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ABSTRACT

Fisheries that are managed by conventional standards are often managed by regulating catches through what are frequently referred to as control rules. These rules involve three components, each of which are treated as distinct issues in this paper:

1) reduction in the abundance of the population of fish being harvested,
2) changes in suggested harvest rates depending on the abundance of the resource population, and
3) the magnitude of these variable harvest rates.

Of course, these components are not isolated from each other and, in their implementation, they are used in combination. Overall, the application of control rules involves lines of reasoning based on our scientific understanding of at least a few of the basic principles of population dynamics. In part, control rules represent attempts to avoid recognized risks of overharvesting.

In this paper, we make use of information from natural patterns to address each of these three elements of control rules to illustrate how each can be treated in a way that fully accounts for all of the complexity involved (i.e., the infinite set of relevant factors). Specifically, macroecological patterns are used to identify some of the problems caused (rather than solved) through the conventional application of control rules. We find that 1) harvested populations should be maintained at levels from 60-100% larger than what is often considered desirable in conventional management, 2) control rules should be curvilinear (rather than involving two linear segments) with harvests at levels that are between 56% and 72% of maximum when resources populations are at 40% of unharvested levels, and 3) harvest rates commonly need to be less than 10% of the magnitude of those used in much of today's management.

Our approach to arriving at these findings is based on information that is holistic in nature; among the things that get taken into account are the full complexity of evosystems, ecosystems, and all of their associated dynamics—including all associated risks. We emphasize the importance of our work by providing examples of the kind of information that achieves this holism. Key in this regard is the match between the natural patterns used for guidance and the management question being addressed. The discrepancies noted for the conventional application of the three components of control rules on which we chose to focus, can, in large part, be attributed to ignoring the importance of this match. Although full holism can be achieved for each management question addressed with empirical patterns, the degree to which full holism is achieved more generally depends on the extent to which other management questions are asked and addressed, and management action taken, following the examples provided both in this paper and elsewhere.

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APPENDICES

INTRODUCTION

Today, we are witness to an increasing number of failures of conventional approaches to fisheries management. By conventional standards, about 28% of the world's fisheries can now be seen as either recovering from being overfished, or still overfished (FAO 2009). As will be presented below, by more systemic (or holistic[1]) standards, virtually all commercial fishing involves harvesting of a magnitude that is well beyond being fully sustainable[2] (Belgrano and Fowler 2011, Fowler et al. 2013**)**. In spite of progress toward the goal of accounting for ecosystems (and to a very limited extent, evosystems[3]) in decision-making and management, overfishing continues to be a problem.

Most of the work to explain the extent, prevalence, and history of overfishing contributes to a growing list of the factors involved—and, more generally, an understanding that each one is included in the complexity with which we are confronted. Another part of our understanding is that this list is incomplete. Politics, international affairs, and economic factors (Botsford et al. 1997, Finley 2011) count among the many anthropogenic factors often thought to be involved in overfishing. Leading up to the emphasis on adopting an ecosystem-based approach to

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[1] Lest the term "holistic" generate a temptation to stop reading at this point, we emphasize its importance as a quality repeatedly identified as critical for effective management. We want to counter any potential aversion by explaining our use of this word. We apply the term in reference to using integrative patterns to provide a full accounting of the complexity of reality as laid out in Fowler (2009) and Fowler et al. (2013). In this paper, we are presenting examples of an approach that takes the mission of achieving holism to its natural limit for each management question we can address.

[2] The word "sustainable" will be used repeatedly below. The term is used in this paper to refer to systemic sustainability so that the sustainability of all systems involved is included. Thus, the sustainability of evosystems, as well as the sustainability of ecosystems, are included. It links directly to the concept of doing what is possible to ensure that all systems (e.g., ecosystems, evosystems, and fisheries) exhibit normal form and function (Fowler 2003, 2009). It is *not* meant to imply that maintenance of the status quo is necessarily an option (terminology from MacCall 2011); much of what we are doing now is clearly not sustainable.

[3] The term "evosystem" refers to the coevolutionary web of interactions among species, cooccurring with, and involving, ecological interactions (i.e., the ecosystem). For further consideration of the history of the origin of this term, see footnote 1 of Belgrano and Fowler (2011). For treatment of a growing appreciation of its importance in management see Faith et al. (2010).

management was the clear lack of sufficient consideration of the innumerable forms of ecological interconnectedness (Christensen et al. 1996), including population dynamics (Lima 2011) and behavior (Svedäng et al. 2011). Added to this are the complicated aspects of evolutionary/coevolutionary dynamics (Palkovacs 2011). There is also the matter of horizontal transfer of genetic material (Woese 2004). Such things are given very superficial consideration in conventional management if they are thought about at all. The importance placed on achieving holism stems from a recognition that, in conventional management, we have not found a way to completely and objectively account for all of the things recognized as important and influential (as well as those that remain, and which may always remain, undiscovered).

Through recognition of the need to account for such complexity, holism has been seen by many as crucial to management[4]. To meet the need for such holism, there is an alternative form of management that involves rejecting and replacing many (but not all) of the processes upon which conventional management depends. This approach (systemic management, Fowler 2009), takes into account all relevant factors, including those that historians, scientists, and managers have identified (including those that will be identified in the future as well as those that will never be identified) by making direct use of integrative empirical patterns that provide guiding information. These patterns are very carefully chosen to provide a strict match with the management question being addressed (i.e., consonance[5] between questions and patterns; Fowler

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[4] Advice to seek more holism is common in the literature, not only with specific reference to fisheries (e.g., Busch et al. 2003, Browman and Stergiou 2004, Francis et al. 2007), but also more generally regarding our (human) interactions with the nonhuman (see the references of Appendices 4.1 and 4.2 of Fowler 2009 and the multiple works of Thomas Berry as exemplified by Berry 2009). Over time, a great deal of emphasis has been placed on taking more and more into account in setting policy and managing not only fisheries but other aspects of our influence on the environment (e.g., see the "integrated systems approach" of Fiksel et al. 2009). Holism has been stressed frequently as a requirement for fisheries management (DeMaster et al. 2006), often in terms of taking interdisciplinary approaches. To overcome the inadequacies of conventional management, many have stressed the importance of more holism (e.g., Botsford et al. 1997). It is one of the "ten commandments" listed by Francis et al. (2007). See also footnote 1.

[5] Consonance involves a strict isomorphism, one-to-one mapping, and congruence between the management question, the research question, and the pattern providing guidance (for more detail, see Belgrano and Fowler 2008, Fowler 2009, Fowler and Hobbs 2009, 2011).

and Hobbs 2009, 2011). Owing to their integral nature (or integrative nature; Fowler et al. 2013), what is essentially full holism is achieved for every management question addressed with a matching pattern; owing to their empirical nature, these patterns bring a level of objectivity impossible to find in conventional approaches (Belgrano and Fowler 2008). Here, we apply the approach of pattern-based management to the formulation of control rules in fisheries management to meet the goals of management (e.g., achieving sustainability, accounting for complexity, seeking objective guidance, and undertaking management action that avoids abnormal human influence on all non-human systems; see Fowler 2003, 2009).

FROM INSIGHT TO QUESTIONS

Figure 1 shows the basic elements of control rules as frequently applied in fisheries management (see similar graphs and descriptions in other papers such as those by Caddy and Mahon 1995, Thompson 1999, Restrepo and Powers 1999, Gerrodette et al. 2002, Apostolaki and Hillary 2009). Each axis is presented with measurements represented by indices for comparison across a variety of applications.

Thus, the abscissa (X-axis) is an index of the abundance of the resource population scaled from 0.0 to 1.0. This index is the ratio of two estimated (observed) population sizes: the abundance occurring under the influence of fishing divided by that found in the absence of exploitation by fisheries. The ordinate (Y-axis) represents an index (F_I) of the recommended fishing rate (F_{rec}, also referred to below as the recommended harvest rate or consumption rate). As such, the F_I depicted in Figure 1 are calculated as the ratio of F_{rec} to F_{max}, where F_{max} is the harvest rate allowed when the population of a particular resource species corresponds to levels it exhibits when free of the effects of fishing. The fishing rate itself (whether the recommended rate, F_{rec}, or F_{ob}, the observed rate) is expressed as a portion[6] of the resource population taken in a specified unit of time. Thus, in Figure 1, both F_I and P are displayed in the range of 0.0 to 1.0.

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[6] We are cognizant of the distinction between instantaneous and crude rates. The approach we are taking, and the conclusions we reach apply to both.

Even though they both can take on values greater than 1.0, each is represented within the range of 0.0 to 1.0 and are thereby standardized to make comparisons across various applications.

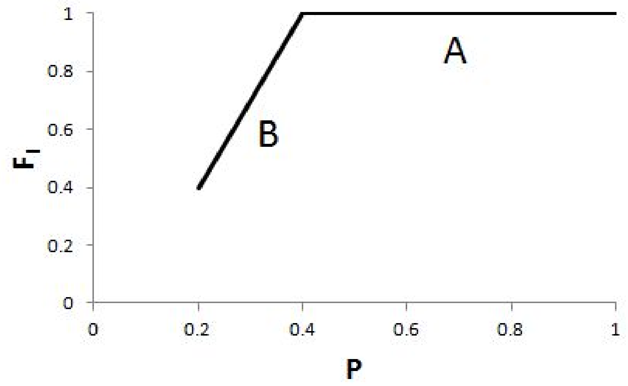

Figure 1. -- Schematic representation of conventional fishery control rules showing an index of fishing rates (F_I) in relation to an index of resource population levels (P). Line A corresponds to $F_I = 1.0$ (the recommended fishing rate is equivalent to the maximum) for a range of P above a specific threshold, and line B reflects the recommended reductions in fishing rates when the resource population is smaller than that threshold (in this case the threshold corresponds to P = 0.4[7]).

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[7] The value 0.4 is used for more than simple illustrative purposes. It is a value often used in fisheries management, especially historically, as either a target, or threshold (or both). As indicated in Restrepo, et al. (1998), National Standard Guidelines (as published in the Federal Register) established in the U.S. in 1997 recommended 0.4 as an acceptable value for P. The use of this standard is frequently found in management recommendations and policy (e.g., Casey, et al. 2009; see also: Apostolaki and Hillary 2009). Values for P less than 0.5 are expected when management is based on population models representing typical life history strategies of many species of fish (Fowler 1981, 1988; Mangel et al. 2013). See Appendix I for further detail regarding the setting of standards (goals) for P in fishing policy.

The lines (A and B) (Fig. 1) are examples of control rules typical of historic (and much of today's) fisheries management[8]. In this approach, there is a maximum fishing rate (F_{max}) implemented at the outset of a new fishery. This is often based on attempts to maximize the harvest (often involving the theory behind the concept of maximum sustainable yield [MSY] as based on a growing understanding of population dynamics). This rate is considered to be a viable option under conditions of a resource population subject to initial harvests when one of the objectives is to reduce the population to stimulate a density-dependent reaction in which population-level productivity typically increases. Shown at the upper right (right end of line A, Fig. 1), this initial harvest index is represented by a value of 1.0 (at this point the recommended fishing rate, F_{rec}, is equal to the maximum, F_{max}, or $F_I = F_{rec}/F_{max} = 1.0$) and corresponds to a population index of 1.0 (where the ratio of the observed population to that of an unharvested population is 1.0; $P = 1.0$).

In many conventional applications of control rules, the recommended fishing rates remain close to F_{max} across a range of resource population levels; line A (Fig. 1) shows a constant fishing rate between a lower threshold of $P = 0.4$ and $P = 1.0$. As the resource population declines, fishing rates are monitored (requiring data on catches and assessments of the resource population). At a predetermined level of the resource population, a threshold is established below which recommended fishing rates are reduced; if assessments of the resource population indicate that it is below this threshold, reduced harvest rates are recommended (and enforced to the extent that conventional control-rule policy is actually implemented). In Figure 1, the extent of such reductions is indicated by the sloping line (B) descending from the flat line; F_{rec} ($F_{rec} = F_I \bullet F_{max}$) becomes a declining function of smaller estimated resource population sizes (for which P serves as an index).

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[8] There are numerous publications which provide more detail regarding this description of control rules (e.g., Caddy and Mahon 1995, Thompson 1999, Restrepo and Powers 1999, Gerrodette et al. 2002, Wallace and Fletcher 2001 and Apostolaki and Hillary 2009). Such references should be consulted also to better understand the variation inherent to actual applications (especially in regard to suggestions for change from the generic set of control rules being described here). Control rules are prevalent in much of today's fisheries management (e.g., see Eikeset et al. 2013 as just one specific example).

It is not unusual, in conventional management, for F_{max} to be close to the fishing rate implied by the theory of population-dynamics involving any one of a number of well established models. Among these models (including the well-known logistic model) are those of Schaefer (1954), Beverton and Holt (1957), and Pella and Tomlinson (1969). Many books and peer-reviewed papers treat these models and their use in establishing F_{max} (e.g., Polacheck, et al. 1993). The implementation of these models will be treated again below in terms of the ways they fail to provide consonant information.

In addition to their use in deciding what F_{max} should be in conventional applications, these same models, and the general theory of population dynamics behind them, are used to establish the extent of permissible, or advisable, resource population reduction to stimulate density-dependent increases in relative productivity. Various risks, including those of lost production and depletion are taken into account in establishing the position and slope of line B to promulgate regulations resulting in reductions in harvest rates to help guard against such risks. As more of the complexity of ecosystems is brought to bear in management, some of the risks to ecosystem structure and function are also taken into account in making decisions about the position and shape of line B, including the option of terminating the harvest completely if the resource population drops too low (i.e., line B drops to zero at a resource population level greater than zero, often referred to as another threshold; e.g., Sainsbury et al. 2000).

Within the control rules applied in conventional management, there are three important elements that can be considered individually. These three aspects of control rules are the primary focal points as treated in the next three sections (and Appendices I-III, respectively). They are:

1. The extent to which a resource population can be reduced; this establishes limits on the extent to which populations can be reduced as a result of harvesting. In reference to Figure 1, we are seeking an advisable P (the ratio of observed population levels in response to harvesting to that in the unharvested state, i.e., the ratio R of Appendix I), especially in terms of a threshold below which management needs to contribute to rebuilding the population. Should it be different from 0.4; if so by how much?

2. The extent to which harvests should be reduced as a function of P. In Figure 1, these reductions are depicted as a portion (F_I) of the harvest rate implemented when P is 1.0. Should the same rate be applied for the full range of population sizes for the resource population between P = 0.4 and P = 1.0?
3. The magnitude of the rate at which harvesting is sustainable in extracting fish from the resource population when that population is at unharvested levels (F_{max}). This is the actual harvest rate (not the index), or consumption rate, at a population index of 1.0 (P = 1.0). Actual harvest rates recommended at other levels of P are determined as $F_{rec} = F_I \bullet F_{max}$. Should harvest rates be as high as they are based on models of population dynamics which predict rates of production?

These three aspects of control rules are not alone, and are interrelated (inseparable) in various ways. Additional factors that might be addressed include the level of the resource population at which harvesting should be terminated or where line B should intersect the abscissa in each case. Each additional factor lends itself to a distinct management question, and (with further research) each question can be treated in future work. In this paper, we focus on the three aspects of management listed above to illustrate how the various aspects of fisheries management can be addressed holistically—each as a distinct part of control rules considered individually. In each case, the element of control rules being considered will be represented by a management question with its consonant research/science question. These three elements are treated in the next three sections with their corresponding appendices. The posing and answering of the questions will involve a process of finding a strict match among 1) the management question, 2) the research question to address the management question, 3) the consonant empirical pattern that research reveals, and 4) the action needed to avoid abnormality based on the resulting guiding information (as described in Fowler and Hobbs 2009, 2011).

To initiate this process, we note that there is the option of more reality to control rules than is achieved by the simplicity of the straight lines in Figure 1. Progress in this regard is shown generically in Figure 2. The curved line in this graph is similar to curves presented in graphic form by Thompson (1999). For purposes of our analysis, we represent such curves with the equation:

$$F_I = aP/(1+bP) \qquad (1)$$

where P is the index of resource population abundance, and a and b are parameters that determine the shape of the curve (b is a shape parameter, and a is the parameter that determines the height of the curve representing the magnitude of F_I). This formulation is used to exemplify the process that we are describing rather than as a statement that it is the only option, or best representation of the relationship. Equation 1 is the well known Holling (1959) "disk equation" and serves to represent the functional response of predators to their prey—responses that are well known fundamental aspects of the relationships between predators and their prey and is used here in regard to predator/prey systems in which we are involved in managing human participation (commercial fishing). In other words, there is an observed pattern in predator/prey interactions which is relevant for managing humans as predators where fish are the prey.

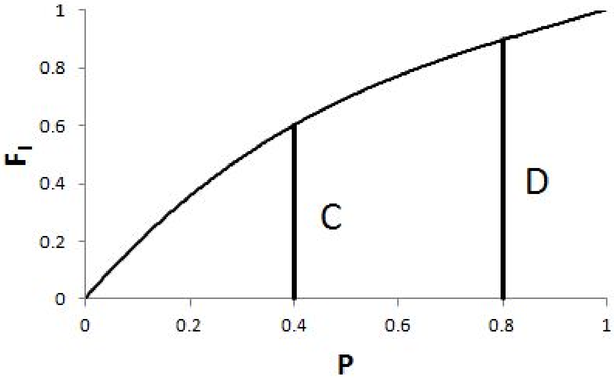

Figure 2. -- Schematic representation of the Holling (1959) functional response of predators to the population abundance of their prey, showing an example of curvilinearity distinct from the straight line segments shown in Figure 1. See text for details regarding the use of information represented by lines C and D.

Note, in Figure 2, that the concepts depicted in Figure 1 are preserved. These include 1) resource population reduction caused by harvesting/consumption (P less than 1.0), 2) reduction in advisable harvest/consumption rates in response to changes in the abundance of the population of the resource/prey (F_I is a declining function of P), and 3) a maximum harvest (or consumption) rate (where $F_I = 1.0 = a/(1+b)$, and implemented fishing rates are F_{max} when $P = 1.0$, all from Equation 1).

In the sections that follow, we will be presenting information that establishes a preliminary representation of Equation 1 not only to initiate its use in fishery management, but more importantly, to initiate research to refine the characterization of such relationships as they vary in regard to the many influential factors involved. The process takes advantage of the fact that information on the position and height of a line (such as line C) determines the parameters a and b, given that at $P = 1.0$, $F_I = 1.0$, and at $P = 0.0$, $F = 0.0$. In other words, if we have an observed value for F_I and P, the equation above can be solved for a ($a = (F_I - P\ F_I)/(P - PF_I)$), and b ($b = a - 1$). For example, with observed information indicating that F_I is observed to be 0.6 at $P = .4$, we can infer that $a = 2.25$, and $b = 1.25$. Thus, with patterns which simultaneously provide information about F_I at the corresponding P, we are closer to being able to supply specific management advice. Still missing is information about the appropriate level for the harvested population (advisable P) and the corresponding advisable F (in contrast to the simple index, F_I).

We begin the consideration of our three management questions with the matter of the extent to which the population of the resource species can be reduced sustainably. What is an advisable P?

RESOURCE POPULATION REDUCTION

To what extent can we sustainably reduce the population of a resource species that we are harvesting? This question, like all questions in systemic management, is asked holistically. That is, to what extent can we reduce a population without causing unsustainable reactions in the resource population, among its other predators, among the populations of the prey on which it feeds, among its competitors, or in the ecosystem and evosystems of which it is a part? The overall mission is one of avoiding *any* unsustainable reactions, particularly abnormal reactions, whatever they may be, and whether they involve scales of time, space, or hierarchical complexity.

The next step is that of revealing the natural empirical pattern in which the answer to the management question is found. As such, we need to ask a consonant research question: *To what extent do populations of nonhuman predatory species reduce the populations of their prey (resource species)?* The consonance achieved in asking this question involves, among other things, the fact that we humans (through commercial fishing) are serving as a predatory species wherein there is a population that is involved in consumption or harvesting of the resource population. Another step toward consonance is achieved insofar as the management issue and the research question both involve changes observed as reactions to harvesting/consumption by the population serving as a resource.

We are not the first to express interest in this question; it has been addressed many times in the published ecological literature. In considering the matter of population reduction by nonhuman predators, Pimm (1991) indicated that between 22 and 44 percent of the cases studied in research to address such a question were counterintuitive (i.e., the effects of predator populations actually resulted in increases, rather than reductions, in the populations of their prey—based on work by Sih et al. 1985). Depending on the variance structure of such measures, the mean index of the reduced population could be well above the 40% often used in conventional fisheries management (Grafton et al. 2009, PFMC 2009). We must remain open-minded to the possibility that values such as 0.4 as practiced in conventional management are too low—abnormally low.

Figure 3 shows the results of our search of the literature (see Appendix I) on the effects of predators on their prey. This analysis involved studies providing measures of the changes in prey populations upon the introduction (or removal) of one of their predators. Consistent with the results reported by Pimm (1991), about 21% of the 119 cases for which we found data indicated that prey populations responded counter-intuitively (remaining unchanged or increasing) as a result of the effects of predation within the system of which they are a part. The mean reduction in prey populations responding to predation was about 37%; in other words, the resulting prey population was, on average, about 63% of the population expected in the absence of predation by the predator for which the effect was being studied.

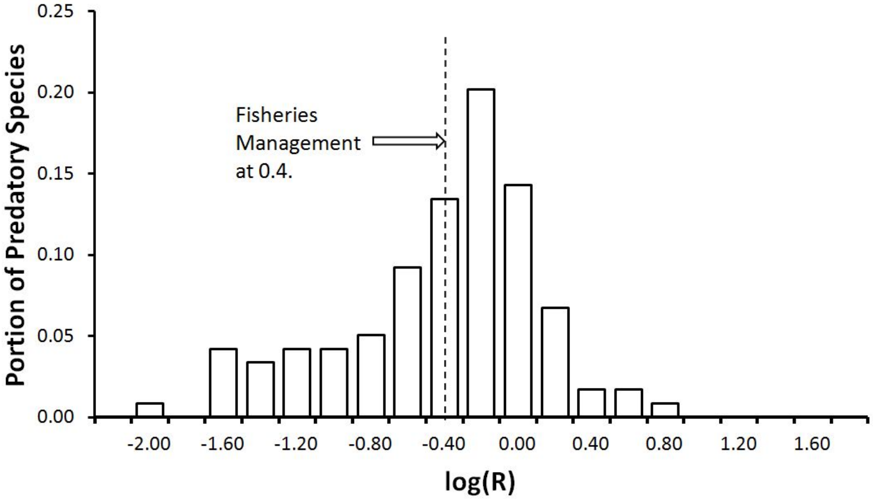

Figure 3. -- The frequency distribution of 119 published measurements (see Appendix I) of the effects of consumer species on their resource populations, compared to the reductions often sought in fisheries management (40% of unfished population levels; P = 0.4, keeping in mind that the ratio R of Appendix I is the measure of P). The changes attributed to consumers involved a mean reduction of about 37%, or a reduction in the resource population to about 63% of it abundance in the absence of predation (i.e., P = 0.63).

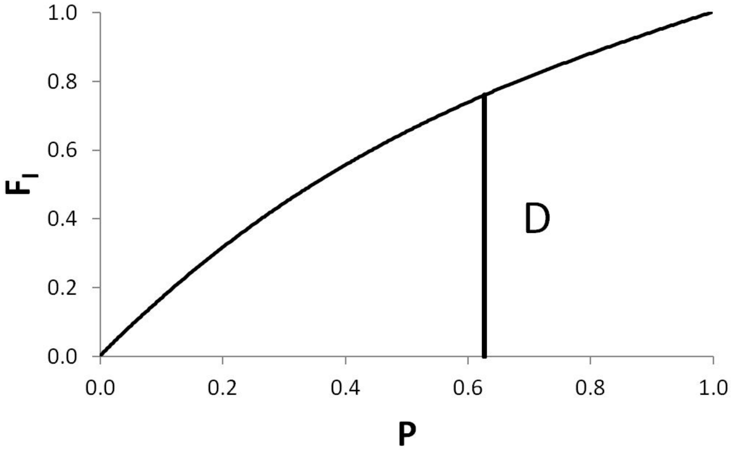

Figure 4. -- The curve of Figure 2 with information concerning a specific sustainable resource population level to which a corresponding fishing rate would apply. In this diagram, the position of line D on the abscissa corresponds to the mean relative population (P) of 0.63 (the height involves a value yet to be determined).

Figure 4 shows this information as represented by a vertical line (D) corresponding to a mean relative population abundance (P) for the prey of 0.63. This represents a rough idea of one option for the position of line D on the abscissa. After treating the matter of reductions in sustainable harvest rates in response to prey population abundance (the shape of the curve as treated in the next section) we will proceed to estimating the approximate height of the curve corresponding to the position of the top of line D on the ordinate. We still need information that will specify the curvature of the relationship shown in Figures 2 and 4 (representing the Holling disk equation presented above). Such information is considered in the next section—information on a specific point in the curve.

PRECAUTIONARY REDUCTION IN HARVEST RATES

Figures 1, 2, and 4 all have the common element of harvest control that would reduce fishing rates in response to declining populations of the resource species. In Figures 2 and 4 there is *continuous* reduction in reaction to the population level of the resource (measured through resource assessment). In contrast, conventional fisheries management (as depicted in Fig. 1) often allows (even occasionally recommends) fishing rates that are constant (linear) across a range of resource population levels in contrast to the nonlinearity represented by the curves of Figures 2 and 4. In these (conventional) cases, fishing rates are required to be reduced only after reaching a predetermined threshold in resource population levels. Again, this level varies among applications, but is often set at a level of the resource population that is about 40% as large as it would be if free of the effects of fishing. We could have chosen any other value for the exercise in this section, but chose the value 0.40 to reveal another pattern (Appendix II). The pattern of interest is one represented by data characterizing the reduction observed in consumption rates by other predatory species as the populations of their resource species decline in response to the predation.

The management question now before us is: *"Compared to rates advisable for initial harvests, how much should the fishing rate on a population of species X be reduced to achieve a sustainable harvest rate when the population of that resource is at 40% of unfished levels?* In this case, the corresponding (consonant) question for scientific investigation is: *In comparison to* *the consumption rates observed for prey populations free of their predatory effects, to what extent do consumption rates by predators decline when prey populations are at 40% of unexploited levels?* Appendix II presents a set of data and analysis that answer this question. The resulting pattern is represented in Figure 5 as empirical information on the length of line C in Figures 2 and 6.

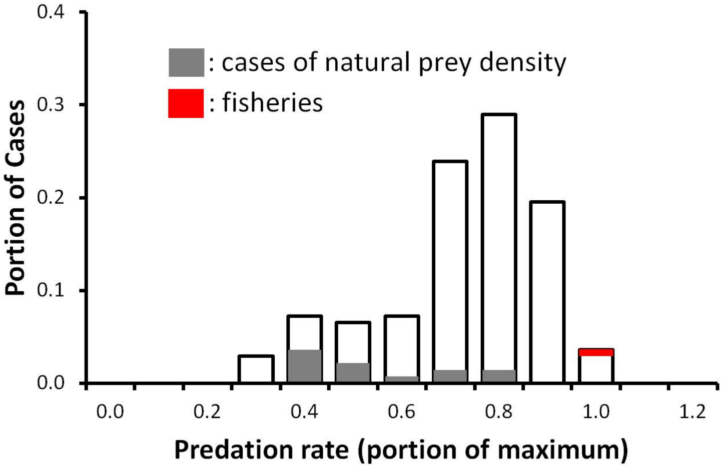

Figure 5. -- The pattern in measures of observed predation rates expressed as a portion of the maximums observed in empirical data for functional responses of predators to the abundance of their prey, all measured at 40% of population levels corresponding to maximum consumption rates (see Appendix II for details).

The overall mean of the data shown in Figure 5 is 0.727. The corresponding mean for cases wherein the comparison involves standards wherein prey populations approximate those expected under natural and normal circumstances is 0.556 (N = 12). Owing to the fact that the latter more effectively takes into account the change in consumption rate relative to naturally occurring population densities of the prey, it is this value that we use in the following sections as an illustration of the use of natural patterns like that represented by Figure 5 to establish control rules of use to the management of fisheries.

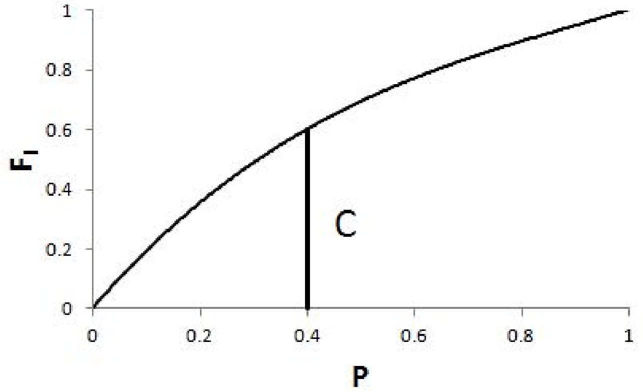

Figure 6. -- The functional response curve of Figures 2 and 4, here illustrating the reduction in the rate at which, on average (line C), nonhuman predators consume prey from a resource population which is at 40% of the level expected in the absence of consumption by the predator. Because the curve is fixed at the two extremes (the paired points 0.0, 0.0 and 1.0, 1.0), and owing to the constraints of Equation 1, the value 0.556 (at P = 0,4; Appendix II) determines the overall shape of the curve between these points as explained in the text.

We are now in a position to specify the shape of the curve to serve as our pattern-based set of control rules. With a value of 0.556 for F_I when $P = 0.4$ (Appendix II), we can estimate values for the parameters a (= $(0.556 - 0.4 \cdot 0.556)/(0.4 - 0.4 \cdot 0.556)$) and b (= a - 1), as 1.88 and 0.88 respectively. The curvature specified by these values is shown in Figure 6. With the curvature established by this information, combined with the information for a sustainable P (= 0.63) from the last section, the F_I corresponding to $P = 0.63$ would be 0.76. Note that in both the case of F_I at $P = 0.4$ and F_I at $P = 0.63$ (0.556 and 0.76 respectively), there is a substantial difference from the 1.0 often assumed in conventional management. Because these values for F_I are indices, they serve to help provide suggested harvest rates, but only with additional information regarding actual sustainable harvest rates. To complete the process, our next task is to establish a value F_{max}.

HARVEST RATES AT P = 1.0

At what rate should we harvest the population of resource species X when its population is at the level it exhibits when free of the effects of our harvesting? This is the generic management question related to finding the value of F_{max}. If we are to use empirical patterns to address this question we will need information on the consumption rates by nonhuman species under circumstances when their prey populations are free of the effect of their predation—a very difficult, if not impossible, task. We have the option, however, of using basic information regarding the shape of curves such as those shown in Figures 2, 4 and 6 to extrapolate from points within the curve. For example if $F_I = 0.556$ when P is 0.4 (Appendix II), we can use the corresponding values for a (1.88) and b (0.88) to find F_I for other values of P. This set of parameters means that at P = 0.63, F_I would be about 0.76. Collectively, this combination of information implies that F_{max} will be 1.32 = 1/0.76 times as large as the sustainable F estimated for P = 0.63. We are thus left with the need for estimating the sustainable harvest levels corresponding to P = 0.63. F_{max} will be 1.32 times greater and an advisable harvest rate to use in initiating a fishery.

We begin with the generic question: *"At what rate can we sustainably harvest species X?"*

In addressing this question, we immediately are confronted with factors that come to mind as important for refining the question. One such factor involves basic population dynamics: we can probably harvest at increasingly higher rates for species with increasingly higher turnover in their populations. It would seem logical to think that more productive populations can be harvested at higher rates. More productive populations often have higher total natural mortality rates (M) which may serve as a proxy for productivity. Thus, to refine[9] the above question with this in mind we might ask: *At what rate should we harvest the population of resource species X, given that its total natural mortality rate is M?* The answer to this question would establish the annual harvest that would be implemented through management so as to be consistent across species, and with other management action, regardless of how it is perceived conventionally. Its use would replace harvests determined through conventional procedures under any of a variety of

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[9] See Fowler and Hobbs (2009, 2011) for treatment of the process of refinement.

terms, including “maximum sustainable yield”, “surplus yield,” “total allowable take,” or “potential biological removal”. Nearly all of these terms actually refer to production rather than consumption and lead to problems (as will be discussed below; see also Fowler and Hobbs 2011).

In the last several paragraphs we have (as also exemplified in previous sections) accomplished much of the first step of systemic management (Fowler 2003, 2009); we have asked the management question and refined it somewhat in order to directly account for M (the total natural mortality rate). As with previous examples, the next step is to ask the consonant research question: *What is the rate at which nonhuman mammalian predators consume the population of resource species X, given that its total natural mortality rate is M?* This completes the second step insofar as we have been specific in asking the management question; this question, as a

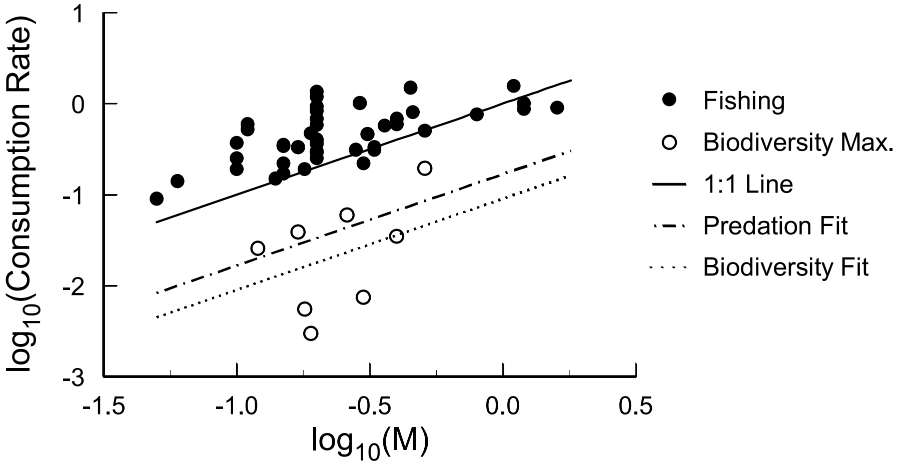

Figure 7. -- The macroecological pattern of predation rates as they maximize biodiversity (open circles) observed for various predators in their consumption of prey as a function of total natural mortality in comparison to fishing rates (filled circles) from 44 species of fish (from Mertz and Myers 1998). The line labeled “Predation Fit” represents the regression line fit to the raw data for individual predation rates; the line labeled “Biodiversity Fit” is the line fit to the data shown in the open circles (see Appendix III for details; Fowler et al. 2013).

question to be addressed in research, matches the management question (Fowler and Hobbs 2011). The total mortality rate is taken into account overtly/directly.[10]

The third step is that of finding the empirical pattern through which the research question leads to information that provides an answer to the management question as guidance for management. Note here that our present goal is an estimate of the rate at which fishing fleets can sustainably harvest (on average) when the resource population is at a level expected while being harvested. The ultimate objective is an estimate of the advisable rate for harvesting upon the initiation of a fishery (when the resource population is at an unharvested level), F_{max}. It is extremely difficult to measure directly the maximum rate at which other species would consume the prey we use as natural resource—such measurements would have to be made in the absence of fishing (especially any abnormal[11] fishing) and in the absence of predation by the predator itself. The populations of their prey are not at levels at which such maxima can be observed and the variable populations of the predators contribute to the variance of such maxima. However, we can estimate such rates by adjusting (using the adjustment factor of 1.32 above) measures of rates corresponding to resource population levels observed in reaction to natural predation. Thus, we can use measures of rates at which other species consume their prey given the existing circumstances (conditions that specifically include both the effects of their prey abundance and the population levels of the predators).

Figure 7 illustrates the empirical pattern (a macroecological pattern; see Appendix III for details) for the relationship between maximized biodiversity in consumption rates among various

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[10] Note here that production is not the sustainable harvest that it is often assumed to be in conventional management. It is (through its proxy, M) to be converted to a sustainable harvest rate through any correlative relationship underlying empirically observed consumption rates.

[11] By abnormal fishing we are referring to fishing rates that are atypical, aberrant, or unusual compared to consumption rates by other mammalian predatory species (see Fowler 2003, 2009; Fowler and McCluskey 2011; Fowler et al. 2013). Abnormal fishing rates are especially obvious when they are well outside the normal range of natural variation of consumption rates by nonhuman mammalian predators (exemplified by the take of mackerel, *Scomber scombrus*, in the northwest Atlantic, which, in the period 1988-1992, was 2.3 times greater the upper 95% confidence limit in consumption rates by 10 species of marine mammals and 62 times greater than the geometric mean; Fowler and McCluskey 2011).

species of mammalian consumers and the estimated total natural mortality rate for the respective populations of the consumed species. The equation representing the correlation between F_{sus} (what might be called a sustainable harvest (or consumption) rate as represented by information from systems in which the observed rates reflect their ecological and evolutionary origins, as well as the population levels of both predator and prey, Appendix III) is

$$F_{sus} = 0.095 M , \tag{2}$$

where M is the total natural mortality rate. Thus, to obtain a reasonable first approximation of the fishing rate that is sustainable for the population level of the resource species corresponding to the sustainable population size (e.g., P = 0.63 from Appendix I) we substitute the total natural mortality rate in the above equation and solve for the sustainable harvest rate to be used in management. One factor ignored in this approximation is the fact that we are adding ourselves as an additional predator; the number of predators must also be taken into account, as discussed below.

In conventional management F_{max} is often implicitly assumed to be roughly equivalent to M (the total natural mortality rate; Die and Caddy 1997). Examples of this are found in numerous publications (e.g., Pitcher et al. 1998, Wakeford et al 2004, Deekae and Abowei 2010), often with reference to Gulland (1971) who suggested that for an optimally harvested population the ratio of F/M would be 1.0 (the ratio of F to total mortality would be 0.5; Mertz and Myers 1998). Thus, among the various reference points and standards considered as options for fisheries management, a frequently chosen option is that of F = M (Mace 1994). With M as a standard of reference for conventional management we can evaluate it using data from natural patterns that are more consonant with the management question. Thus, with the measure of $F_I = F_{sus}/F_{max} = 0.095\ M/F_{max}$, as developed above (and in Appendix III), we find a first approximation of F at P =1.0: F = 1.32(0.095M) = 0.13M, not M. That is, in regard to the relative position of the curves of Figures 2, 4, and 6 compared to that of line A in Figure 1, the maximum height of the curve at P = 1.0 is approximately 0.13 that of the line (i.e., line D in Fig. 2). These steps bring us to the results shown in Figure 8 with the curvilinear control rules well below those of conventional applications.

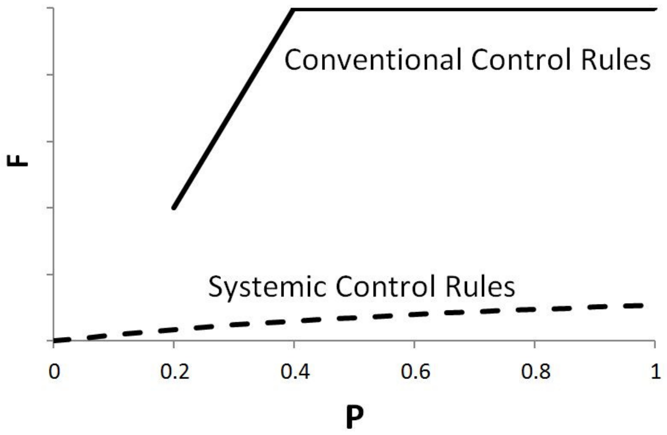

Figure 8. -- A comparison of control rules based on natural patterns (systemic management) and control rules as applied in conventional management of commercial fisheries. There are no units for F as the F_{max} of systemic control rules is shown as a fraction of the F_{max} applied conventionally as it would vary among applications to different species.

Thus, as shown in Figure 8, harvest control rules based in empirical patterns are quite different from the control rules applied in current forms of management in many respects. Not only are conventional control rules abnormal when they make use of linear relationships, and unrealistic in their suggested reductions in resource populations, they are also sources of guidance that result in rates of harvest that are extremely excessive (Fowler et al. 2013). Control rules based on empirical patterns expose the abnormal nature of what has been used in much of conventional fisheries management.

VARIABILITY IN COMBINED RESULTS

One element of simplicity in the process we have exemplified above involves our use of one specific estimate for each element of control rules. This allowed us to illustrate the process. In contrast, the data themselves expose the reality of variability. We have initiated the process of refining management questions to serve as the basis for making reasonable choices of data to find a sustainable P and corresponding F_I. This refinement leads to the realization that various subsets of the data more closely match the management issue involved (i.e., are more consonant in providing guidance). To more clearly emphasize variability, Table 1 presents a range of values for both sustainable P (columns, Appendix I) and indices of consumption rates corresponding to P = 0.4 (rows, Appendix II). The latter represents variability in the curvature of the functional response curve. At the intersection of the corresponding row and column are indications of the multiplier to be applied to the corresponding sustainable harvest rate to obtain F_{max}.

Not only does the information in Table 1 show that there is variability to be taken into account, but it also shows that there are no cases in which the multipliers of Table 1 are sufficiently large to support the assumption that a sustainable harvest rate is approximately equivalent to M (for any population level for the resource). The conclusion that conventional control rules are ecologically abnormal remains clear.

Table 1. -- List of multipliers to be applied to estimated sustainable harvest rates to find F_{max} as they correspond to alternative estimates of sustainable P (P_{sus}, columns) and of sustainable F_I corresponding to P = 0.4 (rows), the combinations of which determine the curvature of the functional response curves. All values for P_{sus} come from Table A1.3, Appendix I. See Appendix II for the values for F_I. The values in parentheses express F_{max} as a multiple of M.

F_I	$P_{sus} = 0.627$[1]	$P_{sus} = 0.631$[2]	$P_{sus} = 0.767$[3]	$P_{sus} = 0.799$[4]
0.522[5]	1.36 (0.129)	1.36 (0.129)	1.18 (0.112)	1.15 (0.109)
0.556[6]	1.32 (0.125)	1.31 (0.124)	1.16 (0.110)	1.13 (0.107)
0.642[7]	1.22 (0.116)	1.22 (0.116)	1.11 (0.105)	1.09 (0.104)
0.663[8]	1.20 (0.114)	1.20 (0.114)	1.10 (0.104)	1.09 (0.104)
0.722[9]	1.15 (0.109)	1.15 (0.109)	1.08 (0.103)	1.06 (0.100)

[1] Arithmetic mean for P from the entire set of data.

[2] Geometric mean for P involving native predators consuming vertebrate prey.

[3] Arithmetic mean for P involving native predators consuming vertebrate prey.

[4] Arithmetic mean for native predators (regardless of type of prey).

[5] Geometric mean of F_I for vertebrate predators with natural prey density

[6] The mean F_I for cases involving natural prey densities.

[7] The mean F_I for cases involving vertebrate predators and vertebrate prey at natural prey density.

[8] The mean F_I for cases involving all vertebrate predators and vertebrate prey.

[9] Mean of the arithmetic means from F_I at P = 0.4 and P at maximum $F_I/2$.

Adding to this conclusion is the likely need for further reductions in sustainable harvest rates to account for the fact that we are adding ourselves as a species to the list of predators preying on a particular resource. As shown by Fowler et al. (2009), in the case of large mammal predators feeding on young of the year from large mammal prey, the sustainable harvest rate per predatory species declines with the number of predators (in that case, about a 60% decline with each additional predator). There is almost undoubtedly a decline in the mean harvest rate per predator more generally, as the number of predatory species increases (e.g., see Lewins 2006), and such a tendency would apply to lumped age classes such as those taken in commercial fisheries. More research is needed to provide more accuracy and precision in this regard. However, such an effect (almost always involving reductions in sustainable harvest rates) is likely to more than counteract the effect of the multipliers in Table 1 (all greater than 1.0 to magnify estimates of sustainable harvest rates, as multipliers to account for estimates of sustainable harvest rates following reduction in resource population levels). These multipliers varied from 6% to 36% greater than 1.00 with the smaller differences more likely than the larger—but all smaller than 60% (as a preliminary and crude estimate of reductions in sustainable harvest rates to account directly for adding ourselves as a species to those serving as predators on a prey species; Fowler et al. 2009).

DISCUSSION

We have shown that various aspects of control rules, as applied in fisheries management today, are flawed. By using empirical patterns to avoid abnormality and achieve sustainability, we can achieve sustainable harvest rates, sustainable reduction of the population of the species being harvested, and advisable changes in harvest rates responding to fluctuations in the size of harvested stocks. Generically, this approach can be applied to fish stocks measured either in terms of numbers or biomass even though the two options may result in different shapes for the functional response curves. In this regard, the parameters for curvilinear control rules may ultimately be found to show patterns that differ not only between numbers and biomass, but also as related to various ecological conditions (e.g., latitude and depth, or temperature and salinity with their annual variability) or the various aspects of life history strategy (e.g., age at first reproduction, maximum age, or generation time). There may be differences associated with taxonomic category. In particular, the rate of increase per generation (Fowler 1988), or the closely related matter of "steepness" (e.g., see Mangel et al. 2013) and their connections with reference points[12] as represented in control rules, are all expected to be influential in determining recommendations for specific cases of single-species fisheries applications. There are undoubtedly differences to be expected between information related to instantaneous rates compared to crude rates. A great deal of research is needed to tease out the details of the correlative relationships involving a long list of factors of the kinds listed above.

As is seen in much of the literature referred to in Appendix II, the Holling disk equation may be an over-simplification of the curvilinearity involved in functional responses in predatory-prey relationships appropriate for guidance in fisheries management. Some relationships may be better represented by sigmoid curves to remind us of the need for even more extreme reductions in harvest rates at very low population abundances in the stocks being fished; work of the rigor exemplified by that of Thompson (1999) is needed to characterize control rules based on empirical patterns so as to directly account for factors such as trophic level, the various elements of life-history strategy, and other relevant factors. The work we are presenting here is merely a first step in abandoning the misleading and problematic nature of conventional management; and it involves only three aspects of management as manifest in control rules.

In this regard, it is important to note that a generic question such as: *What form should control rules take?* is not a good management question. It is not phrased in such a way that scientists can conduct research defined by the question in a way that provides quantitative answers. The work we are presenting here exemplifies a process of breaking the generic question into parts for which consonant measurements can be made, then conducting the research to reveal the natural empirical pattern that matches the question that is consonant with each part. The three components of this paper (and corresponding appendices) represent research addressing science questions defined by the bona fide consonant management questions. The three management

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[12] The influence of steepness and rate of increase per generation are both expected to be important in their contribution to advisable P (the most sustainable population level for a harvested population; Fowler 1988, Mangel et al. 2013).

questions involved three parts of the generic question, asked so that research could provide answers. When faced with a vague question such as: *What form should control rules take?* it is important to identify the measurable aspects of what is involved and address those issues directly.

In addition to the functional responses we have examined here (Appendix II), there is also need to recognize the very real matter of numerical responses. Part of the importance of this distinction involves the fact that fisheries management involves a functional response; all else being equal, reductions in total catches mean a reduction in catch per fishing boat, per fishing fleet, and for the fishing industry as a whole. If reductions in catch result in decreased numbers of boats, there is a form of numerical response. The size of the human population, and certainly that part of the population involved in fishing, as a numerical component of management, involves an issue that is distinct but hardly unrelated (as treated elsewhere; e.g., Fowler 2008); it is part of what contributes to the decision-making and magnitude of realized fishing rates 10-60 fold times larger (Appendix III) than rates that are holistically sustainable and normal.

It is important to emphasize the necessity of achieving consonance between the management question and the empirical natural pattern that provides holistic guidance. This process was exemplified in all three cases of the management questions posed and addressed in this paper. The issues involved were 1) sustainable influence on the population level of the resource, 2) reductions needed in harvest rates responsive to declining populations of harvested stocks, and 3) sustainable harvest rates. Of these, finding sustainable harvest rates serves as a prime example of problems in conventional management that are solved in systemic management. In conventional management, production is used quite directly as a measure of what can be harvested (rather than as a correlative variable as exemplified by total natural mortality in Appendix III). Various models are used for estimating production (e.g., that of Pella-Tomlinson 1969 or that of Beverton and Holt 1957)[13]; other models are used for estimating consumption (see

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[13] A large variety of such models involve production in terms of either biomass or numbers (Fletcher 1978). Classic models in this category include the logistic model, the Ricker model (Ricker 1975), the Schaefer model (Schaefer 1954) and the generalized production model (see Fox 1971). Yield-per-recruit models fall into the same category; they do not provide estimates of consumption.

Innes et al. 1986 and Hunter et al. 2000) especially in combination with population estimates to determine collective consumption rates. It is the former that are used in setting policy in conventional fisheries management rather than the latter. This involves a serious lack of consonance because production is not consumption (Box 1) and it is sustainable consumption rates that we are seeking in our management of the harvest of fish. This problem is solved by using natural patterns in empirically observed consumption rates to provide guidance (with guidance based on avoiding abnormality). This consonance was exemplified by the choice of patterns described in Appendix III.

Another set of factors which we want to emphasize involves the ways in which pattern-based management achieves holism—as exemplified by our work. The most important contribution to holism is likely that achieved through the integrative nature of natural patterns (Belgrano and Fowler 2008). Each natural pattern is infinitely integrative (see Appendix III of Fowler et al. 2013)—nothing is excluded (in comparison to conventional management wherein we have no choice but to ignore most, if not all, of the things about which we are unaware and incapable of thinking; Fowler and Hobbs 2011). In addition to the integrative nature of natural patterns is the matter of taking management action to alleviate natural systems of as many abnormal human impacts as possible—in every way we find ourselves to be abnormal in our impacts. This involves asking as many management questions as we can, conducting the science to reveal the consonant natural patterns, and carrying out management based on the resulting guidance. In this paper we have dealt with three management questions. Others involve sustainable size selectivity in fisheries (to deal with one aspect of evolutionary importance, Etnier and Fowler 2010), sustainable harvests from groups of species, ecosystems, and the entire marine environment (Fowler 2008, Fowler and McCluskey 2011, Fowler et al. 2013), and sustainable species composition of harvests (Fowler 1999). These are a small start; they exemplify a tiny sample of the kinds of issues that can be addressed with natural patterns. There is an essentially infinite set of questions yet to be addressed.

Finally, there is the holism involved in accounting for the complexity of our impacts. This is part of the infinitely integrative nature of natural patterns (especially through the full complexity of all feedback processes); all impacts (direct or indirect, short-term or long-term, involving the full complexity of natural systems) are taken into account (Fowler et al. 2013). Achieving normal influence involves all of the related and interconnected aspects of natural

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Box 1

Production is Not Consumption

Production is not consumption. They are not synonymous; in dictionaries, and in the ecological literature, each is defined as a distinct process. Without consumption (involving the processes of finding and eating resources), a species cannot produce (involving processes such as growth and reproduction); every higher-trophic level species is ecologically "between the bookends" of consumption and production. They are distinctly different processes—intake and output. In the relationship between a predator and its prey, it is the production (numbers or biomass) by the prey that provides the predator with resources to consume; in this case production involves the prey species and consumption involves the predator—two distinct species. It is estimates of the per-species consumption rates that were used in Appendix III to address the management question of a sustainable consumption (harvest) rate for our species. The units used to measure the two processes may appear to be the same (e.g., biomass per unit time per species), but one is biomass per unit time per producing species and the other is biomass per unit time per consuming species (both in terms of particular stocks or regional populations). The fact remains: production and consumption are not the same thing. Production involves the origin of biomass, consumption involves its fate. Confusing them, as is done in conventional management, also involves a logical typing error because consumption by a single predator involves only a part of the fate of production (Fowler and Hobbs 2011). It is sustainability in our (the human) part of the fate of production that we are interested in achieving; this sustainability simultaneously involves that of the ecosystems and evosystems within which we are trying to achieve a sustainable form of participation.

The confusion in conventional thinking, with regard to production and consumption, involves a conceptual conversion of one to the other. In this thinking, we assume, as in the specific case of the concept of maximum sustainable yield (MSY), that the production we have stimulated by reducing a fish stock is all harvestable (consumable) by fisheries. It is the sustainability in the *actual* conversion (rather than the conceptual conversion) of production to consumption that we are, in fact, trying to maximize. Such conversion is a natural process that happens in all predatory/prey relationships in ecological systems and the rates of conversion can be measured or estimated. These measures are information about what works in that conversion—all things considered. In contrast, the conceptual conversion is fallacious (production is not consumption; equating them involves the fallacy of false equivalence); the natural conversion is holistically informative as guidance (consumption is consumption). Consumption rates among natural predators populations from prey populations at observed densities (as exemplified by information used in this paper) serve as guidance for achieving normalcy.

systems. We remain subject to our human limitations in not being able to think of all of the management questions and in our inability (or lack of will) to carry out management that achieves normalcy; complete holism can never be achieved because human limitations prevent asking all management questions. Unasked questions cannot be addressed, and consonant actions cannot be carried out for questions left unasked.

Regarding the specifics of our examples of the implementation of systemic thinking, we emphasize that the results of our work are, as with most science, preliminary. As we have tried to make clear in each of the appendices, much more thorough and extensive research is needed to more precisely and accurately chose appropriate models for control rules and estimate the associated parameters. The sets of data we have used to exemplify the process are subject to a variety of potential and real biases on the part of investigators conducting the studies which resulted in the data we are using (plus, of course, our own human contributions to the process of interpreting published information). The extent of reduction in prey populations by their predators as represented in published estimates may be greater than actually realized in nature owing to the interest of researchers in studying species with significant impacts (e.g., keystone species and alien species). The shape of functional response curves may be biased by laboratory studies in which artificially high prey densities may have been involved—densities higher than observed in normal settings—to result in skewed estimates for the parameters we obtained (we attempted to avoid such bias with our choice of data). Such factors are numerous and a great deal of additional research is needed to sort out the specifics. Our mission was much more one of exemplifying the kind of data (at the expense of quality) needed to establish realistic control rules.

Further caution regarding any tendency to see the results of our work as more than preliminary involves the potential for bias owing to human impact on the systems from which the data used in our research were collected. Specifically, it is important that the rates at which nonhuman predators consume their prey be measured under conditions in which the predator/prey systems, and their ecosystems, have recovered from the extensive abnormal influence of fishing pressure revealed in Appendix III. This kind of return to health also needs to involve recovery from other abnormal influence. These include our abnormal pollution and carbon dioxide production (Fowler 2008), abnormal size selectivity in commercial fishing (Etnier and Fowler 2010), and abnormal harvests from species groups and ecosystems (Fowler 2008).

Nevertheless, our emphasis on the preliminary nature of our findings is not meant to detract from the clarity of the emerging picture of abnormality. The abnormality of conventional control rules is obvious. The simplicity of conventional rules (depicted in Fig. 1) compared to the more realistic curvature of functional response curves (depicted in Fig. 2) is quite clear. Equally obvious is the abnormality of harvest rates overall (as compared in Fig. 8). Both the shape and position of the lines of Figure 1 are quite abnormal. Our emphasis on the preliminary nature of our findings has to do with the need for greater accuracy in the formulation of, and choice of, models to represent holistic control rules, as well as more refined and accurate consonant data, more than it has to do with the risk of incorrectly concluding that there is abnormality. It is always possible that we are making the latter mistake, but it is highly improbable. Fisheries management has far to go to achieve true holistic sustainability.

SUMMARY

Natural patterns, when carefully chosen, can be used to provide guidance for management regarding the various elements, or components, of policy for commercial fishing. This can involve control rules, major parts of which have been the focus of this paper. Such patterns reveal normal variation and its limits and thereby expose abnormality. They also exhibit central tendencies which can serve as guidance for what works (exemplified by our use of means for sustainable population reduction and finding the parameters for the curvilinear control rules) and as guidance for avoiding abnormality. By avoiding abnormality in human influence and participation in natural systems, we can establish sustainable harvest rates, identify changes needed in those harvest rates in reaction to changes in the abundance of harvested stocks, and manage to achieve sustainable population sizes for those stocks. These three elements of control rules were treated in this paper by showing preliminary information for corresponding (consonant) natural patterns. The results show varying degrees of abnormality in current forms of management each of which can be rectified through pattern-based management. Harvest rates are often too large by more than an order of magnitude. This is true whether these harvests are those taken from populations of the resources species that are at levels expected when free of the effects of harvesting, or at population levels reduced by the impact of harvesting (e.g., those forced on the system by conventional management in order to stimulate productivity). Often, populations of species harvested under current management policy are maintained at levels that are nearly half the size that would be fully sustainable in consideration of all other species, their ecosystems and all ecological and evolutionary interactions.

Figure 9 is a graphic summary of the results of the three parts of our work as explained in detail in the three corresponding appendices. The first step (top panel, Appendix I) represents the determination of sustainable reductions in resource populations (less than the 60% often used in historic fisheries management). The second step involves curvilinearity (none of the functional response curves in the literature cited in Appendix II involved extensive straight-line segments of constant intensive harvest rates), and parameterization of the curve (at $P = 0.4$, mean consumption rates were about 55.6% of what they were at prey population levels free of the effects of predation by the predator under study). The third step (Appendix III) provided information for sustainable predation rates (with P at levels established in the first step)—much less than implemented in conventional management (Fowler et al. 2013).

Thus, Figure 9 reveals some of the abnormality in conventional management (i.e., policies used historically in the regulation of fisheries), specifically with respect to what are known as control rules. The simplicity and misleading nature of conventional management is obvious in all respects, but most egregious are the rates of fishing to which resource populations are subjected; these are often much more than 10-fold too large (Appendix III).

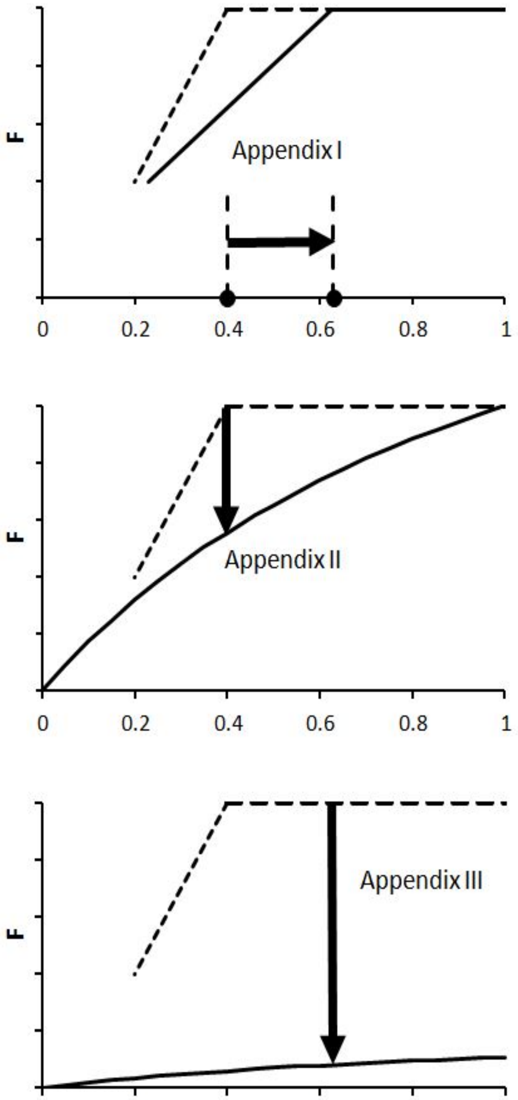

Figure 9. -- The progression of steps involved in establishing pattern-based control rules as presented in this paper. The first step (top panel) involves a revision of sustainable reductions in resource populations. The second step (middle panel) involves holistic guidance regarding curvilinearity (rather than straight-line segments), and parameterization of the curve. The third step (bottom panel) represents information for sustainable predation rates—all as a function of P, and much less than proposed conventionally.

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APPENDICES

APPENDIX I

Responses of Prey Populations to Predation

by

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ABSTRACT

In this appendix, we present information on the pattern observed in the impact of predation on populations of prey. The specific measure of interest is the ratio of the size, or density, of prey populations under the influence of predation to those free of such effects. In all cases, we are interested in the effects of a *single* predator population on its prey. This study is motivated by the fact that populations of species treated as resources in fisheries management are usually reduced intentionally to stimulate productivity; as an individual species, humans serve as the predators. We are thus faced with a management question: *"To what extent can we sustainably reduce a resource population?"*

We found 119 cases in the published literature with data that met our criteria for information on the ratio of interest. Under the influence of predation, the mean prey population was 0.63 (63%) as large as when free of such influence. This is in contrast to fisheries management where it is not uncommon (especially historically) to intentionally reduce harvested fish populations to 40% of their virgin or unharvested levels. In such management, the reductions implemented as a matter of policy are well within the limits of variation for other predatory species but do not correspond to the mean observed among other predatory species. This mean, as derived by our study, is to be considered preliminary in that research more directly matching the management question (involving humans, as a mammalian species, consuming fish), can be expected to produce different results. In other words, it is likely that studies specifically directed toward measuring the impact of mammalian predators on fish populations would be less subject to bias inherent to research of the kinds represented by the publications we found for the purposes of our study.

INTRODUCTION

Much of the management of commercial fisheries worldwide involves what are often referred to as control rules. One of the elements involved in the resulting policy is the reduction of the fish population being harvested[1]. The motivation for such reduction[2] involves the assumption that the productivity of the population will be stimulated—productivity that managers conventionally assume to be available for harvest by humans[3]. The policy of reducing the population of a resource species gives rise to the generic management question: *"At what portion of its unharvested levels is a harvested population when harvested sustainably?"* The sustainability involved, as we are using the term, is holistic to include the sustainability of the ecosystem (and evosystem) in which the harvested population and harvesting occurs. The sustainability of everything impacted, directly or indirectly, and over various time and spatial scales, is at stake.

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[1] Other elements include the magnitude of harvest rates from populations at reduced abundance (treated in Appendix II) and the magnitude of the harvest rate at its maximum (treated in Appendix III).

[2] As indicated in the main text, intentional reductions to a population level of 40% of the unharvested level are often used in fisheries management, especially historically, often as a target (to achieve maximum sustainable yield), or threshold (below which resources are considered over-harvested), or both. The National Standard Guidelines (as published in the Federal Register) established in the U.S. in 1997 recommended 0.4 as an acceptable value for P (Restrepo et al. 1998). The use of this value is often found in management recommendations and policy (Hilborn 2002, Apostolaki and Hillary 2009, Casey et al. 2009, FLSF 2010); smaller values are not rare (Forrest et al. 2010). Values for P less than 0.5 are expected when management is based on population models representing typical life history strategies of many species of fish (Fowler 1981, 1988, Mangel et al. 2013).

[3] Fisheries management has conventionally considered this increase in productivity to be "surplus" (and available for being taken through harvesting) rather than as part of the process required by the resource population to achieve its normal levels within the ecosystem for normal systemic dynamics to occur (to include ecosystems and evosystems). A good description of the how this "surplus" is perceived conventionally is found in Wallace and Fletcher (2001). See Box 1 in the main text regarding the errors involved in conventional assumptions in this regard.

With this management question in hand, we can now follow the protocol of using our management question as basis for formulating a consonant[4] research (science) question (Fowler and Hobbs 2011). In this case, that question is: *"What is the ratio of prey population levels with and without the effects of an individual predatory species?"* Research to address this question results in information that characterizes an informative pattern so that limits to variation exhibited by that pattern can be used to guide management and enable sustainable harvesting of resources (e.g., commercial harvesting of fish); in other words, to promote harvesting that does not result in abnormal reductions in harvested populations—thus avoiding any associated abnormality (e.g., among other species, trophic levels, communities, ecosystems, and the biosphere).

It is with this research question in mind that we carried out the study reported in this appendix.

METHODS

Searches of the literature (using resources available in libraries and online options such as Thomson Reuters' Web of Knowledge, Google and Google Scholar) focused on finding studies of predator/prey systems in which specific predators (populations of an individual species) were either added to the system or removed from the system to evaluate their impact on the populations of specific (individual) prey species[5]. Our search frequently involved finding useful references to similar studies as presented in the literature-cited sections of various papers containing information of the kind we were seeking. Often, publications were found that addressed other focal questions, but provided information of direct use in addressing our research question.

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[4] Consonance involves a strict match between the management question, research question and natural pattern that provides guidance for management (see Fowler and Hobbs 2011 for further detail). See also the examples in Appendices II and III.

[5] The need for individual predatory species as it impacts individual prey species is an element of consonance associated with the management question involving humans as an individual species impacting the resource as an individual species.

Our collection of information focused on predators for which the prey were other animals; herbivores were excluded as the consumer (the management question involves our take of fish, not plants—more consonance). Still more consonance was achieved by recognizing ourselves (humans) as vertebrates; our search of the literature involved accepting only results for predatory species that are vertebrates. Other than avoiding herbivores and invertebrate predators, no attempt was made to focus on any particular set of either predator or prey. We collected information on habitat (e.g., terrestrial vs. marine or fresh water), location, and duration of the study. In each case, the identity (scientific and, if available, common names) of both the predator and the prey were recorded. We distinguished between studies in which the predator was removed and studies in which it was introduced (or reintroduced in cases where it had been absent for lengthy periods), and noted whether or not the predator was a native species or not. Laboratory studies were excluded (the management question involves consumption in natural settings).

The primary focus of our study was a measure of the change in prey populations as they responded to having a predator population either removed or introduced. The measure we chose to record was determined by the research question asked above and reflective of the management question being addressed. Thus, we recorded the ratio, R, of the population level of prey under the influence of predation to that of the population free of the effects of predation—always with the same specific predator. In other words, every case in the data that we collected applied to a single species of predator and a single species of prey. For example, R would be 0.5 if, in the absence of predation by a particular predator, the population level of one of its prey was 1000 individuals (or 100 per square km if the study area was 10 square km) and, under the influence of predation by that same predator, the population level was 500 (or 50 per square km). The ratio R would be 1.2 if the population level under the influence of predation were 1200 individuals (or 120 per square km); this would exemplify the counterintuitive effect of predation as realized through the complex set of interactions involving such things as behavioral impact on other predators, and competition with other prey species also impacted by the specific predator. Information was acceptable if it was expressed in either total numbers (within a fixed area), or density (expressed in a variety of metrics). We accepted a variety of indices of population size or density (e.g., catch-per-unit-effort); these kinds of information are often the only measures available.

Studies that involved the removal of multiple predators were largely ignored. This was because the matter of concern in the management question (and research question) involves the effect of a single predator—humans in our effect on specific resource populations. In a very few cases we accepted the results of studies wherein there were more than one predator removed if the authors indicated that the bulk of predation was attributable to one predator. Studies in which there were measurements of the effects of one predatory species on more than one species of prey were welcome sources of more than one observation—one for each of the prey species in the set of prey involved.

After collection of the data, the information was displayed as a frequency distribution or histogram following the basic procedures outlined by Fowler and Perez (1999). Subsets of the data were treated for purposes of exemplifying the process of achieving consonance in the refinement of the management question.

RESULTS

Table A1.1 lists the primary data collected for this study, with the source of the information indicated by references referred to by number. Table A1.2 is linked to Table A1.1 and is a listing of a variety of potentially important circumstances contributing to the observed impact of predators (e.g., the location of the study and its duration, habitat type, and length of the study). In Table A1.1, R corresponds to the index of population size (P) as presented in the main body of this paper (e.g., Fig. 1).

Table A1.1. -- List of data collected to reveal the pattern in the reduction of prey populations by the effects of populations of individual species of predators. DP is the data point (corresponding to that of Table A1.2), Source is the reference number (see the Literature Cited section), R is the ratio of the prey population as influenced by the presence of the population of predators to that without such influence.

DP	Source	Predator	Prey	CT[1]	TC[2]	R
1	1	*Neovison vison*	*Rana temporaria*	RS	C	0.33
2	2	*Salvelinus fontinalis*	*Baetis bicaudatus*	RS	H	1.69
3	2	*Salvelinus fontinalis*	*Cinygmula* sp.	RS	H	1.07
4	2	*Salvelinus fontinalis*	*Epeorus longimanus*	RS	H	1.45
5	2	*Salvelinus fontinalis*	*Ephemerella coloradensis*	RS	H	1.18
6	2	*Salvelinus fontinalis*	*Ephemerella infrequens*	RS	H	1.32
7	2	*Salvelinus fontinalis*	*Alloperla* sp.	RS	H	1.98
8	2	*Salvelinus fontinalis*	*Zapada haysi*	RS	H	1.73
9	2	*Salvelinus fontinalis*	*Rhyacophila acropedes*	RS	H	1.39
10	2	*Salvelinus fontinalis*	*Rhyacophila valuma*	RS	H	0.65
11	3	*Aquila chrysaetos*	*Urocyon littoralis*	AS	C	0.65
12	4	*Vulpes vulpes*	*Rattus fuscipes*	RT	H	1.00
13	5	*Vulpes vulpes*	*Oryctolagus cuniculus*	RT	H	0.06
14	6	*Vulpes vulpes*	*Oryctolagus cuniculus*	RTS	H	0.11
15	7	*Vulpes vulpes*	*Oryctolagus cuniculus*	RTS	H	0.08
16	7	*Vulpes vulpes*	*Oryctolagus cuniculus*	RTS	H	0.15
17	8	*Vulpes vulpes*	*Macropus giganteu*	RTS	H	0.65
18	9	*Canis lupus*	*Canis latrans*	AT	C	0.72
19	10	*Felis silvestris catus*	*Oryctolagus cuniculus*	RT	H	0.26
20	11	*Neovison vison*	*Fulica atra*	AT	C	0.05
21	12	*Alopex lagopus*	*Haematopus bachmani*	RS	C	0.23
22	12	*Alopex lagopus*	*Cepphus columba*	RS	C	0.09
23	13	*Semicossyphus pulcher*	*Strongylocentrotus*	RTS	H	0.45
24	14	*Dorosoma cepedianum*	*Chaoborus* sp.	RTS	H	0.29
25	14	*Dorosoma cepedianum*	*Diaptomus*	RTS	H	3.75
26	14	*Dorosoma cepedianum*	*Cydopoids copepodids*	RTS	H	0.05
27	14	*Dorosoma cepedianum*	*Diaphanosoma brachyurum*	RTS	H	0.06

DP	Source	Predator	Prey	CT[1]	TC[2]	R
28	14	*Dorosoma cepedianum*	*Keratella* sp.	RTS	H	0.00
29	15	*Enhydra lutris*	*Strongylocentrotus*	PAS	H	0.00
30	15	*Enhydra lutris*	*Strongylocentrotus*	PAS	H	0.00
31	15	*Enhydra lutris*	*Strongylocentrotus*	PAS	H	0.00
32	16	*Enhydra lutris*	*Strongylocentrotus*	AT	H	0.00
33	16	*Enhydra lutris*	*Strongylocentrotus*	AT	H	1.26
34	16	*Enhydra lutris*	*Strongylocentrotus*	AT	H	0.00
35	16	*Enhydra lutris*	*Strongylocentrotus*	AT	H	0.03
36	17	*Canis lupus*	*Rangifer tarandus*	RT	H	0.68
37	17	*Canis lupus*	*Ovis dalli*	RT	H	1.00
38	17	*Canis lupus*	*Alces alces*	RT	H	0.37
39	18	*Lynx lynx*	*Vulpes vulpes*	AT	C	0.78
40	19	*Canis latrans*	*Lepus californicus*	RT	H	0.63
41	19	*Canis latrans*	*Sylvilagus audubonii*	RT	H	1.00
42	19	*Canis latrans*	*Dipodomys ordii*	RT	H	3.36
43	19	*Canis latrans*	*Perognathus flavus*	RT	H	0.24
44	19	*Canis latrans*	*Onychomys leucogaster*	RT	H	0.67
45	19	*Canis latrans*	*Perognathus flavecens*	RT	H	0.44
46	19	*Canis latrans*	*Reithrodontomys megalotis*	RT	H	0.90
47	19	*Canis latrans*	*Peromyscus manicularis*	RT	H	0.44
48	19	*Canis latrans*	*Peromyscus leucopus*	RT	H	0.00
49	19	*Canis latrans*	*Neotoma micropus*	RT	H	0.57
50	19	*Canis latrans*	*Chaetodipus hispidus*	RT	H	1.06
51	20	*Felis silvestris catus*	*Onychoprion fuscatus*	RT	C	0.88
52	21	*Erinaceus europaeus*	*Haematopus ostralegus*	AT	C	1.21
53	21	*Erinaceus europaeus*	*Charadrius hiaticula*	AT	C	0.42
54	21	*Erinaceus europaeus*	*Vanellus vanellus*	AT	C	0.69
55	21	*Erinaceus europaeus*	*Calidris alpina*	AT	C	0.44
56	21	*Erinaceus europaeus*	*Gallinago gallinago*	AT	C	0.45
57	21	*Erinaceus europaeus*	*Tringa totanus*	AT	C	0.59
58	22	*Vulpes vulpes*	*Capreolus capreolus*	RT	H	0.43
59	23	*Vulpes vulpes*	*Petrogale lateralis*	RT	H	0.42

DP	Source	Predator	Prey	CT[1]	TC[2]	R
60	23	*Vulpes vulpes*	*Petrogale lateralis*	RT	H	0.31
61	24	*Vulpes vulpes*	*Petrogale rothschildi*	RTS	H	0.02
62	24	*Vulpes vulpes*	*Petrogale rothschildi*	RT	H	0.04
63	24	*Vulpes vulpes*	*Bettongia penicillata*	RT	H	0.09
64	24	*Vulpes vulpes*	*Trichosurus vulpecula*	RT	H	0.45
65	24	*Vulpes vulpes*	*Macropus eugenii*	RT	H	0.01
66	24	*Vulpes vulpes*	*Macropus eugenii*	RT	H	0.05
67	24	*Vulpes vulpes*	*Bettongia penicillata*	RT	H	0.00
68	24	*Vulpes vulpes*	*Trichosurus vulpecula*	RT	H	0.07
69	24	*Vulpes vulpes*	*Bettongia penicillata*	RTS	H	0.02
70	24	*Vulpes vulpes*	*Trichosurus vulpecula*	RTS	H	0.24
71	24	*Vulpes vulpes*	*Macropus eugenii*	RTS	H	0.18
72	24	*Vulpes vulpes*	*Trichosurus vulpecula*	RTS	H	0.02
73	24	*Vulpes vulpes*	*Trichosurus vulpecula*	RTS	H	0.16
74	24	*Vulpes vulpes*	*Macropus eugenii*	RTS	H	0.00
75	25	*Vipera berus*	*Microtus agrestis*	RTS	H	0.80
76	26	*Vulpes vulpes*	*Clethrionomys glareolus*	RT	H	1.00
77	26	*Vulpes vulpes*	*Microtus agrestis*	RT	H	1.00
78	26	*Vulpes vulpes*	*Tetrao urogallus*	RT	H	0.59
79	26	*Vulpes vulpes*	*Tetrao tetrix*	RT	H	0.59
80	26	*Vulpes vulpes*	*Bonasa bonasia*	RT	H	0.59
81	26	*Vulpes vulpes*	*Lepus timidus*	RT	H	0.59
82	26	*Vulpes vulpes*	*Capreolus capreolus*	RT	H	0.61
83	27	*Rattus norvegicus*	*Crocidura suaveolens*	RT	C	0.02
84	27	*Rattus rattus*	*Gecarcinus ruricola*	RT	C	0.64
85	27	*Rattus norvegicus*	*Anthus petrosus*	RT	H	0.15
86	27	*Rattus norvegicus*	*Prunella modularis*	RT	H	0.55
87	27	*Rattus norvegicus*	*Troglodytes troglodytes*	RT	C	0.36
88	28	*Canis lupus*	*Cervus elaphus*	AT	H	0.75
89	29	*Felis silvestris catus*	*Megadyptes antipodes*	PAS	C	0.42
90	30	*Neovison vison*	*Haematopus ostralegus*	RTS	C	1.25
91	30	*Neovison vison*	*Charadrius hiaticula*	RTS	C	0.25

DP	Source	Predator	Prey	CT[1]	TC[2]	R
92	30	*Neovison vison*	*Tringa totanus*	RTS	C	0.00
93	30	*Neovison vison*	*Arenaria interpres*	RTS	C	0.19
94	30	*Neovison vison*	*Stercorarius parasiticus*	RTS	C	0.17
95	30	*Neovison vison*	*Larus canus*	RTS	C	0.53
96	30	*Neovison vison*	*Larus marinus*	RTS	C	1.11
97	30	*Neovison vison*	*Sterna paradisaea*	RTS	C	0.31
98	30	*Neovison vison*	*Anthus pratensis*	RTS	C	0.75
99	30	*Neovison vison*	*Anthus petrosus*	RTS	C	0.31
100	30	*Neovison vison*	*Motacilla alba*	RTS	C	0.66
101	30	*Neovison vison*	*Oenanthe oenanthe*	RTS	C	0.09
102	31	*Neovison vison*	*Anas platyrhynchos*	RTS	H	0.20
103	31	*Neovison vison*	*Aythya fuligula*	RTS	C	0.00
104	31	*Neovison vison*	*Melanitta fusca*	RTS	C	0.06
105	31	*Neovison vison*	*Tadorna tadorna*	RTS	C	0.00
106	31	*Neovison vison*	*Cygnus olor*	RTS	H	0.81
107	31	*Neovison vison*	*Anser anser*	RTS	H	6.00
108	31	*Neovison vison*	*Somateria mollissima*	RTS	C	2.14
109	31	*Neovison vison*	*Mergus merganser*	RTS	C	0.82
110	32	*Lynx lynx*	*Oryctolagus cuniculus*	PAS	H	3.00
111	33	*Puma concolor*	*Odocoileus hemionus*	RA	H	0.40
112	34	*Mustela erminea*	*Rattus rattus*	RTS	H	0.60
113	34	*Mustela erminea*	*Mus musculus*	RTS	H	1.60
114	35	*Neovison vison*	*Rana temporaria*	RTS	C	0.37
115	36	*Corvus corone*	*Turdus pilaris*	RTS	C	0.21
116	36	*Corvus corone*	*Regulus Regulus*	RTS	C	0.49
117	36	*Corvus corone*	*Turdus philomelos*	RTS	C	0.55
118	37	*Puma concolor*	*Erethizon dorsatum*	AT	H	0.06
119	38	*Ardea herodias*	*Microtus townsendii*	RTS	H	1.00

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[1] CT (comparison type): AT = Predator added (or returned) with comparison over time; RTS = Predator removal with comparisons over time and space; PAS = spatial comparison between areas where predators are present and others where they are absent.

[2] TC is the trophic category of the prey: C = carnivore for species that are of a higher trophic level than herbivore (including omnivores); H = herbivore (including granivores).

Table A1.2. -- Information regarding circumstances involved in the data collected for this study. Corresponding to those shown in Table A1.1, DP is the data point and Ref. is the reference number (in the literature cited section). The status of the predator species (SPD) and that of the prey species (SPY) are indicated (I = introduced, N = native). Habitat is indicated by Terrestrial (T), Fresh Water (F) or Marine (M).

DP	Ref.	Location	Duration (years)	SPD	SPY	T/F/M
1	1	Archipelago Sea, Finland	6.00	I	N	T, F
2	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
3	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
4	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
5	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
6	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
7	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
8	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
9	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
10	2	Cement Creek, Gunnison County, Colorado	4.00	N	N	F
11	3	Channel Islands, California	12.00	I	N	T
12	4	Namadgi National Park, Australia	1.83	I	N	T
13	5	Namadgi National Park, Australia	1.67	I	I	T
14	6	Namadgi National Park, Australia	1.50	I	I	T
15	7	Namadgi National Park, Australia	2.00	I	I	T
16	7	Namadgi National Park, Australia	2.00	I	I	T
17	8	Namadgi National Park, South-East	1.50	I	I	T
18	9	Grand Teton National Park, Wyoming	3.00	N	N	T
19	10	Maquarie Island, Australia	6.00	I	N	T
20	11	Northeast Poland	19.00	I	N	T
21	12	Shumigin Islands, Alaska	2.00	I	N	T
22	12	Shumigin Islands, Alaska	2.00	I	N	T
23	13	San Nicolas Island, California	2.00	N	N	M
24	14	Douglas County, Kansas	0.24	N	N	F
25	14	Douglas County, Kansas	0.24	N	N	F
26	14	Douglas County, Kansas	0.24	N	N	F

DP	Ref.	Location	Duration (years)	SPD	SPY	T/F/M
27	14	Douglas County, Kansas	0.24	N	N	F
28	14	Douglas County, Kansas	0.24	N	N	F
29	15	Surge Bay, Yakobi Is., and Torch Bay,	10.00	N	N	M
30	15	Surge Bay, Yakobi Is., and Torch Bay,	10.00	N	N	M
31	15	Surge Bay, Yakobi Is., and Torch Bay,	10.00	N	N	M
32	16	Torch Bay, Alaska	13.00	N	N	M
33	16	Massacre Bay, Attu Island, Alaska	13.00	N	N	M
34	16	Torch Bay, Alaska	13.00	N	N	M
35	16	Torch Bay, Alaska	13.00	N	N	M
36	17	Aishihik, Southwest Yukon, Canada	5.00	N	N	T
37	17	Aishihik, Southwest Yukon, Canada	5.00	N	N	T
38	17	Aishihik, Southwest Yukon, Canada	5.00	N	N	T
39	18	Orebro County, Sweden	11.00	N	N	T
40	19	Western Texas	2.50	N	N	T
41	19	Western Texas	2.50	N	N	T
42	19	Western Texas	2.50	N	N	T
43	19	Western Texas	2.50	N	N	T
44	19	Western Texas	2.50	N	N	T
45	19	Western Texas	2.50	N	N	T
46	19	Western Texas	2.50	N	N	T
47	19	Western Texas	2.50	N	N	T
48	19	Western Texas	2.50	N	N	T
49	19	Western Texas	2.50	N	N	T
50	19	Western Texas	2.50	N	N	T
51	20	Ascension Island, South Atlantic	6.00	N	N	M
52	21	Outer Hebrides, Scotland, UK	17.00	I	N	T
53	21	Outer Hebrides, Scotland, UK	17.00	I	N	T
54	21	Outer Hebrides, Scotland, UK	17.00	I	N	T
55	21	Outer Hebrides, Scotland, UK	17.00	I	N	T
56	21	Outer Hebrides, Scotland, UK	17.00	I	N	T
57	21	Outer Hebrides, Scotland, UK	17.00	I	N	T

DP	Ref.	Location	Duration (years)	SPD	SPY	T/F/M
58	22	Ekenas, Sweden	15.00	N	N	T
59	23	Kellerberin, Western Australia	4.00	I	N	T
60	23	Kellerberin, Western Australia	4.00	I	N	T
61	24	Dampier Archipelago, Australia	11.00	I	N	T
62	24	Dampier Archipelago, Australia	11.00	I	N	T
63	24	Tutanning Nature Reserve, Australia	13.00	I	N	T
64	24	Tutanning Nature Reserve, Australia	13.00	I	N	T
65	24	Tutanning Nature Reserve, Australia	13.00	I	N	T
66	24	Tutanning Nature Reserve Annex, Australia	11.00	I	N	T
67	24	Tutanning Nature Reserve Annex, Australia	11.00	I	N	T
68	24	Boyagin Nature Reserve, Australia	7.00	I	N	T
69	24	Dryandra Woodland, Australia	3.00	I	N	T
70	24	Dryandra Woodland, Australia	3.00	I	N	T
71	24	Dryandra Woodland, Australia	3.00	I	N	T
72	24	Fitzgerald River National Park, Australia	4.00	I	N	T
73	24	Fitzgerald River National Park, Australia	7.00	I	N	T
74	24	Fitzgerald River National Park, Australia	7.00	I	N	T
75	25	In-Fredeln Island Group, Sweden	4.00	N	N	T
76	26	Grimso Wildlife Research Area, Sweden	19.00	N	N	T
77	26	Grimso Wildlife Research Area, Sweden	19.00	N	N	T
78	26	Grimso Wildlife Research Area, Sweden	19.00	N	N	T
79	26	Grimso Wildlife Research Area, Sweden	19.00	N	N	T
80	26	Grimso Wildlife Research Area, Sweden	19.00	N	N	T
81	26	Grimso Wildlife Research Area, Sweden	19.00	N	N	T
82	26	Grimso Wildlife Research Area, Sweden	19.00	N	N	T
83	27	Bono Island, Sept-Iles Archipelago, France	50.00	I	N	T
84	27	Hardy Island, Martinique Archipelago,	2.00	I	N	T
85	27	Trielen Island, Molene Archipelago, France	5.00	I	N	T
86	27	Trielen Island, Molene Archipelago, France	5.00	I	N	T
87	27	Trielen Island, Molene Archipelago, France	5.00	I	N	T
88	28	Yellowstone National Park, USA	17.00	N	N	T

DP	Ref.	Location	Duration (years)	SPD	SPY	T/F/M
89	29	Stewart Island and vicinity, New Zealand	3.00	I	N	T
90	30	Archipelago Sea, Finland	9.00	I	N	T
91	30	Archipelago Sea, Finland	9.00	I	N	T
92	30	Archipelago Sea, Finland	9.00	I	N	T
93	30	Archipelago Sea, Finland	9.00	I	N	T
94	30	Archipelago Sea, Finland	9.00	I	N	T
95	30	Archipelago Sea, Finland	9.00	I	N	T
96	30	Archipelago Sea, Finland	9.00	I	N	T
97	30	Archipelago Sea, Finland	9.00	I	N	T
98	30	Archipelago Sea, Finland	9.00	I	N	T
99	30	Archipelago Sea, Finland	9.00	I	N	T
100	30	Archipelago Sea, Finland	9.00	I	N	T
101	30	Archipelago Sea, Finland	9.00	I	N	T
102	31	Archipelago Sea, Finland	9.00	I	N	T
103	31	Archipelago Sea, Finland	9.00	I	N	T
104	31	Archipelago Sea, Finland	9.00	I	N	T
105	31	Archipelago Sea, Finland	9.00	I	N	T
106	31	Archipelago Sea, Finland	9.00	I	N	T
107	31	Archipelago Sea, Finland	9.00	I	N	T
108	31	Archipelago Sea, Finland	9.00	I	N	T
109	31	Archipelago Sea, Finland	9.00	I	N	T
110	32	Doñana National Park, Spain	11.00	N	N	T
111	33	Zion Canyon, Zion National Park, Utah,	60.00	N	N	T
112	34	North Island, New Zealand	2.00	I	I	T
113	34	North Island, New Zealand	2.00	I	I	T
114	35	Archipelago Sea, Finland	15.00	I	N	T
115	36	Central Norway	8.00	N	N	T
116	36	Central Norway	8.00	N	N	T
117	36	Central Norway	8.00	N	N	T
118	37	Granite Range, Nevada	5.00	N	N	T
119	38	Westham Island, British Columbia, Canada	0.33	N	N	T

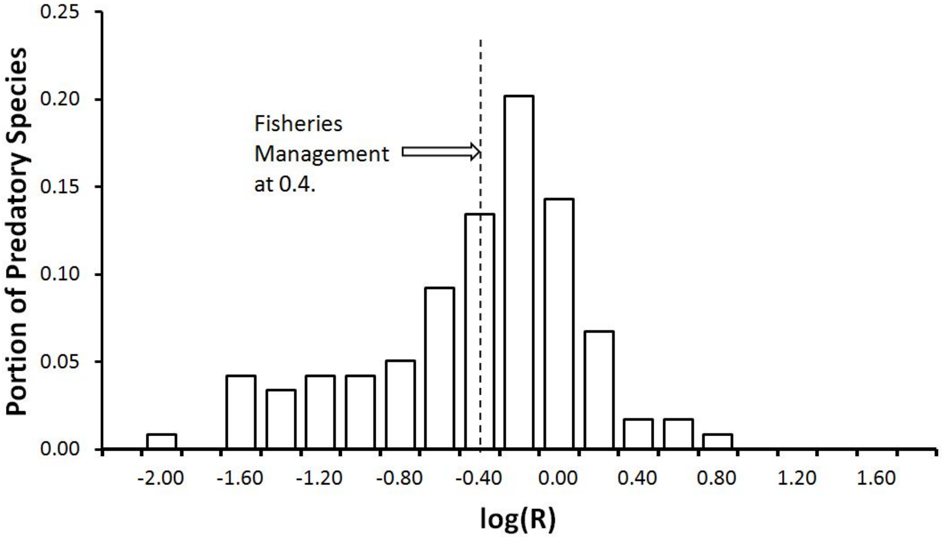

Figure A1.1. -- The frequency distribution of 119 published measurements of the effects of consumer species on their resource populations. The mean ratio (arithmetic mean for R) of prey population with and without the influence of the consumer species was about 0.63 (a reduction of about 37%). This corresponds to a population index (P) of 0.63 compared to the 0.4 often used as a standard in fisheries management.

As seen in Table A1.1, we were able to find 119 cases wherein there was information that met our standards for R, the extent to which predators effect the populations of their prey within the complexity of their ecosystems. Figure A1.1 shows the data from Table A1.1 displayed to show the limits to variation observed in R—a representation of the pattern of central interest to our study (as it bears consonance with the specific management question being addressed in this appendix). The arithmetic mean of this distribution is 0.63. Consistent with the work of Pimm (1991; see also Holt et al. 2008), 25 (about 21%) of the 119 cases showed evidence of prey populations which either remained unchanged or increased as an effect of predation (rather exhibiting the more intuitive effect of decreasing).

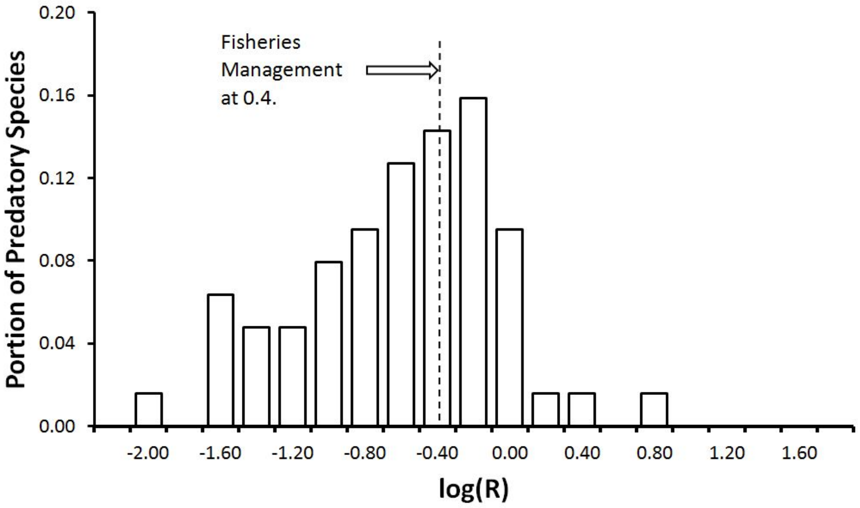

Figure A1.2. -- The frequency distribution of 63 published measurements of the effects of alien (introduced) consumer species on their resource populations as a subset of the data shown in Figure A1.1. The arithmetic mean of R for this set of data was about 0.47 (as compared to the 0.4 of many applications in fisheries management).

The data we gleaned from the published literature involved 21 species of predators and 92 species of prey. There were 56 cases involving native predators; the remaining 63 involved alien (introduced) predatory species. As developed by Salo et al. (2007), there is a tendency for alien predators to have greater impact on their prey populations than native predators. This pattern is seen in comparing the pattern in R for alien species (Fig. A1.2) with that for native species (Fig. A1.3). Conventional management of fisheries involves predatory effects that mimic the impact of alien predators much more closely than that of native predators.

In the management question we are addressing (*"At what portion of its unharvested levels is a harvested population when harvested sustainably?"*) humans, as the predators, fall into the taxonomic category of mammals. In the management of fisheries, the resources are fish. We found no examples of mammalian predatory effects on the size of fish populations, but did encounter 35 cases with information for native mammalian predators consuming vertebrate prey. The data indicative of the effects of these predators on their respective prey populations are shown in Figure A1.4.

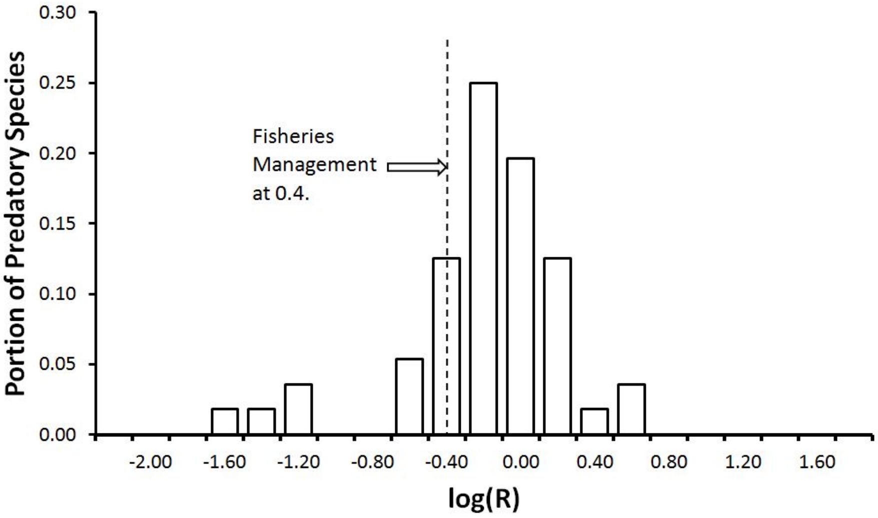

Figure A1.3. -- The frequency distribution of 56 published measurements of the effects of native predators on their resource populations as a subset of the data shown in Figure A1.1. The arithmetic mean of R for this set of data was about 0.80 (as compared to the 0.4 of many applications in fisheries management).

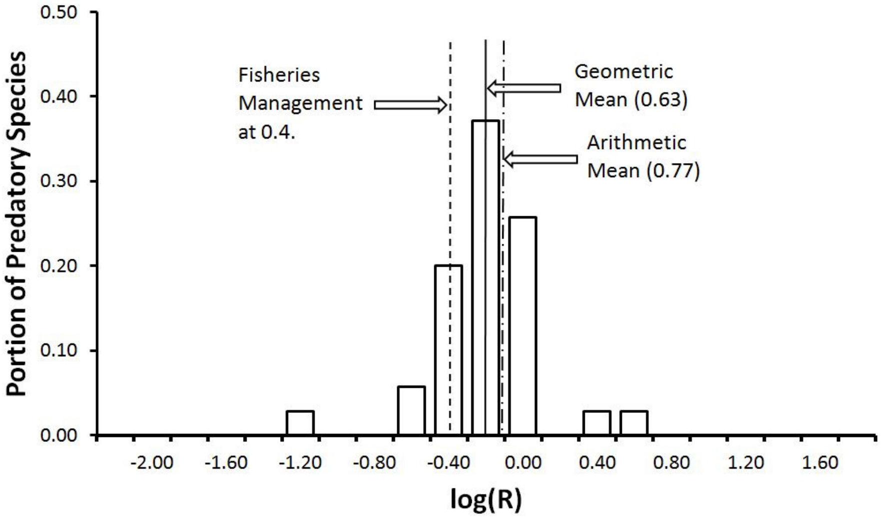

Figure A1.4. -- The frequency distribution of 35 published measurements of the effects of native mammalian predatory species on their vertebrate resource populations as a subset of the data shown in Figure A1.1. The arithmetic mean of R for this set of data was about 0.77; the geometric mean was about 0.63 (all as compared to the 0.4 of many applications in fisheries management).

Table A1.3. -- List of mean values for R from various subsets of data presented in Table A1.1.

Subset of data	Arithmetic mean	Geometric mean	Sample size
Full set of data	0.6273	0.3818	119
Native predators	0.7991	0.6365	56
Alien predators	0.4746	0.2479	63
Native predators/Vertebrate prey	0.7671	0.6306	35
Native mammalian predators/Native mammalian prey	0.8446	0.6695	24
Native large mammalian predators/Native large mammalian prey	0.6533	0.6155	6

Table A1.3 shows a variety of measures of central tendencies for the data from Table A1.1, all of which can be compared to the value of 0.4 that is used in various ways in conventional fisheries management. Although our sample size is small and the studies may be subject to a variety of biases, the data for native mammalian predators and their impact on native mammalian prey would involve more consonance with the management question faced by managers responsible for managing the harvest of large mammals. Further consonance would be achieved with greater specificity in the body size of both predator and prey, with predators chosen to match the body size of humans.

DISCUSSION

It is important to emphasize that the work we are reporting in this appendix exemplifies the process of obtaining information that is *consonant* with a specific management question (in this case, involving part of the application of control rules in fisheries management). The concept of consonance (Fowler and Hobbs 2011) demands that the pattern being characterized by research involve the elements of management in question. For this appendix, we are treating the impact of predation (harvesting) on the prey (resource) population as the pattern consonant with our management question: *“At what portion of its unharvested levels is a harvested population when* *harvested sustainably?"*. The central focus of a consonant study would be values for R, or measures of the impact of predators on their prey populations regardless of any other factors characterizing either of the two species. This involves consonance with the way the management question is posed.

More consonance was achieved in this study when we took into account that fisheries are an expression of predation by humans in which animals (fish, not plants) are harvested. Hence, we rejected studies of the effects of herbivores as consumers from the populations of plants that serve as their resources. Still more consonance was achieved in finding data for animals (we are animals) feeding on animals (fish are animals). In other words, both are of the kingdom *Animalia* to account for at least one level of taxonomic categorization. We are in a process of refining our management question toward the objective of achieving consonance with one specific part of the management action involved in implementing control rules.

Again the management question, as originally posed, was quite generic. This question can be made more specific if we continue the process of refinement (see Fowler and Hobbs 2011) to become: *"At what portion of its unharvested levels is a harvested marine fish population when harvested sustainably?"* To address this question adequately, we would have needed information of the impact of mammalian predators (we are mammals) on marine fish populations in particular. This points to the need for a very specific kind of information—a kind that we did not find in our search of the literature (Table A1.2). Thus, we emphasize the preliminary nature of the numeric results of this study and their implications for management.

Far more important than the preliminary nature of our data, however, are the elements involved in achieving consonance between the management question and the pattern used to address it. As such, the preliminary nature of our data does not detract from the progress made toward useful information and we emphasize the discrepancy between the information regarding R found in this study (e.g., the 0.7991 for the arithmetic mean of native predators; Table A1.3) and that often suggested for the management of fisheries (0.4); the former is nearly double the latter. Different values for R applicable in fisheries management will undoubtedly emerge from further research of the type we found in our survey, but which focus on the effects of mammals consuming marine fish. Further refinement would require research on the impact of mammals on the specific resource species being harvested. Still more would be achieved with such information collected in the location (e.g., specific ecosystem) of the harvest; much of our data came from terrestrial ecosystems (Table A1.2). The extent of research required to provide good management advice becomes more evident with the increasing specificity of management question(s).

Also with regard to the preliminary nature of our work, we note that there is a risk that the mean values for R (Table A1.3) are likely to be subject to various forms of bias. Of concern, for example, would be any tendency on the part of researchers to intentionally choose predatory species suspected to have large impacts on their prey populations. This would be involved in any studies conducted to document cases which substantiate theory regarding the impact of individual species of consumers on the structure and function of ecosystems (keystone species). It would also be a factor behind studies to emphasize the impact of alien species on species native to the habitat to which the predators were introduced. Many of the studies we found in our survey of the literature treated the effects of alien predators (Table A1.2, Fig. A1.2).

Another potential bias involves any tendency on the part of researchers to decide not to publish results in which little or no impact was observed. A similar bias could occur from the effects of papers being rejected for publication if little or no impact was discernable in the research conducted.

The potential for bias mentioned in the last two paragraphs could conceivably result in a mean R less than would be expected on the grounds of a random sampling of predator/prey relationships. An opposing bias could stem from any focus on cases in which the effects of predators on their prey populations were found to be counterintuitive ($R > 1.0$). Owing to the complexity of ecosystems, ecologists recognize this potential, and documenting its occurrence could motivate scientists to publish such results more than would be representative of natural systems.

The complexity of factors behind potential bias, as they involve the kinds of studies involved, is one thing. We failed to see evidence of any strong tendency other than an apparent tendency to study alien species. Are there other reasons to suspect that the data from Table A1.1 show values that are either too large or too small to be of help in guiding management? One factor involves simple population dynamics; the predation rates found to be sustainable (see

Appendix III) are rates that would not be expected to reduce a prey population to any large extent. Although the focus was on the effects of predators on demographic elements of population dynamics, the study reported by Holt et al. (2008) indicated that only a small fraction of bird populations responded to predation. More research is clearly needed, but we seem to be in a position of at least hypothesizing that the data behind Figure A1.4 indicate that predators have more of an effect on their prey populations than actually realized in most cases from natural systems. In the meantime, such patterns provide a first impression of how abnormal fisheries management is by comparison.

Future research to directly evaluate R as its primary focus must take advantage of lessons learned in the conduct of science as represented in the variety of studies listed in Tables A1.1 and A1.2. In particular, meta-analyses such as that by Salo et al. (2010) point toward the need for studies covering enough years to ensure that variance is adequately accounted for in both predator and prey population. Studies such as these also reveal other aspects of the complexity of predatory/prey relationships to help further refine management questions (e.g., to directly account for correlative variables such as those involving various aspects of the life history strategy of the prey). In particular, it is clear that data most useful for guiding management will involve studies that focus on natural predators (rather than alien species; Salo et al. 2007, 2010). There exists the potential for bias in comparing areas with and without predators in studies with an experimental design involving only such comparisons; the assumption that there is no effect of habitat is almost certainly false in many cases. Future studies must be designed to account for such factors. Our point here is that in addition to the matter of achieving consonance with the management questions, the science that produces consonant information must also be conducted to meet the standards of good science.

CITATIONS

Numbered references are references used in Tables A1.1 and A1.2 of this appendix, corresponding to the number listed in the second column of each table. References without numbers are not used in the tables (i.e., these references were used only in the text).

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APPENDIX II

Functional Responses of Predators to their Prey Populations

by

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ABSTRACT

The management of commercial fishing involves a variety of components. Often, policy is based on control rules which themselves involve several distinct elements of importance. Three obvious components of control rules are: 1) the degree to which a fish stock is reduced (owing to the effects of harvesting), 2) the rate at which the stock is fished at these reduced levels (compared to harvest applied to populations of resources free of harvesting), and 3) the rate at which fish can be harvested upon the initiation of a fishery. This appendix treats the second of these three.

Here, we make use of published information to extract data useful for characterizing the shape of curvilinear control rules by considering control rules to be functional responses of fishing to the size of fished stocks. We found 168 published graphic representations of functional responses of predators to the density of their prey. Of these, 136 provided information sufficient for us to make measurements that allow for the formulation of a model representing typical natural functional responses. Our results indicate that, on average, pattern-based control rules would require reducing harvests to less than 70% of the rates that many historic, as well as current, conventional applications of control rules allow when the resource population is at 40% of levels free of the effects of harvesting. These results are, therefore, to be applied as additional reduction in harvest rates beyond reductions necessary for sustainability in the rates applied for stock sizes observed without the impacts of fishing.

INTRODUCTION

The control rules implemented in commercial fishing are effectively managerial functional responses to the population levels (density or abundance) of harvested populations of the various species of resources. Through management, harvest rates are regulated so as to be responsive to such populations—especially when they are at small fractions of the levels they would exhibit if free of the impact of harvesting. In ecological systems, functional responses of nonhuman predators to the abundance of their prey have been the subject of a great deal of scientific research. In the spirit of systemic management[1], this appendix is an examination of a sample of the results from such research to help guide the formulation of control rules for fisheries management that are more realistic than those embodied in current policy. The results of such research represent a characterization of a natural pattern that serves as information regarding sustainability, or what works in natural systems. Management is then a matter of action based on such patterns.

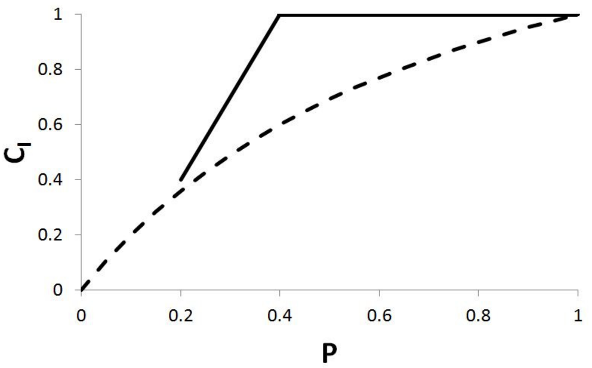

Figure A2.1. -- The control rules of conventional fisheries management, as depicted by the solid lines, compared to the more typical natural functional response curve as shown by the dashed line. C_I represents an index of the consumption rate and P represents an index of the relative abundance of a population of the species serving as a resource (e.g., prey species or species being harvested in commercial fisheries). This illustration is intended to show no more than a comparison of the relative shape of the two relationships; standardized harvest (consumption) rates result in a value of $C_I = 1.0$ at $P = 1.0$ (not a harvest of 100% of the resource population).

Figure A2.1 shows the comparison of current control rules to the generic nature of functional responses observed in natural predator/prey systems. The point that we wish to make clear is that there is a curve involved in natural systems compared to segments of straight lines in applied control rules. In this regard, control rules are abnormal—a problem we hope to help

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[1] Systemic management is a matter of achieving sustainability by mimicking natural systems so as to take advantage of holistic information on what works over all scales of time, space, and hierarchical organization (Fowler 2009) through management with the objective of avoiding abnormal influences, processes and interactions.

alleviate. The general shape, curvature, and position of the natural curvilinear relationship in natural functional responses is the primary focus of our work. The related patterns of variability with their inherent limits are central to our message.

Thus, this appendix addresses the curvilinearity (shape) of the curve shown in Figure A2.1. Having chosen a model to represent that curve (as explained below) it is possible to determine the parameters for the model with information concerning individual points on the curve. This presents the option of addressing a specific management question: *"Compared to rates advisable for initial harvests (i.e., harvests taken from resource populations at levels expected in absence of harvesting), how much should the fishing rate on a population of species X be reduced to achieve a sustainable harvest rate when the population of that resource is at 40% of unfished levels?* The matching (consonant) research question is: *In comparison to their consumption rates observed for prey population levels free of their predatory effects, to what extent do predators reduce the rate at which they consume from their resource populations when those populations are at 40% of unexploited levels?* In essence, we are addressing the management issue of how much harvest rates should be reduced as populations of resource species decline; these are determined by the shape of functional response curves. Data for one or more points on published functional response curves, standardized to be comparable among studies, are used here.

METHODS

We conducted this study based on information presented in functional response curves published in the scientific literature. Our search of this literature involved standard searching tools and efforts to find relevant references as provided by the authors. The published graphs were comparable to the illustration exemplified in Figure A2.2 and found in the numbered citations listed in this appendix. In each case, the information involved the rates at which predators were observed to consume their prey as those rates varied across a range of density or abundance as measured, or manipulated (controlled), for the prey.

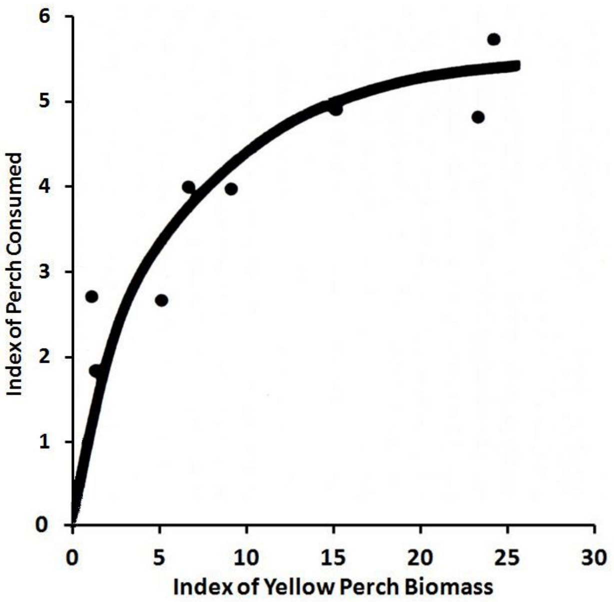

Figure A2.2. -- An example of the kind of information found and used in the study reported in this appendix. This illustration is based on a figure from page 65 of Bailey and Houde (1989) representing the functional response in the consumption of yellow perch (*Perca flavescens*) by walleye (*Stizostedian vitreum*, with data from Forney 1971). Points on the line representing the relationship were the basis for measurements made for this study as described in the main text.

We restricted our search of the literature to studies that involved predators which feed on species that fall into the trophic category of primary consumers or higher; none of the species serving as resources are plants. This begins a process of refinement[2] (a process of specifying management questions and relevant natural patterns) to account for the fact that the fisheries for which we seek management advice are harvesting fish.

To standardize our measurements, and make them comparable across studies, we converted the units measured in each study to indices. Such indices also lend themselves to practical application. The first index is that of prey abundance or density (see Appendix I for a treatment of questions related to indices of appropriate levels of resource abundance). This index

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[2] The process of refinement will be continued later in this appendix as it applies to making the specific management question being addressed even more specific (see Fowler and Hobbs 2011 for more detail; see Appendix I for other examples).

was defined as the ratio of various measures of abundance to that of the maximum measured (as displayed in the graphic presentation of the data). So, if the maximum was 475 prey items per cubic meter of water, a reported consumption rate corresponding to 350 prey items per cubic meter would be associated with an abundance index of 0.737 (= 350/475). The same held for consumption rates. In this case, if the consumption rate (per individual predator, or for a fixed number of individual predators) was found to be 75 per hour when the maximum reported was 200, the consumption index would have been calculated to be 0.375 (= 75/200).

Part of the reason for the standardization just described involves our attempt to describe the shape of functional response curves (in contrast to the "broken-line" shape of control rules with linear segments). As seen in Figure A2.1, the point at which such curves pass through the index of 1.0, 1.0 (consumption index = abundance index = 1.0) will be the same in all cases. As will be discussed below, this carries a risk of serious bias (for which we need to make adjustments). The important point here is that this standardization allows for using information for both variables in the interval between 0 and 1.0 to provide an initial indication of the shape (curvature) of functional response curves between these two endpoints. In both cases, this can be done so as to be independent of the units used in making the original measurements. Through standardization, it is possible to focus specifically on shape; shape is the primary focus of this appendix.

Again referring to Figure A2.1, we assumed that the relationship between consumption rates and the density of prey can be represented by the equation:

$$C_I = aP/(1+bP) \,, \tag{1}$$

where C_I represents the index of the rate at which prey are consumed and P is the index of population abundance. Under circumstances of the standardized index (i.e., when $C_I = 1.0$, $P = 1.0$, and $C_I = 0$ when $P = 0$) $a = 1+b$, and $b = a - 1$. For observed values of C_I and P between 0 and 1.0 it is possible to then solve for a and b to establish the shape of the functional response curve (continuing to recognize and acknowledge the bias inherent to our standardization). That is, $a = (1-(1/P))/(1-(1/C_I))$, and $b = a - 1$. Therefore, for a C_I of 0.6 at $P = 0.4$, $a = 2.25$, and $b = 1.25$.

Our choice of the above equation (1) is based on its frequent use in representing functional response curves starting with the origins of research on such patterns (often referred to as the Holling disk equation owing to work by Holling, 1959b).

Because fisheries often are managed with a reference point of P = 0.4 (the break between the straight-line segments in Fig. A2.1; see Appendix I with regard to the frequent use of 0.4 in fisheries management), we chose to use this index as a reference point for one method of measuring the corresponding C_I. In this method, the point for P = 0.4 was located and the corresponding C_I was measured. For comparison, and to cross-check our work, we employed another reference point. In this case we found the P corresponding to $C_I = 0.5$. In this case, where C_I was half its maximum, we located the corresponding P. In both cases, we obtained information to allow us to determine the values for a and b in the above equation. Both measures were accomplished by using computer software specifically designed to map points digitally located in two dimensional space (Diger3, Golden Software). Thus, with a graph such as that shown in Figure A2.2, scaling could be determined by measurements of labeled points on both axes. Using this scaling, we then measured the maxima for both C_I and P (points chosen along lines representing the data). These measures served as the denominator in ratios wherein measures of the coordinates of any point on the curve could be expressed as the indices defined above.

This process was repeated for all of the graphs that we found in our search of the published literature (as available through 2002, when this research was conducted; our search was not intended to be exhaustive nor are we claiming it to be so). When the estimates for the index of consumption rates from the two methods differed from each other by more than 0.075 we rejected our measurements.

RESULTS

Table A2.1 contains a listing the results of our work expressed in terms of the species (both predator and prey) involved and the accepted measures of C_I at P = 0.4 in the functional response curve representing their predator/prey relationship. We found graphic representations of such relationships for 136 cases as they involve 46 species of predators (including both vertebrates and invertebrates). There were 40 species of prey, mostly invertebrates, including several cases where multiple prey species were involved (see cases found in references15 and 22).

The last column of Table A2.1 contains 12 cases (marked with asterisks) for which the index of consumption rates for cases where the maximum density of prey were considered to be close to natural prey densities (rather than artificially high as part of the experimental design of many of the studies involved in the publications we found). In the following, we use both the full set of data and the subset of 12. To distinguish the two, the symbol C_{I1} will refer to the 136 cases of the full sample, and C_{I2} will refer to the 12 cases described above (and marked with asterisks in Table A2.1).

Table A2.1. -- List of predator/prey pairs represented in the literature by graphic representations of the functional responses of the predators (changes in the rate at which they consume their prey as a function of prey density). The C_I are indices of consumption rates expressed as the ratio of observed consumption rates when the prey population is at 40% of its maximum to that observed at its maximum. Asterisks mark those C_I for which the ratio is that of observed consumption rates at 40% of natural (or normal) prey population levels to that observed for the prey population under natural or normal (or natural) population levels (i.e., the maximum was considered to approximate normal population levels). Numbers in the source column correspond to those in the literature cited section.

Source	Predator	Prey	C_I
1	*Paralabrax clathratus*	*Brachyistius frenatus*	0.748*
1	*Paralabrax clathratus*	*Brachyistius frenatus*	0.829*
1	*Paralabrax clathratus*	*Brachyistius frenatus*	0.418*
1	*Paralabrax clathratus*	*Brachyistius frenatus*	0.514*
2	*Stizostedian vitreum*	*Perca flavescens*	0.469
2	*Stizostedian vitreum*	*Perca flavescens*	0.816
2	*Crangon crangon*	*Pleuronectes platessa*	0.747
3	*Aphelinus thomsoni*	*Drepanosiphum platanoidis*	0.888
4	*Enallagma aspersum*	*Diaptomus spatulocrenatus*	0.738
4	*Enallagma aspersum*	*Simocephalus serrulatus*	0.800
5	*Callinectyes sapidus*	*Crassostrea virginica*	0.795

Source	Predator	Prey	C_I
5	*Callinectyes sapidus*	*Crassostrea virginica*	0.417
5	*Callinectyes sapidus*	*Crassostrea virginica*	0.401
6	*Callinectyes sapidus*	*Crassostrea virginica*	0.396*
6	*Callinectyes sapidus*	*Crassostrea virginica*	0.414*
6	*Callinectyes sapidus*	*Crassostrea virginica*	0.414*
6	*Callinectyes sapidus*	*Crassostrea virginica*	0.427*
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.651
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.716
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.810
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.761
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.838
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.856
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.866
7	*Pleolophus basizonus*	*Neodiprion sertifer*	0.838
8	*Nasonia vitripennis*	*Musca domestica*	0.742
8	*Dahlbominus fuscipennis*	*Neodiprion sertifer*	0.707
8	*Ischnura elegans*	*Daphnia magna*	0.825
8	*Harmonia axyridis*	*Aphis craccivora*	0.877
8	*Aphidius uzbeckistanicus*	*Hylopteroides humilis*	0.541
8	*Plea atomaria*	*Aedes aegypti*	0.817
8	*Aphidius uzbeckistanicus*	*Metapolophium dirhodum*	0.711
8	*Coccinella septempunctata*	*Brevicoryne brassicae*	0.707
8	*Notonecta glauca*	*Asellus aquaticus*	0.732
8	*Notonecta glauca*	*Asellus aquaticus*	0.686
9	*Aphidius uzbeckistanicus*	*Metapolophium dirhodum*	0.657
9	*Coccinella septempunctata*	*Brevicoryne brassicae*	0.830
10	*Salmo trutta*	*Coregonus albula*	0.773
10	*Salmo trutta*	*Coregonus albula*	0.700*
11	*Didinium nasutum*	*Paramecium multimicronucleatum*	0.757
11	*Didinium nasutum*	*Paramecium jenningsi*	0.820
11	*Didinium nasutum*	*Paramecium aurelia*	0.792
12	*Sorex cinereus*	*Neodiprion sertifer*	0.335
13	*Dahlbominus fuliginosus*	*Neodiprion sertifer*	0.771

Source	Predator	Prey	C_I
13	*Dahlbominus fuliginosus*	*Neodiprion sertifer*	0.850
13	*Dahlbominus fuliginosus*	*Neodiprion sertifer*	0.845
13	*Dahlbominus fuliginosus*	*Neodiprion sertifer*	0.683
13	*Dahlbominus fuliginosus*	*Neodiprion sertifer*	0.740
13	*Dahlbominus fuliginosus*	*Neodiprion sertifer*	0.671
14	*Achirus lineatus*	copepod nauplii	0.756
14	*Achirus lineatus*	copepod nauplii	0.816
14	*Anchoa mitchilli*	copepod nauplii	0.708
14	*Achirus lineatus*	copepod nauplii	0.734
14	*Anchoa mitchilli*	copepod nauplii	0.696
14	*Achirus lineatus*	copepod nauplii	0.703
15	*Ischnura ramburii*	*Daphnea magna*	0.881
15	*Anomalagrion hastatum*	*Daphnia magna*	0.764
15	*Anomalagrion hastatum*	*Daphnia magna*	0.780
16	*Apochthonius minimus*	*Folsomia candida*	0.743
16	*Apochthonius minimus*	*Folsomia candida*	0.810
16	*Apochthonius minimus*	*Folsomia candida*	0.673
16	*Apochthonius minimus*	*Folsomia candida*	0.834
17	*Phytoseiulus persimilis*	*Tetranychus urticae*	0.593
17	*Phytoseiulus persimilis*	*Tetranychus urticae*	0.639
17	*Phytoseiulus persimilis*	*Tetranychus urticae*	0.673
18	*Urosalpinx cinerea*	*Balanus balanoides*	0.706
18	*Urosalpinx cinerea*	*Balanus balanoides*	0.745
18	*Urosalpinx cinerea*	*Balanus balanoides*	0.748
18	*Urosalpinx cinerea*	*Balanus balanoides*	0.701
19	*Xylocoris flavipes*	*Sitotroga cerealella*	0.558
19	*Xylocoris flavipes*	*Sitotroga cerealella*	0.514
19	*Xylocoris flavipes*	*Sitotroga cerealella*	0.498
19	*Xylocoris flavipes*	*Sitotroga cerealella*	0.308
19	*Xylocoris flavipes*	*Sitotroga cerealella*	0.429
19	*Xylocoris flavipes*	*Sitotroga cerealella*	0.417
20	*Callinectes sapidus*	*Mya arenaria*	0.789
21	*Mysis mixta*	*Natural zooplankton*	0.577

Source	Predator	Prey	C_I
22	*Callinectes sapidus*	*Callinectes sapidus*	0.650*
22	*Callinectes sapidus*	*Callinectes sapidus*	0.491*
23	*Podisus maculiventris*	*Hyphantria cunea*	0.965
23	*Podisus maculiventris*	*Hyphantria cunea*	0.940
24	*Thais canaliculata*	*Mytilus edulis*	0.734
25	*Acanthina spirata*	*Mytilus edulis*	0.865
25	*Ptychocheilus oregonensis*	*Oncorhynchus* sp.	0.594
26	*Metridia lucens*	*Calanus finmarchicus*	0.641
26	*Centropages typicus*	*Calanus finmarchicus*	0.592
27	*Notolabrus tetricus*	*Haliotis* sp.	0.480*
28	*Cottus bairdi*	*Baetis tricaudatus*	0.852
28	*Agnetina capitata*	*Baetis tricaudatus*	0.503
28	*Cottus bairdi*	*Ephemerella subvaria*	0.318
28	*Agnetina capitata*	*Ephemerella subvaria*	0.445
29	*Chaoborus americanus*	*Daphnia pulex*	0.763
29	*Chaoborus americanus*	*Daphnia pulex*	0.910
29	*Chaoborus americanus*	*Daphnia pulex*	0.850
29	*Chaoborus americanus*	*Daphnia pulex*	0.833
29	*Chaoborus americanus*	*Daphnia pulex*	0.515
29	*Chaoborus americanus*	*Daphnia pulex*	0.742
29	*Chaoborus americanus*	*Daphnia pulex*	0.764
30	*Ischnura elegans*	*Daphnia magna*	0.907
30	*Ischnura elegans*	*Daphnia magna*	0.850
30	*Ischnura elegans*	*Daphnia magna*	0.835
30	*Ischnura elegans*	*Daphnia magna*	0.756
30	*Ischnura elegans*	*Daphnia magna*	0.732
30	*Ischnura elegans*	*Daphnia magna*	0.868
30	*Ischnura elegans*	*Daphnia magna*	0.781
30	*Ischnura elegans*	*Daphnia magna*	0.794
30	*Ischnura elegans*	*Daphnia magna*	0.814
30	*Ischnura elegans*	*Daphnia magna*	0.751
30	*Ischnura elegans*	*Daphnia magna*	0.753
30	*Ischnura elegans*	*Daphnia magna*	0.841

Source	Predator	Prey	C_I
30	*Ischnura elegans*	*Daphnia magna*	0.855
30	*Ischnura elegans*	*Daphnia magna*	0.895
30	*Ischnura elegans*	*Daphnia magna*	0.797
30	*Ischnura elegans*	*Daphnia magna*	0.676
30	*Ischnura elegans*	*Daphnia magna*	0.837
30	*Ischnura elegans*	*Daphnia magna*	0.820
30	*Ischnura elegans*	*Daphnia magna*	0.852
30	*Ischnura elegans*	*Daphnia magna*	0.914
30	*Ischnura elegans*	*Daphnia magna*	0.898
30	*Ischnura elegans*	*Daphnia magna*	0.903
31	*Podisus modestus*	*Neodiprion* sp.	0.927
31	*Podisus modestus*	*Neodiprion* sp.	0.934
31	*Podisus modestus*	*Neodiprion* sp.	0.931
31	*Podisus modestus*	*Neodiprion* sp.	0.828
31	*Podisus modestus*	*Neodiprion* sp.	0.959
31	*Podisus modestus*	*Neodiprion* sp.	0.900
31	*Podisus modestus*	*Neodiprion* sp.	0.925
31	*Podisus modestus*	*Neodiprion* sp.	0.963
31	*Podisus modestus*	*Neodiprion* sp.	0.988
31	*Podisus modestus*	*Neodiprion* sp.	0.854
31	*Podisus modestus*	*Neodiprion* sp.	0.917
32	*Chaoborus americanus*	*Daphnia pulex*	0.561
32	*Chaoborus americanus*	*Daphnia pulex*	0.342
32	*Chaoborus americanus*	*Daphnia rosea*	0.739
32	*Chaoborus americanus*	*Daphnia rosea*	0.579
33	*Paralichthys lethostigma*	*Leiostomus zanthurus*	0.675

Figure A2.3 shows the pattern in reduced consumption rates listed in Table A2.1 for all cases (C_{II}; N = 136); Figure A2.4 shows the pattern in cases for which there was information to specify this ratio relative to densities of prey observed in natural systems (C_{I2}; N = 12). The mean for observed C_{I1} was 0.727 and that for C_{I2} was 0.556.

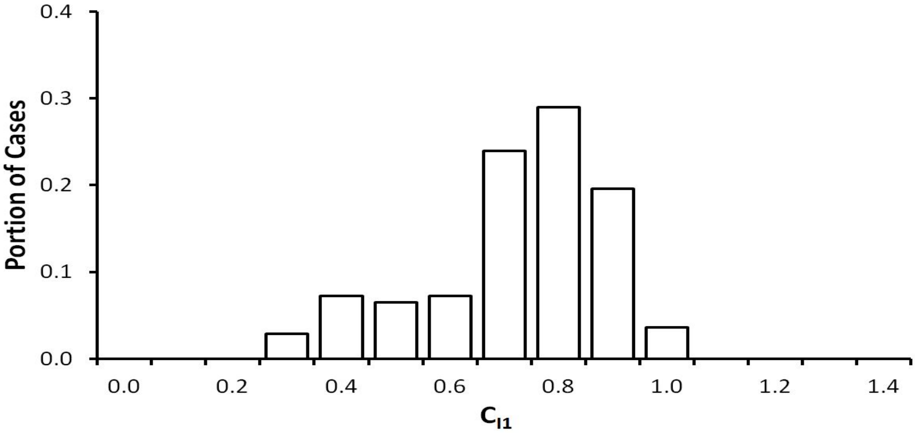

Figure A2.3. -- The frequency distribution of measured C_{I1} (the ratio of consumption rates from functional response curves at points where the prey density was at 40% of its maximum to those observed at the maximum) for 136 cases of published functional response curves.

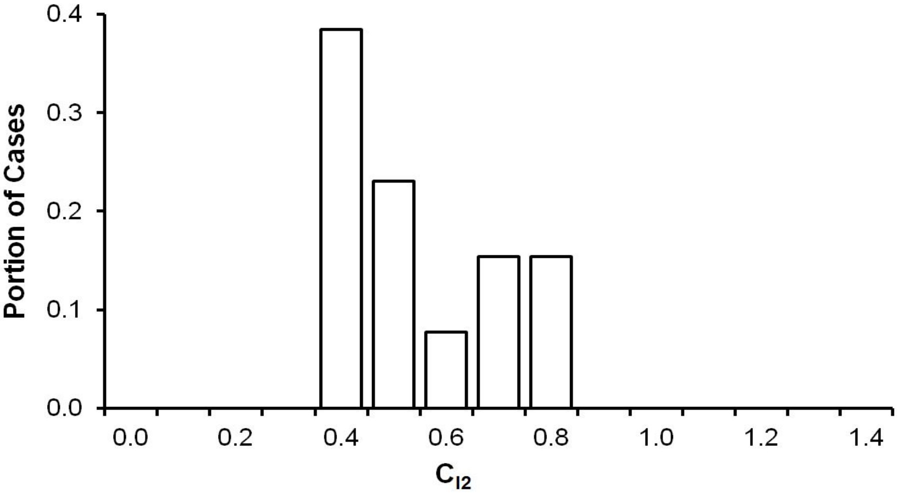

Figure A2.4. -- The frequency distribution of measured C_{I2} (the ratio of consumption rates from functional response curves at points where the prey density was at 40% of its maximum to those observed at population levels approximating those expected when free of the effects of predation) for 12 cases of published functional response curves.

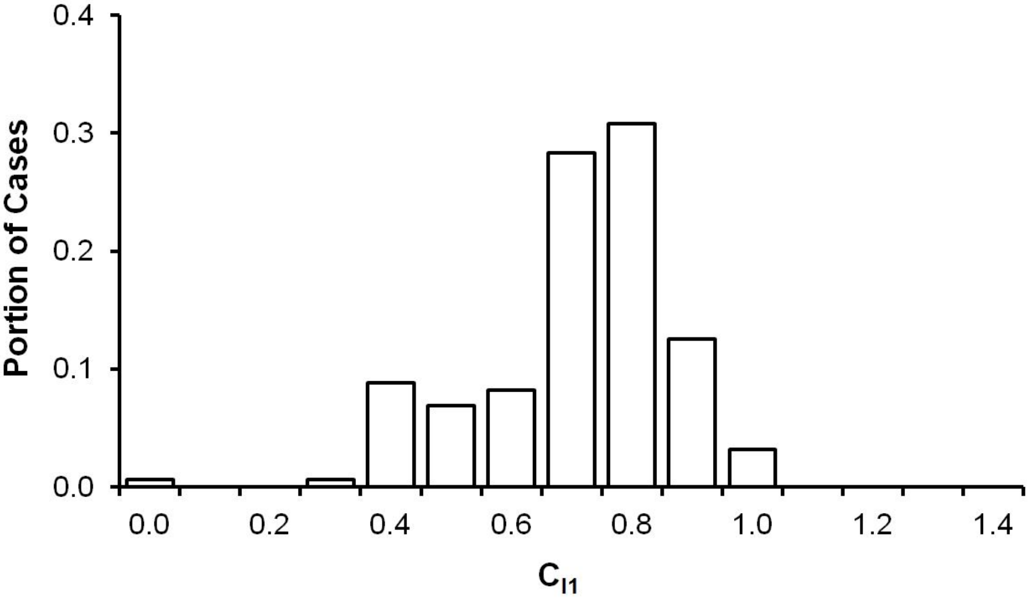

Figure A2.5. -- The frequency distribution of estimated C_{I1} (as for Fig. A2.3, here estimated from measures of P at $C_I = 0.5$ and converted to C_I at $P = 0.4$, using the equation $C_I = aP/(1+bP)$) for 136 cases of published functional response curves.

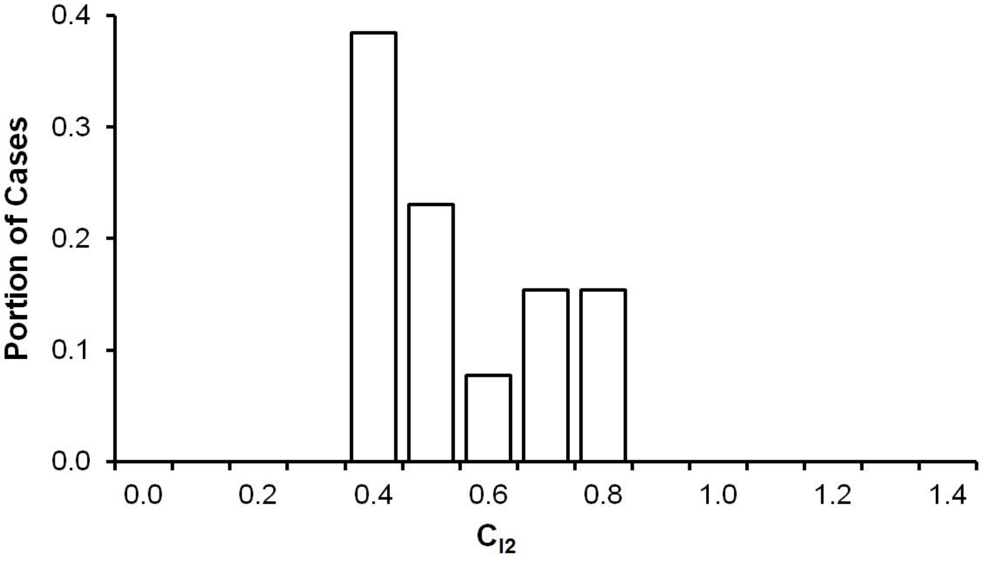

Figure A2.6. -- The frequency distribution of estimated C_{I2} (as for Fig. A2.4, here estimated from measures of P at $C_I = 0.5$ and converted to C_I at $P = 0.4$, using the equation $C_I = aP/(1+bP)$) for 12 cases of published functional response curves.

Figure A2.5 shows the results for the set of data comparable to that of Table A2.1—here representing our estimates of C_I at P = 0.4 for cases in which P was measured where $C_I = 0.5$. In this case, the mean for C_{I1} as estimated for P = 0.4 was 0.727 and that for C_{I2} (Fig. A2.6) was 0.551—quite comparable to the values determined more directly.

Parallel to the case of sustainable prey populations, measures of the central tendencies of empirical information in reductions in harvest rates can be represented by geometric means. Such metrics are less than the corresponding arithmetic means. For example the geometric mean of harvest rates at P = 0.4 for vertebrate predators with natural prey population densities was 0.522 while the geometric mean for vertebrate predators feeding on vertebrate prey was 0.622. In no case were measures of central tendency of these patterns as small as 0.40 which would result in a straight line for the Holling disk equation. This is in spite of the fact that some functional response curves in the literature were represented by straight diagonal lines (e.g., Eggleston, 1990b).

DISCUSSION

In the material presented above (as well as in the other appendices and main text), we have chosen to refrain from presenting statistical information about the variance within the data we are presenting or for the means we have calculated. This was done for two reasons. First, we are presenting a method much more than we are presenting definitive results. Further research is needed with much larger sample sizes and more direct attention to the kinds of questions we are addressing in this preliminary work. This does not mean that we believe that our overall results are not reliable, but it does mean that precision is needed with more intensive and deliberate research taking the kind of approach we have exemplified. Second, within variability there is potential for refined questions which lead to research that explores other significant contributing factors. As will be stressed again below, direct consideration of data representing mammalian predators on fish would bring greater consonance to the task (owing to our being mammals and the harvests central to fisheries management are from fish). Life history characteristics of the fish involved, environmental circumstances, specific taxa, and trophic levels are important to take into account in specific applications. Such factors undoubtedly contribute to the variability in data such as those we have revealed and we wanted to refrain from presenting statistical parameters insofar as they might detract from our emphasis on the need for research to expose explanations for that variability—especially in regard to refining management questions (see Fowler and Hobbs 2011 regarding the details of refinement and Appendices I and III for more examples).

As with the examples provided in the other two appendices for this paper, consonance is primary in the objective of obtaining information that is informative as guidance for management. In the material presented above, the information most consonant with the question we face is that involving measures of systems in which the standard of reference for population levels of prey species is that observed for systems as free of abnormal impact as possible. Therefore, the information from the sample of 12 cases at least approximating normal population levels of the prey species without the effects of predators is preferable to that from highly manipulated experimental research. As such, 0.556 is the value used as it would correspond to P = 0.4 in the combining of information in the main body of this paper. Note that this is quite different from the value of 1.0 represented by conventional control rules used to set policy historically.

We reiterate the importance of extending research of the type we have exemplified here to accomplish a number of objectives. First, a more comprehensive survey of the literature will result in a larger and more current sample. Second, research needs to be done concentrating on studies of consumption rates involving prey populations for which there is information regarding their normal or natural density (as well as consumption rates observed at smaller prey populations to establish the shape of related curves). As indicated in the comparison of Figure A2.3 with Figure A2.4, failure to account for this factor can involve a serious bias. The points that appear as outliers at the far right of Figure A2.4 are probably unreliable on these grounds. We were only partially successful in our attempt to account for this matter and note that it was not an issue of obvious importance in Figure A2.5 (where maximums among the consumption rates would not have been as easily manipulated experimentally as would the density of prey). Third, further refinement of the management and subsequent research questions is needed.

This third point deserves further elaboration. Many of the functional response curves from our study involved invertebrates either as predator or as prey—some both. Taxonomic categories may be important as factors to take into account, although for the 11 cases of vertebrates feeding on vertebrates the mean C_I from our sample was 0.663—not that different from the value for the larger study. In the management question we are addressing, we humans (serving as the predator species) are mammals and the prey we wish to harvest are fish. To adequately refine the management question, followed by a matching research question, the research conducted would involve functional response curves representing mammalian predators feeding on fish. This is the only way to explicitly account for these factors as part of the complexity to be taken into account. Because of the potential that such factors are of significant influence in the patterns of functional responses, it is important that future research involve predator/prey pairs wherein the predators are mammals and the prey are fish. This process is basically without limits. Further refinement of the management question to find even more specific patterns would involve still other factors such as trophic level, body size (see Hewett 1980), numbers of other predators, and numbers of other prey; the potential for further research is immense.

In spite of the preliminary nature of the information we are providing in this appendix, it serves to help clarify the nature of more holistic functional response curves for use in the management of commercial fishing—curves that are more realistic than those representing control rules as implemented in much of today's fisheries management. Thus, we have accomplished two objectives: exemplifying the process by which information for guidance can be gleaned from the literature and future research, and providing a first approximation of points within functional response curves to establish a general idea of the magnitude of abnormality involved in, and resulting from, current forms of management.

SUMMARY

A total sample of 136 published functional response curves makes it quite clear that the commercial harvesting of fish should be managed on the basis of curvilinear control rules rather than the more simplistic process involving linear segments in common use today. Of the full sample, 12 cases of the most directly applicable published functional response curves provide evidence that when a population of harvested fish is at 40% of levels free of the effects of harvesting, the harvest rate should be about 55.6% of maximum rates. The conclusion regarding curvilinearity is a very important, clear, and firm conclusion. The precise nature of the curvilinearity, however, is open to further refinement. It is extremely important that further research be conducted to reveal the functional response of mammals to the abundance of stocks of marine fish in order to provide more precise information for application. Nevertheless, in spite of the preliminary nature of our findings, we expect that the eventual findings of future research will not differ greatly from the information that we have presented here.

CITATIONS

Numbered references are references used in Table A2.1 of this appendix, corresponding to the number listed in the first column. References without numbers are not used in the tables (i.e., these references were used only in the main text of this appendix).

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APPENDIX III

Management to Maximize Biodiversity in Harvesting from Individual Species

by

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ABSTRACT

This appendix treats the third component of control rules listed in the main text: sustainable harvest rates. The rates being treated here are not indices but actual rates which are then treated as indices in the main text in parallel with information from the other two appendices. Those appendices dealt with 1) the sustainable reduction of resource populations (Appendix I), and 2) advisable reduction in harvest rates with declining resource populations (Appendix II).

At what rate can we sustainably harvest fish of species X, accounting for the total mortality rate of that species and our body size as a predator? Expressed this way, the management question being addressed in this appendix involves explicit consideration of factors such as total natural mortality rate and body size. With an answer that also involves direct consideration of biodiversity, it is possible to use other information about predator/prey relationships (as treated in Appendices I and II) to estimate the rate at which species X can be harvested sustainably for any population level of the resource species (including upon the initiation of a fishery—when a fishery is harvesting from a population that is at levels comparable to those free of the effects of commercial harvesting).

Based on maximizing biodiversity within a macroecological pattern consonant with the management question, we found that sustainable fishing rates for a predator of our body size are less than 10% of the total natural mortality rate for populations of harvested species. Slightly higher fishing rates would apply to fish populations at levels corresponding to those free of the impact of fishing. Estimates of such fishing rates depend on the shape of functional response curves as dependent on information such as that presented in Appendix II. Similarly, lower fishing rates would apply to resource populations reduced below sustainable levels (as treated in Appendix I) with reductions again depending on the shape of functional response curves from Appendix II.

INTRODUCTION

Diversity, resource extraction from individual species, and information[1] are all essential elements of management—several among many. Biodiversity is heavily emphasized in the literature regarding the management of human influence on nonhuman biotic systems. Our impacts on other species are part of the complexity of such systems, especially the direct impact of our consumption from species that serve as resources. This appendix presents holistic information (Fowler et al. 2013) concerning the biodiversity among consumption rates of predators that consume from populations of eight different species of prey. Each of these species also is consumed (harvested) by humans. Thus, the information treated includes estimates of consumption from these prey species by both other mammalian predators and humans. This makes it possible to compare the rates at which we humans consume a particular resource with the rates at which that resource is consumed by other predatory species. The combination of this information, across all eight prey species, is used to illustrate a macroecological pattern in consumption rates as a function of the total natural mortality rate for the prey species (M). This pattern can be used to both evaluate existing harvest rates by humans, and to provide guidance for harvests from species for which there are estimates of M.

Patterns in predation rates for individual prey species

The first set of data to be considered are the estimated predation rates for predators preying on a population of white-tailed deer (*Odocoileus virginianus*) in western Montana (U.S.), as presented by Kunkel and Pletscher (1999). The top panel of Figure A3.1 is an illustration of the pattern in consumption rates estimated for five species of predators (including humans) in their take of deer from this population. This pattern is presented as a frequency distribution to illustrate the limits observed in the variability among these rates (shown numerically for

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[1] Using information effectively is a primary tenet of management (see Fowler 2008, 2009). As emphasized in numerous publications, such as that by Christensen et al. (1996), management must be based on information. See Appendix 3 of Fowler et al. (2013) for a treatment of the nature of holistic information (information that accounts for everything).

individual predators in Table A3.1 along with the identity of each of the corresponding predators).

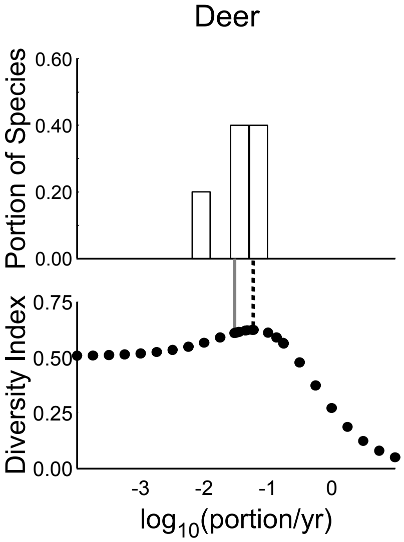

Figure A3.1. -- The pattern in predation rates by mammalian predators on deer (*Odocoileus virginianus*) in western Montana (from Kunkel and Pletscher 1999) showing the information and diversity (based on the Shannon-Weiner information index) resulting from variable harvest levels by humans. The solid gray vertical line represents F_{ob} (the observed harvest rate by humans) and the dashed vertical line represents F_{mb} (the harvest rate by humans which would maximize the diversity for this predatory/prey system).

The bottom panel of Figure A3.1 shows a curve representing a measure of the information and diversity in the predation rates of the predator/prey system involving this deer population and the five species of predators represented in the top panel. These five species include humans and the four other species listed as predators for deer in Table A3.1. The biodiversity represented by the curve in the bottom panel is that corresponding to a variable harvest rate for humans. Thus, the point at the lower end of the solid gray line is the measured diversity of the system in which humans harvested about 3.0% of the deer population each year as observed by Kunkel and Pletscher (1999). The other points represent a sampling of alternative harvest rates for humans to explore resulting variation in the diversity and information inherent to this system as a function of the harvest rate by humans; the diversity of the system can be

Table A3.1. -- A list of the predatory species, and their estimated consumption rates, in their predation on eight species of prey (from Overholtz et al. 1991; Fowler 1999a 1999b; Fowler and Perez 1999; and Kunkle and Pletscher 1999).

Prey	Predator species	Scientific name	Consumption rate (%/yr)
Deer		*Odocoileus virginianus*	
	Cougar	*Puma concolor*	9.000
	Wolf	*Canis lupus*	6.000
	Grizzly bear	*Ursus arctos*	3.000
	Coyote	*Canis latrans*	1.000
Elk		*Cervus elaphus*	
	Cougar	*Puma concolor*	6.000
	Wolf	*Canis lupus*	4.000
	Black bear	*Ursus americanus*	1.000
	Grizzly bear	*Ursus arctos*	2.000
Moose		*Alces alces*	
	Wolf	*Canis lupus*	3.000
	Black bear	*Ursus americanus*	1.000
	Grizzly bear	*Ursus arctos*	3.000
Pollock		*Gadus chalcogrammus*	
	Northern fur seal	*Callorhinus ursinus*	1.460
	Steller sea lion	*Eumetopias jubatus*	0.594
	Harbor seal	*Phoca vitulina*	0.187
	Spotted seal	*Phoca largha*	0.117
	Ringed seal	*Pusa hispida*	0.299
	Bearded seal	*Erignathus barbatus*	0.036
Silver hake		*Clupea harengus*	
	Bottlenose dolphin	*Tursiops truncatus*	0.380
	Grampus	*Grampus griseus*	0.666
	Harbor seal	*Phoca vitulina*	0.898
	Harbor porpoise	*Phocoena phocoena*	1.908
	Common dolphin	*Delphinus delphis*	3.596
	Whitesided dolphin	*Lagenorhynchus acutus*	3.968
	Pilot whale*	*Globicephala melas*	6.260

Prey	Predator species	Scientific name	Consumption rate (%/yr)
Herring		*Merluccius bilinearis*	
	Minke whale*	*Balaenoptera acutorostrata*	0.024
	Harbor porpoise	*Phocoena phocoena*	0.046
	Harbor seal	*Phoca vitulina*	0.096
	Whitesided dolphin	*Lagenorhynchus acutus*	0.099
	Humpback whale*	*Megaptera novaeangliae*	0.187
	Pilot whale*	*Globicephala melas*	0.188
	Fin whale*	*Balaenoptera physalus*	0.664
Sandeel		*Ammodytes marinus*	
	Whitesided dolphin	*Lagenorhynchus acutus*	0.428
	Harbor porpoise	*Phocoena phocoena*	0.470
	Minke whale*	*Balaenoptera acutorostrata*	0.607
	Common dolphin	*Delphinus delphis*	0.633
	Pilot whale*	*Globicephala melas*	2.834
	Harbor seal	*Phoca vitulina*	2.952
	Humpback whale*	*Megaptera novaeangliae*	9.907
	Fin whale*	*Balaenoptera physalus*	37.932
Mackerel		*Scomber scombrus*	
	Bottlenose dolphin	*Tursiops truncatus*	0.022
	Common dolphin	*Delphinus delphis*	0.590
	Fin whale*	*Balaenoptera physalus*	0.666
	Grampus	*Grampus griseus*	0.021
	Harbor porpoise	*Phocoena phocoena*	0.007
	Harbor seal	*Phoca vitulina*	0.030
	Humpback whale*	*Megaptera novaeangliae*	0.162
	Minke whale*	*Balaenoptera acutorostrata*	0.007
	Pilot whale*	*Globicephala melas*	0.894
	Whitesided dolphin	*Lagenorhynchus acutus*	0.037

*Species removed from consideration to explicitly account for human body size as explained in the text.

directly influenced by managing the harvest rate by humans (Fowler 2008). This allows for calculating (iteratively) the harvest rate by humans that would maximize the biodiversity of this predatory prey complex. This maximum is represented by the dashed vertical line. For the set of data for the nonhuman predators listed in Table A3.1, the harvest rate to achieve maximum diversity is estimated to be about 5.9% of the deer population per year (about twice as much as actually taken in the sport harvest reported by Kunkel and Pletscher 1999).

Figure A3.2 represents the predatory/prey system in which the prey species is elk (*Cervus elaphus*, with the predators and their predation rates identified in Table A3.1); otherwise this figure is identical to Figure A3.1. In this case, the biodiversity and information content of the system would be maximized with a harvest by humans of about 3.90%/yr (and the harvest rate observed by Kunkel and Pletscher (1999) was about 4.0% per year—nearly the same as that for maximized biodiversity).

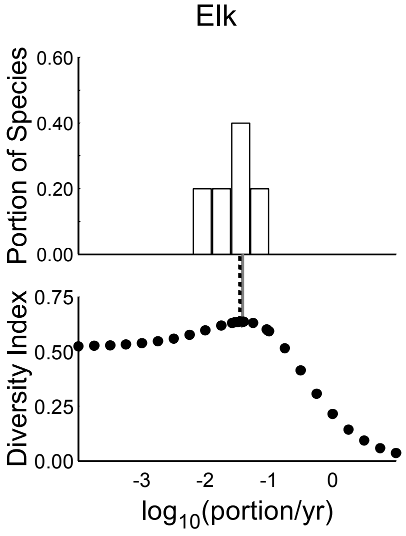

Figure A3.2. -- The pattern in predation rates by mammalian predators in their kill of elk (*Cervus elaphus*) in western Montana (from Kunkel and Pletscher 1999) showing the same kinds of information as depicted in Figure A3.1.

Figure A3.3 is again similar to Figures A3.1 and A3.2, but, in this case, represents the predatory/prey system in which the prey species is moose (*Alces alces*, with the predators and their predation rates identified in Table A3.1). For this prey species, the biodiversity and information content of the system would be maximized with a harvest by humans of about 2.56% (the harvest rate observed by Kunkel and Pletscher (1999) was about 2.0% per year).

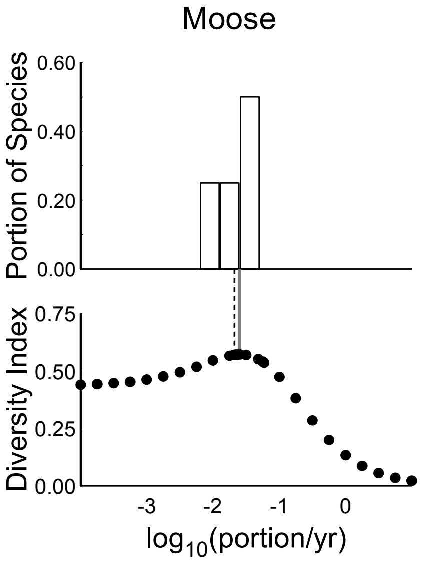

Figure A3.3. -- The pattern in predation rates by mammalian predators in their kill of moose (*Alces alces*) in western Montana (from Kunkel and Pletscher 1999) showing the same kinds of information as depicted in Figures A3.1 and A3.2.

In Figure A3.4, there is a shift to marine systems. In this figure the prey species is walleye pollock (*Gadus chalcogrammus*, with predators and their predation rates identified in Table A3.1). For pollock, the biodiversity and information within the system would have been maximized with a harvest by humans (or a fishing rate, F_{mb}) of about 0.74% of the standing stock per year (the observed harvest rate was about 12.5% per year; Livingston 1993; Fowler and Perez 1999).

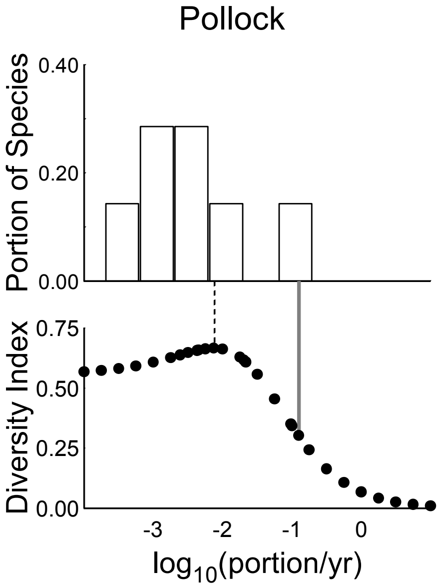

Figure A3.4. -- The pattern in predation rates by mammalian predators in their consumption of pollock (*Gadus chalcogrammus*) from the eastern Bering Sea (from Livingston 1993, Fowler and Perez 1999) showing the same kinds of information as depicted in Figures A3.1 - A3.3.

Figures A3.5 - A3.8 are based on data from Overholtz et al. (1991; see also Fowler 1999b). These graphs also represent marine systems wherein the prey species are herring (*Clupea harengus*), hake (*Merluccius bilinearis*), sandeel (*Ammodytes marinus*), and mackerel (*Scomber scombrus*). As with the previous graphs, the predators and their predation rates are identified in Table A3.1. The values of F_{mb} (fishing rates that maximize biodiversity and information inherent to the system as represented by vertical dashed lines) are 0.30%, 3.48%, 17.78% and 0.55% per year respectively (compared to harvest rates by humans of about 5.7%, 30.8%, 0.05%, and 19.0% per year as represented by the vertical gray lines).

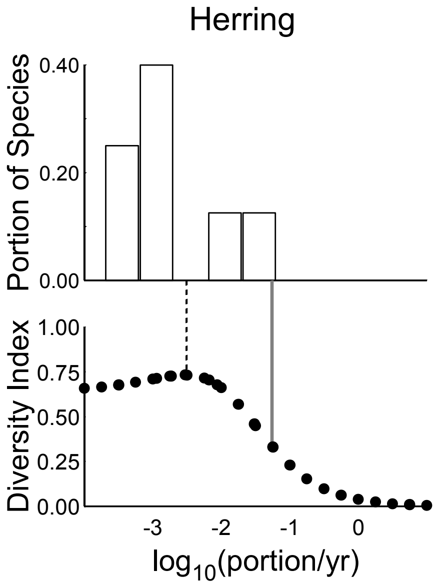

Figure A3.5. -- The pattern in predation rates by mammalian predators in their consumption of herring (*C. harengus*), from the northwest Atlantic (from Overholtz et al. 1991 and Fowler 1999b) showing the same kinds of information as depicted in Figures A3.1 - A3.4.

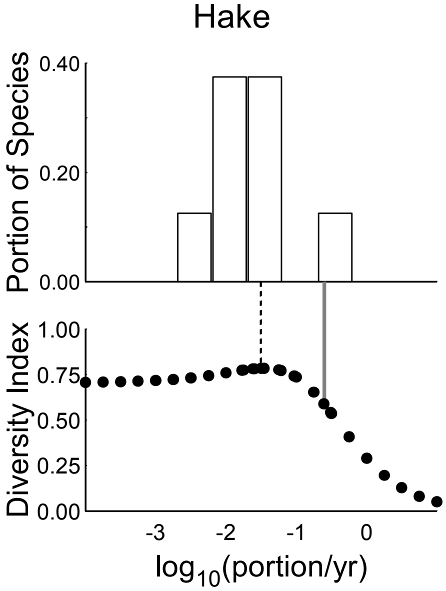

Figure A3.6. -- The pattern in predation rates by mammalian predators in their consumption of hake (*Merluccius bilinearis*), from the northwest Atlantic (from Overholtz et al. 1991 and Fowler 1999b) showing the same kinds of information as depicted in Figures A3.1 - A3.5.

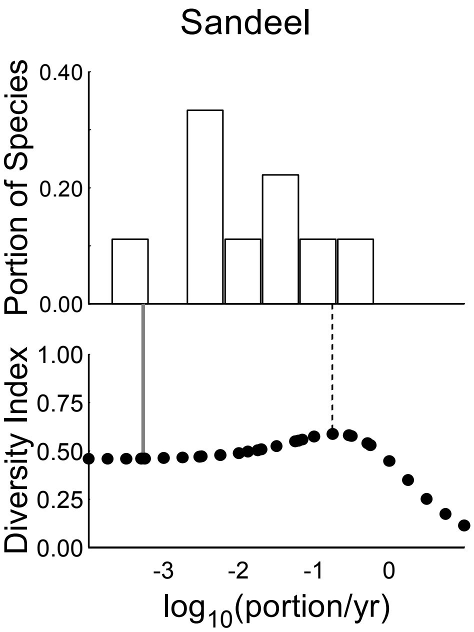

Figure A3.7. -- The pattern in predation rates by mammalian predators in their consumption of sandeel (*Ammodytes marinus*), from the northwest Atlantic (from Overholtz et al. 1991 and Fowler 1999b) showing the same kinds of information as depicted in Figures A3.1 - A3.6.

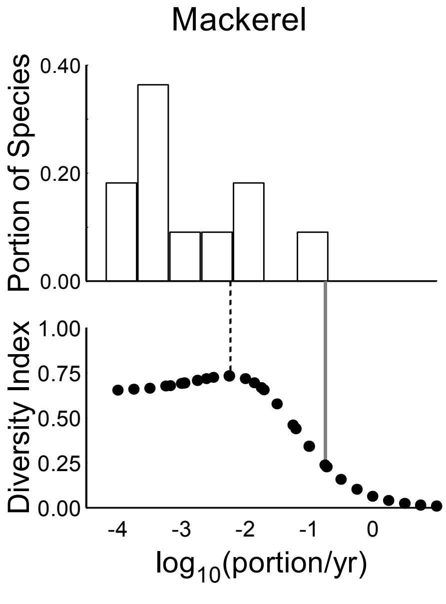

Figure A3.8. -- The pattern in predation rates by mammalian predators in their consumption of mackerel (*Scomber scombrus*), from the northwest Atlantic (from Overholtz et al. 1991 and Fowler 1999b) showing the same kinds of information as depicted in Figures A3.1 - A3.7.

Table A3.2 contains a summary of the values for harvest rates that would maximize biodiversity (F_{mb}) as compared to (F_{ob}), the observed harvest rate as determined for the sets of data presented in Figures A3.1 - A3.8.

Table A3.2. -- List of prey species represented by Figures A3.1-A3.8, listing the harvesting/fishing rate (F_{mb}) that would maximize the biodiversity of the respective predatory/prey system, compared to the observed harvest/fishing rate (F_{ob}), and M, the total natural mortality rate for each prey species (from Kunkel and Pletscher 1999, Mertz and Meyers 1998).

Species		F_{mb}	F_{ob}	M
Deer	*Odocoileus virginianus*	0.0593	0.0300	0.26
Elk	*Cervus elaphus*	0.0390	0.0400	0.17
Moose	*Alces alces*	0.0256	0.0200	0.12
Walleye pollock	*Gadus chalcogrammus*	0.0074	0.1251	0.30
Herring	*Clupea harengus*	0.0030	0.0567	0.19
Silver hake	*Merluccius bilinearis*	0.0348	0.3082	0.40
Sandeel	*Ammodytes marinus*	0.1778	0.0005	0.51
Mackerel	*Scomber scombrus*	0.0055	0.1900	0.18

Note that in each case reviewed above, the management question that was addressed was specific to a particular species and a particular ecosystem. *What portion of species(i) can sustainably be harvested annually within ecosystem(j) (where i is deer, elk, moose, pollock … etc., and j is the ecosystem studied by Kunkel and Pletscher (1999), the ecosystem studied by Livingston (1993), and the ecosystem studied by Overholtz et al. (1991))?* This directly accounts for each specific ecosystem and prey species.

A Macroecological Pattern in Predation Rates

There is a macroecological pattern seen in the combination of data represented by Figures A3.1 - A3.8 and shown numerically in Table A3.1. Figure A3.9 displays this combination as related to total natural mortality rates (from Table A3.2) in comparison to a line representing the case wherein F_{ob} is equal to M (the 1:1) line. As described by Fowler and McCluskey (2011; see also Mertz and Myers 1998), measures of M have often been used to evaluate F_{ob}, and fishing rates in excess of M are considered to be examples of overfishing. As can be seen, empirical examples of what works in these predatory/prey systems show that long-term sustainability is much less than M. Because M is the total natural mortality, a sustainable F to mimic what works in the ecological/evolutionary systems in which these predator/prey systems are component systems has to be, on the average, less than M/N_p, where N_p is the number of nonhuman predators consuming from resource species. How do we find an estimate of F_{es}, where F_{es} is the ecologically/evolutionarily sustainable harvest rate, or a rough measure of what is systemically sustainable—holistic sustainability?

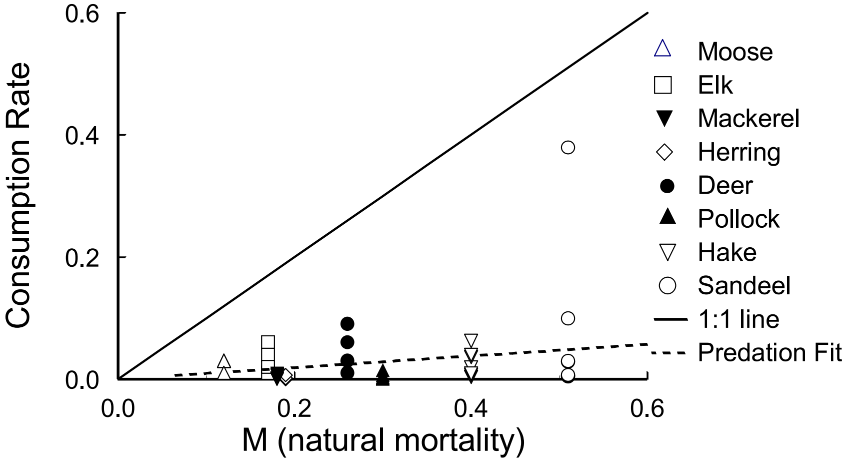

Figure A3.9. -- The macroecological pattern of the combined information from Figures A3.1 - A3.8 representing the data for consumption rates from Table A3.1 plotted as a function of the total natural mortality rates for each of the eight prey species from Table A3.2. The solid line represents the relationship wherein consumption rates (e.g., fishing rates) are equal to the total natural mortality (M). The dashed line is the linear model for the macroecological pattern, as a least squares fit to observed consumption rates forced through the origin.

A first approximation involves fitting a model to the pattern represented by the data displayed in Figure A3.9. Such a model is represented by the dashed line. This model is a linear model in which it is assumed that, when M is zero, all consumption rates (including fishing rates) must also be zero. This model is represented by the simple equation:

$$F_{es} = a\ M.$$

As presented in Fowler et al. (2013), an ordinary least squares fit of this model to the data for consumption rates in Table A3.1, using the estimates of M from Table A3.2, resulted in an estimate of 0.095 for the coefficient (a). Thus, with information for M, an estimate of F_{es} can be obtained with the equation:

$$F_{es} = 0.095M.$$

Figure A3.10 shows the same set of data and relationships, in $\log_{10}$ scale for both F and M. Again, the above equation is represented by the dashed line (predation fit).

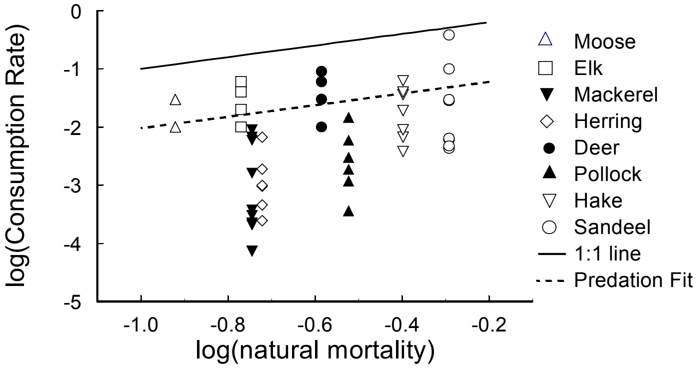

Figure A3.10. -- The macroecological pattern of Figure A3.9 plotted in log scale.

How well does this relationship represent the maximized biodiversity of the eight predator/prey systems illustrated in Figures A3.1 - A3.8? Figure A3.11 shows the relationship between the F_{mb} and the corresponding M of Table A3.2 (again in log scale). A linear least squares fit of a line parallel to that in Figure A3.11 results in as estimate of 0.08925 for the coefficient (a)—very close to 0.095 (only 5.84% different). Owing to the similarity of these estimates of the coefficient, and the preliminary and limited nature of the sets of data involved, the above equation ($F_{es} = 0.095M$) was selected to use in demonstrating the use of the macroecological pattern illustrated in Figures A3.9 - A3.11.

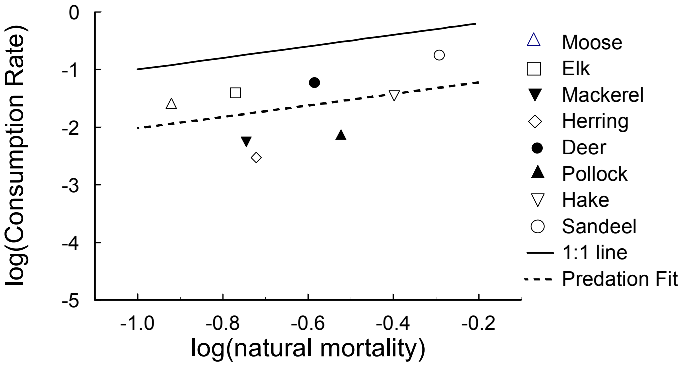

Figure A3.11. -- The macroecological pattern of Figures A3.9 and A3.10 represented by the consumption rates for hunting or fishing by humans that would maximize the diversity of the respective predator/prey systems, in log scale.

Alternative models could have been chosen. One of the first presentations of the macroecological patterns being described here is found in Belgrano and Fowler (2011). They present a model $F_{es} = 0.168M$ with which estimates of F_{es} would be almost twice those produced by the equation being used in this paper (about 1.77 times larger). One of the necessities of good management is to frame the management question so as to explicitly account for relevant factors (exemplified by the specific prey species and ecosystems in the eight sets of data treated above). Other such factors include taxonomy, body size, and trophic level—all of which can be used for further refinement of the management question. The data for predation rates used to derive the equation presented in Belgrano and Fowler (2011) included predation by species that taxonomically do not match ours; some of the predator species were birds (we are not birds), and others were fish (we are not fish). For this reason (along with the close fit to the estimated F_{mb}), $F_{es} = 0.095M$ is being used as the model for demonstrating the use of the macroecological pattern of Figure A3.9.

It must be pointed out, however, that the preliminary nature of this model is emphasized by further refinement of the questions being addressed. Above, we have progressed to the point of addressing the management question: "*Given that we are mammals, what portion of the standing stock of a resource species characterized by a measured value of M can we harvest sustainably each year?*" All of the predatory species of Table A3.1 are mammals—this achieves a limited degree of consonance (see Fowler and Hobbs 2011) in making use of the pattern represented by the information in Figures A3.9 -A3.11. All of the species involved are mammals; as mammals we are comparing ourselves to other mammals. However, body size remains an issue that is not yet accounted for explicitly. If we refine the management question to: "*Given that we humans are mammals, what portion of the standing stock of a resource species with a natural mortality rate of M can we harvest sustainably each year to directly account for our characteristic body size?*" To achieve more consonance in following this refinement of the management question, we can remove the large whales from the analysis (those marked with stars in Table A3.1). This results in an estimate of 0.0478 for the coefficient (a) to result in estimates of F_{es} that are about 50% less than those presented in this paper (based on 0.095 as the coefficient).

Assessing Fisheries Globally

In this section the macroecological pattern illustrated in Figures A3.9 and A3.10 is used to provide assessments of fishing rates applied in conventional management to a variety of species of fish for which values of M are found in the published literature. Table A3.3 is a list of 44 species of fish with their corresponding species-specific estimated total natural mortality rates (M) and fishing rates (F_{ob}) that applied to each species as documented in Mertz and Myers (1998). Figure A3.12 shows the observed fishing rates (filled circles) for these species plotted against the corresponding M. Also shown are the 1:1 line (F = M), the line (dashed) representing the macroecological pattern of Figure A3.9, and the points (open circles)representing the consumption/fishing rates that maximize the biodiversity of the predatory/prey systems for the eight prey species discussed above. Figure A3.13 shows the same sets of information in log scale.

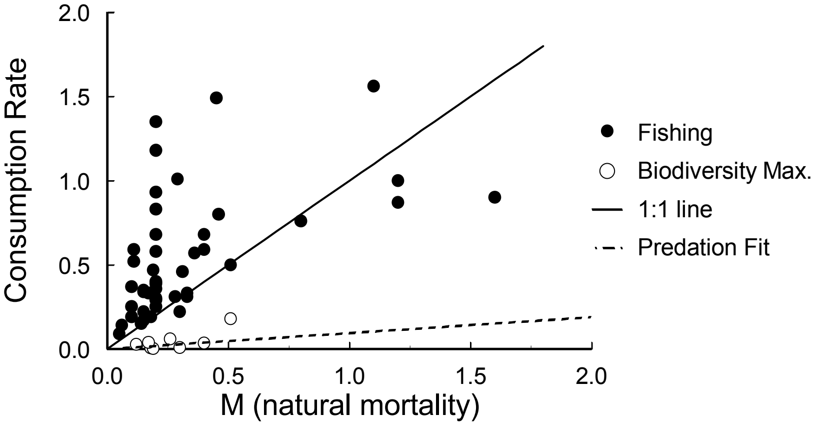

Figure A3.12. -- The observed fishing rates (filled circles; from Mertz and Myers 1998) for 44 species of fish plotted against M, the corresponding total natural mortality rate as compared to the macroecological pattern of Figure A3.9 represented by the consumption rates for hunting or fishing by humans that would maximize the diversity of the respective predator/prey systems (open circles, and dashed line).

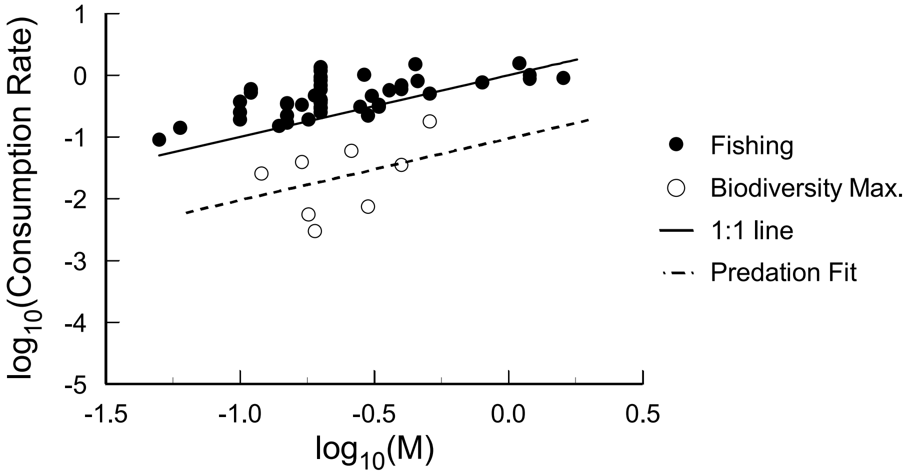

Figure A3.13. -- The information of Figure A3.12 plotted in log scale.

Table A3.3. -- A list of 44 species of fish (from Mertz and Meyers 1998) with their corresponding species-specific estimated total natural mortality rates (M), observed fishing rates (F_{ob}), ecologically sustainable fishing rate (F_{es}), and ecological overfishing index (OI = F_{ob} /F_{es}).

Species (common name)	M	F_{obs}	F_{es}	OI
Brevoortia patronus (Gulf menhaden)	1.10	1.56	0.104	15.0
Brevoortia tyrannus (Atlantic menhaden)	0.45	1.49	0.043	34.9
Clupea harengus (Atlantic herring)	0.19	0.47	0.018	26.1
Sardina pilchardus (Spanish sardine)	0.33	0.33	0.031	10.5
Sardinella brasiliensis (orangespot sardine)	1.20	0.87	0.114	7.6
Sardinops sagax (Pacific sardine)	0.46	0.80	0.044	18.3
Sprattus sprattus (sprat)	0.33	0.31	0.031	9.9
Engraulis encrasicolus (anchovy)	0.80	0.76	0.076	10.0
Engraulis ringens (Peruvian anchoveta)	1.20	1.00	0.114	8.8
Gadus morhua (Atlantic cod)	0.20	0.68	0.019	35.9
Melanogrammus aeglefinus (haddock)	0.20	0.58	0.019	30.6
Merlangius merlangus (whiting)	0.20	0.93	0.019	49.1
Merluccius bilinearis (silverhake)	0.40	0.68	0.038	17.9
Merluccius gayi (Peruvian hake)	0.36	0.57	0.034	16.7
Merluccius merluccius (hake)	0.20	0.29	0.019	15.3
Micromesistius australis (southern blue whiting)	0.20	0.25	0.019	13.2
Micromesistius poutassou (blue whiting)	0.20	0.36	0.019	19.0
Pollachius virens (pollock or saithe)	0.20	0.39	0.019	20.6
Gadus chalcogrammus (walleye pollock)	0.31	0.46	0.029	15.7
Trisopterus esmarkii (Norway pout)	1.60	0.90	0.152	5.9
Ammodytes marinus (sandeel)	0.51	0.50	0.048	10.3
Trachurus symmetricus murphyi (South Pacific horse mackerel)	0.40	0.59	0.038	15.6

Species (common name)	M	F_{obs}	F_{es}	OI
Trachurus trachurus (horse mackerel)	0.15	0.22	0.014	15.5
Stizostedion vitreum (walleye)	0.30	0.22	0.028	7.7
Argyrosomus argentatus (white croaker)	0.29	1.01	0.027	36.7
Scomber scombrus (Atlantic mackerel)	0.18	0.19	0.017	11.1
Scomberomorus cavalla (king mackerel)	0.17	0.33	0.016	20.5
Thunnus thynnus (bluefin tuna)	0.14	0.15	0.013	11.3
Pagrus auratus (New Zealand snapper)	0.06	0.14	0.006	24.6
Pagrus pagrus (red porgy)	0.28	0.31	0.027	11.7
Paralichthys dentatus (summer flounder)	0.20	1.35	0.019	71.2
Hippoglossoides platessoides (American plaice)	0.20	0.83	0.019	43.8
Platichthys flesus (flounder)	0.20	0.40	0.019	21.1
Pleuronectes ferrugineus (yellowtail flounder)	0.20	1.18	0.019	62.2
Pleuronectes platessa (plaice)	0.11	0.59	0.010	56.6
Reinhardtius hippoglossoides (Greenland halibut)	0.15	0.34	0.014	23.9
Lepidorhombus whiffiagonis (megrim)	0.20	0.30	0.019	15.8
Solea vulgaris (sole)	0.10	0.37	0.009	39.0
Salvelinus namaycush (lake trout)	0.11	0.52	0.010	49.9
Anoplopoma fimbria (sablefish)	0.10	0.19	0.009	20.0
Sebastes alutus (Pacific ocean perch)	0.05	0.09	0.005	19.0
Sebastes entomelas (widow rockfish)	0.15	0.35	0.014	24.6
Sebastes mentella (deepwater redfish)	0.10	0.25	0.009	26.4
Sebastes paucispinis (bocaccio)	0.15	0.17	0.014	12.0

Table A3.3 also shows the estimated ecologically sustainable fishing rate (F_{es} = 0.095 M) for each of the 44 species. With these values in hand, an overfishing index (OI = F_{ob}/F_{es}) can then be calculated for each species. The last column of Table A3.3 contains this index for each species. Figure A3.14 shows the pattern in overfishing for all 44 species. Note that overfishing ranges from nearly 6-fold at a minimum to over 71-fold at the maximum. The mean of the overfishing indices from this set of data is 23.4.

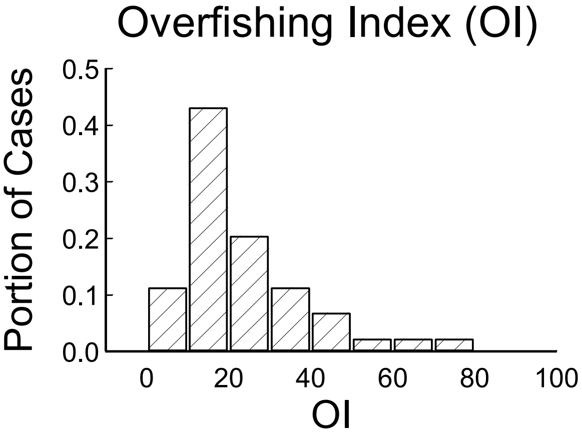

Figure A3.14. -- The pattern in overfishing among the 44 species of fish listed in Table A3.3 expressed as the ratio (OI) of observed fishing rates (F_{ob}) to the systemically (or ecologically) sustainable fishing rates (F_{es}) based on information from the macroecological pattern shown in Figures A3.9-A3.11 and represented by the equation $F_{es} = 0.095$ M.

On the basis of the information from the macroecological pattern shown above, all of the 44 species of Table A3.3 are overfished. This conclusion is to be compared to that of conventional assessments in which it is often claimed that only about 28% are overfished (e.g., FAO 2009). The thinking and belief systems behind such appraisals are part of what is accounted for by the empirical patterns we observe (e.g., all of the patterns represented by the figures of this Appendix; Belgrano and Fowler 2008, 2011; Fowler 2009).

SUMMARY

A macroecological pattern was shown for 50 estimates of consumption rates by predatory mammals on eight species of prey to illustrate how these predation rates are correlated with the total natural mortality rates (M) for the prey species; M serves as a proxy for rate of production. This pattern, as with other patterns, exhibits variability and limits offering the option of finding abnormality, as well as central tendencies that serve to guide management with the objective of aligning ourselves, as a species, with other species as empirical examples of what works in real-world systems with all of their complexity. Estimates were found for consumption rates that would maximize the biodiversity among the mammalian predators in their consumption from populations of each of the eight resource species. These estimates collectively represent the macroecological pattern in a way that treats biodiversity directly. Using the regression equation representing this pattern, it was found that sustainable harvest rates are less than 0.1M. In other words, many (and perhaps most) sustainable harvest rates are less than 10% of M.

Through the use of M as a correlative variable (i.e., accounting for M directly), it is possible to find an estimate of sustainable harvest rates for species represented by information on M. With these estimates, and information on sustainable population levels for resource populations (Appendix I), sustainable harvests can be determined. Appropriate adjustments in harvest rates responsive to changes in the abundance of resource populations can then be applied through the use of information of the kind exemplified in Appendix II.

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