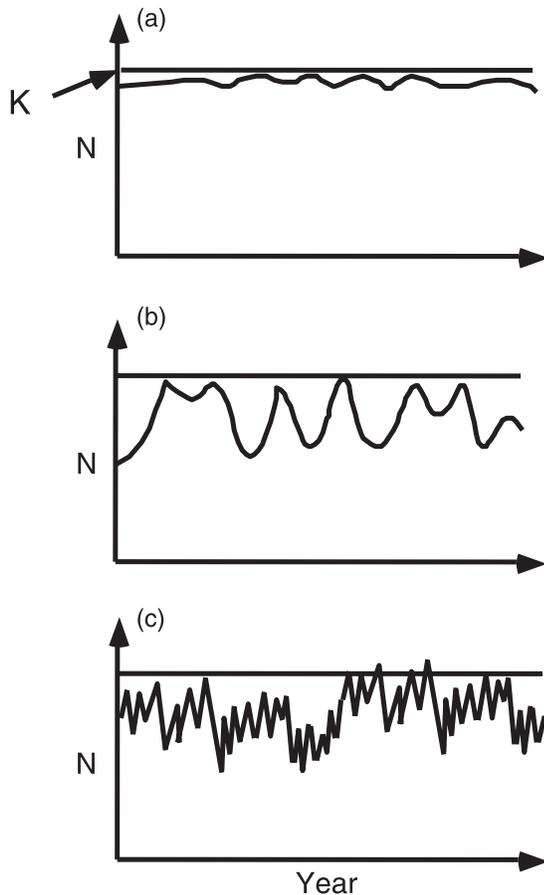
Environmental gradients likely to select for each endpoint strategy are outlined (Fig. 1). Given other factors held constant, the intrinsic rate of increase is more sensitive to changes in generation time than to changes in fecundity or survivorship (Lewontin 1965). Thus, the opportunistic suite of attributes could be considered a colonizing strategy that should maximize fitness in environmental settings dominated by density-independent, ecological influences. Such conditions might be expected in productive habitats subjected to frequent and intense disturbances, such as ephemeral pools, intermittent streams, and salt marshes. Indeed, these habitats often are dominated by species, such as poeciliids (livebearers) and fundulids (killifish), with generation times of only a few months.

The periodic strategy maximizes fitness when environmental variation influencing early life stage survival is periodic (relatively predictable) and large scale (Winemiller and Rose 1992, 1993). In a sense, the periodic strategy could be considered an intergenerational form of bet-hedging, whereby reproductive effort is distributed over several reproductive bouts when variation in juvenile survival is greater than variation in adult survival. By allocating reproductive output across

multiple years, some individuals achieve reproductive success despite long intervals with environmental conditions unfavorable for early life stage survival. The periodic strategy seems to be the dominant strategy observed in fishes, arthropods, mollusks, and plants (Winemiller 1992), which probably reflects ubiquitous large-scale spatial (patchiness) and temporal (seasonality) heterogeneity of ecosystems. Temperate and tropical lotic ecosystems are seasonal, and tropical marine systems are characterized by spatial heterogeneity over large scales (e.g., convergence zones, gyres, coastal currents, and coastal depth and salinity gradients) or are subject to climatic events such as storms and El Niños. Large-scale environmental variation is believed to drive variation in early life stage recruitment for periodic-type marine fishes (e.g., Kawasaki 1985; Hedgecock 1994; Gilbert 1997).

The equilibrium endpoint is essentially the K -selected strategy of high investment in soma and individual offspring at the expense of maximizing per capita growth via reduction of generation time or increases in fecundity. This strategy is a comparatively inefficient means of maximizing the intrinsic rate of increase and appears to be favored in environmental settings having chronic or frequent density-dependent influences (K -selection) or in stressful habitats (adversity selection). The equilibrium strategy is common among fish taxa inhabiting caves (e.g., branchial-brooding amblyopsids), tropical lakes (e.g., mouth-brooding cichlids), and coral reefs (e.g., brood-bearing syngnathids, live-bearing elasmobranchs). It is important to keep in mind that diverse life history strategies may be present among species inhabiting a single habitat (Winemiller 1989). Species with different ecological niches, body sizes, anti-predator defenses, etc., perceive and respond to components of environmental variation in different ways. For example, a large-bodied species, such as a sciaenid, may migrate between an estuary and coastal waters in response to spatial and seasonal variation in food resources and abiotic conditions at the landscape scale. These periodic strategists produce large batches of small eggs that disperse passively and yield high recruitment under appropriate environmental conditions that occur once a year or perhaps even once a decade. In contrast, small

Fig. 2. Predicted population dynamics in relation to a hypothetical carrying capacity (K) imply the relative strength and frequency of density dependence. (a) Equilibrium-type population; (b) periodic-type population; (c) opportunistic-type population.



killifish in the same estuary are restricted to shallow marginal habitats at a local scale. High variance in abiotic (water depth and quality) and biotic (food and predator densities) conditions imposes high and often unpredictable mortality on both juveniles and adults of these relative opportunistic strategists.

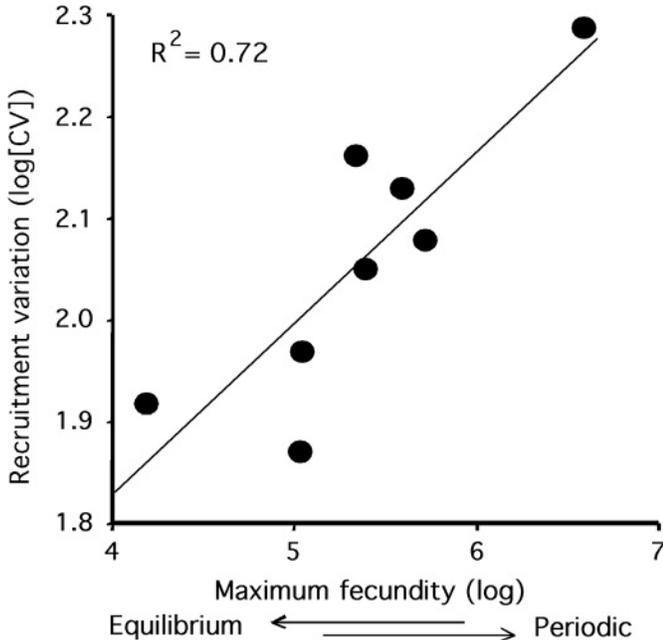
The triangular model of life history evolution was derived from interspecific comparisons and therefore predicts general relationships. Nonetheless, the model's adaptive surface recognizes fundamental constraints. Other aspects of life history variation can be examined in addition to these primary demographic strategies. For example, Balon (1975) defined reproductive guilds based on spawning behavior and specific environmental needs of early life stages. The triangular model qualitatively predicts population responses in relation to a hypothetical carrying capacity, which implies the relative strength or frequency of density dependence influencing population regulation. Here, density dependence includes behavioral, physiological, and demographic responses to predators and interspecific competitors, as well as intraspecific resource competition. Populations of opportunistic strategists would be expected to be well below K most of the time and frequently subject to density-independent sources of mortality (Fig. 2). Periodic strategists should show greater interannual recruitment variation than equilibrium strate-

gists, the latter having relatively low variation with mortality and reproductive success being more strongly influenced by density-dependent influences (Fig. 2). During occasional years of high recruitment, periodic strategists may reach densities that lead to significant density-dependent responses in growth and survival, especially among immature age classes. In long-lived periodic strategists, unusually strong annual cohorts may dominate the adult population for many years. Large spatial variation in environmental conditions can yield large intra-annual variation in recruitment success (Hedgecock 1994), and larger fishes with high fecundity may contribute disproportionately to recruitment (Berkeley et al. 2004). Such patterns are predicted to be weaker for species with opportunistic and equilibrium-type life history strategies.

Is recruitment variation greater for populations with the periodic strategy and lower for populations with the equilibrium strategy? One way to test this hypothesis is to plot recruitment variation (coefficient of variation for annual recruitment) as a function of batch fecundity for a group of related species (i.e., high batch fecundity distinguishes the periodic strategy). A strong relationship is revealed between recruitment variation and fecundity for North American freshwater perciforms (Fig. 3), a group that spans a broad spectrum of strategies. In this data set, all of the low-fecundity species are associated with the equilibrium strategy (delayed reproduction, large egg size, parental care), so that fecundity alone contrasts an equilibrium–periodic gradient. Among North American freshwater perciforms, periodic strategists tend to have higher interannual recruitment variation than equilibrium strategists. Mertz and Myers (1995) found no relationship between the standard deviation of $\log(\text{recruitment})$ versus $\log(\text{fecundity})$ for 41 marine and anadromous fish species. Analyses performed by taxonomic orders yielded weak positive but statistically nonsignificant relationships. Most of the species in their data set were positioned far to the periodic end of the spectrum (fecundities $\geq 15\,000$), and only a single example positioned near the equilibrium endpoint was included (*Squalus acanthias*, fecundity = 3). Rickman et al. (2000) found higher fecundity was significantly associated with higher recruitment variation for 13 of 14 comparisons among exploited marine stocks. When this analysis was repeated without regard for evolutionary relatedness, the trend was not statistically significant.

Stock–recruit (S – R) relationships provide an effective means to view compensatory density dependence in population regulation. The strength of empirical fit to the S – R model indicates the degree to which recruitment is explained by stock density. In theory, the empirical fit should be strong for species with extreme forms of the equilibrium life history strategy and poor for species having opportunistic and periodic attributes (Fig. 4). Moreover, the shape of the S – R curve predicts the manner in which the population responds to variation in stock density, and species with different life history strategies logically should respond differently. Compensation potential, or the capacity for a population to respond rapidly to density-dependent changes at low population abundance, is indicated by the steepness of the slope of the Ricker S – R curve near the origin (Myers et al. 1999; Myers 2001). Rose et al. (2001) grouped 249 populations from the S – R database of Myers et al. (1999) (<http://fish.dal.ca/~myers/data>).

Fig. 3. Plot of recruitment variation as a function of fecundity for North American freshwater perciforms (centrarchid and percid data from R.A. Myers' stock–recruitment database, <http://fish.dal.ca/~myers/data.html>; when multiple databases were available for a species, only the longest time series was analyzed).



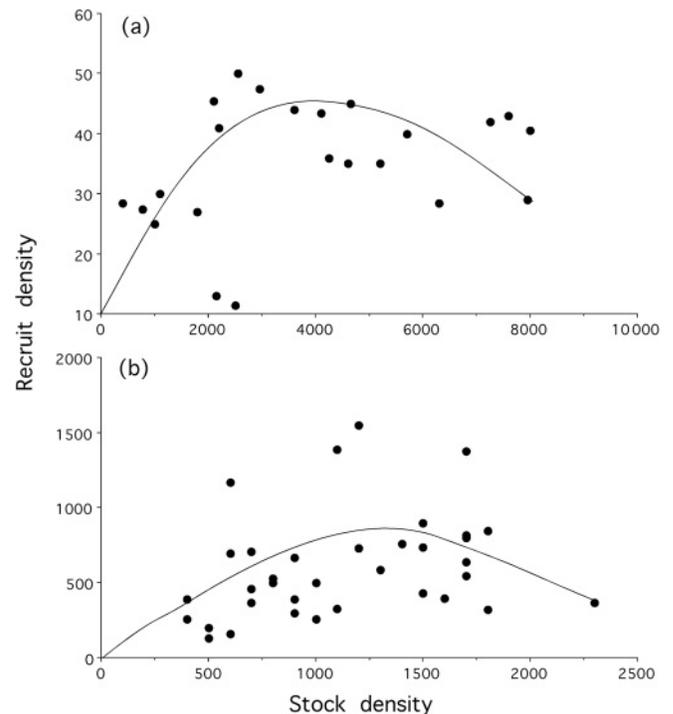
html) according to life history strategies and examined the mean compensation potential (steepness) for each group. As hypothesized, periodic species tended to be associated with a steeper slope than equilibrium and opportunistic strategists. In addition, equilibrium strategists tended to have lower residual variation in fits to S–R relationships, but variance around mean values was high for all three groups. It should be noted that none of the species in this dataset could be considered extreme forms of the opportunistic or equilibrium strategies. An extreme example of the equilibrium strategy would be mouthbrooding and substrate-nesting cichlids of the African rift lakes. For example, several *Lamprologus* species of Lake Tanganyika are entirely dependent on empty snail shells for refuge from predators and for nesting (Konings 1998), and it is likely that shell availability determines population size.

The remainder of this perspective will explore implications of the triangular life history model for fisheries management. I will briefly cover four general issues: (i) sustainable harvest, (ii) conservation of rare and threatened species, (iii) stock enhancement via supplemental stocking, and (iv) equilibrium assumptions of ecological indices. Other issues, including marine reserves and invasive species, also could profit from insights gained by life history theory, but space limitations restrict discussion of those topics.

Sustainable harvest

The traditional view of sustainable harvest was well expressed by McFadden (1977): “Experience with the world’s major stocks has proven both that they have the capacity to withstand impressively high levels of exploitation and pro-

Fig. 4. Examples of data scatter around Ricker stock–recruit relationships. The plot in (a) is for a relative equilibrium strategist, brown trout (*Salmo trutta*) from Black Brows Beck, English Lake District (Elliot 1994), in which stock abundance is the number of fertilized eggs per 60 m² and recruit abundance is the number of age-1+ fish per 60 m² (coefficient of determination = 0.21). The plot in (b) is for a relative periodic strategist, pike (*Esox lucius*) in South Windermere Lake, English Lake District (Kipling 1983), in which stock abundance is kilograms of mature females and recruit abundance is total number of age-2 fish.



duce substantial surplus at population levels well below their pre-exploitation abundance, ...”. This view carries the implicit assumption of density compensation to sustain a population under harvest. The degree to which r is elevated, via compensatory adjustments in population birth (b) and death (d) rates, above replacement level ($r = 0$) defines harvestable surplus yield.

Stock–recruit models have been used extensively in fisheries management to provide a basis for estimating density compensation, maximum or optimal sustainable yield, and biological reference points. This equilibrium view of population dynamics has long been questioned (e.g., Andewartha and Birch 1954; Fletcher and Deriso 1988; Hixon et al. 2002). Because stock–recruitment time-series data are not independent, any persistent cause of low recruitment will result in reduced spawning-stock abundance (Gilbert 2002). In such instances, analyses would yield the erroneous appearance that low spawning-stock abundance yields low recruitment. As noted previously, empirical data generally provide very poor fits to S–R models (Myers et al. 1990; Rose et al. 2001). In these instances where environmental variation has a strong influence on recruitment dynamics, sustainable-yield targets derived from S–R models provide an unsound basis for management. Exceptional cases might involve equilibrium strategists in relatively small, closed ecosystems

(e.g., trout residing in a stream pool, or sunfish in ponds as per the Swingle paradigm discussed below). Christensen and Goodyear (1988) and Hilborn and Walters (1992) discussed potential sources of bias in S–R analyses and quantitative methods for evaluating them, such as time-series analysis of model residuals. They cautioned that management strategies targeting constant stock abundance will not be appropriate in most cases. They also contended that analyses should focus on catch variability just as much as the average catch. Koslow (1992) examined the influence of fecundity and variance in natural mortality during the pre-recruit period on characterization of S–R relationships with strong and weak density dependence. Because small variation in early vital rates result in large changes in population dynamics, simple deterministic S–R models are not applicable to fishes with high fecundity and small egg size (periodic strategists), yet such species comprise the great majority of commercial fish stocks.

Management of most of the world's large commercial fisheries is confronted with "the recruitment problem". What factors and mechanisms limit recruitment at various intervals of the life cycle? For periodic-type species, small differences in mortality of early life stages have huge potential to influence stock abundance. A variety of exogenous factors (e.g., abiotic environmental variation, fluctuations in food supplies or predator densities) are implicated (Cushing 1990; Leggett and DeBlois 1994; Myers 1998). The predictive capability of a stock–recruitment model for American shad increased from 3%–90% when abiotic factors were introduced (Crecco et al. 1986). Fromentin et al. (2001) analyzed 136 time series of juvenile cod and concluded that populations are regulated by an interaction between density-dependent mechanisms and stochastic abiotic factors. Thus, prediction of population dynamics of periodic strategists is confronted by two fundamental problems. Variance in early life stage abundance is almost impossible to estimate with the precision necessary to make even crude population projections, and key abiotic driving variables are difficult to estimate over all but the shortest of time intervals. Large uncertainty is an unavoidable reality for quantitative projections involving periodic-type species, but stochastic models at least can permit managers to assign broad confidence limits around target values (Lande et al. 2003).

In contrast with species near the periodic endpoint, equilibrium and opportunistic strategists should have population dynamics affected by factors influencing later life stages just as much as those influencing early stages. However, these influences should be more density dependent for species with equilibrium life history attributes. For example, both the reproductive success of males and over-winter survival of age-0 smallmouth bass (*Micropterus dolomieu*) at high latitudes is strongly influenced by foraging success and growth during the preceding summer and fall (Shuter et al. 1980; Wiegmann et al. 1992). All populations are subjected to density-dependent population regulation, but the key issue is the relative strength and frequency of these influences. A statistical analysis of diverse taxa with opportunistic life histories showed strongest density-dependent changes in vital rates at low population levels (Stubbs 1977), whereas density-dependent changes were stronger at population levels near carrying capacity for mammals and birds, two groups

that tend to be affiliated with the equilibrium endpoint strategy (Fowler 1981). Guppies (*Poecilia reticulata*) have extreme opportunistic history attributes (early maturation, high continuous reproductive effort); yet detailed experimental research in Trinidad has yielded evidence of interactions among population density, predation level, and food availability (Bronikowski et al. 2002).

Few equilibrium-type fishes are targets for commercial fisheries, and S–R models generally have not been applied to these species. Management methods for sportfishes in small lakes in North America pertain to circumstances in which an assumption of strong density-dependent regulation is probably valid. Small temperate lakes are closed systems with low biological diversity and relatively simple food webs. The Swingle (1956) paradigm of pond management relies on manipulation of predator and prey populations to achieve a balanced community in which individual growth rates are maximized and population fluctuations are minimized. Over the past 50 years, the Swingle paradigm has been developed into a fairly standard technology that has yielded satisfactory results in many regions of the United States, particularly in the South and Midwest (Willis et al. 1993). This technology essentially consists of stocking one or a few species of predator and prey at prescribed densities (Flickinger and Bulow 1993). Fish growth rates, condition, and population size structure are periodically monitored to determine the degree to which predator or prey populations may be showing signs of density-dependent responses to overcrowding and food limitation. The goal is to achieve a balance in the size ratios and densities of predator and prey populations (proportional stock densities).

Why has the technology for managing small lakes succeeded while more extensive efforts to manage the world's commercial marine stocks have been generally viewed as failures? Again, we must recognize that lakes are small, closed ecosystems with few species. This characteristic permits greater relative control over system components, but just as importantly, it greatly simplifies predictions regarding mechanisms controlling population dynamics. It is probably no accident that the Swingle paradigm employs equilibrium-type species for small lake management; sunfishes (Centrarchidae) are recommended as prey for black bass (Centrarchidae) or channel catfish (Ictaluridae). All of these species are substrate-nesting brood guards with life history strategies that should be largely consistent with assumptions of strong density dependence for both juvenile and adult life stages. Similar success has been achieved in management of small lakes in South Africa using brood-guarding tilapia as prey and brood-guarding haplochromine cichlids (*Serranochromis* spp.) as predators. In South America, small lakes generally are stocked with nonindigenous tilapia as forage for brood-guarding peacock cichlids (*Cichla* spp.).

In contrast with species employed in small lake management, most of the species involved in the large commercial fisheries of the world are periodic strategists, usually in an extreme form. These populations should conform poorly to predictions of density-dependent equilibrium dynamics. To a great extent, forecasting of stock dynamics means predicting recruitment dynamics in response to large-scale abiotic drivers, most of which are highly unpredictable. Moreover, these commercial species inhabit large, open ecosystems, such as

oceans, estuaries, large lakes, and floodplain rivers. These systems are heterogeneous, dynamic, and biologically diverse, all of which contribute to more complex interrelationships among variables influencing stock dynamics. This problem is now widely recognized, yet stock management is too often based on strong assumptions of density compensation. Williams and Shertzer (2003) recently analyzed the sensitivity of commonly used biological reference points to life history variation captured by scale invariant parameters (*sensu* Charnov 1993; Charnov et al. 2001). They found that biomass-based reference points were relatively insensitive to life history variation, but a mortality-based reference point was highly sensitive. Moreover, they cautioned that all of the biological reference points were sensitive to the choice of S–R function and the assumed level of population growth at low density (i.e., steepness), which renders universal reference values untenable.

So what should we do? In his last publication, Ray Beverton (1998) provided advice for managing exploited fish stocks in the face of inherent uncertainty. In the short term, we can forecast and track oncoming year classes. For the long term, objectives and targets should be reviewed frequently for medium- and long-lived species, and given our inability to make precise predictions to guide sustainable exploitation, fisheries should not overcapitalize. Beverton's advice, although general, provides a basis for developing more sophisticated means of setting and revising targets following the precautionary principle and adaptive management (Hilborn and Walters 1992). Rose et al. (2001) reviewed density compensation in fish populations and concluded that estimates of density compensation will remain controversial unless underlying mechanisms are understood to some degree. They advocated an approach that integrates life history theory, process-level understanding of mechanisms, analysis of field data, and individual-based simulation modeling. Such efforts require considerable time and resources. In the absence of detailed information, ordination of species according to the triangular life history model allows for rapid, qualitative assessments to guide management as well as research designed to efficiently fill information gaps.

Rare and threatened species

Qualitative predictions from life history theory can greatly assist management strategies for rare and threatened species. In many countries, a prime directive in most regulations designed to protect endangered species is a requirement to limit the take of rare species. Take can be construed as removal or killing of individual organisms, but it also includes indirect means of removal, such as injury or impairment to organisms or essential habitats that support their survival and reproduction. Conservation of rare species by limiting their take implies that each individual in the population is valuable in the sense that its removal will lead to further decline in numbers. In other words, compensatory density dependence is assumed to be very weak.

An assumption of weak or no density compensation is likely not true in many cases, and equilibrium-type species, in particular, are expected to exhibit strong density dependence. Even the large influence of stochastic, abiotic factors on recruitment dynamics of periodic species does not preclude

influence from density-dependent ecological factors. For example, Myers and Barrowman (1996) analyzed 364 S–R time series and found significant relationships between spawner abundance and recruitment levels when a sufficiently broad range of spawner abundances was encompassed. Thus, an important issue for conservation of endangered species is to determine for which species and under what circumstances compensatory mechanisms facilitate population resilience. At low population size, compensatory factors may be cancelled by effects of inbreeding or enhanced sensitivity to environmental variation. Population turnover rate is another key factor that influences resilience. Larger species have longer generation times and greater vulnerability to exploitation because they possess lower potential rates of population increase (Winemiller and Rose 1992; Jennings et al. 1998, 1999a).

What are the attributes of endangered species relative to the triangular model of primary strategies? Review of the current US Fish and Wildlife Service list of 116 fish species listed as threatened or endangered reveals some striking patterns. First, 102 species (88%) are freshwater fishes, 10 species (9%) are anadromous, and 4 species (3%) inhabit nearshore coastal habitats. Freshwater habitats and watersheds have been greatly perturbed, including introductions of invasive nonindigenous species. The status of rare marine species has not yet been assessed to the same extent as freshwater fishes, but even so, impacts on freshwater fishes seem to be particularly serious (Harrison and Stiassny 1999).

Second, 82 species (71%) are small (maximum standard length <15 cm). This percentage of small fishes is greater than the percentage based on the native North American freshwater fish fauna as a whole (64%, based on data compiled by Lee et al. 1980), but not significantly greater ($\chi^2 = 1.12$, $df = 2$, $P = 0.29$). Third, 46 endangered species (40%) can be classified as opportunistic species (maturity ≤ 1 year, high reproductive effort often with multiple spawning bouts), 42 species (36%) are periodic strategists (maturity ≥ 1 year, high fecundity often with pulse spawning), and only 28 species (24%) are equilibrium strategists (relatively large eggs, parental care). Percentages for the continental freshwater fish fauna (estimated in the same manner using information from Lee et al. 1980 and regional fish compendia) are 30% (opportunistic), 54% (periodic), and 17% (equilibrium). Thus, opportunistic and equilibrium-type species tend to be disproportionately threatened ($\chi^2 = 4.64$, $df = 2$, $P = 0.098$).

The observation that more than two thirds of endangered fishes have relatively opportunistic life histories yields an apparent paradox, since these populations should possess a high degree of demographic resilience (low generation times and high reproductive effort yielding high intrinsic rates of increase). But the paradox is solved when one considers the specific circumstances threatening these species. Most of these species occur either in relict habitats in the arid southwestern United States (e.g., *Cyprinodon* and *Gambusia* spp.) or in relatively isolated headwater streams in the southeastern United States (e.g., *Notropis*, *Noturus*, and *Etheostoma* spp.). Small desert fishes are endangered because they are the last survivors from a fauna that was once more diverse during mesic conditions of the past (Smith et al. 1995). High demographic resilience has allowed them to persist in the face of extinctions of species requiring larger and more sta-

ble or predictable habitats. The desert pupfish (*Cyprinodon macularius*) provides a good example. The only remaining population survives in an isolated pool in the Death Valley Basin. Prior to the Pleistocene, the basin received water from extensive drainage systems in the surrounding uplands, but today it is one of the driest places on earth. The species continues to survive with a precarious foothold in a water-filled limestone cavern measuring 3 m × 6 m. Human intervention has managed to stave off extinction of the desert pupfish (Ono et al. 1983). Similarly, populations of opportunistic-type fishes in southeastern streams also should be highly resilient, provided there are refugia from which individuals can reinvade habitats following disturbances. These species frequently are threatened by total habitat destruction (hydrologic alteration, siltation, and pollution) and invasive species.

A second general grouping of threatened fishes identifies relatively large, periodic strategists, the type of life history that should show high recruitment variation with low conformity to density-dependent recruitment expectations, yet also have highest compensatory potential. Endangered periodic fishes fall into two groups: anadromous species and species that inhabit large rivers, mostly in the western United States. Migratory behavior tends to be associated with extreme forms of the periodic strategy (Winemiller and Rose 1992), and a major impact on populations of these fishes is dams and degradation of instream habitats and watersheds. Many of these threatened periodic species migrate long distances to complete their life cycles (e.g., anadromous salmonids and sturgeons), and others use multiple habitats in large rivers during different life cycle stages under variable hydrological conditions (e.g., large cyprinids and catostomids).

The remaining threatened fishes have equilibrium-type life history attributes, which should conform better to predictions of density compensation. These include spring-dwelling fishes (e.g., *Prietella phreatophila*, *Speoplatyrhinus poulsoni*) and trout endemic to small drainage basins of the West (e.g., *Oncorhynchus aguabonita whitei*, *Oncorhynchus clarki seleniris*). Clearly, these fishes are endangered by loss of habitat. The basic issue is not that populations lack resilience or compensatory potential and thus cannot sustain some degree of mortality or take. The problem is loss of habitat or the ecological basis for density compensation. Thus, equilibrium-type species should be resilient to anthropogenic mortality, especially for juvenile life stages, but highly sensitive to habitat loss or degradation. For long-lived equilibrium strategists, such as sharks, the most serious problem is the lack of demographic resilience due to low natural rates of recruitment, long generation times, and low population turnover rates. Sensitivity to harvest by *K*-strategists with long recovery times has been demonstrated many times (e.g., Lewontin 1965; Adams 1980), and the plight of sensitive elasmobranch populations is gaining increasing attention (Musick et al. 2000).

Parent and Schriml (1995) analyzed a suite of 18 life history and 31 ecological variables for fishes of the North American Great Lakes to derive logistic regression models to predict whether or not species were at risk of extinction. The life history variables with greatest contributions to the model were age of maturity and life-span, and dominant ecological variables tended to be associated with spawning and feeding substrates, especially in streams. They inferred that species

maturing at 18 years or greater (in this region, these long-lived species tend to be periodic-types such as sturgeons) faced greatest extinction risk; however, it should be noted that relative to the continent as a whole, the Great Lakes region of North America does not contain a very large number of rare endemic species in relict habitats. Nonetheless, the multivariate statistical approach employed by this study would aid risk assessments of vulnerable species in other regions of the world.

Supplemental stocking of marine fishes

Supplemental stocking has long been a mainstay of fisheries management in freshwater systems. Lakes and impoundments are stocked annually by government agencies to enhance sportfishing, and cool-water streams are stocked with trout to enhance fishing opportunities. In small aquatic systems, there is a high probability that fish stocked at sufficiently large size will eventually be harvested by anglers. In small systems, overstocking can cause adverse density-dependent responses in terms of reduced individual growth rates and reproductive success. Stocking to supplement wild populations in large open ecosystems, especially marine waters, is more controversial (Grimes 1998). Anadromous species have been stocked for decades in areas where dams have impeded migrations to spawning grounds. In the United States, this practice has been essential for preserving local stocks of anadromous salmonids, although perhaps not without risk of deleterious genetic effects. Some regions have initiated supplemental stocking programs for marine species in which millions of fry or juveniles are released into coastal waters in efforts to augment wild populations. Many of the species involved in these programs are periodic strategists in an extreme form. For example, each year state agencies in Florida and Texas release millions of hatchery-reared red drum, *Sciaenops ocellatus*, into bays and estuaries of the Gulf of Mexico. The red drum has a long life-span and extremely high fecundity accompanied by high early mortality yielding high fitness variance (Turner et al. 2002). More importantly, the species displays extremely high variance in natural recruitment. Scharf (2000) analyzed a 20-year data set for juvenile red drum from nine estuaries along the Texas Gulf coast and found that intermittent occurrence of strong year classes was positively correlated across estuaries. This pattern is consistent with the notion that large-scale climatic and oceanographic factors govern early life stage survival and year-class strength in this species. Scharf also discovered evidence suggesting density dependence affecting age-0 survival, but he was unable to detect effects of a decade of stocking fingerlings on the abundance of age-0 or age-1 red drum.

Under all but the most unusual circumstances, supplemental stocking of early life stages is unlikely to translate to enhanced adult stocks for fishes with the extreme periodic strategy. During periods of poor natural recruitment, fishes stocked at a sufficiently large size might enhance coastal populations. In most cases, the numbers required to achieve this effect would be cost prohibitive. During years of strong natural recruitment, supplemental stocking would have virtually no impact on population dynamics. Under optimal conditions for early life stage survival, growth, and development,

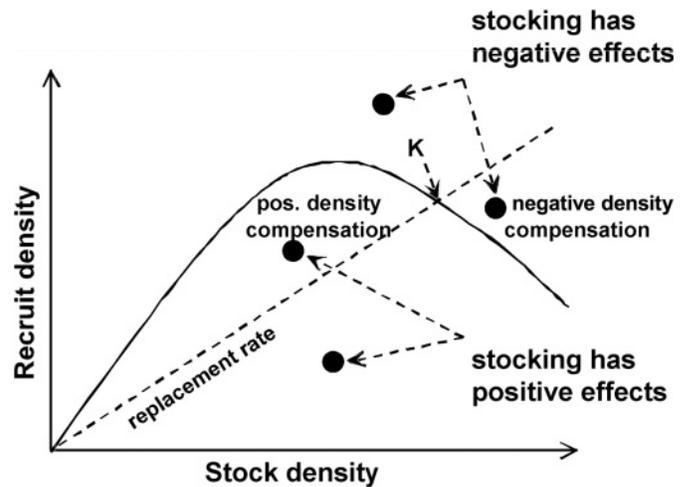
egg production from the wild spawners would swamp out hatchery production. Populations of periodic strategists frequently are dominated by occasional strong year classes.

Potential positive and negative effects of supplemental stocking can be illustrated in an S-R diagram (Fig. 5). If the population is below carrying capacity, then stocking will have positive effects on recruitment, but the amount of benefit depends on the production (trophic) capacity of the ecosystem. In diverse communities with complex food webs, competing species might have enhanced recruitment or growth from available resources during years of low natural recruitment by the target species. During years of high natural recruitment, supplemental stocking would increase the intensity of competition. Given that most years are predicted to be suboptimal for recruitment, this scenario in which stocking yields negative effects should be fairly infrequent. Nonetheless, the high cost associated with supplemental stocking of periodic-type marine fishes would be difficult to justify given doubtful benefits in terms of harvestable stocks. Of course, there could be indirect ecological benefits from stocking even during years of high natural recruitment, such as supplementing the food supply for piscivores; however, this is not likely to be a management objective. Supplemental stocking could be important for populations in which natural production has been effectively eliminated by anthropogenic causes (e.g., dams blocking spawning migrations of salmon or decimation of spawning aggregations of groupers on coral reefs).

Fisheries managers in Texas are examining the potential for supplemental stocking programs to enhance tarpon, *Megalops atlanticus*, a popular marine sportfish that has declined in Texas coastal waters in recent decades. Tarpon are extreme periodic strategists, with maturation at about age 10, a life-span of over 50 years, and batch fecundities from 1 to 20 million (Crabtree et al. 1997). As tarpon pass from a leptocephalus larval stage into the juvenile stage, they enter coastal passes and reside for variable periods of time in coastal wetlands before returning to the sea. Recruitment into wetlands varies between years and is strongly influenced by climate and coastal currents (Shenker et al. 1995). Winemiller and Dailey (2002) developed an age-based matrix model of tarpon to simulate effects of environmental variation and stocking larvae or juveniles of different ages on adult stock abundance. Only stocking huge numbers of juveniles resulted in relatively modest increases in adult stocks. When density dependence was introduced into simulations, the benefits of stocking were eliminated. Simulation of stochastic interannual variation in larval survival had a vastly greater effect on the population than either density dependence or stocking.

Supplemental stocking of opportunistic-type species generally is not practiced in large open ecosystems. In part, this is because most of these small fishes have low economic importance as harvested stocks. But this also may be due to the implicit realization that these fishes tend to have high adult mortality, short life-spans, high population turnover, and high demographic resilience. The fishes that likely would respond best to supplemental stocking are the equilibrium strategists, but would there be benefits in marine systems? Perhaps so, if the population was sufficiently depleted and restricted to a limited region or habitat. Sharks and other el-

Fig. 5. Hypothetical stock–recruit model illustrating regions in which supplemental stocking would have positive (pos.) or negative effects.



asmobranchs inhabiting coral reefs or estuaries might benefit from supplemental stocking. This is because the natural rate of recruitment, population turnover, and demographic resilience are low. Thus, elasmobranchs rank among the most vulnerable marine fishes, and many populations show signs of depletion (Musick et al. 2000). Supplemental stocking of sharks and rays has not been explored, probably because of limited direct economic incentives and high cost that would surely be associated with captive rearing.

Equilibrium assumptions of ecological indices

A variety of indices are used for assessment of the status or relative health of fish populations and aquatic ecosystems. Allocation of limited freshwater supplies is a major issue globally, and assessment of instream flow needs for aquatic ecosystems is a major fisheries management challenge (Poff et al. 1997; Richter et al. 1997). Many instream flow methodologies for protection of lotic systems assume that microhabitat availability controls fish populations (Fausch et al. 1988; Stalnacker 1993; Hardy 1998), but this assumption of density dependence probably is not true for most species most of the time. According to Orth (1987), “microhabitat availability is not the only factor limiting fish populations and does not operate continuously”. Thus, we are again confronted with the challenge of determining the species and environmental settings subject to density-dependent mechanisms of population regulation. Schlosser (1990) noted that fishes inhabiting upstream reaches of temperate streams tend to be smaller with shorter life-spans and earlier maturation than downstream species. He characterized upstream populations as rapid recolonizers of habitats following severe physical disturbances, such as scouring floods or drought. He concluded that high temporal variability of fish assemblage structure in upstream reaches makes it difficult to apply fish-based indices for assessment of subtle changes in ecosystem status due to anthropogenic disturbances. Citing similar issues, Grossman et al. (1995) concluded that “although we

should not ignore studies of the physical habitat requirements of ESUs [evolutionarily significant units], it is likely that the development of more biologically realistic, mechanistic models of habitat selection will facilitate the preservation and management of these fishes”.

Transferability of habitat suitability criteria (HSC) used for instream flow assessments is an issue that life history theory can guide. Freeman et al. (1997) examined HSC relationships with depth, velocity, substrate type, and cover for nine fish species in four unregulated streams of the piedmont and coastal plains in the southeastern United States. Indices were then tested for transferability between the four study sites plus an additional regulated river. HSC transferred reasonably well for three percid species largely restricted to riffle habitats. Tests of HSC transferability failed or were inconsistent for the other six species that commonly occupied a range of pool and riffle habitats. The six habitat generalists were mostly species that lie between the opportunistic and periodic regions of the triangular continuum (three *Cyprinella* spp., two *Percina* spp., *Etheostoma stigmaeum*). The riffle species were *Etheostoma jordani*, *Etheostoma chuckwachatte*, and *Percina palmaris*, species with lower batch fecundities and tending to be positioned between the opportunistic and equilibrium regions of the continuum. Riffles are structurally complex habitats dominated by small species with opportunistic or equilibrium-type characteristics. Equilibrium-type species, such as darters (Percidae), sculpins (Cottidae), and madtoms (Ictaluridae) in North America and armored catfishes (Loricariidae) in South America, frequently occupy microhabitats under or near rocks that provide protection from swift currents as well as from predators. Abundances of these populations may be influenced by the availability of suitable microhabitats. For example, Baltz et al. (1982) demonstrated competition for riffle microhabitats among speckled dace (*Rhinichthys osculus*) in a California stream, and Petty and Grossman (1996) found that habitat use by mottled sculpin (*Cottus bairdi*) in an Appalachian stream was associated with patterns of food availability.

Indices of biotic integrity (IBIs) have become important tools for rapid ecological assessment of streams (Karr et al. 1986). IBIs infer a normal or ideal community structure that should occur in an unimpacted habitat. A numeric scale of overall ecological health is generated by summing values from a series of scaled factors, such as the percentage of species intolerant to degraded water quality and the percentage of species that are top carnivores. Because they can provide relatively rapid and inexpensive ecological assessments, IBIs have been adopted by natural resource agencies worldwide. Yet little research has been conducted to determine the mechanisms that determine population and community structure, such that the conditions that create a normal community are usually not understood. This lack of understanding about processes and mechanisms is overcome by using reference sites as means of calibrating the IBI scale to the ideal or unimpacted context.

Stream fish communities are known to respond to a variety of abiotic and biotic factors that vary stochastically or periodically on different temporal and spatial scales (Horowitz 1978). Fish assemblage structure in an Appalachian stream was more strongly associated with hydrological variation than with biotic variables indicative of species interactions

(Grossman et al. 1998). In a 10-year study of a California stream, discharge differentially influenced year-class strength and relative abundances among species with different life history strategies (Strange et al. 1992). Assemblage structure in a tropical lowland stream was associated with both abiotic and biotic factors that varied with wet-dry seasonality (Winemiller 1996a). Life history strategies influenced species responses to environmental fluctuations and biotic interactions (Winemiller 1989, 1996a). Similar patterns and associations have been described for other low-gradient systems in tropical (Ponton and De Mérona 1998; Mérigoux et al. 1999; Petry et al. 2003), subtropical (Kushlan 1976), and temperate (Winemiller 1996b) regions. In short, opportunistic strategists would be expected to show rapid responses to habitat disturbance and domination of habitats subjected to relatively frequent and stochastic patterns of disturbance. Periodic-type species should dominate habitats with larger-scale and more predictable patterns of environmental variation, such as large floodplain rivers and estuaries. Equilibrium-type species should be favored in stable habitats (e.g., tropical lakes) and respond in a consistent density-dependent manner to changes in habitat quality and quantity in gradually fluctuating systems, such as floodplain pools. Thus, indices of biotic integrity must consider the suite of life history strategies present in the species assemblage to infer the characteristics of a normal or unperturbed system. Ordination of species according to life history strategies could significantly improve predictions about community structure, response to disturbances, and enhance IBIs.

Additional considerations

Life history theory could be used to address a host of management issues in addition to those discussed above. For example, how do we predict effects of invasive species? Most exotic introductions do not become established, so are there common characteristics among species that become established? Kolar and Lodge (2002) examined several life history and ecological attributes of fishes introduced into the Great Lakes of North America. Species that became established had faster growth and tolerated a wide range of temperatures and salinity, but species that spread quickly after establishment had slower growth and tolerated even wider temperature ranges but were intolerant of high water temperatures. Nuisance species have smaller eggs, wider salinity tolerance, and tolerated low temperatures. Their statistical model predicted the sequence of establishment, spread, and impact with >80% accuracy, and it would be interesting to examine life history as correlated suites of attributes (i.e., strategies or syndromes).

Another current issue in fisheries management is the function of artificial reefs and marine reserves. Does the creation of more habitat translate into more fish? According to Grossman et al. (1997), “it appears that both recruitment and post-recruitment processes may limit adult population size of coral reef fishes. The relative importance of the two types of processes depends on the species being examined.” A major goal of marine reserves is to protect a sufficient biomass of adults to replenish regional stocks. In this context, Roberts (1997) noted that fish assemblages contain a diversity of life histories (see also Winemiller 1989; Whitfield 1990), so

that reserves might be one of the only viable means of affording protection for stocks supporting multispecies fisheries.

A major challenge for management of multispecies fisheries is to predict the consequences of altered food web structure for community and production dynamics. As large, long-lived species are depleted, they tend to be replaced in the fishery by species with more rapid life cycles and greater demographic resilience (Jennings et al. 1999b; Rochet 2000; Denney et al. 2002), a sequence commonly referred to as the fishing down phenomenon. Community-level density compensation is evident in the fishing down phenomenon (Pauly et al. 2000). For example, catch data from longline fisheries in the Indo-Pacific region reveal a rapid 80% reduction in stocks of marlin in Pacific waters followed by a compensatory increase in faster growing, earlier maturing species, such as sailfish (Myers and Worm 2003). In relatively simple predator-prey systems, harvest of adult piscivores can lead to depensation in the piscivore population via compensatory cultivation of prey that compete with juvenile life stages (Walters and Kitchell 2001). Two-species models with size-dependent functional response and competition between adult prey and juveniles of the piscivore population can yield complex dynamics (De Roos and Persson 2002). Food web models that simulate density-dependent foraging dynamics and allow species to vary in their life history attributes (e.g., differential allocation of assimilated energy into growth, reproduction, foraging) can yield nonlinear responses that may hinder efforts to find simple correlations between predator and prey populations in time-series data (Walters et al. 2000; Matsuda and Abrams 2004; Abrams and Matsuda 2005).

Fisheries bycatch (estimated at over 27 million tons per year) has the potential to impact nontarget species with unknown consequences for food web dynamics affecting target species (Crowder and Murawski 1998). To argue that bycatch causes no harm to nontarget stocks implicitly assumes significant density compensation and the absence of food web and ecosystem consequences. To argue that bycatch harms nontarget stocks assumes that density-dependence is insignificant or too weak to keep pace with bycatch mortality or that compensatory responses may be impeded by ecosystem impacts affecting resource dynamics (e.g., benthic production disrupted by bottom trawling). Conservation and restoration of stocks affected by multispecies fisheries will be enhanced by examining the manner in which species life history strategies yield density compensation and population resilience (e.g., Schindler et al. 2002).

When we consider the potential for abiotic environmental drivers (affecting recruitment dynamics, migration, and habitat productivity) and life history strategies (slow versus fast life cycles, degree of compensatory density dependence) to influence food web dynamics, the challenge of making predictions seems daunting. Even the most precautionary approaches are risky if we fail to understand the basic mechanisms driving population and community dynamics and the scales on which they operate. In most circumstances, adaptive management (field experiments) and simulation modeling probably will yield more useful guidance than simple management targets based on assumptions of S-R models, such as maximum sustainable yield or biological

reference points. In the absence of guidance from experiments and detailed simulation models, life history theory and species ordination provide a qualitative basis for managing in the face of inherent uncertainty. For example, Pope et al. (2000) used two life history parameters (K from the von Bertalanffy growth equation and natural mortality at length, M , estimated from body weight) to estimate population vulnerability to fishing mortality for two species in the North Sea. Beverton (1998) proposed that such efforts, expanded to the full range of life history strategies, could provide guidance for fisheries management when empirical data are lacking and model predictions are uncertain.

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