Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing[1]

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Abstract: Large, dominant fish species that are the basis of many fisheries may be naturally so successful due partly to "cultivation effects," where adults crop down forage species that are potential competitors/predators of their own juveniles. Such effects imply a converse impact when adult abundance is severely reduced by fishing: increases in forage species may then cause lagged, apparently depensatory decreases in juvenile survival. Depensatory effects can then delay or prevent stock rebuilding. Cultivation effects are apparently common in freshwater communities and may also explain low recruitment success following severe declines of some major marine stocks such as Newfoundland Atlantic cod (*Gadus morhua*). Risk of depensatory effects should be a major target of recruitment research, and management policies should aim for considerably higher spawning abundances than has previously been assumed necessary based on recruitment data collected during adult stock declines associated with fishery development.

Résumé : Le succès des grosses espèces dominantes de poissons qui sont à la base de nombreuses pêches peut être dû en partie à un « effet cultural », les adultes récoltant les espèces fourrage qui sont des concurrents ou des prédateurs potentiels de leurs propres juvéniles. Cet effet a par contre un impact inverse lorsque l'abondance des adultes est fortement réduite par la pêche : les augmentations chez les espèces fourrage peuvent causer des baisses décalées dans le temps, à caractère apparemment dépensatoire, de la survie des juvéniles. Les effets dépensatoires peuvent alors retarder ou empêcher le rétablissement des stocks. L'effet cultural semble courant dans les communautés dulcicoles et peuvent aussi expliquer le faible succès de recrutement qui suit les déclins graves de certains grands stocks marins comme la morue franche (*Gadus morhua*) de Terre-Neuve. Le risque d'effets dépensatoires devrait être un thème majeur de la recherche sur le recrutement, et les politiques de gestion devraient fixer pour objectifs des abondances de géniteurs considérablement plus élevées que ce qu'on jugeait jusqu'ici nécessaire en se fondant sur les données de recrutement recueillies pendant les déclins de stocks d'adultes associés au développement des pêches.

[Traduit par la Rédaction]

Introduction

Single-species stock assessments and harvest policy development generally assume either that recruitment is independent of stock size or that recruitment varies around some compensatory relationship described by a simple saturating or dome-shaped curve. Compensatory effects are assumed to arise through reductions in intraspecific competition and (or) cannibalism when abundance is reduced by fishing. There is now broad empirical support for limits to compensatory response, so that low parental stock sizes can indeed result in lower mean recruitment (Myers and Barrowman 1996; Myers et al. 1999), so most assessments include a recruitment relationship that at least recognizes some risk of recruitment overfishing. But there has been little empirical support for the existence of "depensatory" or "recruitment failure" effects where recruitment decline with stock size is even more rapid than expected from a decrease in egg production combined with high juvenile survival (Myers et al. 1995*a*, 1995*b*; Liermann and Hilborn 1997). However, such effects are likely to be difficult to detect in typical data sets that have few observations at very low stock size (Shelton and Healey 1999). Depensatory effects are not routinely incorporated in assessments except via risk management tactics such as setting arbitrary minimum population size goals. The approach of assuming "stationary" mean stock–recruitment relationships has been criticized on grounds that it does not account for effects of either persistent environmental change or changes in trophic relationships (juvenile predation risk, food) that might accompany overfishing (e.g., see Walters 1987; Walters and Korman 1999; Hall 1999), but criticism has focussed mainly on our inability to forecast short-term recruitment changes. In particular, we have paid little attention to the risk of very severe nonstationarity, in the form of persistent depensatory effects (low juvenile survival) that develop with some time lag following periods of adult stock depletion.

Using Ecosim II (Walters et al. 1997, 2000), we have been conducting exploratory simulations to detect possible depensatory recruitment effects due to trophic interactions.

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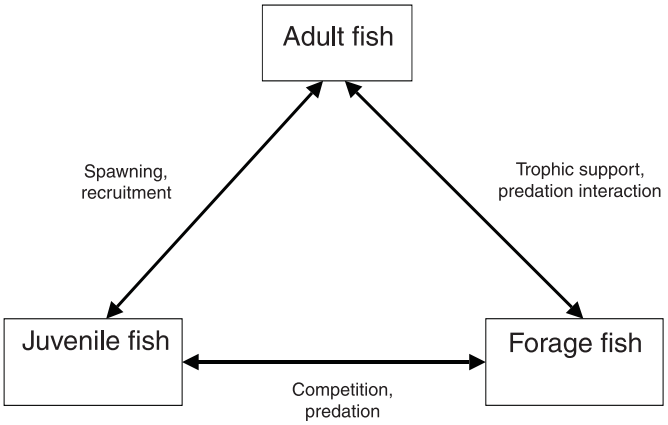
Fig. 1. We envision recruitment depensation at low stock sizes as arising from a trophic triangle: prey organisms of adult fishes can respond positively to reductions in adult fish abundance by fishing and then causing reductions in juvenile survival via competition and (or) predation interactions with the juveniles.



This model combines simple biomass dynamics models for some ecosystem components with age-structured (delay-difference) models for selected species that have strong trophic ontogeny and (or) size-selective fishing impacts. It links recruitment to trophic changes by explicit (and reciprocal, predator–prey) representation of how dynamic changes in food availability and predation risk affect juvenile mortality rates and how juvenile fish may moderate these rates through risk-sensitive changes in foraging times (Walters and Juanes 1993). Most often, the "emergent" stock–recruit relationships predicted by Ecosim II look like the classic Beverton–Holt, broken stick, or Ricker relationships, i.e., we predict mainly strong compensatory (stabilizing) effects due to the usual mechanisms thought to result in increased juvenile survival at low densities (more food, less cannibalism, etc.). But in some cases, we see a catastrophic pattern: as simulated fishing mortality rate is increased over time, recruitment initially appears to be stable or declining along a Beverton–Holt or Ricker relationship with declining spawning stock. But then, juvenile mortality rates "suddenly" increase (over a few simulated years) after some time delay to result in delayed depensatory effects that may result in extinction even if fishing is stopped.

Here, we describe the mechanism that causes models like Ecosim II to predict depensatory recruitment changes that strongly contradict classic compensatory stock–recruitment theory. We propose a "cultivation hypothesis" to suggest why this mechanism could in fact be quite common, especially for large, predatory fish species, and discuss factors that may prevent it from operating in some circumstances. We review case examples where it may have occurred. We conclude that the mechanism is plausible enough, and supported by enough circumstantial case evidence, to warrant immediate policy response in the form of higher spawning stock (lower exploitation rate) goals than would be estimated from single-species population theory.

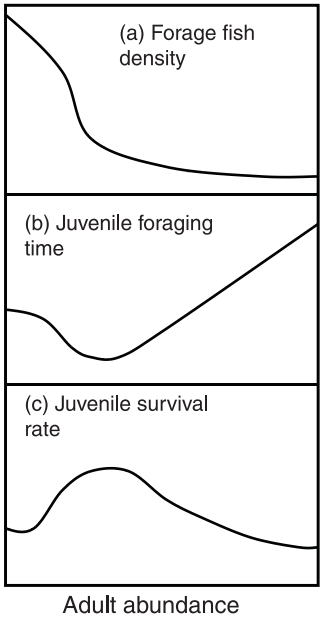
How juvenile trophic interactions can cause depensatory dynamics

Delayed depensatory effects arise in Ecosim II models (Appendix) through the following sequence of events. As fishing reduces the adult population size of a fish species, the total number of juveniles produced per time decreases. In the absence other trophic effects, this results in increased food density in the localized "foraging arena" habitats (usually near predation refuges; see Walters and Juanes 1993) where juvenile feeding is concentrated. Juveniles respond to increased food density by reducing feeding time and hence time at risk to predation (or total time spent at body sizes small enough to be vulnerable to high predation risk). Juvenile mortality rate then decreases, so net recruitment at first stays nearly constant despite fewer juveniles entering the juvenile life stage per time. But if adult abundance is severely reduced, one or more smaller "forage fish" species are "released" to increase in abundance. Then, one or two negative effects can occur. First, the forage fish may directly (even if incidentally) prey on the juveniles, causing increased predation risk per time spent foraging and hence higher juvenile mortality rate. Second, if the forage and juvenile fish share at least some foods (e.g., zooplankton, benthic invertebrates) and use overlapping foraging arenas and tactics for reducing predation risk, increased forage fish abundance leads to reduced food density and hence to increased juvenile foraging time and general predation risk. A simple way to visualize this dynamic is as a "trophic triangle" (Ursin 1982; Cohen et al. 1993; He et al. 1993; Rudstam et al. 1994), "competitive juvenile bottleneck" (Bystroem et al. 1998), or "predator–prey role reversal" (Barkai and McQuaid 1988). The triangle adds prey/competitor dynamics to the usual juvenile/adult dynamic linkage that has traditionally been emphasized in population dynamics modeling (Fig. 1).

Figure 2 presents a graphical model for the elements of this mechanism, in terms of patterns that should be observable in the field if it is operating: (*i*) negative relationship between forage fish abundance and adult abundance ("spawning stock" biomass), (*ii*) depensatory increase in juvenile foraging time (and (or) reduced juvenile growth rate) as the forage fish become more abundant, and (*iii*) declining juvenile survival rate when adult abundance has been low for long enough for the forage fish increase to occur. Additionally, we should be able to observe (*iv*) diet and habitat use overlap between the juvenile fish and the forage fishes and (or) (*v*) direct evidence of predation by the forage fish on juveniles, in stomach contents sampling. Of these observations, we should not be surprised if direct evidence of predation is not found. Forage fish are likely to be much more abundant than the juveniles (and to have high food consumption rates) and may thus cause a high juvenile mortality rate (eat a large total number of juveniles) even if only a very tiny percentage of their diet is juveniles.

Note that this mechanism for causing decreased reproductive performance at low stock size is quite different from the common concern that fishing too hard on a dominant species may allow competitors to increase and "take over" its niche. We are talking not about competitors in general, but very specifically about other small fish (and some invertebrates like squid) that are likely to be directly impacted in abundance and distribution by adults of the fish species in question. These species may be direct competitors and (or) predators of the juveniles of the species during a life history stage where we know from recruitment experience that the

Fig. 2. Elements of a hypothesis for depensatory recruitment changes at low stock sizes. (*a*) Increase in abundance of small "forage" fishes/invertebrates if predatory stock size decreases; (*b*) increasing rather than decreasing juvenile foraging time when adult abundance is low due to competition with forage fishes; (*c*) decreased juvenile survival rate at low adult population size due to increased foraging time and (or) direct predation by forage species.



juveniles are likely to be "sensitive" (to have high and strongly density-dependent mortality rates). In part, this is not a new idea or concern: biologists have long speculated about how predatory fish species are able to achieve large body sizes, given that their juveniles must grow through a predation–competition "bottleneck" involving the very species that will be their prey later in life (Crowder et al. 1992; Wooten 1994). It is familiar in management procedures designed to create "balanced" predator–prey interactions such as those for bluegill (*Lepomis macrochirus*) – largemouth bass (*Micropterus salmoides*) systems (Gutreuter and Anderson 1985), as guidance for size at stocking procedures (Madenjian et al. 1992), and to ecologists engaged in evaluating "size-structured" or "trait-mediated" interactions (Persson and Eklov 1995; Werner 1998).

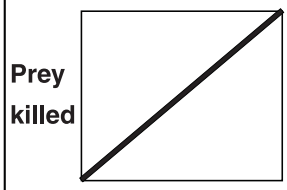
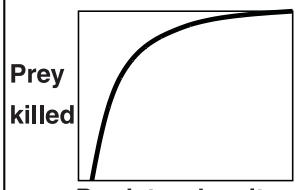
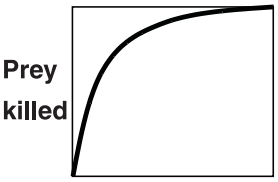
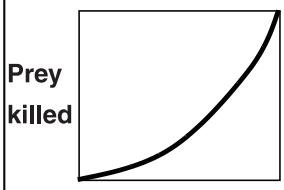
We can of course envision more complex mechanisms by which impacts of adult abundance on trophic structure may modify survival conditions for their juveniles. For example, we found in early Ecosim tests that invasion of Nile perch (*Lates niloticus*) in Lake Victoria was possibly slowed initially by competition/predation from the natural fish community of the lake. Population growth rate then apparently increased as the perch became abundant enough to depress this community and allow increases in an invertebrate (*Caridina*) and a fish (*Rastrinebola*) that later became its dominant foods (Kitchell et al. 1996; Walters et al. 1997). Another example would be the possibility of trophic "quadrangles" in zooplanktivores: if adults feed selectively on larger zooplankters, reduction in adult abundance may allow an increase in abundance of these larger forms with an attendant negative impact on abundance of smaller zooplankters that are needed by smaller juveniles. A third example is argued to account for the progressively increased juvenile mortality rates observed for stocked lake trout (*Salvelinus namaycush*) in Lake Superior. After sea lamprey (*Petromyzon marinus*) and fisheries mortality were reduced, natural reproduction allowed a gradual increase in adult abundance of a deepwater trout race (siscowet). This created a predator population that imposed increased mortality on the stocked juveniles of the shallow water trout race (lean) and may be responsible for the lack of successful reproduction by the latter (Hansen et al. 1995).

The depensatory mechanism described in Fig. 2 is fundamentally different from models for direct depensatory predation effects based on the form of predator responses to prey densities (Fig. 3) (e.g., Collie and Spencer 1993; Spencer and Collie 1997*a*, 1997*b*) or models based on reproductive failure at low population size. In classical "reaction vat" models of predator–prey interaction, decreasing prey mortality rate with increasing prey density is caused by increased handling time or satiation of predators, such that the proportion of the prey population killed by each predator decreases with increasing prey (juvenile fish) density (Fig. 4). This may occur in a few circumstances where prey are particularly vulnerable to predation and predators can be "overwhelmed", for example, during downstream migrations of salmon fry from small streams (Neave 1954), but it is probably not common. In Ecosim, we assume that predation takes place largely in spatial patches or "foraging arenas" where juveniles are forced to accept predation risk in order to forage and where predation rates are limited not by predator satiation but rather by juvenile movement rates into and out of (or time spent in) behavioral refuges and by predation risk per time spent foraging (see Appendix; also see fig. 1 in Walters and Juanes 1993). We think that this model for spatial organization is a much better description of general natural history experience in aquatic ecology (stomach contents data rarely show predator satiation, juvenile fish distributions obviously dominated by tactics to reduce predation risk) than is the classic reaction vat model. Further, it better explains the ecosystem-scale observation that trophic cascade effects are relatively weak and suggestive of ratio dependence in predator–prey interactions (McCarthy et al. 1995; Scheffer and De Boer 1995; Brett and Goldman 1996).

Why perverse interactions could be common: the cultivation hypothesis

Most fisheries develop at least initially to take the largest, most abundant, ecologically "dominant" fishes. This may be precisely the suite of species most vulnerable to depensatory responses because a reversal of these responses may be why such species are dominant in the first place. That is, ecological dominance may well be due at least partly to "cultivation effects": dominants may be species that are fortuitously capable of being especially good at capturing (and otherwise suppressing) the particular smaller forage fishes that could cause the worst competition/predation effects on their own juveniles. Note that this is not a group or population selection argument about selection favoring adults that consume particular forage species so as to protect their own juveniles.

Fig. 3. Contrasting assumptions and predictions in models that explain depensatory effects by the form of predator functional responses in random search (reaction vat) environments versus models that assume spatial organization of predation interactions in patchy "foraging arenas."

Effect of:	Classical predator-prey "reaction vat" models	"Foraging arena" models
Predator density		
Prey density		
Implications	Depensatory increase in prey mortality rate at low prey densities; prey mortality rate highly sensitive to predator abundance; predator satiation common when prey abundance high	Compensatory decrease in prey mortality rate at low prey densities; prey mortality rate relatively insensitive to predator abundance; predators rarely satiated

It simply says that if there are several large species in a system, with varied diets as both juveniles and adults, the dominant large species should end up being that one that happens to cultivate the best survival conditions for its juveniles by having particularly large impacts on its juveniles' competitors/predators.

We usually think of dominant fishes as those capable of best using trophic (food) production and physical habitat and of being long-lived enough to accumulate large unfished population sizes. But when we make this assumption, we ignore the large body of evidence that abundance is generally "limited," not at the adult stage but rather at the juvenile stage (recruitment most often observed to be independent of or flat across a wide range of adult abundance). Dominance may well require adult feeding patterns that efficiently use production by lower trophic levels, but it certainly also requires relatively good conditions for juvenile survival and growth. The cultivation hypothesis is that dominance is a result of not only being able to acquire trophic resources but also to insure the best possible trophic conditions for juveniles.

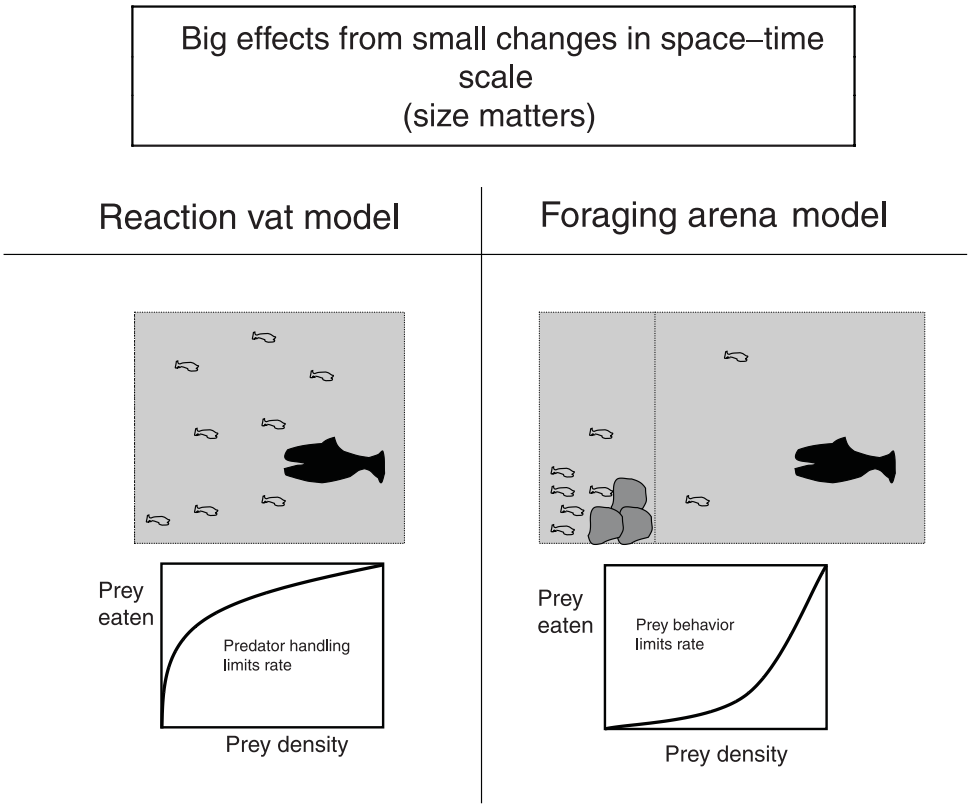
Factors that mitigate against cultivation/depensation effects

An obvious and immediate objection to the cultivation/depensation arguments presented above is that they offer no mechanism by which large, dominant species could become abundant enough to have cultivation effects in the first place. Why is the world not dominated by small forage species that successfully prevent larger predatory species from ever becoming abundant through impacts on juvenile survival of the predatory species? If depensatory effects are common, they must not be so strong as to entirely prevent large predatory species from invading ecosystems, at least when there is no fishing.

At least four factors likely mitigate against very strong depensatory effects: (*i*) niche specialization, (*ii*) limitation of predation impacts in forage species via risk-sensitive behaviors by the forage species, (*iii*) diffuse predation impacts that act to prevent strong population responses by forage fishes, and (*iv*) spatial propagation effects. Niche specialization is an obvious possibility: successful large predatory species may be ones whose juveniles are competent at acquiring particular food resources, relative to forage fish competitors (i.e., competition may not be all that severe). In terms of the graphical model in Fig. 2, such niche specialization would imply a "failure" in Fig. 2*b*: juvenile foraging time not increasing with increases in abundance of forage species competitors.

The second and third factors involve mitigation of the forage fish numerical response to predator abundance, i.e., a less dramatic response than shown in Fig. 2*a*. If the forage fishes have severely restricted habitat use/foraging activities

Fig. 4. Risk-sensitive behaviors by juvenile fish imply a deep reversal of predictions about predation impact. Small increases in the space–time scale of experimentation and modeling can result in a reversal in form of the functional response observed, from a type II response for a reaction vat experiment to type III for an experiment where prey can hide from predators unless prey density is high enough to force the prey to spend more time foraging.



due to predation risk in general (risk-sensitive foraging), they may simply not be limited in abundance in the first place by the predatory species in question. In fisheries terms, their natural mortality rate M and (or) recruitment may not be sensitive to changes in abundance of any particular predator that might be reduced through fishing. Alternatively, any temporary increase in their abundance (due to a decrease in their mortality rate) may be reversed by numerical responses of a variety of other predators (diffuse predation impacts).

In physically large ecosystems with a diversity of habitats, juveniles of large predators may find refuges for persistence in particular sites where predation/competition effects are relatively weak. Such sites may then act as "epicenters" for spatial population expansion, as adults produced from the centers gradually move in enough numbers to other sites so as to generate cultivation effects in these sites. That is, cultivation effects may be critical in the range expansion/contraction dynamics often observed for large fish populations (MacCall 1990).

We likewise would not expect strong cultivation/depensation effects for species that show large-scale ontogenetic habitat shifts (large physical separation between juvenile nursery areas and adult feeding areas), possible mainly in marine ecosystems. In cases like anadromous salmon, it is difficult to see how adults could have much direct effect on competition/predation conditions faced by juveniles (although they may have other indirect effects such as fertilization of rearing areas with carcasses).

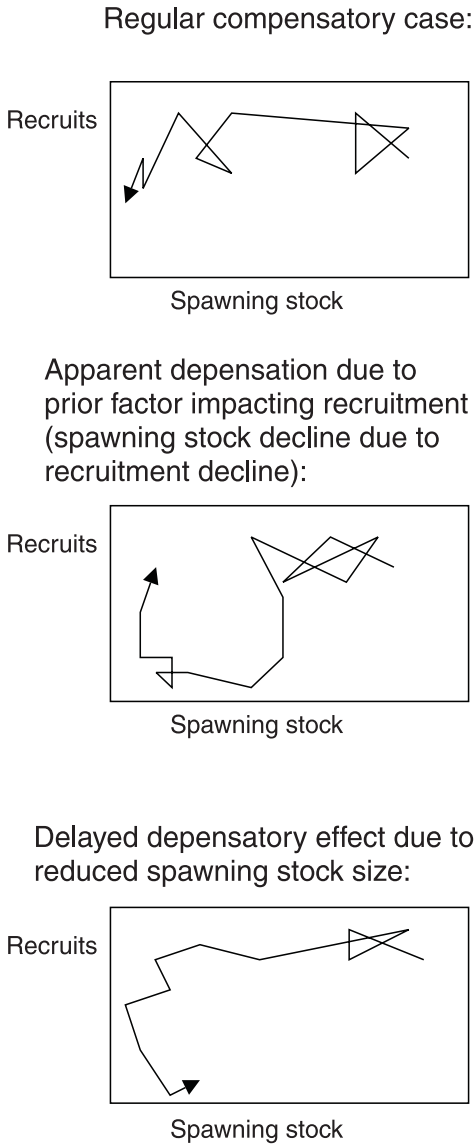
It should be noted that large ecosystem size per se does not imply that predation/competition effects should be weaker because predation is more "dilute," as suggested by Verity and Smetacek (1996) to explain differences between freshwater and marine systems. Since interactions can be spatially patchy (highly localized) in both environments, it is irrelevant that average densities of predators are much lower in the ocean environment.

Examples?

The most obvious examples of apparent cultivation/depensation effects have been in freshwater ecosystems. There has long been a concern about how to establish "balance" in centrarchid communities, which have a nasty propensity to shift toward dominance by stunted sunfish populations when basses are heavily exploited (Swingle 1950*a*, 1950*b*; Hackney 1979; Olson 1996). In these systems, it is obvious how sunfish forage species impact recruitment of bass via both competition and direct predation. There is a south–north cline toward increasing risk of sunfish dominance to the north, most likely related to the impact of growing season length and the duration of the competition/predation window faced by juvenile basses.

Under heavy exploitation, walleye (*Stizostedion vitrium*) populations in Alberta, Canada, have shown persistent recruitment failure, accompanied by dramatic increases in minnow populations that are thought to prey heavily on walleye larvae (M. Sullivan, Alberta Department of Natural

Fig. 5. Patterns in stock–recruitment data expected under alternative hypotheses. In the regular compensation case, juvenile survival rate increases smoothly as spawning stock size decreases. In the apparent (prior) depensation case, recruitment decline precedes (and causes) the spawning stock decline, giving the appearance of depensation unless enough observations are available for the recovery portion of the recruitment "hook." In the delayed depensation case, recruitment may remain high as the stock declines and then finally collapse.



Resources, Edmonton, Atla., personal communication). Similar walleye recruitment failures may have occurred in Wisconsin lakes, and walleye have not become established in some lakes with apparently excellent habitat and forage conditions (D. Beard, Wisconsin Department of Natural Resources, Madison, Wis., personal communication). However, most Wisconsin lakes have maintained strong recruitment despite heavy fishing (e.g., Escanaba; Hansen et al. 1998). The striking difference between these regions supports the possibility mentioned above that "diffuse predation" may prevent delayed depensatory effects: Alberta lakes lack the centrarchids (basses, sunfish) that are prominent in the littoral zones of most Wisconsin Lakes.

The northern (2J3KL) Atlantic cod (*Gadus morhus*) stock off Newfoundland showed declines in apparent juvenile survival rate (recruits per spawning biomass) and also body growth rate during the 1980s, following severe stock reduction during the 1970s (Myers et al. 1996; Anderson and Dalley 1997; Shelton and Healey 1999). That stock has not recovered as expected following fishery closure in 1992, and in particular, there is little evidence of recruitment to the larger, offshore migratory component of the stock. If the cultivation/depensation hypothesis applies in this case, it should be possible to demonstrate substantial increases in some smaller species that are competitors/predators on juvenile cod in nursery areas and were preferred prey of adult cod (note that "preferred" is in the technical sense: a high proportion in the diet compared with the proportion in the environment). One possible candidate species is Arctic cod (*Boreogadus saida*). However, note that for the 10 North Atlantic cod stocks that have undergone severe decline (80% or more) in recent years, 6 have not shown the survival decline predicted by the cultivation/depensation hypothesis (Myers et al. 1996). Bax (1998) suggested that predation on juvenile cod by clupeids could exaggerate fishing effects and help lead to a "planktivore-dominated" ecosystem in the Baltic.

The large number of stock–recruitment data sets assembled by Myers and colleagues (Myers et al. 1995*a*, 1995*b*, 1999; www.mscs.dal.ca/~myers/data.html) provides an opportunity to broadly examine the frequency of occurrence of depensatory effects. Because we were concerned about possible transitory and delayed effects that might not be detected by simply fitting stationary stock–recruitment curves to the data (Fig. 5), we had three independent scientists examine the data sets and provide a visual assessment of whether delayed depensation might be present. Of 330 stock–recruitment data sets excluding anadromous salmonid cases, we found (Table 1) that 44–112 could be interpreted as showing some sort of depensatory response, but these represent almost a third of the cases where there are observations at relatively low (20% or less of maximum) spawning stock sizes. Liermann and Hilborn (1997) also suggested that these data sets might contain more examples of depensation than were detected by Myers et al. (1995*a*, 1995*b*). However, only a small number (17–45) of these possible depensatory cases show the delayed response expected under the cultivation/depensation hypothesis, characterized by a downward "hook" (Walters 1987) in the stock–recruit time series (Fig. 5). Far more common, especially for clupeoids, are hooks of the reverse shape where recruitment initially declines, then the spawning stock declines, and then recruitment begins to recover; these cases should not be interpreted as evidence for depensation. Fisheries scientists have generally interpreted these cases as "bad luck": poor environmental conditions leading to recruitment failure, and persistence of the poor conditions for at least some time following implementation of measures aimed at protecting spawning stocks. While such cases might be due to trophic effects (e.g., increase in predators leading to recruitment decline and then predator collapse allowing recruitment to recover; likewise for food supply

Table 1. Visual characterization of 330 worldwide stock–recruit data sets assembled by Myers and colleages, exlcuding anadromous salmonid cases.

			Possible depensation	
Taxonomic group	No evidence	No depensation	Prior	Delay
Classification by three scientists of data at www.mscs.dal.ca/~myers/data.html				
Clupeiformes	24–32	11–23	14–25	3–7
Gadiformes	36–52	6–18	6–15	7–14
Perciformes	38–47	6–17	1–10	2–11
Pleuronectiformes	27–30	1–11	1–7	1–3
Salmoniformes	16–19	11–16	3–4	2–5
Miscellaneous	11–22	3–8	2–6	2–5
Total	152–202	38–93	27–67	17–45
Classification by Walters of data in Myers et al. 1995*a* and 1995*b*				
Clupeiformes	21	28	3	2
Gadiformes	36	18	4	11
Perciformes	12	5	2	1
Pleuronectiformes	21	7	2	0
Salmoniformes	2	3	1	2
Miscellaneous				
Total	92	61	12	16

Note: Ranges are for three independent scientists. "No evidence" means no observations at low enough spawning stock size (<20% of maximum) to expect depensatory effects, "no depensation" means recruitment relatively high at lowest stock sizes and (or) an upward hook in the recruitment time series, and "possible depensation" means at least a few observations of relatively low recruitment per spawner (juvenile survival rate) at low stock size. In depensation cases, "prior" means that survival decline preceded stock decline, suggesting an agent other than delayed depensation likely responsible for apparent depensation.

dynamics), we would not interpret them as evidence for persistent depensatory effects, delayed or otherwise.

The taxonomic distribution of possible depensation cases in the Myers and colleagues database (Table 1) provides direct support for using foraging arena assumptions in ecosystem models and recruitment analysis (Figs. 3 and 4). Were predator–prey interactions mainly of the mass action or reaction vat functional form, we would expect depensation effects to be most common in taxonomic groups dominated by smaller "forage" species (Clupeiformes fishes) and least common in groups dominated by piscivores (Gadiformes fishes). In fact, we see the opposite: the incidence of depensatory cases is highest in Gadiformes fishes, and the two delayed depensation cases in Salmoniformes fishes are for a large piscivore (northern pike (*Esox lucius*) in the two basins of Lake Windermere, Great Britain). This is just what we expect from foraging arena theory, assuming that there has been strong selection in smaller species for distributional/behavioral tactics to limit predation risk. Also, we generally predict unrealistically violent predator–prey oscillations in Ecosim models and unrealistically large temporal variation in natural mortality rates of forage species unless we assume such tactics.

It is likely that available stock–recruitment data sets provide an underestimate of the risk of cultivation/depensation effects. Most of the data have been collected since the middle of the twentieth century, and many stock collapses due to depensatory effects could have occurred much earlier in world fishery development so that what we have left to study today are mainly the most productive and resilient stocks. It is not unusual to hear laments by older, experienced fisheries observers about the disappearance of various species and stock components, before anyone had the time or resources to study them. Data collected for research purposes are typically among the last things to occur in the developmental sequence of most fisheries. On an even longer time scale, the patterns of mortality imposed by the industrial fisheries of this century are unlike anything in the evolutionary history of most fish species (Frank and Leggett 1994).

Implications for harvest management and research

The arguments presented in this paper imply need for a very particular third step in the evolution of the theory of fishing. The first step in this evolution was the development of simple catch–effort relationships (Baranov, Graham, Scahefer, Gulland) that did not explicitly use any ecological variables for prediction; this approach "worked" in a world of slow fisheries development that did not cause either rapid population size/structure transients or severe depletion. The second step, heralded by Schaefer's (1957) method for fitting logistic population models to time series data, was to recognize population size and structure as dynamic variables. Most of the elaborate machinery of modern fisheries assessment has really just added detail to the population state representation and statistical analysis, allowing better interpretation of data from rapidly changing populations under modern, more violent exploitation regimes. It is noteworthy that we generally do not obtain much better fits to population time series data (or predictions of harvest impact) with the elaborate models than we can with simple logistic or delay-difference models; the really big step was to recognize population size as a critical state variable. Single-species models served us well until very severe stock depletions began to occur.

We argue that in this "new" domain of fisheries system states, where severe depletions and risk of recruitment overfishing are common, that the single-species recruitment models are no longer reliable. While we understand and agree with the call for an "ecosystem approach" to fisheries management (Mooney 1998), we also recognize that this approach is complex and will require a substantial effort before successes can reinforce its value. In the interim, we believe that we must at least try to extend the theory of fishing so as represent some other, particularly important variables (predators/competitors of juvenile fish) in order to predict the pathological dynamics that sometimes accompany severe depletion. That is, we need to take a third basic step toward inclusion of more variables in predictive models, but in a very particular way. Just as population dynamics modelers had much of the modeling and statistical machinery already available when they began the step into modern stock assessment, so do we have the machinery largely in place to begin the next step, via ecosystem analysis tools like multispecies virtual population analysis (Pope 1991; Sparre 1991) and Ecopath/Ecosim (Walters et al. 1997, 2000).

As for any depensatory mechanism, the primary policy implication of cultivation/depensation effects is the existence of a critical population size, defining a division between two qualitatively different domains of population behavior. In the high-abundance domain, traditional single-species assessment procedures and prescriptions should work reasonably well. But should abundance be driven into the lower domain, we expect to see accelerating population collapse toward some low equilibrium or extinction. Reduction in exploitation rates after entering this domain may or may not allow recovery, depending in a quite unpredictable way on the *quantitative* details of how the juvenile survival rate is impacted.

Can we say anything in general about the probability of there being such a critical population size, or what this size might be relative to reference points like unfished abundance? We think not: the development of depensatory effects as population size is reduced depends on the quantitative pattern of forage (competitor/predator) response, i.e., the specific form of the numerical response in Fig. 2*a*. Models like Ecosim II can be used to define a range of possible responses, depending on assumptions about factors ranging from predator feeding rates to behavioral characteristics of the forage fish that may limit their vulnerability to predation. But the parameters that define the "correct" response obviously cannot be estimated reliably from historical data where the response is not yet evident, and these parameters summarize a very complex set of direct and indirect impacts of predation (Bax 1998). Comparative analysis of stock–recruitment data (Table 1; Myers et al. 1995*a*, 1995*b*; Liermann and Hilborn 1997) hints that at least some delayed depensation effects may occur in up to 10–20% of severely overfished cases. But the available data sets do not have enough observations at low stock sizes to make a convincing quantitative case about risk. We suspect that 10% may be a considerable underestimate of the risk for freshwater piscivores and possibly also for larger marine piscivores (particularly Gadiformes). We note, too, that many of the data sets in hand derive from populations that are components of multispecies fisheries. Therefore, the observed responses to exploitation include some degree of ecological change greater than that of simple mortality rates for single stocks. Ecosim may be a particularly valuable tool in evaluating those mixed impacts.

From a biological perspective, we might be willing to treat relatively rare instances (e.g., 10–20% of stocks; Table 1) of delayed depensation as biological curiosities rather than a matter for considerable research investment. But from a social and economic perspective, a 10% risk of stock collapse and (or) delayed recovery can be a very serious matter, especially where a substantial community of people is deeply dependent on the stocks. Would any fishery manager in Canada be willing to step forward and admit to having knowingly accepted a 10% chance that the Newfoundland cod stocks would collapse and show long delays in recovery? We think not, and we conclude from such examples that the risk should be taken very seriously indeed.

Depensation and physical "environmental effects" may interact, making prediction of critical population size even more difficult (Collie and Spencer 1993). Physical changes that impact productivity and size of juvenile nursery areas may move the response curves in Fig. 2 in complex ways, depending on the details of how both juveniles and their competitors/predators are impacted. Outcomes can range from mitigation of effects if there is a differential negative effect on the other species to severe reinforcing of negative effects if the other species are differentially enhanced. Indeed, the cultivation/depensation hypothesis offers an explanation for why correlations between recruitment and environmental factors are so prone to break down over time (Drinkwater and Myers 1987; Myers et al. 1997). Strong immediate responses to physical change are likely to be followed by dampening of the effect as trophic structure adjusts to the change.

If we cannot predict the critical population size in advance, what might we monitor in order to provide the earliest possible management reaction should depensatory effects start to develop? Here there are two obvious recommendations. First, develop survey methods to provide direct, immediate measures of juvenile survival rate and recruitment performance. Age-structured methods based on surveys and harvest of older fish do not provide reliable recruitment/survival estimates for each cohort until that cohort has been in the fishery for at least a few years. Second, also develop survey methods (or use the juvenile survey methods themselves) for abundance trends of a suite of potential competitor/predators in major juvenile nursery and rearing areas. In these surveys, routinely monitor diet compositions of juveniles and these species. Although multispecies surveys may fail to detect potential depensatory effects if such effects occur in concentrated space–time windows (e.g., seasonal impact on a particular size range of juveniles), their failure is the essential next step toward discovering this type of "critical period" or "bottleneck" effect.

As of 1990, assessments based on goals such as $F_{0.1}$, along with general belief that recruitment is poorly correlated with spawning biomass, led to a common view that the spawning biomass for most fish can be safely reduced at least 60–80% from natural levels without a substantial risk of recruitment failure. This view has been strongly challenged in the last decade (Mace 1994; Myers et al. 1994),

thanks particularly to the comparative recruitment studies by Myers and his colleagues along with empirical studies of long-term population change (Patterson 1992). It is now rare to see suggestions that spawning biomass can be safely reduced by more than 60–70%. We suggest that even these more conservative goals are based on very limited temporal experience with initial recruitment responses to stock size reduction and over the long term may be dangerously optimistic. To insure against lagged depensation effects, we suggest that spawning stock abundance goals should generally be no less than 50% of unfished spawning biomass, which in any case should usually produce yields not much less than at the more dangerously low levels (e.g., 30%) often recommended.

Where is the burden of proof?

Ecosystem models have drawn considerable criticism from proponents of single-species assessment methods. Ecosystem models have not been "proven" to work and have not been "tested" by fitting them to available time series data, they have many parameters whose effects are not easily seen in the data, and there is no proof that representations of species interaction effects are really necessary for policy formulation (e.g., see Hilborn and Walters 1992, p. 448: "We believe that the food web modeling approach is hopeless as an aid to formulating management advice"). In short, defenders of single-species assessment have argued that (*i*) you cannot do it and (or) (*ii*) we do not need it. We think that these arguments are deeply misleading and in fact represent a bizarre reversal of the burden of proof: what really demands justification is not attempts to understand consequences of trophic interactions but rather continuing the pretense that we can get away with not doing so!

Consider the "you cannot do it" argument. By appropriate choice of vulnerability parameters in functions for predicting predation mortality rates and foraging time/predation risk responses (e.g., Ecosim eq. A3, Appendix), we can turn ecosystem models into a collection of "independent" single-species models with essentially the same response dynamics as the single-species models now used for most assessment. If we then follow the standard assessment practice of including many nuisance parameters to account for unexplained recruitment variation ("process errors," "recruitment anomalies"), we can then fit these population "submodels" just as well as we can fit their single-species analogs and make the same predictions about policy parameters like maximum sustainable yield. If we then vary parameters so as to strengthen trophic interaction effects, we are almost bound (given many covarying time series) to "explain" at least some of the variation initially attributed to nuisance parameters. Such exercises prove nothing (correlations could be spurious), just as do exercises showing that recruitment anomalies are correlated with environmental factors. At this point, ecosystem model predictions about impacts of extreme abundance changes and impacts of policy changes such as fishing at the bottom of the food chain will begin to depart from the predictions of single-species models. Should we trust such predictions? Of course we should not, any more than we should trust the predictions of single-species assessments: the only "proof" is to see which predictions stand the test of time, and we cannot obtain such proof if we resist making the predictions in the first place.

It is even more misleading to argue that we do not "need" ecosystem models. Most of the apparent success of single-species assessment approaches has come from three tactics employed by experienced assessment scientists like the senior author. First, we take considerable care in choice of case populations and data sets to use as test cases in reporting methods development, when possible avoiding uninformative and (or) perverse data sets (which in fact make up a clear majority in the Myers synthesis of stock–recruitment data sets). Second, we shrug off much of the interesting variation, by calling it "anomalies" or "environmental effects," saying only that we need to perform risk assessments under various alternative hypotheses about future patterns of variation. This tactic leads us directly away from recognizing serious policy issues such as the risk of delayed depensation. Third, we restrict ourselves to asking only the most menial of policy questions, and in this, we do deep disservice to fisheries management by encouraging the use of correspondingly myopic policy approaches (e.g., my model cannot tell you anything about the efficacy of marine protected areas because it does not account for the spatial and trophic effects of such a policy, so let us talk about next year's allowable catch instead). Assessment scientists who use these tactics may soon find themselves left behind by both the science and fisheries decision-making.

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Appendix. "Foraging arena" concept as represented in Ecosim

In trophic models, we need to predict consumption rates Q_{ij} of prey types i by predator types j. Suppose that at some moment in time the total prey population is N_i and the total predator population is N_j. Simple reaction vat or mass action encounter models predict Q_{ij} from encounter rate arguments as $Q_{ij} = a_{ij}N_iN_j$ or as $Q_{ij} = f(N_i)N_j$, where $f(N_i)$ is the predator functional response to overall prey density. But in reality, if we look at any collection N_i of prey, we will find these individuals at any moment to be in a wide variety of "vulnerability states" with respect to N_j, depending on spatial position (e.g., in hiding places) and activity (e.g., resting versus actively feeding). Ecosim attempts to model this vulnerability distribution by treating the prey as being in one of two behavioral states, "invulnerable" and "vulnerable," with exchange between these states possibly representing both behavioral and physical mixing processes. Animals in the vulnerable state are said to be "in the foraging arena for i–j interaction," and we assume that there are V_{ij} of these at any moment. The dynamics of V_{ij} are modeled as having three components: (1) movement of individuals into the vulnerable (foraging arena) state at rate $v_{ij}(N_i - V_{ij})$, (2) movement of individuals out of this state at rate $v'_{ij}V_{ij}$, and (3) consumption of vulnerable individuals at mass action rate $Q_{ij} = a_{ij}V_{ij}N_j$. Note that we ignore predator handling time/satiation in the attack rate component 3, following the observation that predators with full stomachs are not a common field observation (D. Schindler, Department of Zoology, University of Washington, Seattle, Wash., unpublished data). We then assume that the dynamics of V are very fast compared with the dynamics of the Ns, so V quickly adjusts so that the three rates 1–3 remain near balance (dV/dt stays near zero). This variable speed-splitting assumption (similar to speed-splitting arguments used to derive classic type II functional response equations from handling time considerations) leads to the prediction

$$\text{(A1)} \quad V_{ij} = v_{ij}N_i/(v_{ij} + v'_{ij} + a_{ij}N_j).$$

Combining this prediction with assumption 3 above leads to

$$\text{(A2)} \quad Q_{ij} = a_{ij}v_{ij}N_iN_j/(v_{ij} + v'_{ij} + a_{ij}N_j).$$

This model implies Q_{ij} proportional to N_i and saturating in N_j (Fig. 3). In traditional predator–prey terminology, the denominator term $a_{ij}N_j$ represents a "ratio dependence" or localized "predator interference competition" effect. From eq. A2, instantaneous prey mortality rate Z_{ij} due to predator j is predicted to vary as

$$\text{(A3)} \quad Z_{ij} = Q_{ij}/N_i = a_{ij}v_{ij}N_j/(v_{ij} + v'_{ij} + a_{ij}N_j).$$

That is, Z_{ij} is not simply proportional to predator abundance but rather increases asymptotically toward maximum rate v_{ij} as predator abundance increases; for low v_{ij} and high predator search rate a_{ij}, Z_{ij} is predicted to be nearly constant (constant natural mortality M assumption).

In Ecosim, we allow users to introduce additional variation into predation mortality rates Z_{ij} by assuming changes in v_{ij} due to intraspecific competition among prey i and risk-sensitive behavioral responses. We monitor simulated food consumption rates by N_i and increase/decrease v_{ij} as feeding rate decreases/increases; the "target" feeding rate can be made inversely proportional to predation risk per time foraging. A basic implication of these time adjustment hypotheses is that for fixed predator abundance (all N_j constant) and N_i representing juveniles of some fish species, Z_{ij} will vary linearly with N_i so as to produce the widely observed Beverton–Holt form (flat-topped) of stock–recruitment curve (Walters and Korman 1999).

We see four common mechanisms that can decrease the vulnerability parameters v_{ij} so as to create stabilizing effects (Abrams and Walters 1996) and the appearance of "ratio-dependent" or "bottom-up" control of consumption rates (Q_{ij} limited to maximum $v_{ij}N_i$ no matter how many predators are present).

(1) Risk-sensitive prey behaviors

Prey may spend only a small proportion of their time in foraging arenas where they are subject to predation risk, otherwise taking refuge in schools, deep water, littoral refuge sites, etc.

(2) Risk-sensitive predator behaviors (the "three to tango" argument)

Especially if the predator is a small fish, it may severely restrict its own range relative to the range occupied by the prey, so that only a small proportion of the prey move or are mixed into the habitats used by it per unit time; in other words, its predators may drive it to behave in ways that make its own prey less vulnerable to it.

(3) Size-dependent graduation effects

If N_i represents an aggregate of different prey sizes, and predator j can take only some limited range of sizes, v_{ij} can represent a somewhat slower process of prey graduation into

and out of the vulnerable size range due to growth. Size effects may of course also be associated with distribution (predator–prey spatial overlap) shifts.

(4) Passive, differential spatial depletion effects

Even if neither prey nor predator shows active behaviors that create foraging arena patches, any physical or behavioral processes that create spatial variation in encounters between i and j will lead to local depletion of i in high-risk areas and concentrations of i in partial predation "refuges" represented by low-risk areas. "Flow" between low- and high-risk areas (v_{ij}) is then created by any processes that move organisms.

These mechanisms are so ubiquitous that any reader with aquatic natural history experience might wonder why modelers have ever chosen to assume mass action, random encounter models (or infinite v_{ij}) in the past.

For readers who might think it practical to avoid simplifications like eqs. A1 and A2 by explicitly modeling the full space–time structure of individual predator–prey encounters, be warned that the foraging arena structure arises from biology and physics operating at very small scales indeed. Foraging and movement dynamics generally take place at time scales of minutes to hours and involve complicated spatial movements at scales of a few metres to a few hundred metres. Indeed, it is probably because we have not thought carefully about heterogeneity at these very difficult scales that we have been willing to use mass action models in the past. Note further that just complicating the trophic model state representation by including details of size structure and macroscale spatial overlaps of predators and prey (e.g., Stefansson and Palsson 1998) does not solve the microscale representation problem at all and could still be completely misleading if only simple mass action interaction rates are used in the detailed calculations.

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