

# Lack of relationship between simulated fish population responses and their life history traits: inadequate models, incorrect analysis, or site-specific factors?<sup>1</sup>

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**Abstract:** Relationships between fish population responses to changes in their vital rates and commonly available life history traits would be a powerful screening tool to guide management about species vulnerability, to focus future data collection on species and life stages of concern, and to aid in designing effective habitat enhancements. As an extension of previous analyses by others, I analyzed the responses to changes in fecundity and yearling survival of age-structured matrix and individual-based population models of 17 populations comprising 10 species. Simulations of the matrix models showed that the magnitude of population responses, but not the relative order of species sensitivity, depended on the state (sustainable or undergoing excessive removals) of the population. Matrix and individual-based models predicted population responses that appeared to be unrelated to their species-level life history traits when responses were plotted on a three-end-point life history surface. Density-dependent adult growth was added to the lake trout (*Salvelinus namaycush*) matrix model, and simulations demonstrated the potential importance to predicted responses of density-dependent processes outside the usual spawner–recruit relationship. Four reasons for the lack of relationship between population responses and life history traits related to inadequate population models, incorrect analysis, inappropriate life history model, and important site-specific factors are discussed.

**Résumé :** Les relations entre les réactions des populations de poissons aux changements de leurs taux vitaux et les caractéristiques démographiques communément disponibles pourraient être des outils puissants de dépistage pour renseigner les gestionnaires sur la vulnérabilité des espèces, pour mieux cibler les récoltes futures de données sur les espèces et les stades de développement qui sont des sujets de préoccupation et, enfin, pour aider à mettre au point des améliorations efficaces des habitats. En continuité avec des analyses antérieures par d'autres chercheurs, mon analyse porte sur les réactions aux changements de fécondité et de survie des animaux de 1 an de modèles démographiques matriciels structurés d'après l'âge et de modèles centrés sur l'individu de 17 populations comprenant 10 espèces. Les simulations des modèles matriciels montrent que l'importance des réactions de la population, mais non l'ordre relatif de sensibilité des espèces, dépendent de l'état (récolte soutenable ou retraits excessifs) de la population. Les modèles matriciels et ceux centrés sur l'individu prédisent des réactions des populations qui semblent indépendantes de leurs caractéristiques démographiques spécifiques, lorsque les réactions sont portées sur un graphique démographique comportant trois points extrêmes. Si on ajoute une croissance adulte reliée à la densité au modèle matriciel du touladi (*Salvelinus namaycush*), les simulations montrent l'importance potentielle pour les réactions prédites de processus reliés à la densité distincts des relations habituelles entre les reproducteurs et les recrues. La discussion porte sur quatre raisons qui expliquent le manque de relation entre les réactions des populations et leurs caractéristiques démographiques, soit des modèles de population inadéquats, une analyse fautive, des modèles démographiques non appropriés et des facteurs importants spécifiques aux sites.

[Traduit par la Rédaction]

## Introduction

Understanding and forecasting how fish populations will respond to changes in their vital rates (reproduction, mortal-

ity, growth) has been the focus of research and speculation for decades. Marine fisheries management in the United States is governed by the Sustainable Fisheries Act, whose implementation includes estimation of the current status of the fish

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stock, forecasts of annual yields under different harvesting scenarios, and if needed, specification of recovery plans for overfished stocks (Restrepo et al. 1998). Forecasting population trajectories and estimating sustainable harvests have focused fisheries management on stock-assessment methods based on surplus-production models, age-structured statistical models (e.g., virtual population analysis and catch-at-age), and age-structured matrix projection models (Quinn and Deriso 1999). For populations with sufficient site-specific data, this quantitative population-oriented approach is reasonable, although ecosystem-level considerations are receiving increasing attention (Alaska Sea Grant 1999; National Marine Fisheries Service 1999).

Often, even when data are sufficient for development of a site-specific model, certain model parameters are estimated from information on other populations or species. For example, Rose and Cowan (2003) used red grouper (*Epinephelus morio*) in the Gulf of Mexico to illustrate how models and data can affect management decisions. One of the most critical parameters of the age-structured matrix projection model used for determining stock status and forecasting yields into the future was the steepness of the spawner–recruit relationship. Steepness is a measure of how quickly the predicted number of recruits approaches the maximum recruitment level with increasing spawning stock, and is defined as the fraction of maximum recruitment expected when the spawning stock is at 20% of its virgin (no fishing mortality) level (Haddon 2001). Because there were no spawner–recruit data for red grouper, several values of the steepness parameter were used, based on values from similar species that had spawner–recruit data. Life history theory was used to assign species to one of three end-point strategies (Rose et al. 2001), and steepness values from the strategy most similar to red grouper were used in the analysis.

The need for simple rules that use readily available life history traits to infer parameter values or population sensitivity to harvesting is even more important for the many species for which data are simply too sparse to support formal population modeling. The National Marine Fisheries Service (2003) reported that in 2002 the status of fish stocks in the US Exclusive Economic Zone with respect to overfished was unknown for 99 of 259 major stocks (> 90 909 kg landed) and for 596 of 673 minor stocks (< 90 909 kg landed). Meta-analysis offers a promising approach for estimating parameter values from other populations and species (e.g., Myers 2001). Some simple rules for inferring which of the data-poor species might be most vulnerable to harvesting would provide a systematic method for prioritizing already-stretched fisheries-management people and monetary resources.

Data limitations can also arise when the investigation changes from determining the effects of harvesting to other issues such as the effects of changes in habitat. The inclusion of habitat issues in the Sustainable Fisheries Act, and general concerns about accelerating habitat losses, have led to increased interest in habitat effects on fish (Benaka 1999). Recently, US Environmental Protection Agency rules regarding the permitting of power-plant withdrawals of water for cooling include an option that the permittee can use enhancements (e.g., add habitat, stocking) to offset power-plant-induced mortality (Anonymous 2002). Without extensive site-specific data and detailed models, quantifying the

effects of various changes in habitat on fish populations is very difficult (Rose 2000). Yet in a given situation there are many options for habitat enhancements, and information on the species and life stages most likely to respond would be useful.

There is clearly a great need for general rules about how species respond to changes in their vital rates, and about the relative sensitivity among life stages to these changes. Life history traits are available or estimable for many species. If rules could be developed that use these readily available life history traits, a potentially powerful management and screening tool could be formulated. Such a tool could be used in data-poor situations to guide management about species vulnerability, to focus future data collection on species and life stages of concern, and to aid in designing the effective habitat enhancements.

In this paper I use a suite of population-dynamics models of a variety of populations and species to determine if the magnitude of their long-term simulated population responses to changes in fecundity and survival can be related to their life history traits. I first briefly review examples where life history theory has been used to qualitatively and quantitatively relate fish population responses to life history traits. I then present an analysis that used a mix of 17 matrix projection models and individual-based models (IBMs) that simulated long-term fish population dynamics. Fecundity and yearling (age 1 to age 2) survival rates were systematically varied, and percent changes in average population abundance were compared among populations and related back to species-level life history traits. Given that I could not find any obvious patterns in the results, I conclude with a discussion of the possible reasons for this non-result and its broader implications for fisheries management and modeling.

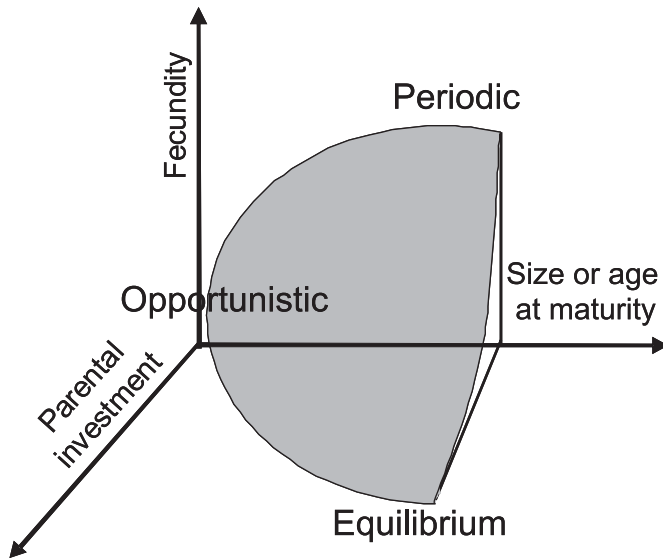
## Life history theory and population responses

### End-point strategies

The literature is rich with analyses that focus on life history traits and how demographic or physiological constraints limit the combinations of traits that result in viable and persistent populations (Roff 1992; Stearns 1997). Less common are studies that use life history traits to infer how populations should respond to changes in their vital rates. The classic  $r$ – $K$  continuum remains an area of active discussion in the literature today (Reznick et al. 2002). Qualitatively,  $r$ -selected species are thought to be more resilient to harvesting and quicker to recover than  $K$ -selected species (Musick 1999).

Winemiller and Rose (1992) modified the  $r$ – $K$  approach to better accommodate the life histories of North American fish species. They analyzed 245 species and proposed a three-end-point continuum (Fig. 1). They concluded that fishes fell on a surface defined by the three extreme strategies denoted equilibrium, periodic, and opportunistic. The equilibrium strategy was similar to  $K$ -selected species, and was characterized by delayed maturity, small clutches of large eggs, a high degree of parental care, and intermediate adult survival rates. Opportunistic strategists were characterized by early maturity, many small clutches over a protracted spawning season, and low adult survival rates. Periodic strategists were

**Fig. 1.** The three-end-point life history surface for fish proposed by Winemiller and Rose (1992). The end-point strategies are labeled equilibrium, opportunistic, and periodic.



characterized by delayed maturity, large clutches, and high adult survival rates. Species that are representative examples are smallmouth bass (*Micropterus dolomieu*) for the equilibrium strategy, bay anchovy (*Anchoa mitchilli*) for the opportunistic strategy, and striped bass (*Morone saxatilis*) for the periodic strategy. Winemiller (2005) discusses the implications of the three end-point strategies for sustainable harvest, endangered species, stocking, population health indicators, and multispecies interactions.

Several subsequent analyses generally supported the three end-point strategies proposed by Winemiller and Rose (1992). Vila-Gispert and Moreno-Amich (2002) performed a very similar analysis to that of Winemiller and Rose (1992) on 25 freshwater fish species from European waters. Their analysis was in general agreement with that of Winemiller and Rose (1992), but European fish species showed a more restricted range of strategies. European species included periodic and opportunistic species, but no true equilibrium strategists; those authors also noted that some of their periodic strategists were intermediate between periodic and equilibrium strategists. McCann and Shuter (1997) looked at the allometry of reproduction within the context of the three end-point strategies of Winemiller and Rose (1992). They found that the three end-point strategies did provide constraints that were consistent with empirical relationships between ovary weight and body weight and between age at maturity and weight at maturity. They also concluded that salmonids are likely best considered a fourth strategy. Spencer and Collie (1997) analyzed time-series data of catch-per-unit-effort or catch of 30 stocks and related their six groupings of population fluctuations to the three end-point life history strategies of Kawasaki (1983), which directly map to the three end-point strategies of Winemiller and Rose (1992).

Using a different statistical approach than that used by Winemiller and Rose (1992), Rochet et al. (2000) analyzed the interpopulation and interspecific variation of seven traits among 84 populations of 49 species. They applied an

autoregressive model to a suite of traits such as time to 5% survival and body length at sexual maturity. The autoregressive model was used to explain variation in each of the traits across populations within species (intraspecific) and among species (interspecific). Each population also had an associated fishing-mortality rate. Principal components analysis was then applied to the “corrected” values of the traits (predicted from the autoregressive models) to identify groupings, and mean values of corrected traits were computed for each of three groupings of fishing-mortality rates. Rochet et al. (2000) interpreted the results of the principal components analysis as two axes: one was a slow-turnover to fast-turnover continuum and the second was the schedule of how energy is allocated to growth versus reproduction. They related their axes to the three end-point strategies of Winemiller and Rose (1992) and concluded that periodic species should have the highest resilience to fishing.

### Predicted responses to mortality

Rose et al. (2001) ventured further with the Winemiller and Rose (1992) framework and suggested how the three different end-point strategies would respond to changes in mortality rates. Rose et al. (2001) distinguished between compensation and compensatory reserve. Compensation is the net effect of the density-dependent processes that cause negative feedback on population size. Compensatory reserve is “excessive reproductive capacity under ideal conditions for individual reproduction (Christensen and Goodyear 1988)”. Stronger compensation implies less variation in population size over time, while higher compensatory reserve implies greater resilience to increases in mortality. Rose et al. (2001) hypothesized that periodic strategists should show the weakest compensation (high population variation) but the highest compensatory reserve, while equilibrium strategists should show the strongest compensation but the lowest compensatory reserve. They evaluated this hypothesis by comparing estimates of steepness and residual variation of spawner–recruit relationships of 249 populations (57 species) from the Myers spawner–recruit database (Myers et al. 1995). Steepness is the fraction of maximum recruitment at 20% virgin (unfished) stock biomass, and is a measure of compensatory reserve. Residual variation (defined below as the standard deviation ( $\sigma$ ) of the spawner–recruit fits to data) was interpreted as an indicator of compensation. Plotting the steepness and residual-variation values with species grouped into Winemiller and Rose’s (1992) three end-point strategies, Rose et al. (2001) inferred that the highest steepness values for periodic species and lowest residual-variation values for equilibrium species were consistent with life history theory, and that periodic species should be relatively resilient to fishing. However, there was much variation in steepness and residual-variation values within each life history strategy.

Jennings et al. (1998) included phylogenetic considerations in their analysis of 18 exploited northeast Atlantic fish stocks (9 species), and showed that the decrease in abundance of stocks that matured later, attained a larger maximum body size, and had lower population growth rates decreased in abundance was greater than would be expected from the fishing-mortality rate. They suggested that some simple life history trait, such as maximum body size, could

**Table 1.** The 17 population models involving 10 species used to relate population responses to life history traits.

	Model <sup>a</sup>	Food web <sup>b</sup>	Location
Bay anchovy	I	Population	Chesapeake Bay, mesohaline region
Brook trout	I	2-species competition	Appalachian stream, third order
Lake trout	M	Population	Lake Opeongo; after cisco introduction
Menhaden	M	Population	Mid-Atlantic Bight
Northern anchovy	M	Population	Central California
American shad	M	Population	Connecticut River
Smallmouth bass	M	Population	Lake Opeongo
Striped bass	M	Population	US east coast
	I	Population	San Francisco estuary
Winter flounder	M	Population	Niantic River
	I	Population	Niantic River
Yellow perch	I	Population	Lake Mendota
	I	2-species LV	Lake Mendota
	I	2-species HV	Lake Mendota
	I	3-species competition	Lake Mendota
	I	6-species LV	Lake Mendota
	I	6-species HV	Lake Mendota

**Note:** The six alternative food-web configurations for the yellow perch (*Perca flavescens*) individual-based model are shown in Fig. 2.

<sup>a</sup>M, matrix projection model; I, individual-based model.

<sup>b</sup>LV, low variability; HV, high variability.

be used to indicate the vulnerability of a population to fishing.

### Quantitative evaluations with population models

There have been several analyses that have used population models to quantitatively evaluate the predictions of life history theory for fish. These approaches have generally used age-structured matrix projection models to examine how population responses to changes in mortality rate can be related to life history traits.

Fromentin and Fonteneau (2001) used principal components analysis to analyze the life history traits of 10 tuna and tuna-like species, and determined that the tropical species were characterized by a shorter life-span, smaller body size, longer spawning season, more rapid growth, and younger age at maturity than temperate-zone species. They then developed age-structured models with a spawner–recruit relationship for eggs to young-of-the-year juveniles for species with two contrasting life histories: tropical skipjack tuna (*Katsuwonus pelamis*) and temperate-zone Atlantic bluefin tuna (*Thunnus thynnus*). The models were modified to accommodate monthly spawning over the entire year for the tropical skipjack tuna. Several scenarios of fishing-mortality rates were simulated for 200 years. They concluded that the tropical skipjack tuna (*r*-selected traits) was resistant to fishing, whereas the temperate-zone Atlantic bluefin tuna (*K*-selected traits) was vulnerable to collapse if harvest was imposed prior to their age at maturation.

Rochet (2000) used deterministic, density-independent stage-based matrix models to compare life history traits during high and low population abundance periods for Greenland halibut (*Reinhardtius hippoglossoides*) and plaice (*Pleuronectes platessa*). She computed the sensitivity of the finite population growth rate ( $\lambda$ ) and, by comparing high- and low-abundance periods between the species, concluded that changes in life history traits towards a younger age at maturity,

decreased proportion of repeat spawners, and increased fecundity at age could be used to infer the effects of fishing and population viability.

Schaaf et al. (1987, 1993) used age-structured matrix projection models of 12 populations (8 species and one population divided into three time periods) to relate predicted population responses to life history traits. They used density-independent, deterministic age-structured matrix models, solving for the survival rate in the first year that would stabilize each population trajectory. They decreased either first-year or age-1 and older survival rates for 1 year only or permanently, and computed various metrics of population responses. The population response to one-time reductions in survival was the number of years required for the population to stabilize, which was positively related to a heuristic index of reproduction based on age-specific survival rates and fecundity. Stabilization was longer for those species that delayed reproduction and quickest for those species whose reproduction was well dispersed among ages. Responses to permanent changes in first-year or age-1 and older survival rates were compared among populations by computing the finite population growth rate ( $\lambda$ ) for a series of reductions in survival rates. Schaaf et al. (1993) summarized each population's response as the slope of the regression of changes in  $\ln(\lambda)$  versus percent changes in survival rates. They then related the slopes to differences in the life history traits and habitat-usage patterns of the populations.

Barnthouse et al. (1990) used age-structured matrix projection models to compare the responses of Gulf menhaden (*Brevoortia patronus*) and striped bass to increased mortality. Their matrix projection models included both density-dependence (Ricker spawner–recruit relationship) and interannual stochasticity in young-of-the-year survival. They used laboratory toxicity data as the basis for reducing young-of-the-year survival, and performed one hundred 100-year simulations for baseline (no contaminant) and three lev-



els of increased mortality. They inferred the importance of life history by noting that Gulf menhaden (small bodied, short-lived) had greater tolerance to increases in young-of-the-year mortality than striped bass (large bodied, long-lived).

### Segue to my analyses

My analyses in this paper can be viewed as an extension of these previous analyses. I used models that included both density-dependence and stochasticity, and I simulated a wide variety of species. The previous analyses were heading in the right direction in terms of quantitative evaluation of life history theory predictions, but used either density-independent or deterministic matrix models (Schraaf et al. 1993; Rochet 2000) or included density-dependence but simulated only a few species (Barnthouse et al. 1990; Fromentin and Fonteneau 2001). I also attempt to place my results in the context of the Winemiller and Rose (1992) framework of three end-point life strategies, which appears to be a robust representation of life history strategies of fish.

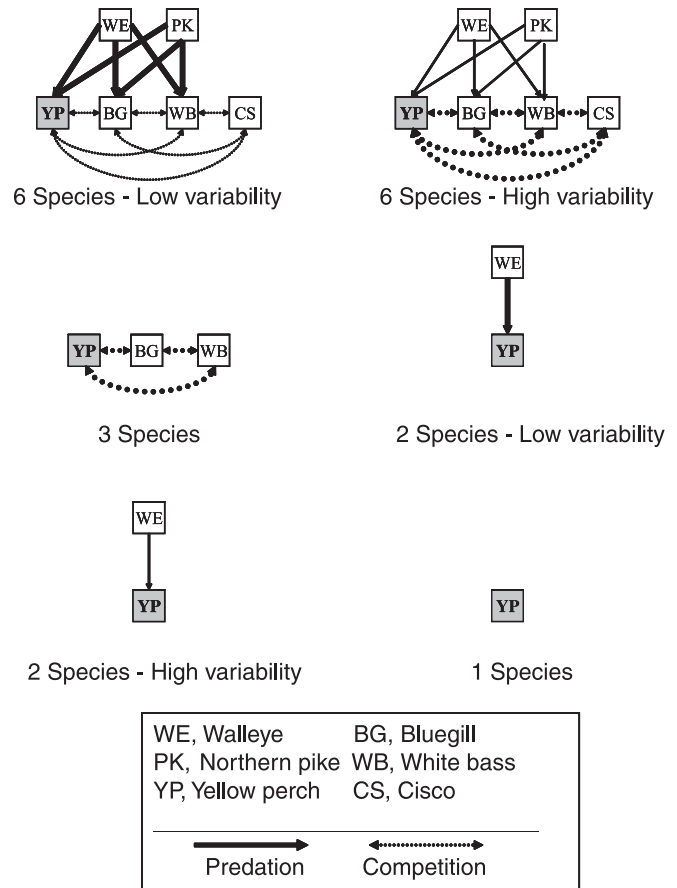
### Methods: population models and simulations

I used models of 17 populations comprising 10 different species (Table 1). These models were of two types: age-structured matrix projection and individual-based. I had matrix models and IBMs of the same population (Niantic River winter flounder, *Pleuronectes americanus*) and for two different populations of the same species (Chesapeake Bay and San Francisco Estuary striped bass). For yellow perch (*Perca flavescens*), the IBM was configured for the environment of Lake Mendota, with yellow perch imbedded into six different food webs (Fig. 2). The remainder of the matrix projection models and IBMs were of different species. The species simulated with matrix models were selected on the basis of the availability of spawner–recruit data and well-documented survival, maturation, and fecundity rates by age. IBMs are much more difficult to use than matrix models because each involves a customized computer code. The species simulated with IBMs involved my participation and I had first-hand knowledge of the history of model development and the computer code. When put together, the species analyzed had a wide variety of life history strategies and traits.

### Matrix projection models

The matrix projection models were formulated similarly among species. The species were selected to ensure a range of life history strategies, and because these particular populations had long time series of (what I judged to be high-quality) spawner–recruit data. The models followed the total numbers of male and females (females only for winter flounder) on an annual basis; age-specific survival, maturity, and fecundity (eggs per mature female) rates were obtained from literature reviews (Public Service Electric and Gas Company 1999) and from data provided by investigators familiar with the populations (Tables 2 and 3). First-year survival was represented as a Beverton–Holt spawner–recruit function fitted to the data (Fig. 3). Both Beverton–Holt and Ricker functions were fit using nonlinear regression, and in all cases the Beverton–Holt function provided a similar or better fit.

**Fig. 2.** Six alternative food webs for the yellow perch (*Perca flavescens*) individual-based model. All versions used the same environmental conditions representative of Lake Mendota. Arrows denote whether the dynamics were dominated by competition for common prey resources among the planktivores (high variability) or by piscivore predation on the planktivores (low variability).



Based on the Beverton–Holt fit, the mean ( $\bar{x}$ ) and standard deviation ( $\sigma$ ) of the natural-log-transformed residuals (log predicted – log observed) were computed and used as parameters of a lognormal distribution (Cordue 2001). For each year of the simulation, a random deviate was generated from the lognormal distribution (exponentiation of normal distribution with  $\bar{x}$  and  $\sigma$ ), and used to multiply the recruitment for that year. All matrix-model simulations except lake trout (*Salvelinus namaycush*) were for 200 years, with average values of total population number computed for years 51–200. Lake trout simulations were for 500 years, with means computed for years 201–500, to allow the simulated population to completely respond to changes in fecundity and yearling survival rates.

For striped bass and northern anchovy (*Engraulis mordax*), the weight of spawners in the spawner–recruit relationship was reported in metric tons. I determined a multiplier for each of these species that converted total eggs computed in the model to metric tons for use in the spawner–recruit relationship. Using trial and error simulation, I found multipliers of total eggs of  $3 \times 10^{-10}$  for northern anchovy and  $5 \times 10^{-9}$  for striped bass that resulted in

**Table 2.** Age-specific mortality (fraction per year), fraction mature times fecundity per mature female (eggs-female<sup>-1</sup>), and weight per individual (grams wet weight) for the American shad (*Alosa sapidissima*; SH), Atlantic menhaden (*Brevoortia tyrannus*; ME), and northern anchovy (*Engraulis mordax*; NA) matrix population models.

Age	Annual mortality			Maturity × fecundity (× 10 <sup>4</sup> )			Weight per individual		
	SH	ME	NA	SH	ME	NA	SH	ME	NA
1	0.32	0.81	0.75	0.00	0.63	2.02	140.0	114.6	8.7
2	0.32	0.79	0.75	0.00	7.34	9.35	530.0	266.1	14.6
3	0.32	0.79	0.75	0.00	18.44	19.45	1050.0	427.5	18.3
4	0.49	0.79	0.75	5.75	29.13	27.99	1590.0	566.7	21.2
5	0.76	0.79	0.75	2.15	39.29	32.75	2070.0	674.2	24.5
6	0.85	0.79	0.75	41.53	47.78	32.75	2480.0	752.1	24.3
7	0.85	0.79	0.75	45.97	54.31	32.75	2810.0	806.6	24.5
8	0.85	0.79		49.36	59.06		3070.0	843.7	

**Note:** Mortality is defined as the fraction dying from age  $i$  to age  $i + 1$ ; survival from egg to age 1 was determined by a spawner–recruit relationship. A female to male sex ratio of 1:1 is assumed for all species. Data for American shad and Atlantic menhaden are from Public Service Electric and Gas Company (1999) and for northern anchovy from Butler et al. (1993).

**Table 3.** Age-specific mortality (fraction per year), fraction mature times fecundity per mature female (eggs per mature female), and weight per individual (grams wet weight) for the lake trout (*Salvelinus namaycush*; LT), smallmouth bass (*Micropterus dolomieu*; SM), striped bass (*Morone saxatilis*; SB), and winter flounder (*Pleuronectes americanus*; WF) matrix population models.

Age	Annual mortality				Maturity × fecundity				Weight per individual			
	LT	SM	SB	WF	LT	SM	SB	WF	LT	SM	SB	WF
1	0.12	0.26	0.67	0.4	0	0	0	0	3.81	5.2	175	4.98
2	0.12	0.26	0.25	0.3	0	0	0	0	29.9	30.1	620	56.7
3	0.12	0.48	0.20	0.3	0	0	0	0.3	94.4	83.8	1388	251.3
4	0.12	0.30	0.30	0.5	0	0.1	0.1	1.3	205.2	178.3	2427	367.9
5	0.12	0.40	0.36	0.5	0	0.5	0.8	5.2	364.1	276.4	3658	494.0
6	0.35	0.51	0.37	0.5	0	1.0	4.3	7.8	568.7	469.9	5000	624.6
7	0.35	0.57	0.37	0.5	0	1.5	11.9	10.0	813.8	627.5	6384	746.2
8	0.35	0.62	0.37	0.5	0	2.0	16.2	12.0	1093.0	781.6	7756	849.6
9	0.35	0.58	0.37	0.5	0.1	2.4	21.1	13.6	1399.7	937.0	9078	933.1
10	0.35	0.58	0.37	0.5	0.20	3.0	24.9	15.0	1726.5	1157.6	10322	999.3
11	0.35	0.60	0.37	0.5	0.30	3.3	28.6	15.9	2067.0	1307.2	11474	1045.1
12	0.35	0.64	0.37	0.5	0.36	3.53	32.0	16.8	2415.0	1358.9	12526	1084.1
13	0.35	0.62	0.37	0.5	0.41	3.53	35.2	17.5	2766.5	1360.8	13478	1116.3
14	0.35		0.37	0.5	0.46		38.1	18.0	3115.9		14328	1141.3
15	0.35		0.37	0.5	0.52		40.7	18.5	3460.0		15084	1157.6
16	0.35		0.37		0.57		430.8		3795.7		15752	
17	0.35		0.37		0.62		451.6		4120.9		16339	

**Note:** For comparison with other species, the fecundity values for winter flounder used in this table are double those used in the matrix-model simulations (i.e., convert female eggs per mature female to eggs per mature female). The fraction mature × fecundity is × 10<sup>4</sup> for lake trout and smallmouth bass and × 10<sup>5</sup> for striped bass and winter flounder. Mortality is defined as the fraction dying from age  $i$  to age  $i + 1$ ; survival from egg to age 1 was determined by a spawner–recruit relationship. A female to male sex ratio of 1:1 is assumed for all species. Data for lake trout and smallmouth bass were provided by B. Shuter, Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada, personal communication; data for striped bass are from Public Service Electric and Gas Company (1999), and for winter flounder from Northeast Utilities Environmental Laboratory (2002).

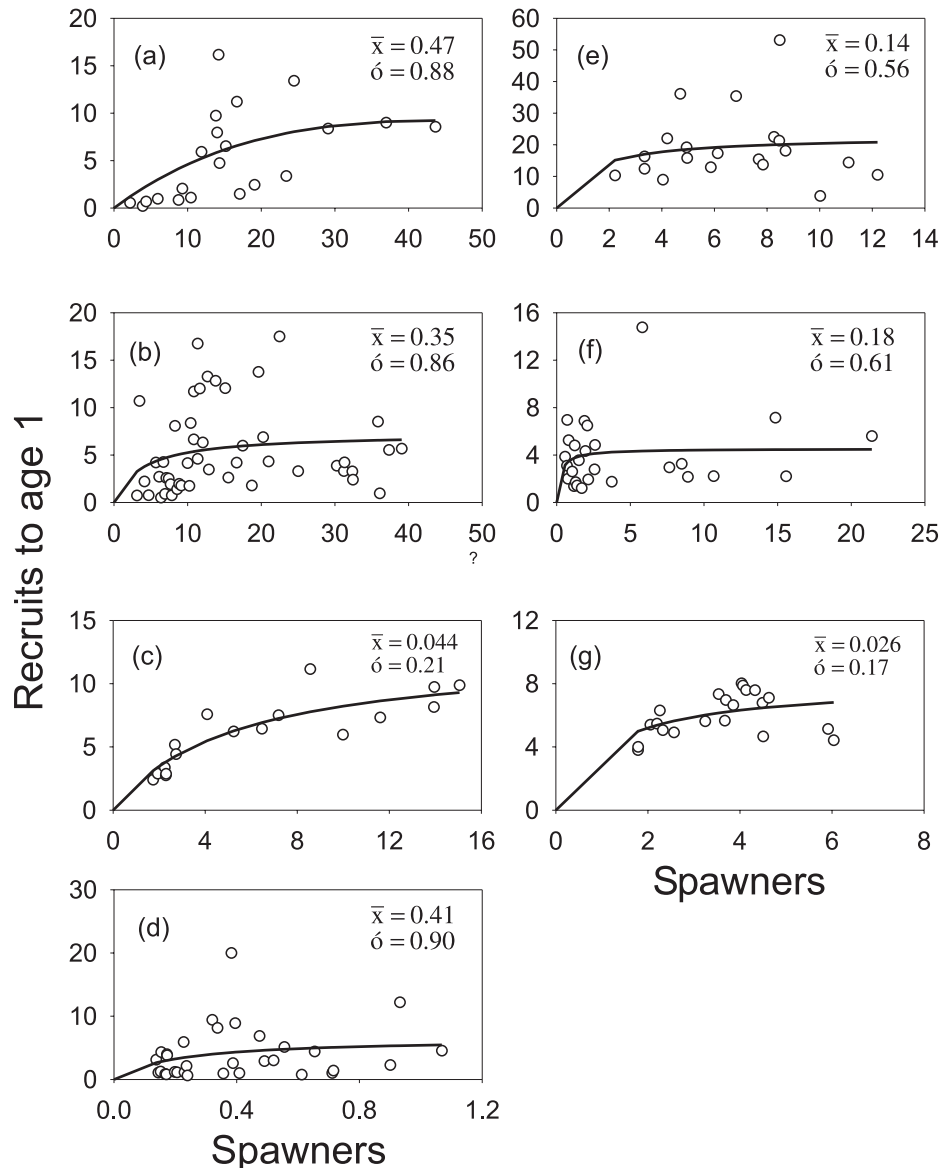
recruitment values that were in the middle of the range of their observed recruitment levels.

### Standardization of matrix models

I standardized the population state simulated by the matrix models across the seven populations. Predicted responses to changes in fecundity and survival rates could depend on the state of the population, which would confound comparisons among species. Depressed populations

would likely show greater responses than populations near their carrying capacity. I therefore assessed the effects of population state on predicted population responses. I did not adjust the spawner–recruit relationships because they were site-specific. Rather, I achieved a variety of population states for each matrix model by adjusting the annual survival fractions of the age-1 and older age classes. Natural and fishing survival rates were less site-specific than the spawner–recruit relationships. Changing adult mortality is a

**Fig. 3.** Spawner–recruit data and fitted Beverton–Holt relationships used in the matrix models. The mean ( $\bar{x}$ ) and standard deviation ( $\sigma$ ) of the log-transformed residuals used to generate lognormal variability in recruitment are shown. (a) Winter flounder, *Pleuronectes americanus* ( $10^9$  female eggs and  $2 \times 10^4$  female recruits). (b) Smallmouth bass, *Micropterus dolomieu* ( $10^6$  eggs and  $10^3$  recruits). (c) Striped bass, *Morone saxatilis* ( $10^3$  tonnes (t) and  $10^6$  recruits). (d) Northern anchovy, *Engraulis mordax* ( $10^5$  t and  $10^7$  recruits). (e) American shad, *Alosa sapidissima* ( $10^{10}$  eggs and  $10^6$  recruits). (f) Atlantic menhaden, *Brevoortia tyrannus* ( $10^{13}$  eggs and  $10^9$  recruits). (g) Lake trout, *Salvelinus namaycush* ( $10^{10}$  eggs and  $10^6$  recruits). Sources are as follows: winter flounder, Northeast Utilities Environmental Laboratory (2002), data for age-1 recruits were approximated from reported fully recruited individuals assuming average survival rates; smallmouth bass, B. Shuter, Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, personal communication; striped bass, Myers et al. (1995); northern anchovy, Pacific Fishery Management Council (1998), recruits were converted from biomass on 1 July to numbers on the following 15 February (about 1 year old) assuming an individual weighed 8.7 g and the survival rate was 40% (Butler et al. 1993); American shad, Savoy and Crecco (1988); Atlantic menhaden, Vaughan and Smith (1988), Vaughan (1990); lake trout, B. Shuter (personal communication).



reasonable way to put the populations in depressed versus sustainable states.

I standardized the matrix models using an approach analogous to that used in marine fisheries management in the United States (Rose and Cowan 2003). US fisheries management uses the metrics of long-term average yield and the spawning stock associated with this yield. Because I specified total mortality rates for adults, I computed the sustainable total removal (analogous to yield from fishing) as the

annual biomass (number by age times mean weight by age) generated from mortality of age-1 and older age classes. The spawning stock associated with each level of sustainable removal was computed as the average annual total number of eggs produced. I ran series of simulations for each population in which I incrementally increased or decreased age-1 and older survival by a multiplier (e.g., 0.9, 1.0, 1.1). This resulted in a plot of sustainable removals on the y axis versus the associated changes (multiplier value) in adult sur-

**Table 4.** Characteristics of the five individual-based models used in the analysis: bay anchovy, *Anchoa mitchilli* (BA), brook trout, *Salvelinus fontinalis* (BT), striped bass (SB), winter flounder (WF), and yellow perch (YP).

Model	Time step	Spatial grain	Currency	Source
BA	Daily	Single box	Individuals	Rose et al. 1999
BT	Daily	Series of 45 hydrologically linked pool, run, and riffle habitat cells	Individuals	Clark and Rose 1997a, 1997b, 1997c
SB	Daily for YOY; annual for age 1 and older	Four connected boxes representing upper Sacramento, lower Sacramento, San Joaquin, and Suisin areas	Individual for YOY; age classes for age 1 and older	K.A. Rose, J.H. Cowan, L.W. Miller, D.E. Stevens, W.J. Kimmerer, and R.L. Brown, unpublished data
WF	Daily for YOY; annual for age 1 and older	Single box	Individuals for YOY; age classes for age 1 and older	Rose et al. 1996
YP	Daily	Connected epilimnion, hypolimnion, and littoral habitat boxes	Individuals	McDermot 1998; McDermot and Rose 2000

**Note:** YOY, young-of-the-year.

vival on the  $x$  axis. In all cases, these plots were dome-shaped, although some populations generated relatively flat curves. The dome shape implies that some intermediate level of adult survival generated the maximum removable biomass, which is analogous to the commonly assumed dome-shaped relationship between yield and fishing-mortality rate. I determined the multiplier of adult survival that resulted in the maximum sustainable removal (MSR), which was the peak of the dome-shaped relationship, and the spawning stock (total eggs) associated with that level of MSR (denoted  $SS_{MSR}$ ). For each population I then determined the multiplier needed to achieve a spawning stock at 25%  $SS_{MSR}$  (sustainable), 10%  $SS_{MSR}$  (heavy removal), and 5%  $SS_{MSR}$  (over-removal). I also included the initial set of adult survival rates estimated from the literature, which I termed arbitrary. All simulations involving changes in egg or yearling survival were applied for each of the four versions of each population model (arbitrary and 5%, 10%, and 25%  $SS_{MSR}$ ).

The designations sustainable, heavy removal, and over-removal were based on population responses to further decreases in adult survival. For most of the matrix models, populations at the 25%  $SS_{MSR}$  state, deemed sustainable, were able to withstand further decreases of at least 25%–30% in their adult survival multiplier (i.e., withstand 25%–30% higher annual mortality) with only small decreases in their long-term average abundances. The 10%  $SS_{MSR}$  state was labeled heavy removal, based on further decreases of 25% in adult survival, resulting in persistent but noticeably lower population abundances. The 5%  $SS_{MSR}$  state was labeled over-removal because further decreases of 25% in adult survival generally caused populations to barely persist or to approach extinction. US fisheries management has used a general guideline that is risk-averse and sustainable to remove 60%–70% of a virgin stock's reproductive potential (Mace and Sissenwine 1993; Myers et al. 1994).

### Individual-based models

The IBMs shared several features but, in contrast to the matrix models, differed greatly in their details (Table 4). All of the IBMs simulated growth, mortality, and reproduction for the full life cycle of each population. Models that included multiple spatial boxes also simulated movement of individuals among the boxes. All of the models tracked

young-of-the-year individuals on a daily time step, and all represented growth of young-of-the-year life stages with a bioenergetics model. Some of the models tracked individuals throughout their lifetime (yellow perch, brook trout (*Salvelinus fontinalis*), and bay anchovy), while others used simpler age-structured approaches for the adult portion of the life cycle (striped bass and winter flounder). All of the models included potential density-dependent growth in one or more life stages by simulating prey densities through time as the net result of prey production and fish consumption. Depending on the model, density-dependent growth affected survival and reproduction because mortality, maturity, and fecundity rates were size-dependent. Several of the models also included density-dependent mortality (winter flounder, striped bass, and yellow perch). In the spatially explicit models, movement was represented in a variety of ways: inferred from particle-tracking results for eggs and yolk-sac larvae for the San Francisco Estuary striped bass model; based on short-term growth maximization for the trout model; and dependent on water temperature and dissolved oxygen concentrations for the yellow perch model.

In contrast to the matrix models, I did not standardize the population states among the IBMs. The IBMs were developed to be as site-specific as possible. While they used information from other populations and species for model inputs, each of the IBMs was calibrated and evaluated, to varying degrees, against data from the population of interest. In some instances I was wary of running the models under conditions much different than their original site-specific applications without substantial recalibration.

### Life history traits

I used the values of life history traits reported by Winemiller and Rose (1992) for the 10 species in this analysis (Table 5). Another option would be to use population-specific values of life history traits consistent with each of the population models. I initially used the general values of the life history traits reported in Winemiller and Rose (1992) in this analysis, as one purpose of the analysis was to see if life history traits could be used to infer population responses in data-poor situations. Subsequent attempts to use life history traits derived from the site-specific models did not significantly alter the results of the analysis. The 10 species



**Table 5.** Values of the life history traits for the 10 species for which there were matrix or individual-based population models.

	Maturation length (mm)	Clutch size (eggs·batch <sup>-1</sup> )	Investment per progeny <sup>a</sup>
American shad	461	538 767	2.04
Northern anchovy	49	685	0.59
Lake trout	419	7902	2.56
Striped bass	633	2 462 000	1.72
Smallmouth bass	292	7708	2.71
Winter flounder	250	600 000	0.59
Atlantic menhaden	257	224 134	0.96
Bay anchovy	45	687	0.59
Brook trout	119	1210	2.45
Yellow perch	127	43 680	1.53

**Note:** The values of the life history traits are the same as those used in analyses reported in Winemiller and Rose (1992).

<sup>a</sup>Computed as  $\log[(\text{parental care} + 1) \times (\text{egg diameter} + 1)]$ , where parental care was coded as 1, 2, 3, or 4 depending on whether eggs were placed in special habitats, whether nests were involved, the duration of parental protection of nest, and the parental contribution to the nutrition of the larvae.

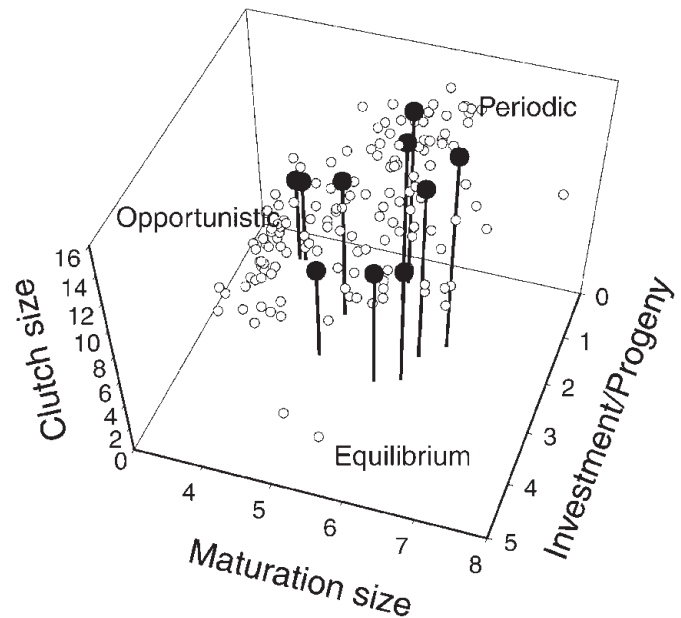
analyzed here cover a reasonable portion of the life history space formed by the 245 species analyzed by Winemiller and Rose (1992) (Fig. 4).

### Design of simulations

I performed three sets of simulations. The first set used the matrix projection models to assess how population state affected population responses. The second set then used the matrix models (under a selected population state) together with the IBMs to predict population responses to changes in fecundity and yearling survival rates, and to relate these responses to life history traits. The third set of simulations used the matrix model of lake trout, without and with adult density-dependent growth rates, to assess how density-dependence in post-young-of-the-year life stages (i.e., outside the spawner–recruit relationship) could influence population responses.

All simulations used  $\pm 25\%$  changes in fecundity of all mature age classes and  $\pm 25\%$  changes in the yearling (age 1 to age 2) annual survival rate. For the IBMs that represented the yearling life stage on a daily time step, the 25% changes were imposed so that 25% annual changes were achieved (e.g., 25% reduction was a daily multiplier of  $^{365}\sqrt{0.75} = 0.9992$ ). Model predictions of population responses are likely sensitive to whether changes are imposed before or after density-dependence operates. My changes to fecundity generally corresponded to a time prior to density-dependence in all of the models. Changes to yearling survival occurred after density-dependence in the matrix models, but were fuzzier in the IBMs. Most of the IBMs included density-dependence during young-of-the-year life stages, but some of the IBMs also predicted significant density-dependent growth and mortality in older life stages.

The first set of simulations imposed the  $\pm 25\%$  changes in fecundity or yearling survival in the matrix models for the four different population states. For each, I computed the average total population just prior to reproduction, so that the youngest individuals were just about to turn age 1. The average population was computed for years 51–200 (201–500 for

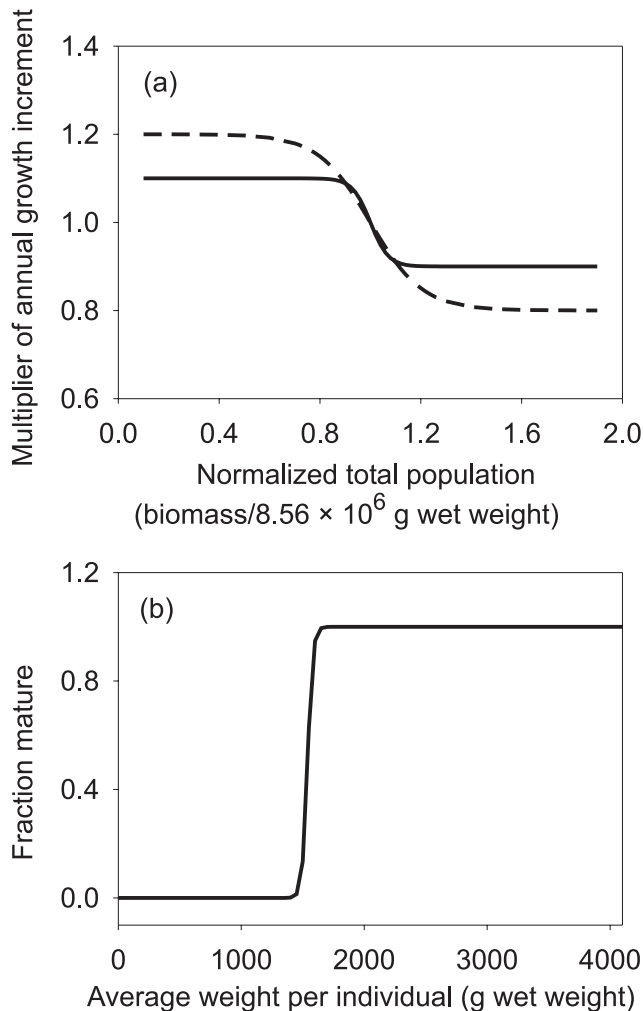
**Fig. 4.** The positions in life history space of the 10 species used in this analysis (●) compared with those of the 245 species analyzed by Winemiller and Rose (1992) (○).

lake trout) for each of the five conditions (baseline, +25% and –25% fecundity, and +25% and –25% yearling survival) at each of the four population states (arbitrary and 5%, 10%, and 25%  $SSB_{MSR}$ ). I report the population responses as percent change in average population number from the baseline value:  $\% \text{ change} = 100 \times [(Y - Y_{\text{baseline}})/Y_{\text{baseline}}]$ .

The second set of simulations used both the matrix models and the IBMs to simulate population responses to  $\pm 25\%$  changes in fecundity or yearling survival. Because population state did not greatly affect matrix-model predictions of species sensitivity, I used the adult survival rate corresponding to the 5%  $SSB_{MSR}$  for all of the matrix models. Percent change in the average total population number from baseline was computed and plotted in life history space. The plots used log maturation size, log clutch size, and investment per progeny for the three axes (Table 5); the height of the symbol was that species' position in life history space, and the size (diameter) of the symbol was scaled proportional to the absolute magnitude of its population response. To confirm the interpretation of the three-dimensional surface plots, I also show the responses to the changes in fecundity as a series of three two-dimensional scatter graphs (each graph is a pairwise combination of the three life history traits), with the size of the symbol scaled to the absolute magnitude of the population response.

The third set of simulations added density-dependent adult growth to the matrix model of lake trout to explore the consequences of including density-dependence in the matrix models outside the spawner–recruit relationship. Recent reviews suggest that density-dependent growth in adult fishes may be more widespread than was previously thought (Lorenzen and Enberg 2002). Density-dependent growth has been well documented in adult lake trout (Matuszek et al. 1990; Ferreri and Taylor 1996), and therefore permitted realistic specification in the matrix model. Annual growth in weight increments (grams wet weight per year) were specified as functions of

**Fig. 5.** Density-dependent multiplier of annual growth increments (a) and fraction mature as a function of weight (b) for the density-dependent adult growth addition to the matrix model of lake trout. In a, the solid line represents 10% and the broken line represents 20%.



age from differencing successive weights from the baseline weights at age schedule (shown in Table 3). Two levels of density-dependent adult growth were simulated. I specified two functions (denoted 10% and 20%) that acted as a multiplier of the annual growth increments that were dependent on the total adult (age 1 and older) biomass (Fig. 5a). The 10% and 20% density-dependent functions were chosen to very crudely bracket the magnitude of changes in growth rate and age at maturity of adult lake trout observed in Lake Opeongo between the high-abundance period (before the introduction of cisco, *Coregonus artedii*) and the low-abundance period (after the introduction of cisco) (Matuszek et al. 1990). The baseline fecundity and maturity at age values used in the matrix model were converted to functions of body weight using the baseline mean weight at age schedule (fraction mature shown in Fig. 5b; fecundity =  $0.068958 + 1.506 \times \text{body weight in grams}$ ). Model simulations were begun with the baseline weight at age values, and each year total population biomass was computed, which determined the density-dependent multiplier of the weight increments.

Weight at age was then updated by applying the density-dependent multiplier to the weight increment and adding this to the previous year's weight. Fecundity and fraction mature by age for that year were then determined from the mean weights at age. Simulations of the model under baseline conditions using the dynamic, density-dependent growth were very similar to the simulations that used the fixed fecundity and maturity by age. The  $\pm 25\%$  changes in fecundity and yearling survival were repeated using the matrix model that included both the spawner–recruit relationship and density-dependent adult growth, and responses were compared with the matrix model that included the spawner–recruit relationship only.

### Replicate simulations

All results shown are based on single matrix-model and IBM simulations. Both types of models involve stochastic simulation using Monte Carlo techniques. While mean total population varied among simulations that used different random-number sequences, percent change from baseline values varied little among replicate simulations. For example, predicted percent responses of the winter flounder matrix model for the 5%  $SS_{MSR}$  condition for two different random-number sequences were 20% and 22% for increased fecundity,  $-36\%$  and  $-39\%$  for decreased fecundity, 50% and 52% for increase yearling survival, and  $-52\%$  and  $-54\%$  for decreased yearling survival. Predicted responses of the IBMs were also robust to whether simulations were run for 50 or 100 years, and among replicate simulations that used different random-number sequences.

## Results

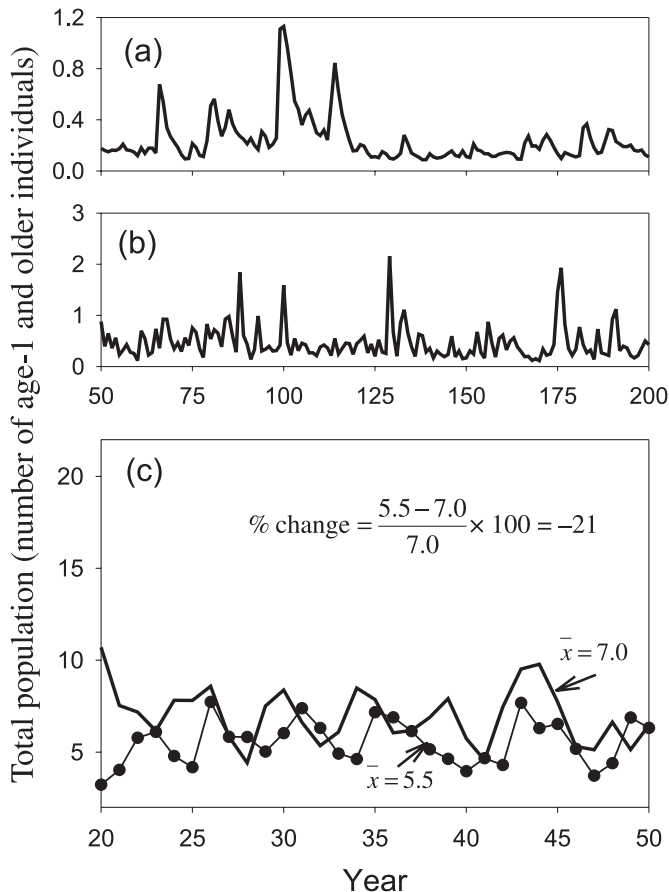
### Population trajectories

Representative simulations of the population trajectories for the matrix models and IBMs are shown in Fig. 6. Small-mouth bass (Fig. 6a) and Atlantic menhaden (*Brevoortia tyrannus*) (Fig. 6b) are used to illustrate the interannual variation in total population numbers typical of the baseline matrix-model simulations. Years 20–50 of the yellow perch IBM for the 2-species low-variability food web for the baseline and  $-25\%$  yearling survival simulations are shown as well (Fig. 6c). Also illustrated, using the yellow perch IBM, is the calculation of percent change from baseline for the reduced yearling survival simulation.

### Effects of population state

Population state affected the magnitude, but not the general patterns, of population responses among matrix-model species (Fig. 7). For a given species, responses to increased fecundity and decreased fecundity decreased in absolute magnitude with improving population state (the bars get smaller from 5% to 10% to 25%  $SSB_{MSR}$  in Fig. 7a). However, responses to fecundity across species generally maintained the same rank ordering with improving population state. For each population state, winter flounder and northern anchovy consistently showed the largest responses, while Atlantic menhaden and American shad (*Alosa sapidissima*) consistently showed the smallest responses. The responses to changes in yearling survival (Fig. 7b) were generally larger, showed less variation among species, and were relatively less

**Fig. 6.** Time series of total population (number of age-1 and older individuals) for baseline simulations of the smallmouth bass matrix model ( $10^5$  individuals) (a), Atlantic menhaden matrix model ( $10^{10}$  individuals) (b), and yellow perch individual-based model (IBM;  $10^5$  individuals) (c) in the 2-species low-variability food web. Also shown are the total population numbers for the reduced yearling survival simulation of the yellow perch IBM and the calculation of the population response as percent change from baseline. In c, the thick line represents baseline values and the thin line with solid circles represents the reduced yearling survival simulation.



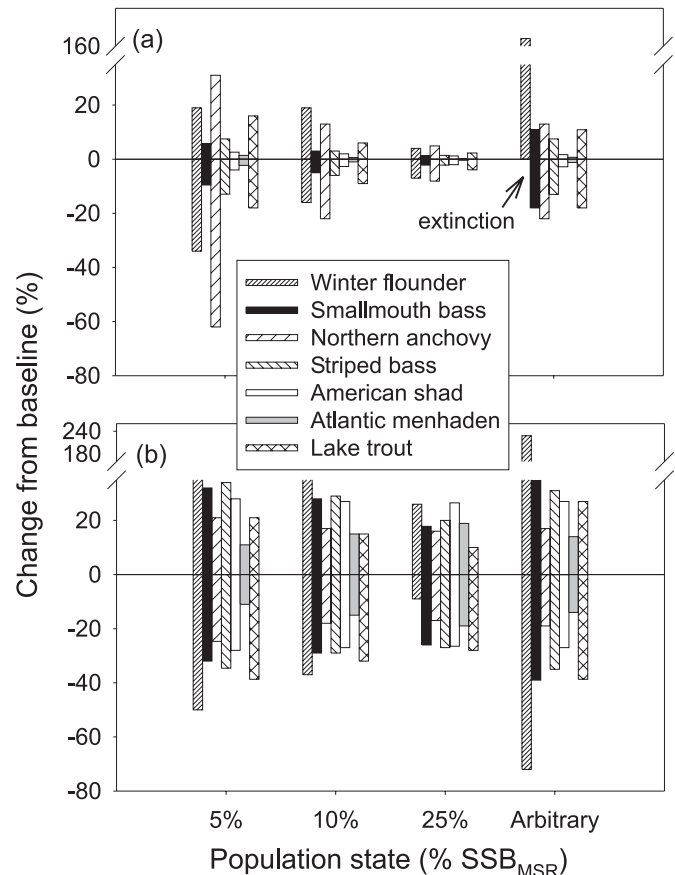
affected by the state of the population than the responses to changes in fecundity. For changes in both fecundity and yearling survival, population responses with the arbitrary values of inputs generally showed the same patterns of species sensitivity as those predicted with the populations in standardized states.

#### Responses in life history space

The magnitude of responses of the matrix models and IBMs showed no obvious relationship to the three life history traits. Neither large nor small symbols seemed to cluster in particular regions of the life history surface for changes in fecundity (Fig. 8) or for changes in yearling survival (Fig. 9). Pairwise examination of the three life history traits for changes in fecundity also did not show any obvious patterns or clustering in the sizes of symbols (Fig. 10).

The range of responses of yellow perch among its different food webs was, in some cases, comparable to the range of responses across all species. For example, increased fe-

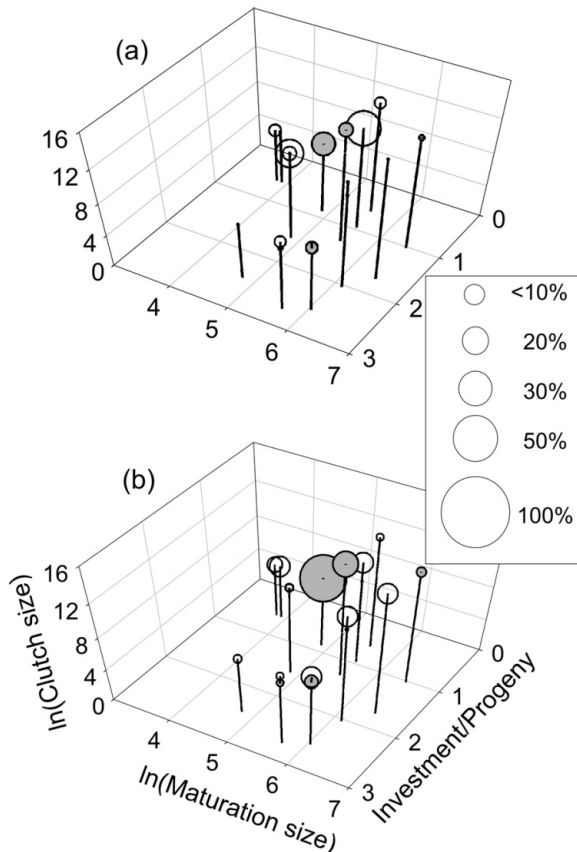
**Fig. 7.** Predicted population responses (percent change from baseline) for changes in fecundity (a) and yearling survival (b) for the matrix models adjusted to 5%, 10%, and 25%  $SSB_{MSR}$ , and with the initial arbitrary values of input parameters.



cundity resulted in a range of responses of 1%–31% among all matrix models, 2%–46% for the IBMs other than yellow perch, and 2%–37% among the six alternative yellow perch food webs. These matrix-model predictions were based on the population state of 5%  $SSB_{MSR}$ , which generally resulted in the largest matrix-model responses. The wide range of predicted responses among the alternative yellow perch food webs was not due to unrealistic food webs. The 2% and 37% responses were obtained from the two 6-species food webs, which were both reflective of the food web in Lake Mendota but were calibrated differently (McDermot and Rose 2000). The yellow perch IBM did not always predict wide-ranging responses. Decreased fecundity resulted in responses of –2% to –62% among the matrix models and –10% to –27% among the IBMs other than yellow perch, compared with a range of only –1% to –6% for yellow perch among all six different food webs.

There were no consistent differences in the responses between the matrix models and the IBMs, although such a comparison is weak because of small sample size. Examination of the matrix-model and IBM results separately did not show any obvious clustering of the small or large symbols (open versus shaded circles in Figs. 8 and 9). However, the number of species becomes relatively small when matrix-model and IBM results are viewed separately. Winter flounder responses predicted by the matrix model and IBM were

**Fig. 8.** Predicted population responses (percent change from baseline) from the matrix models (shaded circles) and IBMs (open circles) for increased fecundity (a) and decreased fecundity (b) plotted in Winemiller and Rose (1992) life history space. The height of the symbol is the position of the species on the life history surface, and the size of the symbol is proportional to the absolute magnitude of the predicted response. All responses to increased fecundity were positive (higher average population abundance than baseline), and all responses to decreased fecundity were negative (lower average population abundance than baseline).

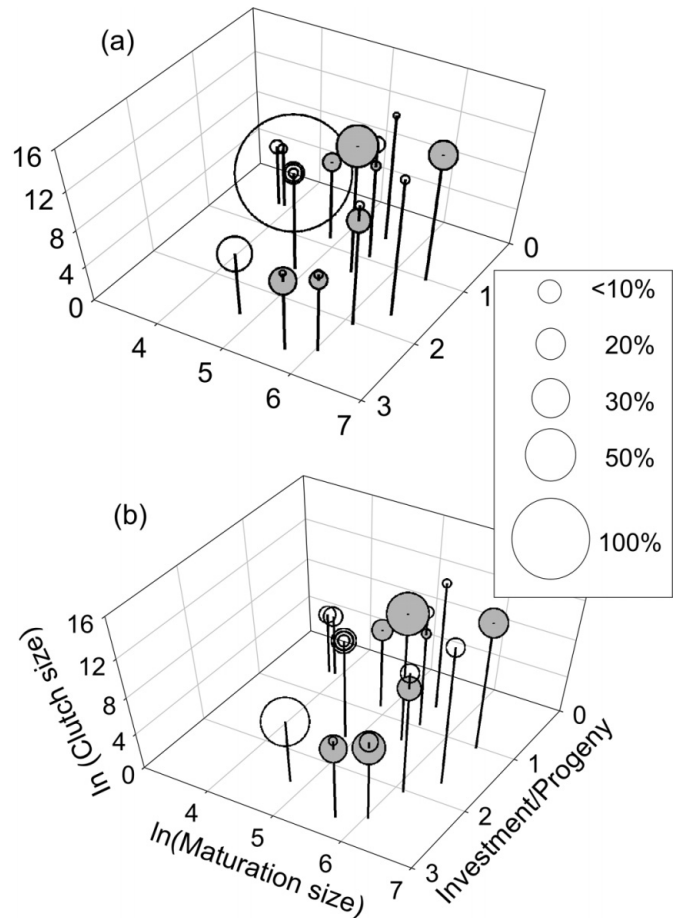


not consistent, even though both models were based on the same Niantic River winter flounder data. Predicted responses for the winter flounder matrix model and IBM were 20% versus 46% for increased fecundity, -36% versus -27% for reduced fecundity, 50% versus 18% for increased yearling survival, and -52% versus -14% for reduced yearling survival.

#### Effects of adult density-dependent growth on lake trout responses

Realistic levels of density-dependent adult growth dampened population responses of lake trout to changes in fecundity and yearling survival (Fig. 11). The 10% density-dependent function eliminated the lake trout response to increased fecundity and approximately halved the responses to decreased fecundity and to changes in yearling survival. The stronger 20% density-dependent function essentially eliminated (offset) all of the population responses, resulting in population responses of less than 6% for all changes in fecundity and yearling survival.

**Fig. 9.** Predicted population responses (percent change from baseline) from the matrix models (shaded circles) and IBMs (open circles) for increased yearling survival (a) and decreased yearling survival (b) plotted in Winemiller and Rose (1992) life history space. The height of the symbol is the position of the species on the life history surface and the size of the symbol is proportional to the absolute magnitude of the predicted response. All responses to increased yearling survival were positive (higher average population abundance than baseline) and all responses to decreased yearling survival were negative (lower average population abundance than baseline).

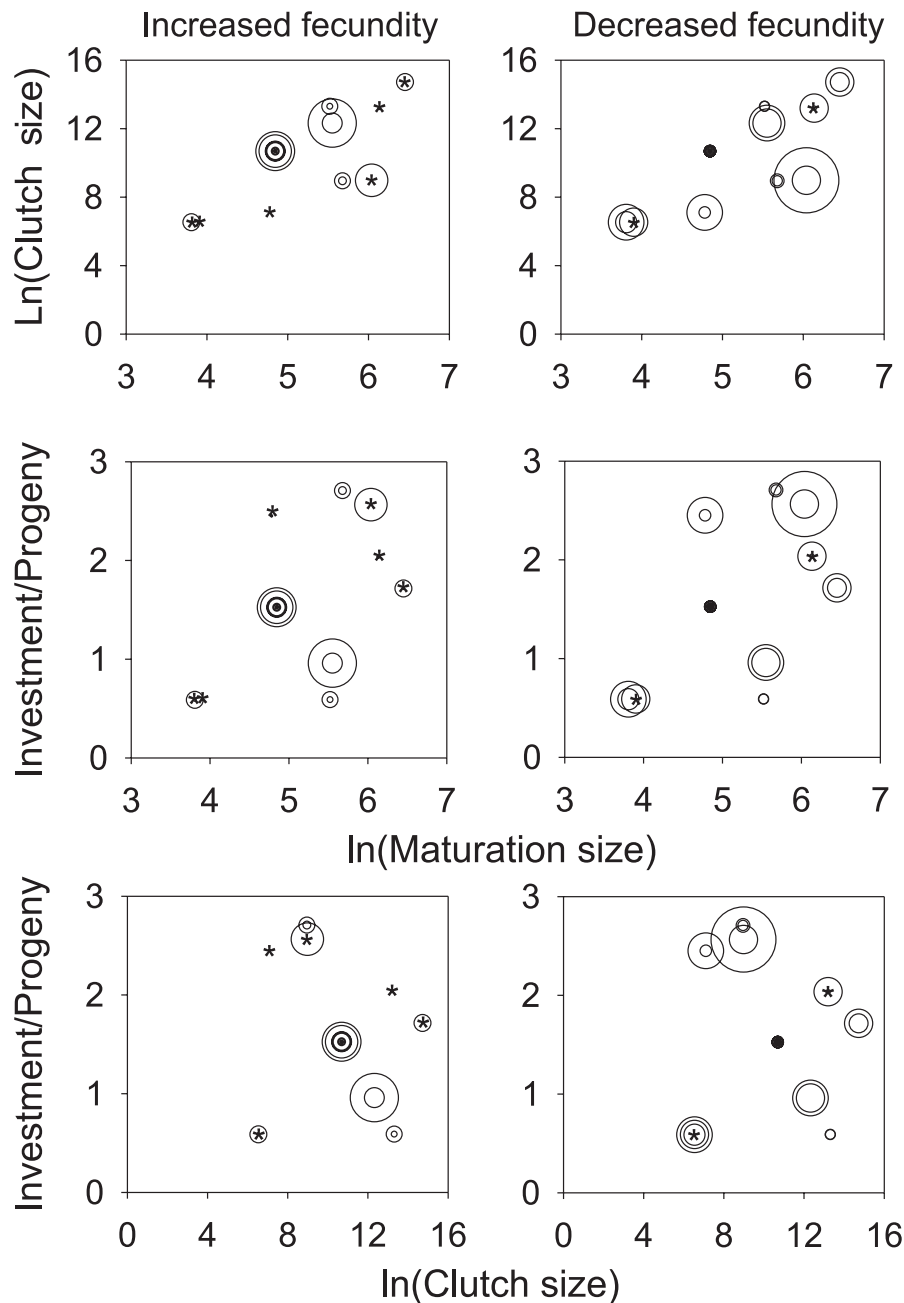


#### Discussion

Using life history theory to infer likely fish population responses to changes in vital rates, such as fecundity and survival, has many attractive features. While many species are data-poor, we often know or can estimate their basic life history traits. I would argue that, with some extrapolation and a little effort, we could place many species on the surface shown in Fig. 1. Thus, if population responses to changes in fecundity and survival showed consistent patterns in this life history space, we would have a powerful screening tool for identifying species potentially at risk and the species likely to be most responsive to habitat enhancements. Unfortunately, my analysis did not yield consistent patterns. There are four reasons that could explain my results: inadequate population models, incorrect analysis, inappropriate life history model, or important site-specific factors. I discuss each



**Fig. 10.** Scatterplots of predicted population responses of the matrix models and IBMs to increased and decreased fecundity for pairwise combinations of the three life history traits used to define the Winemiller and Rose (1992) life history surface. The size of the symbol is proportional to the absolute magnitude of the predicted response. All responses to increased fecundity were positive (higher average population abundance than baseline) and all responses to decreased fecundity were negative (lower average population abundance than baseline). A star indicates responses  $\leq 5\%$ .



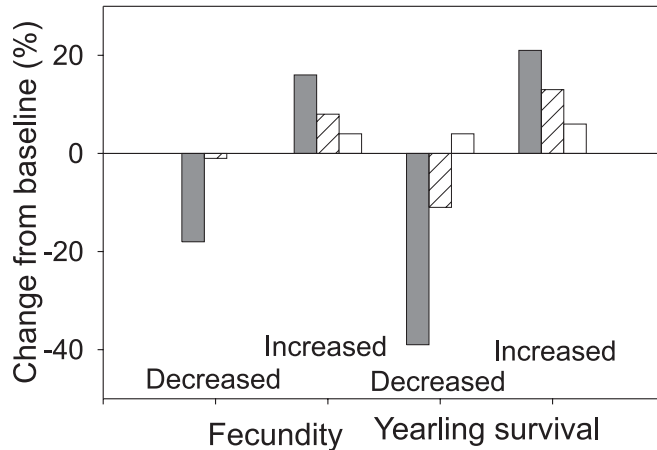
of these below in the spirit of encouraging others to investigate this apparent non-result (see Koricheva 2003).

The first reason for my results could be that the matrix models and IBMs were inappropriate for the analysis. The use of matrix projection models with spawner–recruit relationship for eggs to age 1 seemed reasonable. Indeed, such matrix models are a logical extension of previous analyses that inferred life history influences on population responses (e.g., Barnhouse et al. 1990).

Furthermore, age-structured matrix models with spawner–recruit relationships are commonly used in both theoretical analyses (e.g., DeAngelis et al. 1980; Punt 2000) and fisheries management (e.g., Southeast Fisheries Science Center 2002).

Justification of the use of IBMs in this analysis, based on past use of similar models, is more difficult because the IBMs are more complex than the matrix models and they varied greatly in their details. I was involved in the develop-

**Fig. 11.** Predicted population responses (percent change from baseline) for increased and decreased fecundity and yearling survival for the lake trout matrix model with the spawner–recruit relationship only (shaded bars) and with the spawner–recruit relationship and 10% (hatched bars) or 20% (open bars) adult density-dependent growth.



ment of all of the IBMs used, so one would hope that I understood the capabilities of the models and thus did not misuse them in this analysis.

Despite the widespread use of the matrix model and my familiarity with the complex IBMs, it is possible that both types of models were not sophisticated enough to capture important species differences to enable population responses to be related to life history traits. Spatial heterogeneity and density-dependence are two areas that the models likely oversimplified. All of the matrix models represented a single well-mixed box, and many of the IBMs represented one or only a few spatial boxes. The exception was the brook trout model, which represented many habitat boxes of a small stream. Clark and Rose (1997c) showed that density-dependent reproduction, growth, and mortality in the brook trout IBM were tightly coupled to the explicit representation of space and the movement of individuals among the spatial boxes. The interaction between density-dependence and spatial heterogeneity has been discussed for fish (e.g., MacCall 1990), and remains an area of much discussion in ecology (Hixon et al. 2002). Furthermore, important differences among species responses could be related to density-dependence in post-young-of-the-year life stages. For example, density-dependent growth of adults, and its effect on reproduction, have been documented in variety of fish species (Helser and Almeida 1997; Rose et al. 2001; Lorenzen and Enberg 2002).

I initially attempted to use a more general form of the matrix projection model (based on stage or stage within age), with density-dependence and stochasticity in all appropriate life stages. I was unable to develop such models for more than a few species, and even those models were based on too much conjecture to ensure that species differences in responses were real or simply a result of my subjective decisions during model development. Nevertheless, including realistic levels of adult density-dependent growth in the lake trout matrix model significantly affected predicted population responses, and showed the potential importance of

density-dependent processes outside of the first year of life. While many of the IBMs allowed for density-dependence in the adult life stages, perhaps too few IBMs were used in this analysis to show clear patterns. More sophisticated matrix projection models, especially those having better representation of spatial heterogeneity and density-dependence of adult life stages, and additional IBMs might be needed to clarify the relationship between population responses and life history traits.

A second explanation for the lack of consistent results is that I may have made mistakes in the analysis. Assuming that the matrix models and IBMs were adequate and appropriate for the analysis, I may have done the analysis in a way that masked an underlying relationship between population responses and life history traits. Perhaps I did not standardize the population states appropriately, so species responses were confounded with populations being in different states. While the patterns of responses in the matrix models were similar across  $SS_{MSR}$  values, the magnitude of responses to changes in fecundity did depend on population state. The magnitude of responses is important when matrix-model results are mixed with IBM results. Masking of relationships by mixing matrix-model and IBM results is possible but seems unlikely. Matrix-model responses to changes in yearling survival were insensitive to population state, and responses to changes in yearling survival did also not show any patterns in life history space. Furthermore, when I substituted the predicted responses obtained from the matrix models based on 5%  $SS_{MSR}$  with the results based on the arbitrary and 10% and 25%  $SS_{MSR}$  population states, I again did not find any obvious clustering of small or large responses on the life history surface.

Other aspects of the analysis where I could have gone wrong were in making incorrect assumptions concerning the values of the life history traits and how the changes in fecundity and yearling survival were imposed. These are also possible, but I think unlikely, explanations. I used the life history traits reported in Winemiller and Rose (1992), which may not accurately reflect the life history traits of the actual populations represented in the models. I replotted Figs. 8–10 using the fecundity (mean batch size) and maturation size derived from the matrix-model inputs and IBM simulations; investment per progeny did not change because egg size and parental care were not dependent on model inputs. Very similar non-patterns of responses in life history space were obtained. Use of other values of species' life history traits would reshape the surface, but likely not re-sort the larger or smaller responses towards a particular region of the surface.

It is also possible that the changes in fecundity and yearling survival were not imposed consistently between the matrix model and IBMs. Perhaps larger changes would have resulted in a clearer pattern of responses. I repeated the matrix-model and IBM analyses with 10% and 40% changes in fecundity and yearling survival and obtained results similar to those based on 25% changes. Given the straightforward way in which changes were imposed and the wide range of responses predicted by both types of models, I do not see obvious problems in how fecundity and survival were changed.

The third possible explanation relates to the three-end-point life history surface. Perhaps species' life history strategies

nicely map onto the Winemiller and Rose (1992) surface, but this does not mean that the magnitude of population responses to changes in survival and fecundity necessarily map onto the same surface. The Winemiller and Rose life history surface is appealingly simple, but may not be appropriate for quantitatively relating life history strategies to population responses. The magnitude of density-dependence in a population is fundamental to determining the population's response to changes in survival. Rose et al. (2001) showed that the steepness of the spawner–recruit relationship, which measures the magnitude of density-dependence, showed wide variation when grouped into the three end-point strategies of Winemiller and Rose.

Perhaps I needed to correlate the responses to life history traits other than the three (maturation, fecundity, parental care) that define the Winemiller and Rose (1992) life history surface. For example, Schaaf et al. (1987) related population responses to an index of reproduction based on the mean and standard deviation of reproductive contributions by age, and Parent and Schriml (1995) included piscivory in their suite of life history traits to help determine fish species at risk of extinction.

I tried, with only moderate success, several correlation analyses using my predicted responses and a variety of life history traits. For example, I correlated predicted responses by the matrix models to the life history traits of mean age of the population, age at maturity, longevity, number of eggs per mature adult, first-year survival rate, and steepness of the spawner–recruit relationship, all estimated from the baseline matrix-model simulations. Predicted matrix-model responses to changes in fecundity were correlated with steepness ( $r^2 \approx 0.8$ ) but not with any of the other life history traits. Given that the only density-dependence in the matrix model was in the spawner–recruit relationship, this result was expected and not especially useful in data-poor situations that likely would lack spawner–recruit data. Predicted responses to reduced yearling survival were moderately correlated with longevity ( $r^2 \approx 0.5$ ), but responses to increased yearling survival were moderately correlated with mean number of eggs per mature adult ( $r^2 \approx 0.5$ ). I also added the predicted responses from the IBMs to the matrix-model results. I derived average values of five of the same life history traits (not steepness) from baseline simulations of the IBMs, even allowing for different values for the six yellow perch versions, and the correlation results remained murky. Perhaps including additional species in the analysis would help identify the elusive life history traits that are cleanly related to population responses.

The fourth and final possible explanation for my results is that population responses may have a strong site-specific component. Perhaps the models and the analysis were adequate, but the responses of the populations were dominated by the site-specific aspects of each of the models (e.g., Rose and Cowan 2000). The shape of the spawner–recruit relationships used in the matrix models, which was the only density-dependent aspect of the matrix projection models, was critical to the magnitude of responses predicted. I purposely selected spawner–recruit data from specific locations so that the estimated Beverton–Holt relationships were more easily defensible. The IBMs were also developed using data from one or a few similar locations. Perhaps the responses

predicted by the models have a strong population (site-specific) component. If this is so, then inclusion of many more populations would enable me to observe the species-level patterns in the responses. Unfortunately, while there are hundreds of spawner–recruit data sets (e.g., Myers et al. 1995), the vast majority involve spawners or recruits reported on relative scales, and involve mostly periodic strategists (Rose et al. 2001). The availability of long-term, absolute-scale spawner–recruit data, especially involving equilibrium- and opportunistic-strategy species, is quite limited. Some candidate equilibrium and opportunistic species that have sufficient spawner–recruit data that could be included in future analyses are the brown trout (*Salmo trutta*) (Elliott 1994; Bell et al. 2000), Pacific sardine (*Sardinops sagax*) (Jacobson and MacCall 1995), alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*) (Jessop 1990). Other IBMs (e.g., Wang 1998) are also available that could be added to the analysis.

Life history has been invoked previously to infer fish population responses to changes in their vital rates (e.g., Jennings et al. 1998; Rochet 2000). Many of these studies were either qualitative, used a limited of species, or made simplifying assumptions concerning density-dependent processes. I assembled a suite of matrix models and individual-based models that addressed these limitations. My analysis did not yield any obvious relationships between the magnitude of population responses and life history traits.

The lack of obvious patterns in the results could be explained by inadequate population models, incorrect analyses, inappropriate life history model, or important site-specific factors. In the case of incorrect analyses and an inappropriate life history model, the problem may be solved with additional empirically based and theoretical analyses, likely performed by others taking a fresh look at the problem. The explanations in terms of inadequate population models and important site-specific influences are more problematic. Both of these explanations have broader implications. Inadequate population models are troublesome because age-structured approaches (e.g., matrix models) with spawner–recruit relationships are widely used (e.g., Barnthouse et al. 1990; Restrepo and Legault 1998), and IBMs are continuing to gain popularity (DeAngelis et al. 1994; Grimm 1999). If site-specific factors play at least a partial role, then my results imply that predictions based on life history theory should remain qualitative, and that quantitative predictions should be based on site-specific data. Some progress on the issue of the role of site-specific factors is possible using multiple populations of a few well-studied species (e.g., Shuter et al. 1998), but such data being limited to a relatively few species will preclude definitive conclusions. Whether adding many more populations to the analysis presented in this paper would allow at least semiquantitative predictions with only minimal site-specific data remains to be determined.

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