

## **Evaluating the strength of interactions between predators and prey species in food webs: an Index of Predator Influence (IPI) on controlling available production of prey.**

by

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### **Abstract**

A modelling approach developed for use in the CCAMLR Working Group on Ecosystem Monitoring and Management has been extended to examine whether removal of a predator (all or part of the population), such as whales, will enhance a fishery on a target species i.e. surplus production of the target species will persist after the removal of the predator and be available to be taken by the fishery. To date, two approaches have been used, which derive from classical single species models and from food web modelling. Given the difficulties associated with both the surplus yield approach and developing robust food web models, a cost-effective assessment method is needed that will be robust against the uncertainties in both model structure and estimates of model parameters. This paper presents a hybrid approach that can use available information to test (i) whether culling might result in greater catches available to a fishery and, as such, (ii) whether food web models need to be further developed in specific cases. Ultimately, and most importantly, this approach provides an index of the strength of influence that a predator might have on controlling the available production of prey (Index of Predator Influence – IPI). The index incorporates uncertainties in the model parameters, such as abundance, consumption rates and diet composition, and particularly accounts for the magnitude of precision and variability in the abundance of the target prey species. Thus, the index provides a mean expectation of the proportion of target prey production that might remain if the subject predator was removed from the food web and all other relationships remained unchanged. A further Index of Surplus Yield (ISY) is developed with the purpose of providing, through the use of an extreme case (the extirpation of the predator), an indication of whether the removal of a subject predator might substantially increase the available production of a target prey species and be available to the fishery. The utility of the index is illustrated and its implications are discussed in the paper.

## Introduction

The question currently being posed to managers of marine ecosystems is whether removal of a predator (all or part of the population), such as whales, will enhance a fishery on a target species i.e. surplus production of the target species will persist after the removal of the predator and be available to be taken by the fishery. Models of the relationship between the predator and the target species are needed to provide justification for such a conclusion. These models need to be robust against both natural variability as well as the uncertainties in both model structure and estimates of the underlying parameters. To date, two approaches have been used, which derive from classical single species models and from food web modelling. This paper presents a hybrid approach that can use available information to test (i) whether culling might result in greater catches available to a fishery and, as such, (ii) whether food web models need to be further developed in specific cases.

### *Surplus Yield*

The logic of such a question is based on the notion of “surplus yield”. In its simplest form, this question has been considered in terms of reallocating sources of natural mortality of the target species to the fishery. The usual model for the total mortality rate for a target species,  $Z$ , of which includes the sum of the natural mortality rate,  $M$ , and the fishing mortality,  $F$ , is

$$Z = M + F \quad (1)$$

Theoretically, the natural mortality rate can be partitioned between predators of the target species as well as natural mortality arising from other causes. The optimistic expectation in a surplus yield model is that the mortality of prey arising from a subject predator species,  $\hat{p}$ , can be readily made available to a fishery by culling the predator species, such that

$$Z = (M - mM_{\hat{p}}) + (F_t + mM_{\hat{p}}) \quad (2)$$

where  $m$  is the fraction of the mortality rate arising from a subject predator removed through the culling program and made available to the fishery.

Beverton (1985) used this ‘surplus yield’ approach to examine the potential effects of a change in predator abundance on the natural mortality rate of a target species and, therefore, the consequent effect on yield. Beverton identified some aspects of why the simple formulation presented above might fail in practice. For these and other reasons, this approach is now known to be simplistic and inappropriate because (i) food web systems are not in static equilibrium and the relationships between species in a food web may change to varying degrees over time, (ii) the productivity of the

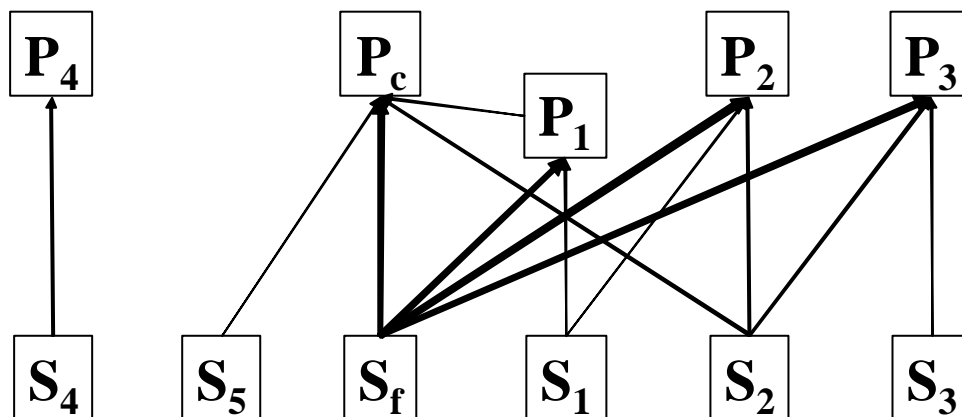
target species released through culling a predator may not be captured by the fishery and (iii) other predators might sequester the apparent surplus in production.

### *Food Web Models*

This is explored further in a review by Yodzis (2001), who indicates that what happens to a prey species following the culling of a predator species may be unpredictable because of the complexity of food webs and the potential for a variety of indirect effects.

Figure 1 illustrates a theoretical food web model showing the potential linkages between species that might influence how the culling of predator  $P_c$  might be translated into changes in abundance and/or available production of the targeted prey species  $S_f$ . Outcomes will vary depending on the importance of the targeted prey species to the different predators, the degree to which species compete for resources, either the predators or the prey, the relative competitive abilities of species and the spatial and temporal relationships between species.

**Figure 1:** Schematic of a food web of predators,  $P$ , and their prey,  $S$ , including a culled predator,  $P_c$ , and the target species of a fishery,  $S_f$ . Bold arrows are linkages between the target species and its predators.



Food web models are a common method currently being employed to investigate the likely response of a target prey species to changes in abundance of predators and/or the catch from a fishery (e.g. Walters *et al.* 1997). The added complexity required of such models does not necessarily translate to better predictions because of the paucity of data on most interactions. Most data will relate to the target prey species because those species are of interest to the fishery. The availability of data is likely to diminish rapidly for species more distant in the food web. Also, estimates of key parameters, such as abundances of many species, are imprecise and uncertain at best.

Consequently, the success of a food web model for predicting the outcomes of food web manipulation will be highly dependent on (i) how the model behaves with most available information concentrated in only a subset of the food web, (ii) the degree of uncertainty surrounding each model parameter, (iii) the ability for the model to capture dynamic properties of the system, including stochastic events that dramatically reduce target prey species to low levels, and (iv) the reliability of underlying assumptions and dummy parameters needed to close the model, i.e. make the model work in the absence of more information.

### *A new approach*

Given the difficulties associated with both the surplus yield approach and developing robust food web models, it is important to find a method that can provide robust and relatively cost-effective assessments of whether culling a predator might give rise to increased catches in a fishery. Such a method will need to be robust against the uncertainties in both model structure and estimates of model parameters. A new method for helping achieve this task is set out below.

In this paper, we return to a basic “surplus yield” assessment of the impact of a predator on the mortality of prey but endeavour to account for current theoretical and practical knowledge on ecological processes as well as for uncertainty in such processes and estimates of parameters.

The potential for the culling of a predator to increase catches in a fishery on a target prey species will only arise if all of the following conditions are satisfied:

- i) resource competition (*sensu* Underwood 1986) amongst predators is occurring, i.e. the predator guild plus the catch of the fishery are capable of removing quantities of the target prey greater than that which can be sustained by the available production of the prey,
- ii) the culled predator has a sufficiently strong influence on controlling the abundance of available production of prey that some of that production will remain for some undetermined time following the removal of the predator, and
- iii) the fishery is able to catch the surplus of production arising from (ii) within that same time.

In addition, although not explored further in this paper, the expectation is that culling will not have other effects on the food web e.g. cause a change in abundance of competing predators because the fishery is expected to supplant the culled predator or a change in the composition of prey species.

In terms of the first condition, competition between two predators is considered not to be occurring if the consumption rate of one predator is not affected by another predator even though they may eat the same target prey. Competition is considered to be occurring between these predators only when available production is in short supply to both predators (Underwood 1986).

The second condition will not arise if competition is sufficiently intense between two predators that the removal of one predator (all or in part) does not reduce the potential consumption by the remaining predators to less than the available production.

As Beverton (1985) points out, there would be no point to a culling program if the ‘surplus yield’ is unavailable to the fishery. This would occur if the fishery exploits a different pool of production than that available to the predators either through spatial differentiation or in terms of age/size structure of the population. If the culled predators exploit younger fish than the fishery then the production may be utilised by other predators before the fishery has access to the prey species. If the culled predators exploit older fish then the surplus production will be unavailable to the fishery.

It is important to be clear that in circumstances where a predator and a fishery share a resource and the production of that prey exceeds extraction from those sources, competition does not exist and yield to the fishery and that predator are effectively independent.

The method developed here uses available information on the predators of a target prey species without needing to explicitly consider the relationships with species from other more distant parts of the food web or with the ecosystem, including with other prey species or the potential for indirect positive and negative feedbacks from other trophic levels. It is an assessment based on a plausible “current” scenario incorporating the abundances of predators and the target prey, their estimated/predicted linkages and the uncertainties in all parameters. Conceivably, the method could be used to explore different scenarios as information becomes available.

The approach is not dissimilar to the general approach for understanding the ecology of populations advocated by Andrewartha & Birch (1984) in their development of envirograms. Such an approach placed the species of interest at the centre of the system knowing that the boundaries of the system will vary depending on which species is of greatest interest.

This method draws on the modelling approach of Constable (2001), in which the part of the food web to be modelled is that part related directly to the consumption of fished species. This paper addresses the opposite interaction of the effect of predators on a target species and concentrates on the relevant subset of the food web in a similar way.

Ultimately, and most importantly, this approach provides an index of the strength of influence that a predator might have on controlling the available production of prey (Index of Predator Influence – IPI); it is solely concerned with characterising a single one-way interaction. The index incorporates uncertainties in the model parameters, such as abundance, consumption rates and diet composition, and particularly accounts for the magnitude of precision and variability in the abundance of the target prey species.

Thus, the index provides a mean expectation of the proportion of target prey production that might remain if the subject predator was removed from the food web and all other relationships remained unchanged. A further Index of Surplus Yield (ISY) is developed with the purpose of providing, through the use of an extreme case (the extirpation of the predator), an indication of whether the removal of a subject predator might substantially increase the available production of a target prey species and be available to the fishery.

### **Index of Predator Influence (IPI)**

The vector of numerical abundances of predators,  $N$ , of the target species and the biomass of the target species,  $B_{\tilde{s}}$ , define the status of a predator-prey complex of interest. The index of predator influence (*IPI*) is the proportion of the target prey production,  $P_{\tilde{s}}$ , remaining when the subject predator,  $\tilde{p}$ , is removed from the vector of predators. The production remaining is given as the difference in total consumption of the target prey,  $\tilde{s}$ , for the system when no predators are absent,  $\hat{C}_{\tilde{s},0}$ , less the total consumption when the subject predator is absent,  $\hat{C}_{\tilde{s},\tilde{p}}$ . Depending on the level of detail available, this index of predator influence can be estimated for each age (or size) class of the target prey species,  $a$ , and for different geographic locations,  $g$ , and/or different times,  $t$ . Similarly, the model can be stratified for different age and sex classes of predators that may be subject to removal, but this is not developed here.

Thus, the *IPI* for a given relationship between the subject predator,  $\tilde{p}$ , and a target prey species,  $\tilde{s}$ , is

$$IPI_{\tilde{p},\tilde{s}}(a, g, t) = \frac{\hat{C}_{\tilde{s},0}(a, g, t) - \hat{C}_{\tilde{s},\tilde{p}}(a, g, t)}{P_{\tilde{s}}(a, g, t)} \quad (3)$$

The accumulated IPI is a summation across all ages of the target prey across a whole region over a given time interval

$$IPI_{\vec{p},\tilde{s}} = \frac{\sum_a \sum_g \sum_t \hat{C}_{\tilde{s},0}(a, g, t) - \hat{C}_{\tilde{s},\vec{p}}(a, g, t)}{\sum_a \sum_g \sum_t P_{\tilde{s}}(a, g, t)} \quad (4)$$

### *Prey Production*

An estimate of production of the target prey species is given by

$$P_{\tilde{s}} = b_{\tilde{s}} B_{\tilde{s}} \quad (5)$$

where  $B_{\tilde{s}}$  is the biomass of the target prey species and  $b_{\tilde{s}}$  is an estimate of the production to biomass ratio. The inclusion of age-specific production and the potential for the production rate per biomass to vary between geographic locations and over the prescribed time interval would result in

$$P_{\tilde{s}}(a, g, t) = b_{\tilde{s}}(a, g, t) B_{\tilde{s}}(a, g, t) \quad (6)$$

### *Total Consumption*

The total consumption,  $\hat{C}_{\tilde{s},\vec{p}}(a, g, t)$ , of a target prey species,  $\tilde{s}$ , by a vector of predators,  $\vec{p}$ , can be modelled similar to the formulation of Walters *et al.* (1997) such that

$$\hat{C}_{\tilde{s},\vec{p}}(a, g, t) = \sum_p I_{p,\tilde{s}}(a, g, t) W_p(a, g, t) N_p(a, g, t) + U_{\tilde{s}}(a, g, t) \quad (7)$$

where  $I_{p,\tilde{s}}$  is the ingested biomass of target prey per predator biomass over the time interval of interest, say one year,  $W_p$  is the mean weight of an individual predator and  $N_p$  is the numerical abundance of the predator.  $U_{\tilde{s}}$  is the consumption added for known predators but for which consumption could not be estimated directly. This would usually be set to 0.

The amount ingested of a particular prey species may be dependent on:

- i) the abundance and availability of the target prey species, where availability could be influenced by fine-scale parameters including avoidance behaviour by prey, aggregation density and ‘patchiness’,
- ii) the foraging ecology of the predators, which includes consideration of the abundance and availability of the prey species relative to other prey species and the feeding

preferences/behaviours of each of the predators, including prey switching, all of which may vary over time, and

- iii) intra- and interspecific competition between predators, which includes the potential dependence of the ingestion rates on the abundance of other predators relative to the abundance of prey.

Most of these factors can be incorporated into the functional feeding response of a given predator to the abundance of the target prey species. Variability in some of the characteristics and relationships may need to be included in the methods for accounting for uncertainty. However, the influence of most, if not all, of these characteristics will be approximated at best. A general model of the functional feeding relationship for a given predator,  $f_{p,\bar{s}}$ , based on the relationships developed by Holling (1959), refined by Gurney & Nisbet (1998) to include the abundance of prey,  $B_{0.5\bar{s}}$  when  $f_{p,\bar{s}}=0.5$ , and with the addition of the effects of predator abundance by Beddington (1975) can be developed as

$$f_{p,\bar{s}} = \frac{B_{\bar{s}}^{(q+1)}}{B_{0.5\bar{s}}^{(q+1)} + \left( B_{\bar{s}} + \sum_{p'} g_{p,p'} P_{p'} \right)^{(q+1)}} \quad (8)$$

where  $g_{p,p'}$  is the relative influence of a predator,  $p'$ , on the predator,  $p$ , and  $g_{p,p'}$  is the degree of influence by an individual predator on the other. The parameter,  $q$ , provides for the difference between Holling Type II ( $q=0$ ) and Holling Type III relationships ( $q>0$ ). The consumption rate may remain constant by setting  $B_{0.5\bar{s}}$  to 0 and  $q$  to 0 (Holling Type I).

Although not considered here, careful consideration may need to be given in formulating the functional feeding relationship for a predator if it feeds on the target prey species as well as one of the other predators considered in this index, e.g. the interaction between the subject predator and predator 1 in Figure 1.

In addition to the impact on consumption rate, a predator may be selective for which age (or size) classes are consumed. The probability of an age class being ingested in a given geographic location and at a given time,  $i_{p,\bar{s}}(a, g, t)$ , and the functional feeding relationship can be combined to estimate the biomass of prey ingested

$$I_{p,\bar{s}}(a, g, t) = i_{p,\bar{s}}(a, g, t) f_{p,\bar{s}} \hat{I}_{p,\bar{s}} \quad (9)$$

where  $\hat{I}_{p,\bar{s}}$  is the maximum biomass of the target prey species that could be ingested over the time interval of interest.

### *Effects of Competition*

If predators are capable of consuming more than the available production then the biomass of the target prey species will decline and competition will be occurring. The index is to determine the proportion of production remaining after the removal of the subject predator. Thus, if there is potential for all production to be consumed by a suite of predators then total consumption will be set to equal production, i.e.

$$\hat{C}_{\bar{s},\bar{p}} = P_{\bar{s}} \quad (\text{if } \hat{C}_{\bar{s},\bar{p}} > P_{\bar{s}}) \quad (10)$$

### **Index of Surplus Yield**

The Index of Surplus Yield is an extension of the Index of Predator Influence in Equation (4) as it takes into account the vulnerability to the fishery of an age (or size) class of prey in a geographic location at a given time,  $v_{\bar{s}}(a, g, t)$ . Thus,

$$ISY_{\bar{p},\bar{s}} = \frac{\sum_a \sum_g \sum_t v_{\bar{s}}(a, g, t) \left[ \hat{C}_{\bar{s},0}(a, g, t) - \hat{C}_{\bar{s},\bar{p}}(a, g, t) \right]}{\sum_a \sum_g \sum_t P_{\bar{s}}(a, g, t)} \quad (11)$$

### **Accounting for Uncertainty**

Two types of uncertainty may be present in the assessment of this index. Obviously, the values of parameters used in the index will have some uncertainty. In addition, it is important to account for temporal variation in the abundance of the target prey species. For example, most prey species will vary in abundance at a much faster rate than the response of predators to that abundance. It would seem reasonable to incorporate the variability of prey abundance to ensure the index is not biased

by the value of prey abundance used in a single assessment. Similarly, the influence of time trends in prey abundance/availability on index values could be explored.

Parameter uncertainty and variation in prey abundance can be easily incorporated into the assessment of the mean expectation of the IPI by using Monte Carlo trials to integrate across all the uncertainties and to vary the abundance of prey used in the calculations to provide a mean expectation for the index with confidence intervals. Such simulations could also incorporate a suite of options including the potential for dramatic mortality events of prey.

## Examples

The application of the Index of Predator Influence using Monte Carlo simulations to take account of uncertainty is illustrated using three simple trials showing the effects of different functional feeding relationships, and a fourth example showing the effect of uncertainty in the abundance estimates for predators. Parameters for these trials are listed in Table 1. Values of the parameters were chosen for illustrative purposes but reflect crude differences between birds (Predator 1), seals (Predator 2) and whales (Predator 3).

The Index of Surplus Yield is a minor extension of the IPI and is not illustrated here.

The functional feeding relationships (foraging efficiency) for each predator in each trial are shown in Figure 2. The notable difference between Trials 2 and 3 is that Predators 1 & 2 maintain relatively constant foraging efficiency until critical abundance is reached (different for each case) at which point the foraging efficiency is dramatically reduced. In contrast, the foraging efficiency is gradually reduced for Predator 3 with reductions in prey abundance.

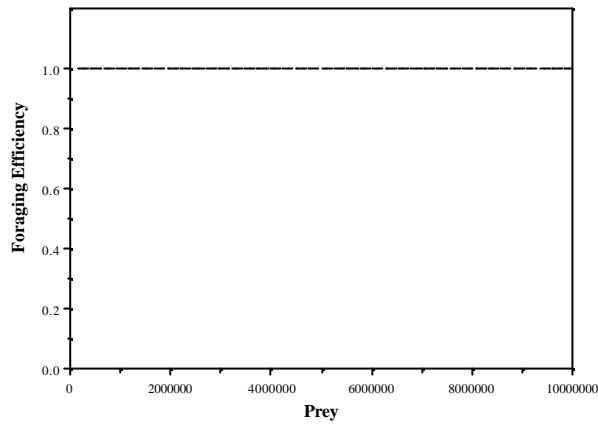
The consumption of the predators given different levels of prey abundance is shown in Figure 3. Also shown is the overall productivity of the target prey species. The consumption of predators in the absence of each of the subject predators is also shown to indicate the relative influence of each predator on the total consumption, little change means little influence. This figure illustrates the basis for calculating the Index of Predator Influence, noting (i) the difference between total consumption and consumption without a given predator and then (ii) relating this difference to the magnitude of production of the prey species.

For Trial 1, the Index of Predator Influence is shown relative to prey abundance in Fig. 4. Competition under this scenario is intense and resulted in the mean IPI being very small for each predator (see Table 2). Thus, box plots of the IPI following Monte Carlo simulation trials over variation in prey abundance are not shown in this case.

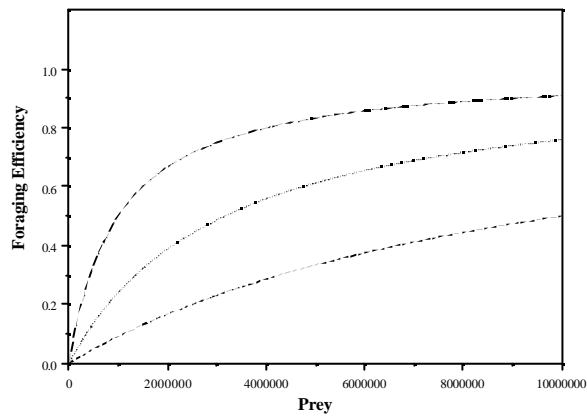
**Table 1:** Parameter values for 4 example trials showing the development of the Index of Predator Influence.

<i>Parameter</i>	<i>Parameter Values</i>			
<b>Target Prey Species</b>				
Biomass of the target prey species, $B_{\bar{s}}$ :	Mean = $10^6$			
	CV = 0.8 (trial 4)			
	log-normal			
Production to biomass ratio, $b_{\bar{s}}$	1.0			
<b>Predator 1</b>				
Numerical abundance of the predator, $N_p$	$10^6$ (Trial 4 - CV = 2.0)			
Mean weight of an individual, $W_p$	0.01			
Functional feeding relationships with target prey species	Trial			
	1	2	3	4
$B_{0.5\bar{s}}$	0	$10^6$	$10^6$	$10^6$
$\mathbf{g}_{p,p'}P_{p'}$	0	0	0	0
$q$	0	0	2	2
Predator selectivity $i_{p,\bar{s}}(a, g, t)$	1 (all ages)			
Max target prey ingested, $\hat{I}_{p,\bar{s}}$ as ratio to body mass	100			
vulnerability to the fishery, $v_{\bar{s}}(a, g, t)$ .	1			
<b>Predator 2</b>				
Numerical abundance of the predator, $N_p$	$10^5$ (Trial 4 - CV = 1.3)			
Mean weight of an individual, $W_p$	0.1			
Functional feeding relationships with target prey species	Trial			
	1	2	3	4
$B_{0.5\bar{s}}$	0	$10^{6.5}$	$10^{6.5}$	$10^{6.5}$
$\mathbf{g}_{p,p'}P_{p'}$	0	0	0	0
$q$	0	0	4	4
Predator selectivity $i_{p,\bar{s}}(a, g, t)$	1 (all ages)			
Max target prey ingested, $\hat{I}_{p,\bar{s}}$ as ratio to body mass	200			
vulnerability to the fishery, $v_{\bar{s}}(a, g, t)$ .	1			
<b>Predator 3</b>				
Numerical abundance of the predator, $N_p$	$10^3$ (Trial 4 - CV = 0.8)			
Mean weight of an individual, $W_p$	1.2			
Functional feeding relationships with target prey species	Trial			
	1	2	3	4
$B_{0.5\bar{s}}$	0	$10^7$	$10^7$	$10^7$
$\mathbf{g}_{p,p'}P_{p'}$	0	0	0	0
$q$	0	0	0	0
Predator selectivity $i_{p,\bar{s}}(a, g, t)$	1 (all ages)			
Max target prey ingested, $\hat{I}_{p,\bar{s}}$ as ratio to body mass	300			
vulnerability to the fishery, $v_{\bar{s}}(a, g, t)$ .	1			
<b>General</b>				
consumption added for known predators but for which consumption could not be estimated directly, $U_{\bar{s}}$	0			

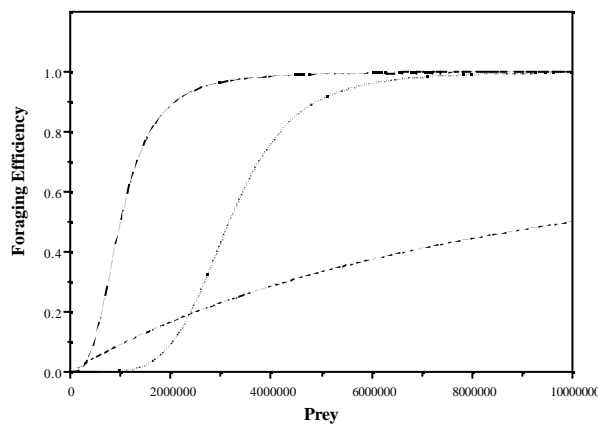
**Figure 2:** Functional feeding relationships (foraging efficiencies) between three predators and the target prey species used in four trials. **a.** consumption is constant at the maximum ingestion rate (Trial 1). **b.** Holling Type II relationship (Trial 2). **c.** Holling Type II relationship (Trials 3 & 4). (Long dashes – Predator 1; dots – Predator 2; short dashes – Predator 3)



**a.**

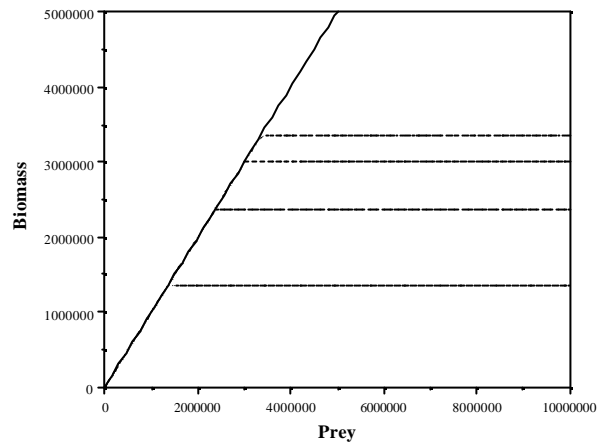


**b.**

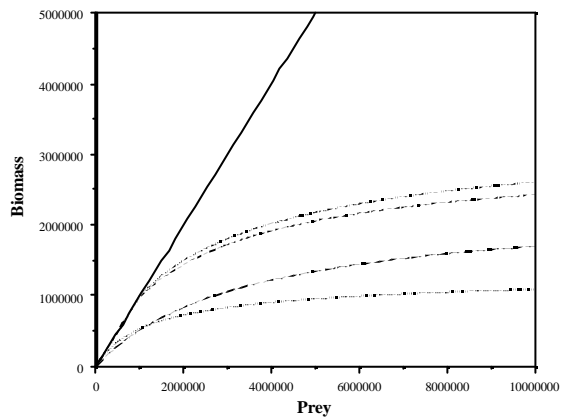


**c.**

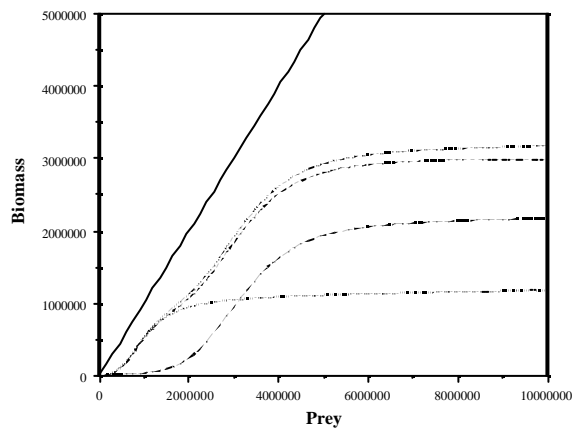
**Figure 3:** Estimated consumption of the target prey species by three predators in the three trials influenced by the respective functional feeding relationships in Figure 2. Letters correspond to the same panels in Fig. 2. Solid line – total production by target prey species, Dot-Dash – Total consumption, Remaining lines: consumption in the absence of Predator 1 - long dashes; Predator 2 – dots, Predator 3 - short dashes.



a.

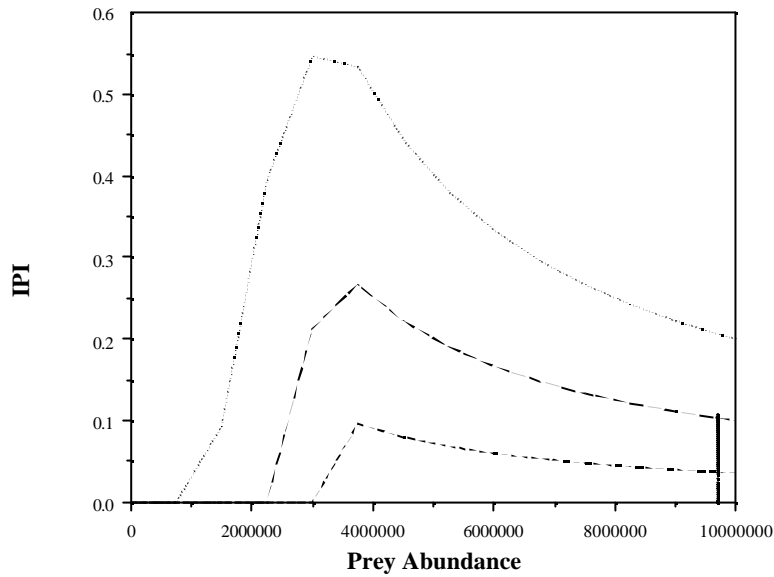


b.

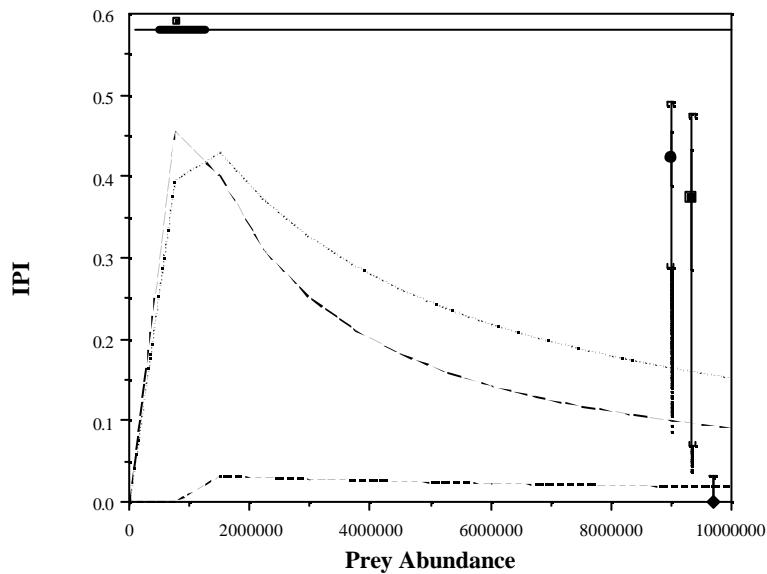


c.

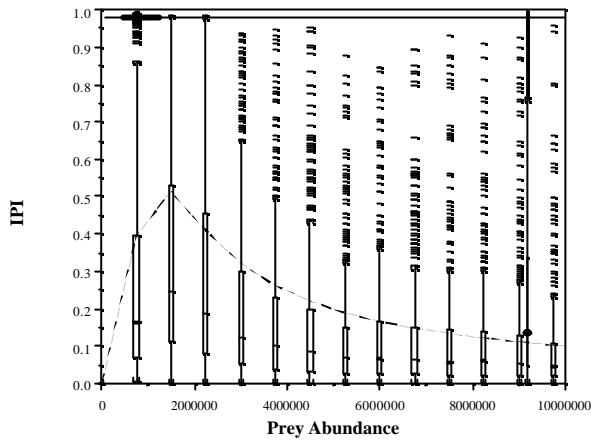
**Figure 4:** Indices of Predator Influence for three predators in Trial 1 where the foraging efficiency was equal to 1.0. Lines - Predator 1 - long dashes, Predator 2 – dots, Predator 3 - short dashes.



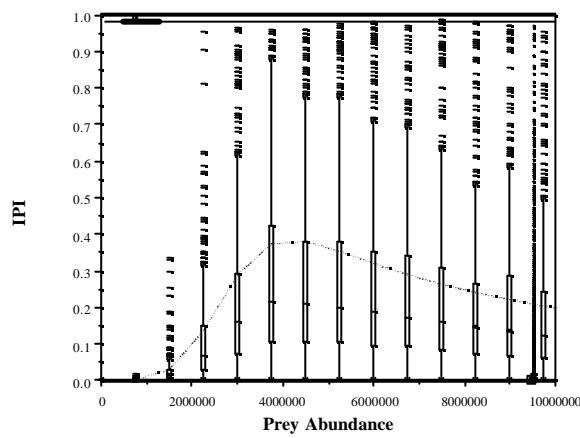
**Figure 5:** Indices of Predator Influence for three predators in Trial 2 where foraging efficiencies were Holling Type II. Lines - Predator 1 - long dashes, Predator 2 – dots, Predator 3 - short dashes. Horizontal box plot showing distribution of prey abundance given mean and CV in Table 1. Symbols with high low bars, which are not to be read in conjunction with the prey abundance, show the median IPI and its maximum and minimum for each of the predators arising from 10 000 Monte Carlo simulations of the prey abundance - Predator 1 - circle, Predator 2 – square, Predator 3 –diamond (part covered).



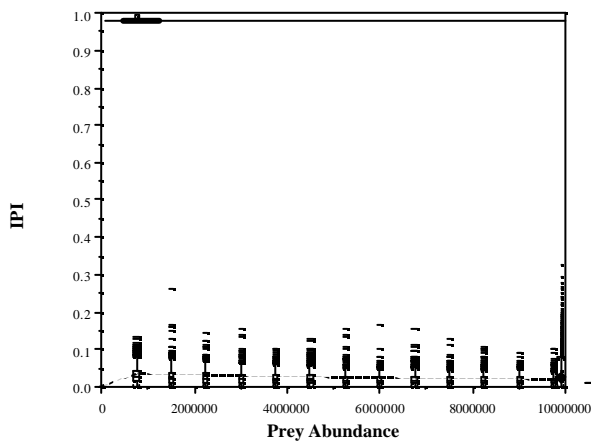
**Figure 6:** Indices of Predator Influence for three predators in Trial 3 and 4 where foraging efficiencies were Holling Type III. The line is derived from Trial 3 for which there was no uncertainty in predator abundance. The series of box plots relative to prey abundance show the resulting distributions of the IPI from 500 Monte Carlo simulations for the given prey abundance. The horizontal box plot shows the distribution of prey abundance given mean and CV in Table 1. Symbols with high low bars, which are not to be read in conjunction with the prey abundance, show the median IPI and its maximum and minimum for each of the predators arising from 10 000 Monte Carlo simulations of the prey abundance - Predator 1 - circle, Predator 2 – square, Predator 3 –diamond.



Predator 1



Predator 2



Predator 3

**Table 2:** The mean Index of Predator Influence (proportion of production of target prey species) and its coefficient of variation for three predators in each of 4 illustrative trials. Results of these trials are presented in Figures 4-6.

	<i>Predator</i>	<i>Mean</i>	<i>CV</i>
<b>Trial 1</b>	1	0.01	4.4
	2	0.06	2.3
	3	< 0.01	6.2
<b>Trial 2</b>	1	0.41	0.1
	2	0.35	0.3
	3	0.01	1.3
<b>Trial 3</b>	1	0.34	0.5
	2	0.02	2.4
	3	0.03	0.1
<b>Trial 4</b>	1	0.25	1.1
	2	0.02	3.5
	3	0.03	0.9

The results of Trial 2 are illustrated in Fig. 5. In this case, the box plots of the Monte Carlo simulations used to integrate over the variation in prey abundance shows that Predator 1 has the highest IPI while Predator 3 has the lowest, almost negligible, IPI. The variability in the index for both Predators 1 and 2 illustrate the degree of uncertainty in the outcome for these species.

Trials 3 and 4 show the effect of uncertainty in predator parameters on the IPI for each level of prey abundance. The consequent effects on the mean IPI for each predator are given in Table 2. The increased uncertainty resulted in a reduction in the mean IPI only for the most abundant predator but increased the uncertainty substantially for all three predators.

In reference to Figure 6, some of the differences may have arisen because of the small sample size (500) in the simulations for each level of prey abundance. A greater sample size will be used in the final work.

## Discussion

The Index of Predator Influence and its extension, the Index of Surplus Yield, provide indicative assessments of the strength of interaction between a subject predator and a target prey species. They are estimated using an extreme case, the total removal of a predator and not just a partial removal. Therefore, the assessment provides a potentially overly optimistic view of the production of a target species in surplus after the removal of a predator. Unlike previous “surplus yield” models, this approach takes account of some levels of uncertainty and the variability in the

abundance of prey. A fishery and its historical and/or future effects can easily be included in this method using the parameter framework presented here.

Another outcome of using such an index is to readily identify which predators may be important in a food web i.e. which are the strongest interactions, a need identified by Paine (1966). For example, the effect of a predator may be negligible if competition is so great that all its consumption is taken up by another species. In this case, the primary effect of the predator in the food web will be as a competitor to other predator species but not as a primary determinant of the population dynamics of the prey species.

The utility of the index is dependent on the plausibility of the model structures used to estimate consumption and prey production. The different components of the index can be made more or less complex depending on the information available. It will be important to ensure that the data quality and quantity are appropriately reflected in the uncertainties for each parameter. An important issue will be to determine appropriate values of the availability of prey, including consideration of the proportion of predation of the target prey species being described. Varying the unknown predation from zero would need to be undertaken with sound reasons and made prior to the assessment of the index.

The simplest assumptions in this index is for complete overlap of each predator as competitors for prey with the same foraging capability and selectivity. Providing greater discrimination between these predators will inevitably reduce the relative importance of predators to controlling the availability of production of the target prey species. Thus, once the potential for a predator to be a substantially important consumer is demonstrated then refinements in knowledge will be necessary to determine how important that consumer might be.

This model takes a 'static' view of relationships between predators and prey. Given that foraging studies are increasingly showing the plasticity of feeding behaviour (responsive to, among other things, changes in prey behaviour and availability) then it is reasonable to expect that an increase in the 'surplus' production of a prey species will influence the behaviour of other predators. These other predators may not have previously been important consumers. Similarly, if a fishery fails to absorb the additional productivity of a prey within a particular timeframe, production of competitive predators will increase and continue to consume the surplus into the future.

If the index results in only competition occurring, i.e. potential predator consumption is always greater than prey production, then the model may be incorrect, particularly if consumption is greater than the sum of prey biomass plus its production. Alternatively, the system may have changed irrevocably and the predators will begin declining in abundance. This may arise, for example, from

overfishing. Under these circumstances, it is unlikely that any production will be “released” following the removal of a predator.

The next stage in the development of this index is to determine the sensitivity of the index to uncertainty in each of the parameters. For example, Boyd (2000) has argued that estimates of prey consumption by predators is most sensitive to the estimates of abundance of the predators. This suggests that diet studies are less critical model inputs. Certainly, information on whether different predators consume a particular target species is required (such as by the methods discussed by Jarmin & Gales, 2002). However, the accuracy and precision of the partitioning of the diet amongst different prey is probably not necessary for the purposes of this index beyond using broad categories such as trivial (<5%), small (5-20%), medium (20-60%) and large (60-100%).

The method can be extended relatively easily to apply to a guild of harvested prey species by summing the estimate of production for all prey species in the guild, subtracting the consumption of prey production by other prey as appropriate and then estimating consumption of all targeted prey species by the relevant predators as described in Constable (2001).

This method provides a pragmatic and conservative approach to assess the likely efficacy of extreme options for managing fisheries like culling of predators. The approach is not intended to supplant the development of carefully managed fisheries. It is designed as an adjunct to the planning process so that it can be determined *a priori* whether particular actions may warrant further investigation, such as culling or the further collection of data for food web modelling to refine analyses pertaining to this question. Ultimately, caution must be given to ecosystem engineering, which is the manipulation (reduction) of one species to indirectly manipulate (increase) the abundance of another species. The utility of such actions needs to be carefully evaluated because they are potentially fraught with difficulty and have not necessarily achieved the desired outcomes, such as in pest management.

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